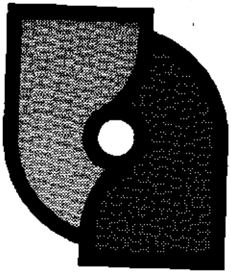

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Proceedings of the First International Congress of Ecology

STRUCTURE, FUNCTIONING AND MANAGEMENT OF ECOSYSTEMS

The Hague
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SPECIAL SYMPOSIA

PREFACE

A.J. Cavé

Secretary of the Local Organizing Committee

The First International Congress of Ecology has been organized by the International Association for Ecology (INTECOL) under the auspices of the Division of Environmental Biology of the International Union of Biological Sciences (IUBS).

It brings together ecologists of several disciplines such as limnology, botany, zoology, microbiology and agriculture.

All these specialisms have their own organizations and international meetings, often with a long tradition. They have developed scientific concepts of their own and speak to a certain degree a different language. This creates problems, especially with regard to the urgent development of ecosystems research.

In ecosystems research all disciplines based on taxonomic groups or on specialisms such as parasitism or population dynamics find a common ground. In the study of ecosystem dynamics real progress depends on mutual understanding and close cooperation.

To stimulate such an integrated approach the congress of ecology sollicitated a number of main papers on "unifying concepts in ecology" which discuss notions such as energy flow, productivity, diversity, stability and maturity from different points of view.

The contributions to the A-sessions report on investigations, relevant to these general themes.

The purpose of the B-sessions is to bring together the results of more than a thousand research projects of the International Biological Programme, widely scattered throughout the world, in the form of general conclusions.

These sessions have been organized by the IBP-organization.

The C- and E-sessions comprise special symposia on important techniques such as systems analysis, remote sensing and methods of experimentation with ecosystems. Other symposia of this series deal with special branches of ecological research work, e.g. biological control, parasitic systems, aerobiology and human ecology.

The participants were urged to give special attention to the contribution of these specialisms to general ecology.

Concern about the fate of tropical forests resulted in a symposium on: ecological consequences of deforestation for vegetation, soil and aquatic systems in the tropics.

In these proceedings the contributions to the plenary sessions are represented only in the form of abstracts. Full texts and summaries of the discussions during the congress will be published in a separate book: Unifying Concepts in Ecology.[1]

The speakers of all other sessions have been asked to contribute to the proceedings with a full text which had to be sent in ready for reproduction in offset litho.

Not all of them have succeeded to accomplish this before the closing date.

The Organizing Committee acknowledges with gratitude the efforts of all those who have supported the publication of these Proceedings. We are confident they will serve to stimulate exchange of ideas and discussions during and after the congress.

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[1] Van Dobben, W.H.; Gradwell, G.R. (Editors); 1975. Unifying concepts in ecology. Dr W. Junk Publishers, The Hague; Pudoc, Wageningen, Netherlands. ca 250 pp.

Presidential Address

UNIFICATION OF LAND-WATER ECOLOGICAL SYSTEMS

Arthur D. Hasler

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Respected colleagues from around the world:

Through much of my career I have conducted research on the ecology of fishes. I have elected to draw an example from this experience to illustrate an effective relationship between land-water systems. My example concerns the guideposts from land used by salmon to find their way home from the sea.

In a small stream of a river system a pair of coho salmon returning from their strenuous oceanic migration lay and fertilize their eggs. Once hatched, these young salmon live in the stream for about a year, eating food organisms which thrive from nutrients flowing off the land. As fingerlings they undergo a biological change called smolting, preparing them for the long trip downstream to the ocean. At sea, they spend about two years feeding on shrimp and small fish, growing rapidly toward maturity. Finally, some still unknown stimuli initiate the homing migration back to their home stream. Across many kilometers of open water, the fish travel to a large river which earlier had brought them to sea. Once in the river system the sexually mature salmon stop eating, seemingly concentrating only on the search for one stream in many, the stream of their birth. Leaping waterfalls and climbing fish ladders around man-made dams, the fish swim relentlessly upcurrent rejecting one branch after another in search for the home stream. Then, often scores of miles inland in a tiny tributary, they stop to spawn, thus the beginning of another generation. For tens of thousands of years, since before the time of man, this behavior has remained essentially unchanged. Through the years man has made ample use of the salmon, from satisfying the hunger of primitive cave dwellers to delighting the sports fisherman. Yet through decades salmon have held tightly the aura of mystery surrounding their incredible migratory journey.

What we've known for many years is that they do have the capability of returning to the precise home stream. But there was no good explanation for what the cues or guideposts were that directed them and helped them to identify this home site. Hence, it was here, with my interest in ecology and sensory physiology of fishes, that my students and I were able to explore this problem.

When I first began to investigate the homing behavior of salmon, my principal goal was to satisfy a scientific curiosity and explain, by new facts, the mechanisms used by salmon to find their way home. One of my working hypotheses was an ecological one, namely, that the home stream of a salmon carried an odor, a fragrance which was different from all other streams. I reasoned that because the soils and plant communities of each catchment basin were different, then each stream was unique and bore a characteristic bouquet, as do wines from grapes raised on different soils. My hypothesis proposed that the young salmon became imprinted to this odor before they migrated; hence after attaining sexual maturity at sea, they returned to this area and recognized their home stream odor, having retained it in memory since their departure for sea.

My students and I conducted a number of experiments in the laboratory and in the field (Hasler, 1966) which provided circumstantial evidence that this hypothesis might be valid. First off, we demonstrated that fish could be trained in the laboratory to discriminate two different streams by olfaction (Hasler and Wisby, 1951). The next question was to determine if adult salmon need their noses to find their way in the river. To answer this, we captured 300 homing salmon and displaced them downstream below a fork in the Issequah River. In one-half of these we plugged their noses with cotton while one-half served as controls. These were appropriately marked. The normal salmon returned correctly to the stream from which they were displaced while those with plugged noses confused the confluence and made mistakes (Wisby and Hasler, 1954).

While this evidence suggests strongly that a stream odor is unique and serves as a cue for homing salmon, I felt it was essential to conduct the following experiment as a more conclusive test: young smolting salmon raised in a hatchery would be imprinted with an artificial odorous chemical which they had never experienced in the history of their evolution. They were to be marked and released to swim to sea. Upon the return of the mature adults, the synthetic imprinting chemical that could be smelled by salmon at low concentrations would be dripped into a tributary downstream from the original imprinting site to determine if they could be decoyed into a tributary of a river different from their birth.

In a doctoral thesis, one of my students, Warren Wisby (1954), undertook the task of screening various chemicals to find a suitable synthetic substance which we could use for a test of this hypothesis. The chemical should have the following characteristics:

1. to be detectable by olfaction at low concentrations, as low as 10^{-6} mg/l.
2. to be neither a natural repellent nor an attractant.
3. to have reasonable chemical stability.

Morpholine fulfilled these specifications, but we were unable to perform field tests during the ensuing years because of our location so far from salmon territory. Now over 20 years later in collaboration with my students and associates we could conduct these experiments on coho salmon which have been stocked and now flourish in nearby Lake Michigan.

In 1971 we (Scholz et al., 1973; Hasler, 1974) raised 16,000 and in 1972 38,200 coho salmon to the smolting stage (100 mm) in an inland hatchery through the cooperation of the Wisconsin Department of Natural Resources. These fish were transferred to large tanks near Milwaukee where one-half of them were imprinted to morpholine at 10^{-5} mg/l for 2-4 weeks. Water from Lake Michigan flowed through the tanks, hence an association with any stream water was avoided. Both control and experimental fish were marked and released to the lake without the fish having had exposure to any stream odors.

In the subsequent spawning seasons when the salmon returned to the area, morpholine was dripped into a small Lake Michigan stream (Oak Creek) to scent it with the imprinting odor. Traps were set at the mouth of the stream where returning salmon were captured with a combined total of 1,710 imprinted fish and 193 controls, a ratio of 9:1, thus verifying our original hypothesis that an odor is the basis for identifying the "home" water - in this instance, a simulated home stream scented by the imprinting synthetic odor. In addition, we fastened ultrasonic transmitters to some of the homing salmon and displaced them out into the lake 5 km. Our tracking boats were then able to follow them with hydrophones. Meanwhile, from another boat we dripped a small quantity of morpholine into the water along the fish's path. When the imprinted fish reached the area containing morpholine, they stopped short and milled around. Control fish, however, swam right by. If the morpholine was not dripped into the water, imprinted fish also swam by without hesitating. Physiological experiments on imprinted and non-imprinted salmon provided additional neural evidence of retention of odor memory (Cooper and Hasler, 1974). Hence, using three different methods, our hypothesis of odor imprinting was again confirmed.

Because the unifying principles of ecology are the principal themes of this Congress, I cite our research because it exemplifies the linkages between land and water.

In this instance salmon rely upon the fragrances from the landscape's soil and vegetation to provide them the guidepost to their spawning ground upon returning from sea.

Moreover, this example from our research was used because a series of experiments designed to test a theory yielded, in the end, facts which not only satisfied our initial scientific curiosity, but had, as well, application to a human need, food, because artificially imprinted salmon may now be attracted at sexual maturity to a point of easy accessibility, a stream near the coast where the protein rich adults may be harvested. Moreover, ripe eggs can be readily salvaged and shipped to hatcheries where salmon can be raised, unfortunately at a greater cost but at least to provide stock to maintain a population of fish in an area where streams have been:

a. dammed with non-passable barriers
b. warmed by cooling water
c. polluted beyond biological restoration
d. rendered inhospitable to salmon by eroded sediments.

In considering the management of our biota, I emphasize that salmon are essentially a free resource. At sea they need no stalls. There is no manure to haul and no one is required to feed them, treat them for domestic diseases and herd them; instead they deliver themselves at our "back door" for harvesting, free of middleman charges. Their food, shrimp and small fish, is supplied free of charge by nature. Man, without expending energy uneconomically, could not harvest for himself these smaller organisms that the salmon eat. It is more logical to rely upon salmon to convert them into larger units more readily harvestable.

An example of the cost of replacement of a free resource can be found in Sweden which expends over a million dollars per year to rear young salmon in hatcheries for release at the smolting stage into the Baltic Sea. Society in this instance is paying for a service previously rendered free by its salmon streams but which are now obstructed by power dams.

Salmon are a major protein resource from the northern seas. Continuous surveillance of the ecosystem which supports them must be maintained in order to offset harmful practices which would deprive society of these stocks of high quality food.

A series of interacting ecological systems comprising vegetation, soil, rivers, estuaries and ocean have been utilized in the evolution of a species that became an important protein source for man. Moreover, the sheer beauty of this complex system fills one with admiration for nature's "inventiveness". It gives the ecologist respect for nature's ebullient harvests; moreover, this example demonstrates how closely man lives with disaster when he tampers with nature's free resources, the productivity of landscape and ocean. Ecological knowledge is needed to avoid misuse of resources and to help correct its damages.

International cooperation in resource management

I have used here an example of ecological research in which an investigator and his immediate associates are the participants.

We are gathered in The Hague this week as members of the International Association for Ecology. How can we profit from this collaboration? What can ecologists accomplish through these multi-institutional and international organizations that will augment our understanding of ecosystems? In the past we have made only modest use of scientific organizations in acting responsibly to the need for better management of our resources, but the need increases; hence we must strive to be of greater service.

I am heartened that it was ecologists who developed the plan which led to the creation of an international commission for managing the declining stocks of the Pribilof Island seals. The nations involved agreed to assign their sovereign rights for managing these aquatic mammals to this commission. As a result of ecological planning, the seals have now increased to their former abundance.

Again, it was the ecological logic and the meaningful statistics of fishery ecologists which made possible a management plan for reducing, by international agreement, the slaughter of whales, some species of which are now so near extinction.

These instances of applying ecological knowledge which lead to reasonable cooperation can become models upon which greater ones can be based. A new ecological ethic is gradually emerging which will help to create a responsible concept of world order in which concession and agreement will replace opposition and disagreement.

Perhaps in the area of ecology rests a key to cooperative attitudes among nations. Sharing the products of common ownership, such as the fish of the oceans, will encourage each nation to act responsibly and in concert on other problems confronting society.

"Achieving the international cooperation needed to cope with existing and emerging threats to human well being is dependent on creating a new concept of world order in which the basic emphasis is more on cooperation and a sense of community and less on conflict and competition." - Lester R. Brown, World Without Borders, 1972.

New organizations to cope with crises

I urge ecologists everywhere to apply their talents to basic and applied problems for closing the leakages from our industrial, agricultural, and aquacultural systems. It is the leakages of pollutants into the environment which are damaging to the structure and function of our natural systems.

I endorse plans to form an assemblage of competent international experts for the study of ecological crises. Their task would be to identify potential crises and forecast the possible date of onset. They would also prepare plans and set forth corrective measures to avoid or reduce the severity of the perturbations and to specify logical processes to deal with them should they arise. Such an orderly approach would replace the haphazard practices applied in the past.

An example of an early warning of a dwindling resource is that from a workshop on Global Ecological Problems organized by The Institute of Ecology (1971) in which one of the tasks was to estimate the rate of decline of phosphorus reserves at varying world population levels. Phosphorus is a very special element in nature because it is the only non-substitutable mineral essential to all living things; hence increased future demands on it as a fertilizer of crops become an international concern.

Table 1. Estimated use of phosphorus fertilizer to feed world populations of various sizes at the present average nutritional level combining data from the UN and the Pres. Sci. Adv. Comm.

Population (thousand millions)	Phosphorus Use/ Year (millions metric tons)	Lifetime of Known Reserves (years)
1.8	1.7	11,700
3.6	11.3	1,750
7.2	73.0	271
12.0	291.0	68
20.0	1170.0	17

Taken from page 54 of Man in the Living Environment, a report of the Workshop on Global Ecological Problems sponsored by The Institute of Ecology and the National Science Foundation, Madison, Wisconsin, June 1971. These estimates were based on known deposits containing 8% P and an estimated rate of increase in use of 2.7.

This study has since generated a number of thoughtful evaluations and is yielding new facts which will help to meet future emergencies. In addition, ecological studies have been initiated on: phosphate metabolism in plant communities, recycling studies, chemistry and physics of phosphorus, in addition to genetics of phosphorus utilization by various plant species.

We need more ecological research on the intensive management of our natural and agricultural systems in order to provide the food and fiber needed by society. It will require a cooperative effort on the part of ecologists, working in concert with industry, forestry and agriculture. To examine the wasteful and harmful practices in man-made systems and develop techniques for correcting them, ecologists can lead the way by devising multidisciplinary and multi-institutional working groups for solving urgent societal problems where ecological knowledge is needed.

It is my hope that this First International Congress of Ecology will be viewed as a large leap forward in the progressive advance of ecological knowledge and the application of this knowledge.

We who are assembled here today are grateful indeed for many persons and organizations who have made possible this Congress.

On behalf of the International Association for Ecology, I extend sincere thanks to you all for your support of our Association and especially to:

Prof. van Dobben, the chairman of the Congress, for three years of unselfish dedication to this responsibility,

all members of the Dutch Organizing Committee for personal service,

the Dutch Academy of Sciences for providing support to the Committee's efforts,

the people of Holland for financial support and for their conviction that consideration of the unifying ecological principles can help to alleviate many of the adverse effects of man's activities on living systems in water and on land.

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Structure, functioning and management of ecosystems

P1 - P5 Unifying concepts in ecology (abstracts)

A1 - A5 Research communications

P1 A1

Flow of energy and matter between trophic levels

INTRODUCTION TO THEME ONE

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Abstract

Just now Ecology is a science in search of a theory. Until recently we had many rules, or theories of low generality, and one theory of high generality, neo-Darwinian evolutionary theory. In this phase, Ecologists tried to fill the gap between high and low with theories of intermediate generality. Recently there has been a growing, but tacit awareness that although neo-Darwinism is a satisfying thought paradigm, it never yields useful predictions about specific situations. I suggest that this awareness has led us to search for new patterns of explanation and that the energy-flow approach, exemplified by IBP, is one of these.

The description of the purpose of this Congress suggests that we are dissatisfied with our unifying concepts or theories and Theme 1 in particular suggests that the energy-flow approach must be fused with the nutrient cycling approach if we are to achieve useful theories. I suggest that there are some serious difficulties waiting for us when we attempt this union.

The first of these are inherent in studies of energy flow. (a) Studies of energy flow have tended to accept the taxonomy common to evolutionary biology - the species system. To simplify the task of describing ecosystems the species were grouped into superunits called trophic levels. This produced a classification scheme in which the taxa are hybrids of old morphological units and trophic functional units. Since these taxa cannot be identified operationally, any theories about these units will be empty of predictions. (b) Energy flow is rarely measured in ecosystem studies. Normally we measure flux of a substance such as carbon, oxygen or dry weight and use a flexible factor to convert our results into energy units.

The second type of difficulty arises from the different classification system adopted by students of nutrient cycling. Their categories began independently of the species and their taxa tended to be operationally defined.

It is suggested that the present need is not to combine the study of nutrient cycling and energy flow, but to reconcile two incompatible systems of classifying ecosystems. Real progress will only be made by revising one or both systems, provided the revised system has components that can be identified with operationally defined entities.

PRINCIPLES OF ENERGY AND MATERIAL EXCHANGE IN ECOSYSTEMS[1]

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Recent advances in the scientific analysis of ecological systems have elucidated a number of ecosystem attributes, consistent in pattern among ecosystems and emanating from basic ecosystem properties. These properties are the result of the mechanistic processes of the flow of energy and cycling of elements between trophic levels -- in complete, autonomous ecological systems. This paper will formalize some of the concepts that have evolved from the International Biological Programme concerning the fundamental principles governing ecosystem structure and function. Hypotheses are presented for scrutiny and critique as to their utility in explaining ecological phenomena. These hypotheses represent a developing, unifying theory of ecosystem function and provide an operational framework for synthesis and comparative interpretation of ecosystem data.

Ecological systems are conceived as energy-processing units, ordinarily not radiant energy limited, but constrained by the availability of essential nutrient elements and water. Energy is the fuel upon which ecological processes operate, but the rates at which processes occur are controlled in natural systems by nutrient availability. It is hypothesized that ecosystems adopt strategies to expend readily available energy to minimize the constraints imposed by limiting nutrients and water. Ecosystems display adaptive control mechanisms associated with heterotrophic activities (e.g., grazing and decomposition) that lead to conservation of nutrient capital. Therefore, patterns of energy flow and element cycling in ecological systems cannot be interpreted independently without introducing errors as to ecosystem objectives and strategies for optimization and stability.

[1] Research supported in part by the U.S. Atomic Energy Commission under contract with the Union Carbide Corporation, and in part by the Eastern Deciduous Forest Biome, US-IBP, funded by the National Science Foundation under Interagency Agreement AG-199, 40-193-69 with the Atomic Energy Commission - Oak Ridge National Laboratory.

[2] Operated by Union Carbide Corporation for the U.S. Atomic Energy Commission.

Contribution No. 160 from the Eastern Deciduous Forest Biome, US-IBP.

GENERATION AND UTILIZATION OF ATP IN CHEMOORGANOTROPHIC BACTERIA

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Chemoorganotrophic bacteria derive their energy for growth from the aerobic or anaerobic oxidation of organic compounds. These serve both as energy- and C source. Continuous culture studies of organisms grown under nutrient limitation at submaximal rate have revealed some principles which contribute to understanding their activities in natural environments. The amount of cell material produced per mole of organic substrate consumed as well as per mole of ATP generated is a function of growth rate, irrespective of the kind of nutrient limitation. These yields decrease with decreasing growth rate as a result of a growth rate-independent requirement of ATP for maintenance purposes. This requirement is a function of environmental conditions (e.g. osmotic pressure).

The molar growth yield with respect to C- and energy source is highest at any submaximal rate when this nutrient limits growth rate. The lower the growth rate, the larger the difference in yield between C-limited cells and cells limited by other nutrients. Thus, N-limited cells growing at low rate may contribute considerably to oxidation of organic molecules, while producing little biomass.

In the extreme case of absence of essential nutrients other than the C-source, no biomass is formed at all, and all energy produced during oxidation is dissipated as heat. A similar situation may also occur when there is complete uncoupling between dissimilation and assimilation due to other factors (e.g. superoptimal temperatures). Except for these extreme conditions catabolism and anabolism, or in ecological terms nutrient cycling and biomass formation, are inseparable in the bacterial cell, and therefore in any ecosystem in which they participate. However, there need not necessarily be a fixed correlation between biomass and oxidative activities.

FLOW OF ENERGY AND MATTER BETWEEN TROPHIC LEVELS (WITH SPECIAL REFERENCE TO HIGHER LEVELS)

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On the basis of field investigations the following questions are discussed:general patterns in the biogeocenosis(BGC)structure in different biomes and in different types of BGC within the limits of separate landscape zones;biological unity of BGC,consisting of several ecological subsystems;populational mechanisms of maintaining the biogeocenotic equilibrium; flow of energy,migration and accumulation of chemical elements during the populational peak of dominant consumers.

Any trophic level is represented by a small number of dominant species which provide for the accumulation of the biomass and the basic flow of energy within the BGC and by a large amount of species-satellites that encourage the energetic activity of the dominants.

In various types of tundra BGC differing in a number of consumer species(from 60 to 200)and productivity(zoomass from 335 to 1887 mg/m2) dominants create from 86 to 93% of the biomass.

The analysis of such examples proves the great effectiveness of the populational mechanisms of regulation of the biogeocenotic processes - the populational peak is followed by the "populational collapse"before the equilibrium of the BGC is disturbed.Moreover,observations have shown that the mass reproduction of the dominant species often becomes an important factor of the biogeocenotic enrichment.Thus,the increase of the *Dicrostonyx torquatus* to 1000 animals per ha in the southern tundra brings to the sharp disturbtion of the stand of grass which,however, recreates during one vegetational season. This is greatly promoted by the enrichment of soil with organic and ash elements.

In the period of intensive reproduction lemmings attribute to the soil(kg/ha):Si-6,0;Al-5,0;Fe-0,5; P-4,0;Ca-6,0;Mg-3,0;Mn-0,2;K-15,0; Na-1,8.

The analysis of the ecological consequences of the mass reproduction of some insects(*Limantria dispar*, etc.)brings to the same conclusions.

The increase of the number of consumers causes compensating reactions of species of the lower trophic levels.As a result of this the maximum productivity of producers is observed not when consumers are absent but when their number is relatively high. This was proved in a direct field experiment. Maximum production of nothern plants was observed in the sites where 20% of vegetation was destroyed by consumers (*Microtus middendorffi*).This corresponds to the density of voles of about 100-120/ha during 100 vegetational days.

At meadows in forest-steppes a population of voles with density of about 650/ha causes some changes in the phytocenosis which decreases the CO_2 absorbtion 1,4 times. In a month however, the photosynthetic activity and the association structure renew. This corresponds well with field observations.In the region under investigation the offsprings of 6 overwintered pairs of voles per ha consumed during the vegetational period more than 30% of the total (1645 kg/ha) plant production and circa 9 kg K, 3 kg Na, 0,4 kg P but it had not influenced the productivity of the phytocenosis (the standing crop more than 5500 kg/ha).

The optimal functioning of the BGC is assured not only by the populational mechanisms and reactions of the organisms belonging to different trophic levels but also by the composition of separate trophic levels. Specific role of homotherm and poikilotherm animals in the life of an ecosystem is discussed.

Combination of animals differing in energy spent for the preservation of their average number and in their influence over the lower trophic levels ensures the dynamic equilibrium of the ecosystems.

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THE PHYSICAL FOUNDATIONS OF GLOBAL ECOLOGICAL PROCESSES

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Summary

Certain ecological generalizations such as photosynthetically driven material cycling and the nature of the input molecules for this cycling are shown to be derivable from chemical reaction network theory and the second law of thermodynamics. The outline features of global ecology are, thus, not uniquely biological. These results demonstrate the extent to which biological processes, even in the large, can be reduced to physical analysis.

Introduction

The purpose of this paper is to discuss two generalizations of global ecology and to show that they may be deduced from concepts of physics and chemistry. Thus the constructs are not uniquely ecological, but embed ecology in the structure of the physical sciences. Those areas of formal background we shall call upon are structure representation in organic chemistry, chemical reaction network theory and nonequilibrium thermodynamics. Our presentation will be directed at exploring the physical content of the approach rather than striving for mathematical precision. As a result the approach will be more in words than in equations.

The two ecological generalizations we wish to direct attention to are as follows: 1) The global ecological system is characterized by major material cycles, flows of matter involving transformations from one chemical form to another. 2) The material inputs to the flow cycles are thermodynamically low lying molecules such as H_2O, CO_2, N_2 and NO_3.

Theory

To introduce the theoretical foundations we first start with a result which arose from computer representations in organic chemistry. In an effort to encode molecular structures into computer form it was necessary to transform the information from a two-dimensional drawing or a three-dimensional model into a one-dimensional sequence of symbols. There are many alternative ways of doing this and it seems perfectly general to assert that any organic molecule, ion, or free radical can be represented by a finite sequence of linear symbols. Since any symbol can be given numerical representation, any molecule can be represented by an n-tuple of the form $\{x_1, x_2, x_3, x_4 \; . \; . \; . \; . \; . \; x_n\}$. Some encodings may be better than others for specific purposes, but the precise encoding does not concern us here, only the principle that linear representation is possible.

If we now form a multi-dimensional space of dimension n (n is determined by the largest size molecule we wish to include in the representation), each type of organic molecule can be represented by a point in this abstract n dimension space. The space is not dense with points because each point does not represent a quantum mechanically possible organic structure.

Chemical reactions may now be represented by lines drawn between points in the abstract space. For an isomerization we simply connect two points with a line . Condensation reactions of the form A+B→C are represented by a gamma connection . Condensation splitting reactions, A+B→C+D, can be shown as a chi connection . If short lived intermediates are allowed as points in the space then all of the reactions of organic chemistry can be described in terms of these three types of connections between points. The allowable points and lines are ultimately generated by the laws of quantum chemistry. Thus the space as formulated can be used to represent any chemical system; it is an abstract representation of real chemistry that we designate "Platonic Space."

Real homogeneous systems can be represented by assigning to each point a number corresponding to the number of molecules of that type in the system. To each connection we assign a number representing the net flow rate of molecules along that reaction pathway. Thus a set of occupation numbers and flow values describes all real systems. Occupation numbers correspond to structure and flow numbers correspond to function in the system.

Next consider a model system which consists of a container of organic molecules which is in contact with an infinite isothermal reservoir. The container has one side which may either have an adiabatic wall or a nonabsorbing window open to a beam of electromagnetic energy of constant flux and constant spectral distribution including visible and ultraviolet radiation. The system is a highly idealized model of the surface of the earth undergoing solar flux. We will consider two states of the model systems: 1) The equilibrium state with the adiabatic wall in place and the system aged for a long time, 2) The steady state with the window in place and the electromagnetic energy flowing into the system balanced by the flow of heat to the reservoir.

At equilibrium the state of the system is fixed by the atomic composition, volume, and total energy. Computer optimization programs are available for determining the molecular distributions and these are dominated by a group of energetically low lying small molecules. (Dayhoff et al., 1964) At equilibrium the molecule numbers are time invariant and the flow values are all zero. The latter result follows from the principle of detailed balance as discussed by Onsager. (Onsager, 1931).

The steady state system has time invariant molecule numbers but some flows must be nonzero since some energy inputs are of sufficiently high frequency to lead to electronic transitions, while all of the energy transfers out of the system are thermal. This means there must be nonzero flows from the input molecules to the electronically excited state input molecules to the products of reactions of these excited state molecules. Some of the subsequent reactions must be exothermic. The existence of some nonzero flows at a point must be compensated by other nonzero flows since the molecule number is time invariant. This constitutes a form of the Kirchhoff current law for steady state chemical networks. The previous conditions can be fulfilled only by cyclic flows of matter which leave a point, flow through the chemical network and return to the point.

Thus any chemical system with steady states of high frequency energy input and lower frequency energy outflow must be characterized by cyclical flows of matter around the reaction network. The analogy to global ecology is now clear, the major cycles such as the carbon, nitrogen and sulfur cycles are examples of such flows driven by solar energy. They are not however to be thought of as exclusively biological; they are an example of the cyclical flows that would occur in any reaction network taking in energy from a source with a color temperature of 6,000 K and releasing energy to a sink of color temperature 300 K, (if one considers the earth's surface), or 2 K, (if one considers outer space which is the ultimate heat reservoir for the process). Some such cycles must have predated cellular biology and must have been part of the functional processes which led to cellular life.

Next compare the steady state system with the equilibrium system that would develop if the window in the steady state system were replaced by the adiabatic wall. The equilibrium system would have a much more uniform distribution; it would be dominated by a few chemical species, characterized by large negative free energies of formation. However, even in the steady state the equilibrium distribution represents an attractor toward which the steady state system is constantly flowing. This follows from the formulation of the second law in irreversible thermodynamics. If the steady state cycles did not involve the dominant equilibrium species, these points would drain the cycles and steady states could not be maintained. Therefore the material cycles must involve inputs from those species of molecules that dominate in the equilibrium distribution. For the biosphere the equilibrium distribution would be dominated by CO_2, H_2O, N_2 and NO_3. Therefore these molecules are necessary inputs into the photosynthetic cycle. Thus we have another result relating to ecological cycling which turns out not to be uniquely biological but a consequence of steady state thermodynamic constraints.

Two major global ecological generalizations are thus shown to be derivable from physics and chemistry. The following principles were employed: 1) The representation of generalized chemical reaction networks as points and flow lines, 2) The steady state specification which is equivalent to Kirchhoff's current law for these networks, 3) The attractor nature of the equilibrium point which follows from the second law of thermodynamics.

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MODELS DESCRIBING ENERGY FLOW AND NUTRIENT CYCLES IN ECOSYSTEMS

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Summary

Models of energy flow and nutrient cycling should attempt to explain ecosystem behaviour rather than describe it. This is best approached by deriving the mathematical expressions from basic functional biological relationships and mechanisms. With our present state of knowledge, this is rarely possible but empirical models should be robust and admit of various functions whose numerical behaviour is similar.

Resource management is an area where decision making should be guided by production models of one of these types, even if available data is incomplete. Adaptive control of the model is well suited to this type of problem.

Introduction

There are a number of ways to describe the flow of energy and matter in ecosystems. One could have (and must, as a prerequisite for any description) a set of tables which quantify production, respiration and the like at each trophic level, and the amount of energy or nutrient passed to higher levels. More graphically, energy and nutrient flow diagrams can be used and are a useful means of gaining insight into energy values and transfer. Measures of the multitudinous efficiencies (Kozlovsky, 1968) can be made and valuable theoretical conclusions drawn, especially about production (see, for example, Ryther 1969). But, to my mind, such descriptions are really little more than collections of data. Despite the intensive effort and experimentation required to accumulate such vital and comprehensive data, these models do not analyse the structure of a system itself. They cannot attempt to trace the development in time of an ecosystem or to explicate the nature of the interactions between the elements of a biocoenosis. Rather, such energy and nutrient budgets serve as sources of kinematic data in our attempts to understand the dynamic characteristics of biological systems.

Now the most natural way of portraying modes of dynamic behaviour is by mechanical (Pearson 1960) or mathematical models. In the mathematical approach, an ecosystem is usually modelled by differential or difference equations. These contain rates of change of energy or nutrients within components of the system and rates of transfer between components. By using mathematical analysis or simulation, one can study quantitative and qualitative aspects of the system. Such properties as the steady states and their stability, the flow of energy through the system in a steady state, oscillations, and the effect of deterministic or random disturbances in the environment can all be examined. We can compare the relative importance of different parameters, interactions, and even of whole subsystems. All these characteristics can be compared with observation. Agreement with qualitative behaviour would make us more confident about our understanding and description of causal mechanisms in ecosystems. If sensitivity analysis leads us to believe that some parameters are more important than others in determining system behaviour, greater research effort can be devoted to these areas (Smith, 1970). Discrepancies will not only lead us to consider recasting the model and its assumptions, but also to more closely examine the data and the way it was collected and interpreted.

Even within this class of dynamical systems there is often a difference between models used for theoretical purposes and those required for resource management. In the first, our mathematics attempts to describe basic functional and structural relationships between elements of the system. Reddingius (1970) has cogently described many of the uses to which such models may be put as tools for reasoning, and for testing hypotheses. On the other hand, it may be considered sufficient, for management, to predict, to some required degree of accuracy, the quantitative progress in time of the system. This could be done by an empirically fitted model, not based on a priori knowledge of the biological situation, which is successfully predictive. Such models usually arise when there is a lot of numerical information, and not much else, and are often the only type then available. But it is precisely the ignorance of biological mechanisms and interrelationships which make attempts at resource management, on the basis of ad hoc empirical models, so dangerous. The strong interactions and feedback, largely responsible for the stable persistence of ecosystems, can exaggerate disturbances when pushed beyond the limits of regulation (Collier et al., 1973). Clearly, for rational management, a model should include these basic relationships whenever possible. It might be argued that it is better to begin with a general model whose assumptions and biological relations are 'right', despite lack of the detailed numerical data which varies according to locality. I shall return to this point later.

The mathematical functions with which we try to reflect biological mechanisms may be 'plausible' such as those of Lotka-Volterra systems, growth saturations (Canale, 1970) and predator saturation (Nicholson and Bailey, 1935; Watt, 1959; Rosenzweig, 1971). Although great insight can be obtained by such an approach and lack of specific knowledge of behaviour may preclude anything else, there is the nagging worry of being superficial. Holling (1959) has highlighted the difference between functions which describe system behaviour and those which explain it in a biologically meaningful way. This is distinct from the point made by Levins (1966) concerning generality and precision. Rather I would feel more comfortable about features of a model if they were derived from observed behavioural responses at the biological level, somewhat along the lines of deduction used in the physical sciences. Some recent examples of this approach are the use of the prey refugium in zoo-plankton grazing (McAllister, 1970; Parsons and LeBrasseur, 1970) and the use and derivation of parasitoid area of discovery (Diamond, 1974a, b; Hassell, 1971; Rogers and Hassell, 1974).

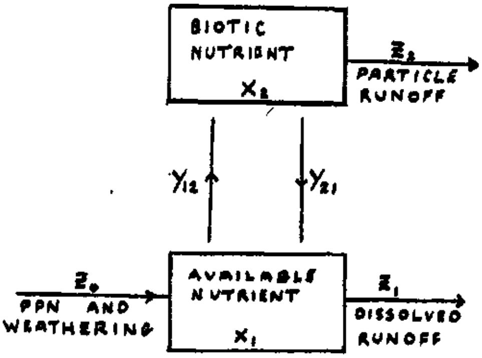
Certainly if one is to be confident about a model which is only plausible (in the above sense) it should be robust (Levins, 1966; Reddingius, 1970) in the sense that many similar functions incorporated in our equations will give similar results. A good example of this technique is displayed in Rosenzweig (1971).

Perhaps the greatest advance to be made in realistic model making is to include random fluctuations. Some theoretical progress has been made in drawing very general conclusions (May 1972, 1973) and some more specific results have been deduced for small systems (Levins, 1969; Lewontin and Cohen, 1969; Diamond 1974c). But the stochastic remains arcane. Difficulties in the numerical integration of random differential equations (Clements and Anderson, 1973; Wright, 1974) have shown digital simulation of stochastic systems to be a perilous exercise. The mathematical theory of stochastic simulation is not well understood and a great deal of mathematical theory is yet to be done.

An example of nutrient cycling

An exceedingly simple illustration of some of the ideas and problems sketched above is furnished by the well known Hubbard Brook study (Bormann and Likens, 1967). The simple empirical system described below is not a unit in itself, but is to be viewed as a subsystem of a larger biogeocoenosis, perhaps associated with a model for optimal forest exploitation. It is represented by figure 1, adapted from Bormann et al (1969). The macronutrient chosen was potassium, because of its rapid cycling. Difference equations, at yearly rests, are used because of extreme seasonal variation and the deciduous nature of the forest.

FIG. 1



Expressing the concentrations at year t, $x_1(t)$ and $x_2(t)$ in kg./ha., and precipitation content in kg./ha./yr., then

$$x_1(t+1) = z_0 - z_1 - y_{12} + y_{21} + x_1(t)$$

$$x_2(t+1) = y_{12} - y_{21} - z_2 + x_2(t) .$$

If $f(t)$ $D(t)$ are the precipitation and stream runoff, then $f(t) = \gamma D(t)$ (Johnson et al, 1968). The input $z_0 = a\, D(t)$ is proportional to the precipitation content (1.4 kg./ha./yr.) and ground leaching (.1 kg./ha./yr.) achieved by runoff. At a yearly average of $D(t) = 70$ cm., $a = .021$. The output $t_1 = b\, D(t)\, x_1(t)$, taken at 1.5 kg./ha./yr., depends on the available nutrient $x_1(t)$ and on $D(t)$. Despite the very great and intensive labours of the study, no publications list potassium levels in the nutrient pool. Rodin and Bazilevich (1967) and Duvigneaud and Denaeyer-De Smet (1970) give values for northern deciduous hardwood forests. With some misgivings, bearing in mind that the watershed is regarded as oligotrophic (Siccama et al, 1970), I chose x_1 approximately 400, well within the range of the values given by the above references. This gave $b = .53 \times 10^{-4}$. The organic particulate z_2 was only o.5% of soluble potassium (Bormann et al, 1969) and was ignored.

Of more interest are the interaction terms y_{12} and y_{21}, the expected stabilising influences upon the system. The term y_{21} describes leaching from tree crowns, and litter fall. For potassium, nearly all comes from leaching, and the data of Rodin and Bazilevich (1967) shows a closely linear relationship between this and x_2, $y_{21} = \beta x_2$, in older forests and this also appears reasonable (sic!) as a first order kinetic term. Results of Duvigneaud and Denaeyer-De Smet (1970) put $\beta = .125$ at Wavreille forest and $\beta = .155$ at the younger, more vigorous Virelles. I have taken $\beta = .14$.

The rate y_{12} represents an interaction at an interface between organic and inorganic solutions and should depend on both x_1 and x_2. But data of Rodin and Bazilevich (1970) and Duvigneaud and Denaeyer-De Smet (1970) suggests that, after an early period of intensive growth has passed, if $y_{12} = \alpha x_1 x_2$, the constant α is much larger in young forests than in more mature forests. I took α to $\alpha_0 - \alpha_1 x_2$. The model is robust enough to take many decreasing functions for α. The figures from Warreille and Virelles give
$\alpha = 2.9 \times 10^{-3} - .43 \quad 10^{-5} x_2$

The progress of the system, in its approach to equilibria $x_1 = 396$, $x_2 = 593$, is shown in fig. 2. Analysis shows the equilibria to be stable for an enormous range of values of the various parameters. The relative sensitivities are

$a : 1.0$, $b : 1.0$, $\alpha_1 : .88$, $\alpha_0 : .78$, $\beta : .11$,

where a relative sensitivity of 1.0 indicates a 1.25% total error in equilibria coming from a 1% error in estimating the parameters.

As noted by Bormann and Likens (1969), the critical input-output relationships are geared to the hydrologic cycle. Precipitation can be randomised, as may the runoff parameter b. The steady state is a random variable, but still stable in the sense of Bucy (1965). The system development when b has a mean of 0.53×10^{-4} and a standard deviation of 0.1×10^{-4} is much the same as fig. 2.

The effects of various practices such as adding fertiliser, culling, inhibiting nitrification and so on, can be predicted by increasing inputs or outputs or embedding in a larger system. Ulrich et al (1971) have constructed a much more detailed, but purely linear model. Even if one is confident of the theoretical or empirical formulation of inter-relationships, paucity of data remains a serious problem for management of such ecosystems.

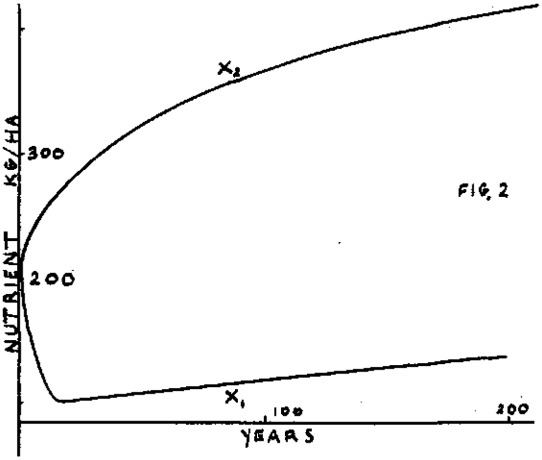


FIG. 2

Energy cycles in marine ecosystems

Photosynthetic production by algae is generally limited by lack of nutrients rather than of energy. Further, the relationships between trophic levels involve us in population dynamics and predator-prey interactions. The question of electivity and the rate at which herbivores and carnivores can assimilate different types of organisms complicates the situation (Dickie, 1970; Parsons and LeBrasseur, 1970). Also the food value of a given species might change (Petipa, 1959). Although energy is the name of the game, the rules are determined by nutrient cycles and the dynamics produced by behavioural and functional mechanisms. Any model of production and energy cycling should take all these features into account, but the difficulties and complexities of gathering data and model construction are staggering.

This approach would proceed as follows: let $x_{ij}(t)$ be the calorific value in cal/m^3 of the j-th species of the i-th trophic level. Writing $x = (x_{ij})$,

$$dn/dt = M(n_I - n) + F(x)$$

$$dx_{ij}/dt = (P_{ij}(n) - r_{ij} - D_{ij})\, x_{ij} - f_{ij}(x)$$

$$dx_{ij}/dt = (g_{ij}(x) - r_{ij} - D_{ij})\, x_{ij} - f_{ij}(x)$$

$i \geqslant 2$.

Here n is the limiting nutrient, x_{ij} the producers, P_{ij} photosynthetic coefficients, r_{ij} and D_{ij} respiration and death/sinking rates. The biological interactions are expressed by F, describing uptake and return of nutrient by the various levels, and f_{ij}, g_{ij} which contain food relationships and utilisation, defaecation and moulting. The energy flux through the i-th level is, at the steady state,

$$\sum_j (r_{ij} + D_{ij}) x_{ij} + f_{ij}(x) .$$

It is the nature of these functions which is mysterious. Steele (1958) and Riley (1965) have achieved some success with empirical models of phytoplankton, zooplankton interacting with a phosphorus cycle. McAllister (1970) has successfully combined Ivlev's empirical function and a prey refugium to obtain nice phytoplankton-zooplankton interactions. The addition of a nutrient cycle, however, apparently reduces asymptotically stable orbits to limit cycles (McAllister et al, 1972). The use of Ivlev's function can be made plausible by basing a mathematical argument on certain assumptions not clearly derived from physiological considerations (Gause, 1934, p55; Monod, 1958, p122). There is a clear need to derive such formulations from basic behavioural responses. Until some progress is made in this regard, realistic and usable models of several trophic levels will remain remote.

Resource management

It is certain that the already heavy demand on biological resources will increase. History abounds with examples of resources destroyed by human over-exploitation and we may be witnessing another in Peruvian waters (Idyll, 1973). Clearly exploitation must allow a resource to persist whilst still producing worthwhile harvests. It is my particular prejudice that this can best be done by utilising a mathematical model. Yet even if we have a model which fully expresses the dynamic interactions of the system, crucial numerical data concerning deterministic or random parameters may be lacking. Moreover, some functional relationships may themselves change, either in a natural cycle (Dobzhansky, 1971) or as a result of management practices. Resistance to insecticides is a paradigm of the latter. In such cases the model is forced into adaptive control procedures, and consequent mathematical complications.

As an example, consider a fertilisation program for the forest model previously described, with incomplete knowledge of the random runoff parameter b. In the year ending t, $q(t)$ fertiliser is added. We have some production/cost function $g(x(t), q(t))$, and over a period of N years want to maximise the expectation $f_N(c,b)$ of

$$R_N = \sum_{t=1}^{N} g(x(t), q(t)) , x(0) = c .$$

Assuming b to be normally distributed, and making yearly observations $b(t)$, at every k-th year we modify the distribution of b to have mean $\overline{b}(k)$ and standard deviation $s(k)$ given by $\overline{b}(k) = \sum_{t=1}^{k} b(t)/k$, $s^2(k) = \sum_{t=1}^{k} (b(t) - \overline{b}(k))^2/(k-1)$. At each step this gives a frequency function $G(k,b)$. It follows (Bellman and Kalaba, 1965) that

$$f_N(c,b) = \max_q \int (g(c,q)+f_{N-1}(A(c,q,b),b)) \times G(1,b)db , n \geqslant 2 ,$$

$$f_1(c,b) = \max_q \int g(c,q)G(1,b)db ,$$

where $A(x,q,b)$ describes the fertilised model

$$x(t+1) = A(x(t),q(t),b) ,$$

by the relation

$$x_1(t+1) = D(t)(a+q(t)-bq(t)-bx_1(t))+\beta x_2(t) -\alpha(q(t)+x_1(t))x_2(t)+x_1(t)+q(t) ,$$

with a similar equation for x_2. The adaptive control problem is thus reduced to solving the functional equations for f_N and making a decision at each year. Probably the cost function g should include some component which takes downriver entrophication into account. Solution is difficult, even for such a simple model as has been described.

Conclusions

1. Mathematical models of energy flow and nutrient cycling should aim at explaining basic mechanisms of ecosystems, and to describe the dynamic character of such systems.

2. Models have a crucial role to play in resource management. Lack of knowledge will force reliance on adaptive control processes and randomised models.

3. The subject is in its infancy and is one of the most difficult and challenging to biologists. Yet the area must be urgently and intensively researched to maintain the world's supply of natural resources.

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ENERGY FLOW RELATIONSHIPS IN A SHORTGRASS PRAIRIE ECOSYSTEM

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Summary

Energy flow through all major anabolic and catabolic compartments of a water-limited shortgrass prairie ecosystem was determined. The majority of net primary production was by roots and crowns. Likewise, catabolic activity was dominated by microbes in the belowground system. Energy flow through biophages was minuscule compared to saprophages. Grazing by cattle has a minor effect on primary production. In contrast, it is postulated that grazing by invertebrates, such as the plant parasitic nematodes, may have a major impact on primary production.

Introduction

The flow of energy through an ecosystem has long been recognized as providing the driving force for form, function, and diversity in nature. With a few exceptions, the history of ecological energetics parallels fragmentary ecological studies of the first one-third of the 20th century. Thus early plant physiologists such as Brown (1905) noted the energy balance phenomena of individual leaves, and Transeau (1926) estimated the accumulation of chemical energy by a corn crop. Lotka (1924) developed an energy-flow scheme for "the energy transformers of nature," which was prescient in certain respects, but incomplete in others, coming 11 years before Tansley's (1935) landmark paper on the ecosystem concept. Lotka considered that the role of consumers (i.e., all catabions, be they animals or microorganisms) was principally to accelerate or facilitate the return of mineral elements to the plants or primary producer component. The role of saprophagous components in the ecosystem was given strong emphasis by Lindeman (1942). However, he placed them in a level (A_4) even higher than carnivores, presumably indicating that their respiratory energy loss with respect to growth would be similar to that of many homoiothermic carnivores.

More recently, ecologists have attempted to document global patterns in energy flow (Jordan, 1971) and also to further understand the influence of consumers on ecosystem anabolism and nutrient cycling. Wiegert & Owen (1971) have emphasized the two-pathway nature of dissimilation of organic matter; biophagic, via living substrate, and saprophagic[2], i.e., dead or dying substrate. These are separate, largely independent pathways, and as is pointed out by Wiegert & Owen (1971) and McCullough (1970), only the grazing by primary biophages has immediate "feed-back" effects on the producer components. Contrasting examples of such effects are producer stimulation due to moderate grazing by livestock (Vickery, 1972), or alternately, depletion of plant amino-acid pools, possibly causing as much as five-fold greater decreases in net primary production than calories ingested (Wiegert, 1964). In the saprophagic pathway, grazing by collembolans, mites, nematodes, etc., may stimulate bacterial and fungal growth, thus immobilizing more or less mineral nutrients in grazed than in ungrazed controls, depending on grazing stresses (Witkamp, 1971).

The US/IBP Grassland Biome was established to study the "structure, function, and utilization" of grassland ecosystems. Energy flow is a concept that unites these ecosystem properties. The objective of this paper is to summarize energy flow for the shortgrass prairie. Ecosystem energetics were determined by measuring all major facets of primary production and biophagic and saprophagic catabolism. These measurements were made on areas with different livestock grazing intensities as well as on a long-term nongrazed control area in order to determine the effects of grazing by large herbivores on other consumers and upon primary production. Quantification of energy flow for the shortgrass ecosystem allows the testing of hypotheses about the dynamic nature of such grasslands and the energy flow concept per se. One pertinent hypothesis is that the stress of grazing by large herbivores will cause a significant shift in energy-flow patterns, shifts that are in excess of caloric intake values. Furthermore, an assumption used in many studies of energy flow that harvest methods adequately

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1. On leave from the Department of Botany, Kurukshetra University, Kurukshetra, India
2. We agree with Allee et al. (1949): "The terminology, more or less apt," of itself, "explains nothing."

describe the organic production and decomposition events in grasslands can be evaluated.

Because of limitations of space only a very brief accounting of procedures we used in determinations of energy flow can be presented herein. However, detailed information will be given in Coleman et al. (in preparation) and in part can be found in the included references. Discussion of tabular material is and will be presented in papers being prepared by the authors.

Site description

Our studies were conducted on the Pawnee National Grassland in northeastern Colorado. The vegetation on the Pawnee Site is typical of the widely-distributed and water-limited shortgrass prairie association. Warm season grasses (C-4 pathway of carbon fixation) are dominant (Williams & Markley, 1973): the most important on the Pawnee Site is blue grama (Bouteloua gracilis (H.B.K.) Lag.). Average annual precipitation for the area is 30 cm, about 72% of which is received during the growing season as a result of convective storms. Rainfall is erratic with variations ranging from 56% below to 66% above the long-term average. However, 1972, the year for which we present data, was a near "normal" year with 33 cm of rainfall recorded. Daily maximum air temperatures during the growing season average 25°C. The frost-free season when most active vegetation growth takes place averages 135 days, but the thermal potential growing season ranges from 160 to 210 days. For more detailed descriptions of the site see Klipple & Costello (1960).

Design and methods

The experimental design included a long-term ungrazed, a lightly grazed (1 steer/10.8 ha for 180 days), and a heavily grazed (1 steer/4.8 ha for 180 days) treatment, with two replicates each. Time-series data, recorded approximately at biweekly intervals during the growing season, on shoot, crown, and root biomass were collected by the harvest technique. The aboveground net primary production was determined by summing the peak live weights of individual species. The net production of crowns was estimated by summing significant ($P > 0.95$) positive increments in the standing crop of crowns. Net root production was calculated as the sum of positive increments by depth for the ungrazed treatment. In the lightly grazed treatment and the heavily grazed treatment sampling for roots was confined to the 10-cm depth only. Therefore appropriate correction factors were used to obtain the net root production value for the 0 to 60 cm depth. The dry matter values were multiplied by appropriate conversion factors to express the results in kcal/m^2. Plant matter consumed by herbivores was then added to the above estimates in order to obtain total estimates. The gross primary production and aboveground respiration values for the ungrazed treatment were determined by a data-based primary productivity model (Brown, 1974). Steady state gross photosynthesis data collected at the Pawnee during 1972 on 100% blue grama sods was read directly into the model through four-way interaction graphs. Aboveground respiration values were determined in a similar manner with the exception that two-way interaction graphs of soil water potential and temperatures were used to arrive at the respiration rate. Belowground respiration was calculated as the difference between gross photosynthesis and the sum of shoot respiration plus total net production. For the other two treatments, gross photosynthesis, shoot respiration, and belowground respiration were estimated from known relationships among these properties and net production values in the ungrazed treatment.

The biophagic and the faunal saprophagic groups for which energy flow determinations were made include large herbivores (cattle), small mammals (rodents) passerine birds, macroarthropods, microarthropods (mites and collembolans), nematodes, and microbial populations. Because of census difficulties some relatively large and widely dispersed vertebrates, including raptors, coyotes, and lagomorphs, could not be included in the determinations. Assimilation and consumption determinations were made from appropriate standing crop censuses and pertinent energetic parameters from the literature (cattle--Hyder et al., 1971; small mammals--French et al., MS; birds--Wiens & Innis, in press; macroarthropods--Swift & French, 1972; Reichle, 1971; Andrews, in prep.; nematodes--J. Smolik, unpubl. data; Klekowski et al., 1972; Andrews & Anway, in prep.; microarthropods--Zinkler, 1966; Webb, 1970a,b; Wood & Lawton, 1973).

Microbial population turnover was estimated in two ways: (1) respirometry and (2) assumed turnover time of standing crop. In the first instance, respiration was measured on a Gilson respirometer (20°C), concomitant with ATP determinations (Sparrow & Doxtader, 1973). Assuming that production efficiency was about 50% (Payne, 1970), mg C fixed/24 hr/g soil were calculated, then converted to g C/m^2/200-day season. The second approach assumed a turnover time of 0.001 standing crop × hr^{-1} (Babiuk & Paul, 1970). In subsequent calculations, microbial tissue was assumed to be 5.5 kcal/g. Total soil respiration was measured every 3 to 4 weeks, for 24 hr, by alkali absorption, and season-long soil respiration was calculated by integrating under parabolic regression curves of daily CO_2 evolution × m^{-2} by time. Microbial respiration energy equivalents were calculated using an RQ of 0.7 (Klein, 1972). Further details on methodology appear in Coleman (1973a).

Results

Producer subsystem

The energy allocations of the primary producers are given in Table 1. During the 154-day growing season 5.6 × 10^3 to 6.5 × 10^3 kcal/m^2 were metabolized through the growth and respiration processes of the plant community. This amounted to 1.4 to 1.7% of the total usable solar radiation incident during the same period. For the ungrazed treatments 66% of this gross production was retained in the system as net production, and this was assumed for the other treatments as well. The production of roots and crowns was 78 to 85% of the total net production. There were no significant differences in net primary productivity between the various treatments as a result of heterogeneity of the replicates and lack of a severe grazing stress (utilization on our heavily grazed treatment was about half that suggested for the maintenance of shortgrass rangeland in "satisfactory" condition, Klipple & Costello, 1960). However, the trends in the data suggest grazing effects. Energy partitioning among roots, crowns, and shoots varied with intensity of grazing. Thus, roots accounted for 59% of total net production in the ungrazed treatment, 60% in the lightly grazed, and 69% in the heavily grazed treatment. The proportion in crowns decreased from 27%, 17%, to 12%, respectively. The proportion in shoots was 14%, 22%, and 19%, respectively. Thus, shoot production appears to have been stimulated in the lightly grazed treatment while crown production declined with increased grazing pressure and the production of roots increased.

Biophagic subsystem

Total biophagic assimilation on the ungrazed, lightly grazed, and heavily grazed treatments was 43.6, 65.0, and 86.6 kcal/m^2, respectively (Table 1). All subsequent series of numbers refer to the sequence: ungrazed, lightly grazed, and heavily grazed. The major herbivores were cattle and invertebrates. Cattle accounted for 0%, 39.0%, and 64.8% and invertebrates 81.7%, 49.5%, and 29.1% of the total herbivore assimilation. About 90% of the herbivorous invertebrate assimilation was contributed by four taxa: Nematoda, Homoptera, Scarabaeidae and adult Carabidae (in the phytophagous tribes Amarinae and Harpalinae). Secondary consumers accounted for 16.3%, 10.1%, and 5.2% of the total biophagic assimilation with Nematoda and larval Asilidae being the major contributors. Among invertebrates about 90% of the energy transfers took place in the belowground system and more than 50% of the total energy was processed by nematodes. Assimilation by birds (seven species) and small mammals (four species) amounted to 5.6%, 3.7%, and 2.7% of the total biophagic assimilation. For both these groups values were greater for secondary consumption because of the high level of insectivory during the summer months. Although birds and small mammals had similar biomasses on the various treatments (about 85 and 74 g/ha, respectively), assimilation by birds was about twice as high as that of the small mammals. With the possible exception of lagomorphs, most of the vertebrates not considered in this study would presumably have relatively small energy flow values. For example, Bauerle (1972) estimated the biomass of snakes on the Pawnee Site to be 84.3 g/ha. However, assimilation for this group was less than 0.05 kcal/m^2 as compared to 1.6 kcal/m^2 for birds that had similar biomass figures.

Saprophagic subsystem

The saprophagic subsystem was dominated by microbial activity which accounted for more than 99% of total saprophagic assimilation (Table 1). Microbial production, measured by respirometry of "active" components in 1971 (Sparrow & Doxtader, 1973) totaled 1474 kcal/m^2/200 days. Estimates of total microbial turnover (Babiuk & Paul, 1970) of 4.8 per 200 days with an average standing crop of 65 g/m^2 gave 1715 kcal/m^2 of microbial production for that time period. Because of the similarity of these independent estimates, a mean of 1594 kcal/m^2 was used across all three treatments. Microbial respiration was determined as a fraction of total soil respiration. Overall soil respiration for 200 days was 780 and 600 g CO_2/m^2 for the ungrazed and heavily grazed treatments, respectively. To correct for root respiration, 20% of the total CO_2 was subtracted from these figures (Clark & Coleman, 1972; Coleman, 1973b; Warembourg & Paul, in press). Thus, in caloric equivalents, 598 and 461 kcal/m^2 were evolved as root respiration and 2990 and 2304 kcal/m^2 were due to microbial respiration for the ungrazed and heavily grazed treatments, respectively.

Saprophagic grazing by invertebrates was dominated by nematodes, which accounted for 95% of the total saprophagic invertebrate assimilation. Tenebrionidae (Coleoptera) adults were the most important arthropod

Table 1. Energy flow data (kcal/m^2) on the shortgrass Pawnee Site, 1972. AG = aboveground, BG = belowground; (Days) indicate the length of the measurement period; a = not measured on this treatment, b = not measured on this treatment; values would be similar to the lightly grazed treatment. Solar radiation for 154 day plant growing season: received = 8.28×10^5 kcal/m^2, photosynthetically active = 3.89×10^5 kcal/m^2.

Primary production (154 days)

Energy pathways	Ungrazed	Lightly grazed	Heavily grazed
Gross production	5838	6508	5596
Net production	3852	4296	3694
net production AG	562	958	728
net production BG	3290	3338	2966
net root production	2256	2594	2539
net crown production	1034	744	427
Net respiration	1986	2212	1902
net AG respiration	936	1134	944
net BG respiration (model)	1050	1078	958
net BG respiration (lab)	598	a	461

Saprophagic activity (200 days)

	Ungrazed	Lightly grazed	Heavily grazed
Microbial respiration	2990	a	2304
Microbial production	1594	a	a
Microbial assimilation	4584	a	a
Saprophagic-grazing consumption	45	a	35
Saprophagic-grazing respiration	16.2	a	12.5
Saprophagic-grazing production	3.7	a	3.0
Saprophagic-grazing assimilation	19.9	a	15.5

Biophagic activity

	Invertebrates (180 days)			Vertebrates		
	ungrazed	lightly grazed	heavily grazed	ungrazed	lightly grazed	heavily grazed
	Belowground herbivores			Cattle (180 days)		
Consumption	46.7	42.5	34.1	0	46.1	107.9
Respiration	22.8	21.0	17.4	0	22.2	49.2
Production	7.2	6.8	5.4	0	3.2	7.0
Assimilation	30.0	27.8	22.8	0	25.4	56.2
	Belowground carnivores			Herbivorous small mammals (180 days)		
Consumption	6.2	5.8	3.2	b	0.3	0.4
Respiration	3.9	3.6	2.1	b	0.3	0.3
Production	1.2	1.1	0.6	b	<0.1	<0.1
Assimilation	5.1	4.7	2.7	b	<0.3	0.3
	Aboveground herbivores			Carnivorous small mammals (180 days)		
Consumption	9.6	6.8	4.3	b	0.8	0.8
Respiration	4.0	3.4	1.7	b	0.6	0.6
Production	1.6	1.1	0.7	b	<0.1	<0.1
Assimilation	5.6	4.4	2.4	b	0.6	0.6
	Aboveground carnivores			Herbivorous birds (150 days)		
Consumption	0.6	0.3	0.2	b	0.8	0.6
Respiration	0.3	0.2	0.1	b	0.6	0.4
Production	0.1	<0.1	<0.1	b	<0.1	<0.1
Assimilation	0.4	<0.3	<0.2	b	0.6	0.5
				Carnivorous birds (150 days)		
Consumption				b	1.4	1.4
Respiration				b	1.0	1.0
Production				b	<0.1	<0.1
Assimilation				b	1.0	1.0

taxa. Assimilation by microarthropods was very low. Over 80% was due to prostigmatid mites, which accounted for less than 0.01% of the total saprophagic invertebrate assimilation.

Discussion

Large herbivores are indigenous consumers in shortgrass ecosystems. Thus, although cattle now represent the bison, pronghorn, elk, and other large herbivores that evolved with the grasslands of central North America, we can assume that energy flow on our lightly grazed treatment may be representative of the ecosystem in a reasonably natural state. For this reason, we will use the data for this treatment as the basis for discussion and comparison.

The primary producer, biophagic and saprophagic subsystems of the shortgrass ecosystem have been presented as separate entities. By interconnecting these components we encounter the question of balance: there is clearly greater catabolic assimilation than apparent anabolic production. Microbial production plus respiration (assimilation) = 4635 kcal/m^2/200 days + 393 kcal/m^2/165 (respiration during the winter months, Coleman, unpubl. data) = 5028 kcal/m^2/yr. In contrast, net primary production (corrected for consumption) was 4210 kcal/m^2 during the 154-day growing season. This leaves 818 kcal/m^2 which are not accounted for by the data in Table 1.

There are several considerations relevant to the lack of a year-long energetic balance for the Pawnee data. First, the determination of net primary production by the harvest method is a conservative means of determining production. The belowground net production estimates do not include estimates of short-term sloughing of root tissue, exudates, or nongrowing-season growth. Observations by Jorge Ares (pers. comm.) and Singh & Coleman (in press) suggest that these factors may make a significant contribution to production in the belowground system. Furthermore, the consumption figures for herbivorous invertebrates in Table 1 are based on intake alone and do not include potential impact on the plant community. For example, it is well known that many insects destroy more than they consume. Thus, our estimate that orthopterans consume 3.6 kcal/m^2 should be multiplied by a factor of 6 to 10 for an estimate of effective consumption (Andrzejewska & Wójcik, 1970). Such underestimates of arthropod consumption for this and other groups result in low estimates of net primary production. A second consideration is the pervasive technical difficulties associated with measuring the activity of microbial populations (Clark & Paul, 1970). By assuming a conservative turnover rate we probably underestimate microbial production and thus minimize the disparity between the estimates of primary production and catabolic assimilation. A further consideratio is whether or not all production need be accounted for by catabolic activity. The possible accumulation of organic material would preclude a year-to-year balance. Therefore, because of the "unknowns" involved we feel compelled to leave the flow chart of Table 1 energetically unbalanced if only to point out the ecosystem interfaces that sorely need more information.

Apart from the general problem of balancing the anabolic and catabolic processes, the salient features of energy flow in the shortgrass ecosystem are clearly demonstrated by the data in Table 1. One notable feature is the dominance of the belowground system for both production and catabolism. About 78% of net primary production was roots and crowns and more than 99% of catabolic assimilation was by the soil microbes. Concomitantly, the amount of energy transferred through the biophagic pathway is minuscule. Even the relative amount of aboveground net primary production that is assimilated by aboveground herbivores is very small, only about 3% (or about 5% apparent consumption). Such low estimates of assimilation and consumption seem to be typical of invertebrate dominated aboveground systems (Menhinick, 1967; Reichle & Crossley, 1967; Bray, 1964). On the heavily grazed treatment, cattle consumed about 15% of the aboveground net primary production, or about 3% of the total production. Thus, consumption by cattle was lower than the 30 to 50% consumption that seems to be typical of temperate grasslands (Lewis et al., 1956; Herbel & Anderson, 1959; Klipple & Costello, 1960). Another feature of interest is the contrast of the vertebrate (cattle) and invertebrate herbivores. Apparent consumption by herbivores is similar for the aboveground and belowground systems (despite the major differences in magnitude of primary production) with the herbivorous invertebrates consuming 43 kcal/m^2 belowground and cattle consuming 46 kcal/m^2 aboveground. There was a slight, but far from compensatory response, of arthropod herbivores to the change in grazing intensity of cattle. Thus, although consumption by cattle was 0, 48, and 108 kcal/m^2 on the ungrazed, lightly grazed, and heavily grazed treatments, respectively, arthropod consumption was only 17% lower on the lightly grazed (34 kcal/m^2) than on the ungrazed (41 kcal/m^2) and only 29% lower for heavily grazed (24 kcal/m^2) than for the lightly grazed treatment. Perhaps a more important contrast between invertebrate and vertebrate herbivores is that of potential impact. We have mentioned that within the grazing stresses of this study a significant impact on the plant community is difficult to demonstrate. In contrast, Smolik (in press) was able to demonstrate the marked influence that plant parasitic nematodes have on the midgrass prairie in South Dakota where application of a nematicide was followed by 30 to 60% increases in aboveground plant production. If such an impact can be extrapolated to the shortgrass prairie (the numbers of nematodes are similar), one could conclude that nematodes are the major competitors with man for the available resources of the shortgrass ecosystem.

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ON THE REGULARITIES OF MATTER AND ENERGY TRANSPORT IN THE TROPHIC LEVELS OF THE MARINE COMMUNITIES

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Summary

Trophic complicity, energy specific flow and respiratory expenditures in the trophic levels of the communities as well as efficiency of matter and energy transport through the trophic levels are evaluated on the base of all-round investigations in nutrition, respiration and energy balance of main planktonic species.

It is established that constant specific rates for energy flow and energy expenditures, constant index (27-28%) of matter transport efficiency through all the heterotrophic levels are found for stable temperate and tropical communities.

In nonstable systems these indices rapidly change from the first heterotrophic level to that last. In particular, specific rates of energy flow and respiratory expenditures increase while matter and energy transport efficiency decreases.

Introduction

Food inter-relations of different organism groups significantly affect both turnover of organic matter in the sea and functioning of marine ecosystems. So analysis of trophic relationships between individual organisms, populations and living forms in pelagic ecosystems as well as estimation of the amount of matter and energy transferred in the food webs may be considered as the main stages in the investigation of organics turnover and consequently of certain aspects of pelagic ecosystems functioning.

The aim of our work is to reveal the dependences between trophic structure, stability and some aspects of functioning of marine ecological systems of temperate and tropical oceanic regions - direction and rate of matter and energy flows, energy expenditures in respiration, matter and energy transport efficiency in the trophic levels. It is one of the most important, recently arising and widely developed problem of modern marine ecology.

Extensive data as the result of the investigations carried out in the Black sea and tropical stable area of the Pacific ocean/Petipa et alles,1970; Petipa et al.,1974; Vinogradov et al .,1971/ are summarized and present in our report.

Results and conclusion

Trophic webs in temperate neritic and tropical oceanic ecosystems

The description of marine communities actual trophic chains or webs with determined amount of energy transport through these chains requires an extensive research work's complex on the all-round investigation of organism nutrition and energetic balance. In particular, to create the scheme of trophic relations between separate organisms or between their grouppings in the model community one must not only know a concrete composition of animals gut contents but evaluate animals potential abilities to consume different food in shape, size, weight, value etc. Potential abilities of animals and some heterotrophic plants to consume different food depends upon pecularities of oral apparatus construction and manners of food catching, of composition,distribution and abundance off food objects in the sea and of animals electivity. Principle nutrition characteristics and food balance in mass plankton specimen representatives certain ecological groups habe been studied. Creation of the whole scheme on trophic relations in the sea is simplified by division of plankton communities into ecological groups or life forms. Character and quantitative nutrition process regularities of large number species in ecological groups of organisms may be evaluated by their typical representatives.

It has been found out that such environmental conditions as composition,size and amount of food as well as light and temperature have a serious effect upon animals preference to this or that mode of moving and nutrition. It is especially typical in Copepods that compose the main mass of animals in marine communities. Animals usually choose those food objects,movements and mode of capture depending on available food objects. Thus ,main ecological organism grouppings or living forms with a certain ecological type of nutrition were segregated with account of materials obtained during investigation of large complex questions of food inter-relations.

In our opinion ecological type of nutrition is defined with totality of functional-morphological pecularities of oral and digestive apparatus of consumer. These pecularities display on environmental conditions and above all on the quality and amount of food,temperature and light.

Quantitative indices for the trophic relationships and for the matter and energy flows through food chains have been determined by magnitudes of planktonic organisms daily rations in each species of food objects and by the amount of utilized food.

All the energetic balance elements and food composition of the ecological groups' main representatives have been calculated by radiocarbonic method or by direct registration of eaten food, of weight body increment,and respiration.

Rapid changes in water density and other physico-chemical ingredients in the sea caused by some or other reasons divide vertical water thickness into natural more or less independent water masses or layers which are inhabited by certain communities of organisms. That is why the differentiation and investigation of communities and ecosystems in pelagial have been carried out with the account of natural water masses demarcation.

Two communities are marked out in the Black sea euphotic zone - epiplankton occupying the surface strata above the thermocline (12-25m layer) and bathyplankton inhabiting water space under the thermocline (layer from 12-25m to 100m and deeper) (Petipa et all.,1970).

One community may be distinguished in the euphotic zone of the equatorial Pacific approximately up to 70-100m.It is delimited from deeper living communities by little thermo-or picnocline or by the layer of dynamic equlibrium of two life limiting factors: the amount of light penetrating from above and the rate of biogens carrying out from deeper layers or by combination of the first two factors (Sorokin,1959) .

Studies in ecological nutrition types resulted in the following data: plankton forms of nerithic Black sea communities are more or less distinctly distinguished into hervivores and carnivores with an unsufficient number of omnivores while in the oceanic tropical communities mixed-food organisms predominate with preferable predation or detritophagy.

For the lack of animal food in rations energetic requirements of organisms usually are not fulfilled even at high levels of plants and bacteria assimilation (Petipa et all,1974).

The increase of omnivoreness and necessity of predation in the ocean tropical areas is determined by low magnitudes of phyto- and zooplankton biomasses, high plankton diversity and absence of predominating form. In temperate and tropical upwelling waters with reverse picture of plankton state plants,bacteria and protozoa may be the only animals' food satisfying their energetic requirements.

The number of ecological grouppings (g) in investigated communities is not equal.It is known that tropical plankton have higher species diversity compared with that of temperate latitudes.As a result the number of ecological plankton groups in the Pacific tropical community (g_3=24) is approximately two times as much as that in the Black sea nerithic communities ($g_{1,2}$=13). The number of trophic relations among the tropical plankton (m_3 = 164) is also thrice as more as that of the Black sea plankton communities ($m_{1,2}$ = 50). The Black sea infusoria and bacteria are not accounted in present calculations as well as tropical Salpae and Pteropoda.The average number of trophic inter-relations per one groupping in the tropical community equals 8,2 and in the Black sea one 3,85. An introduced index ($f = \frac{m}{g}$) may be called an index of communities trophic complicacy.The higher it is the more complicate community is.Comparing all the observed communities by this index we may see that oceanic tropical communities appear to be more complicated.

Flow, expenditures and efficiency of energy transfer through communities trophic levels

The main matter and energy flow within the Black sea epiplankton ecosystems is transferred by smaller and medium-sized forms of all trophic levels, such as: dinoflagellates (Pyrrhophyta) and diatoms (Bacillariophyta) up to 50μ in size and animals (Nauplii, Copepodites I-III of smaller-sized copepods, IY-Y copepodites of Paracalanus, Acartia clausi and Oithona minuta, small forms of Sagitta and Pleurobrachia) up to 1,5-4,0mm in size. They generate small biomass but develop high rates of matter production. All these organisms constitute the main volume of plankton community and are the principal food stock for all levels.

The epiplankton community gets a significant part of energy from detritus: its daily consumption rate constitute 49% from all alive community organisms' biomass put into energetic units.

The greater part of matter and energy flow in the bathyplankton ecosystem in contraty to epiplankton one is transmitted principally by large-sized forms of trophic levels and partially by smaller one. The most powerful matter and energy flows from producers and saprophagous organisms' level are transmitted to secondary and tertiary carnivores by large-sized diatoms and dinoflagellates, especially by Noctiluca (60-800μ), by the migrating stages of large-sized Pseudocalanus elongatus and Calanus helgolandicus (1,4-3,3mm) by males and females of Oithona similis (0,7-0,9 mm) to large-sized forms of Sagitta, Pleurobrachia and Medusae (4-10 mm).

Bathyplankton organisms consume detritus nearly as intensive as epiplankton ones. The daily rates of its consumption constitute 45% from the biomass of all alive bathyplankton community organisms put into energetic units.

All the ecological groups in the tropical oceanic ecosystem are closely connected with each other by food inter-relations. The major matter and energy flow is transmitted here through small-sized as well as large sized forms. In particular, powerful energy flows are transmitted by nauplii and copepodites of small and large-sized copepods, small-sized species of "Calanus type" to large forms of "Euchaeta type" and to small forms of "Oithona-Oncaea" type. Bacteria take a significant part in food relations within tropical communities. They receive particularly powerful energy flows from dissolved organic matter through destructing of detritus. This energy is then got by nauplii, copepodites and other ecological groups.

The daily rates of detritus consumption within tropical ecosystem equals 9% of the tropical community organisms' biomass. The comparative estimation of studied ecosystems has shown that in spite of the low detritus consumption rate in tropical community the average detritus percentage in the average animals rations is the highest (53,7) just in tropical ecosystem (in the bathyplankton system - 50,4%; in the epiplankton - 46%). The total detritus amount in the 100 m layer/m^2 tropical system is higher than in the Black sea communities.

Studies on selection of food by the main ecological groups' representatives of all three investigated systems confirm the materials and conclusions about the energy flow character in these systems.

Moreover, obtained materials indicate that not only composition and biomass of ecological grouppings but relation of organics income rates (nutrition) to organic matter expenditure (respiration) also cause the direction and magnitude of energy flow through the food webs of the Black sea and tropical Pacific communities. For example rapid increase of energy respiratory expenditures from the Herbivores level to that last in the epiplankton temperate community determines analogical enlargements of energy flow specific rate in the same direction. The values for energy expenditures are relatively equal for all the levels of bathyplankton and tropical communities. So specific energy flow is more or less constant value. This dependence is shown in Table 1.

Results of calculations on ecological trophic levels' efficiency (Slobodkin, 1962) or of matter and energy transfer efficiency by communities heterotrophic levels in the Black sea and in the tropical Pacific are represented in Table 2. The energy transfer's efficiency (E) from the first heterotrophic level to the last one in the Black sea epiplankton system constantly decreases from 59 to 8%, while in bathyplankton and tropical ecosystems this ingredient

Table 1. Matter flow and energy respiratory expenditures in the communities of temperate and tropical waters.

Trophic levels	Epiplankton community			Bathyplankton community			Plankton community of tropical oceanic area		
	B $\frac{cal}{m^3}$	$\frac{U}{B}$ %	$\frac{T}{B}$ %	B $\frac{cal}{m^3}$	$\frac{U}{B}$ %	$\frac{T}{B}$ %	B $\frac{cal}{m^3}$	$\frac{U}{B}$ %	$\frac{T}{B}$ %
Herbivores mainly	110,57	47,1	34	66,01	65,0	60	11,55	74,3	40
Mixed-food consumers	22,20	75,7	68	1,94	39,2	35	10,28	26,3	28
Primary carnivores	24,00	155,0	150	3,51	78,3	70	-	-	-
Secondary and tertiary carnivores	9,38	67,7	58	23,44	25,3	21	0,65	56,6	48

B - biomass of the levels put in energetic units,
U - amount of assimilated food or matter flow through the levels put in energetic units, per daily.
T - energy expenditures in respiration, per daily.

Table 2. Energy transfer efficiency (ecological efficiency - E = $\frac{G}{R}$) through the heterotrophic levels of temperate and tropical communities.

Trophic levels	Epiplankton community (0 - 12 m)			Bathyplankton community (12 - 100 m)			Plankton community of tropical Pacific oceanic area (0-100 m)		
	R $\frac{cal}{m^3}$	G $\frac{cal}{m^3}$	E%	R $\frac{cal}{m^3}$	G $\frac{cal}{m^3}$	E %	R $\frac{cal}{m^3}$	G $\frac{cal}{m^3}$	E %
Herbivores	62,35	35,67	59	51,00	10,47	24	14,35	4,61	32
Mixed-food consumers	18,40	8,87	48	0,97	0,36	37	6,64	1,66	25
Primary carnivores	36,90	4,90	12	3,05	0,59	19	-	-	-
Secondary and tertiary carnivores	10,50	0,87	8	10,30	0 *	0 *	0,60	0,0048*	0,8**

* - levels are not eaten, ** - complete eating is unknown,
G - amount of energy extracted from the level on the account of eating,
R - amount of energy consumed by the level, total daily ration.

is relatively constant for all the levels and its average percentage is 27-28. The analysis of obtained material has declared that the energy transfer efficiency and matter and energy specific flow at all communities trophic levels of the observed ecosystems as well as respiratory energy expenditures are evidently conditioned by different ecosystem stability. It is well known that high species diversity within any ecosystem and consequently high complicacy of food inter-relations provides higher stability of ecosystem as a whole. Hence, one may consider that the tropical oceanic ecosystem because of the higher trophic complicacy (see above) is more stable compared with the Black sea ones. However stability of state in the researched Black sea epi- and bathyplankton communities are not equal. V.V. Menshutkin has computed their stability by some ingredient $\sum \frac{\Sigma /K/}{m}$, where Σ /K/ is a sum of absolute magnitudes of biomass declinations of all ecosystems' elements (ecological groups) under the experimental perturbation effect upon the ecosystem; m- the amount of trophic relations within a system.

The obtained results indicate that the bathyplankton community (0,318) is more stable compared with the epiplankton one (0,249). As the numbers of trophic relations (connections) and ecological groups of the Black sea epi-and bathyplankton community is practically the same then different stabilities of these communities may be explained by heterogenous conditions of their existence i.e. by different environmental conditions. In fact the bathyplankton community inhabits comparatively deep waters with constant during a year temperature, salinity and other factors, while life conditions of epiplankton are greatly influenced by seasonal changes of different factors, by fluctuation in rivers indraft etc. As a result the bathyplankton community has a firm-formed in the course of time stable structure and physiological characteristics.

The following conclusion may be made out.

Stable temporary and tropical communities are characterized by relatively constant specific energy flow (U/B) through all the levels and constant specific energy expenditures in respiration. In stable communities constant index (with average percentage 27-28) of energy transfer efficiency through all the heterotrophic levels or in other words constant ecological efficiency of all the levels is observed.

On the contrary increase of specific energy flow and energetic respiratory expenditures from the first heterotrophic level to the last one is found for any nonstable system.

For the nonstable system the index of energy transfer efficiency (E) more rapidly decreases from the first heterotrophic level ($\approx$ 60%) to that last (8%), however its average value for all the levels is approximately the same as for stable systems. Inconstancy of all the marked values for the trophic levels and high indices (E) for the first heterotrophic level in the nonstable systems indicate of strained inter-relations between producers and consumers in these systems.

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Comparative productivity in ecosystems

COMPARATIVE PRODUCTIVITY IN ECOSYSTEMS - THE PRIMARY PRODUCTIVITY

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Summary

The primary productivity, as used in this paper, is the total amount of biomass assessable as day weight within a given period of time. To enable world wide comparisons the units used are g dry weight per square meter during one calendar year.

Assessments of primary productivity levels in natural ecosystems are difficult to achieve and usually not more accurate than to the 10% level. Various research groups all over the world have tried in the last decade to make such measurements with various methods. Our discussion of world productivity patterns is based on these measurements, mainly provided by IBP groups.

The world pattern of primary productivity may be discussed best either in combination with the traditionally distinguished physiognomic vegetation types or in comparison to environmental parameters and controls.

The methodological details of productivity assessments of simple plots and regional levels as well are discussed in a volume by Lieth and Whittaker, ed., "The Primary Productivity of the Biosphere", Springer Verlag, New York, in press. We can, therefore, concentrate in this paper on presenting and evaluating existing numbers and facts.

Summarizing the existing information for the net primary production, we find that about 155×10^9 t dry matter are produced by the entire biosphere with about 100×10^9 t for the terrestrial vegetation. This is about equal to 2.9×10^{21} Joule (686.9×10^{19} cal) with 1.8×10^{21} J (426×10^{19} cal). The solar energy conversion, assuming an input of 2.1×10^{24} J (510×10^{21} cal) has a mean efficiency of 0.13%, with 0.3% for the terrestrial areas and 0.07% for the oceans. Gross patterns of global productivity were presented in the past decade by Lieth, Rodin and Bazilevitch, and other teams.

Of considerable importance is the examination of correlations between net primary productivity and environmental parameters. This can greatly facilitate regional pattern prediction. On a global scale, this was done by Lieth and several students. The procedure is such that correlation models are built based on a limited set of actual productivity measurements paired with environmental data, construction of a regression equation and conversion of a large, world covering set of environmental data into the biological values. So far, we have constructed 4 models of this type

(1) $P = 3000(1 - e^{-0.000664N})$ for precipitation N in mm; Lieth, Wolaver and Box

(2) $P = \dfrac{3000}{1 + e^{1.315-0.119T}}$ for temperature T in C°; Lieth, Wolaver, Box

(3) $P = 3000(1 - e^{-0.0009665(E-20)})$ for actual evapotranspiration E in mm; Lieth and Box

(4) $P = -1.57 + 0.0517S$ for photosynthetic season in days, S in days; Reader.

Each model is convertible into a map showing the global productivity pattern. The combined use of (1) & (2) is known as the Miami Model, (3) as the Thornthwaite Memorial Model. (4) was constructed from the productivity profiles of the Eastern deciduous forest biome. It uses a data set completely different from the models (1)-(3). In its present form, it reads the maximum productivity possible for 365 days as about 1800 g/m^2 whereas the other three formulas operate with a hypothetical maximum value of 3000 g/m^2.

Future use of the primary productivity data produced in the last decade is a starting point for a variety of scientific programs ranging from geophysics to biochemistry. Ecologists should be prepared now to cooperate with many other disciplines inside and outside of biology.

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COMPARATIVE PRODUCTIVITY IN ECOSYSTEM - SECONDARY PRODUCTIVITY

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The subject of this review is vast - microbial and faunal production in terrestrial, freshwater and marine ecosystems, including discussion of trophic efficiencies, food selection etc. Comprehensive data are rare for most types of ecosystem and much of the IBP research remains to be digested. Therefore the paper will concentrate on a few general features or concepts of secondary production which have been recognised in recent years.

Major problems are associated with the measurement of secondary production, especially with micro-organisms where the approach adopted for higher organisms of measurement of population or biomass change with time is not particularly applicable. Are such estimates feasible and is an estimate of microbial productivity useful?

With increasing size, estimation of production usually becomes easier but for many invertebrates there are major problems in defining and quantifying feeding relationships and there are still very few studies in which estimates of total faunal productivity are available. Therefore we cannot expect even when IBP syntheses are complete, a clear picture of the patterns of secondary production between ecosystems. However we can obtain some broad ideas from recent information and these should clarify, and require revision of, some current concepts.

Many of the current ideas concerning secondary productivity and trophic relationships are based on an understanding of plant-herbivore-carnivore food webs. These ideas require extension to cover faunal and microbial productivity and inter-relationships within the decomposer sub-system. This applies particularly to terrestrial ecosystems where usually 70-100% of the primary productivity passes to decomposition.

It is a simple, but fundamental, fact that the productivity of microflora and fauna is dependent on primary productivity for energy, carbon and nutrient supply. Thus knowing that in most or all ecosystems the equivalent of more than 90% of primary production is recycled annually, the upper limit to total secondary production per unit area per year is set by the level of primary production. Using estimates of production:respiration for various types of organisms, and of the main pathways of carbon circulation in different ecosystems the approximate pattern of productivity of fauna and microflora in major ecosystem categories can be estimated. Some variation in the pattern can be attributed to the influence of organic matter quality, to changes in life history of organisms and to climatic factors.

ENERGY AND MATTER ECONOMY IN ECOSYSTEMS

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Abstract

The productivity of an ecosystem is determined by its energy and matter economy. In general terms, the production of a system per unit of time is proportional to the quantity /mass/ of available material and the amount of energy for the transformation and turnover of matter involved in production processes. An important feature of the economy of an ecosystem is that energy is stored in the same substances which are involved in production processes, that is in organic matter. The autotrophs of an ecosystem set the amount of available energy, while the heterotrophs influence the turnover of matter in ecosystems. The efficiency of both groups of organisms is influenced by abiotic sources of energy /climatic, ect./ as well as by the physical and chemical properties of the habitat. The photosynthetic efficiency of ecosystems is in turn influenced by a structure of producers which can by demonstrated by comparisons of the utilization of solar radiation in forest, grassland and cultivated fields situated on the same soil and climatic conditions. The turnover of organic matter is more rapid in cultivated fields and grassland ecosystems than in forest and aquatic ones. In cultivated fields, grasslands and water ecosystems physical factors influence organic matter turnover to a greater degree than in forests. Cultivated fields are ecosystems which are artificially maintained at an early stage of succession, with a simple structure, small possibilities of modifing the effect of climatic factors, low energy cost of the production of a biomass unit, and with open cycles of mineral circulation. Man influences practically all of the ecosystem processes.

Grassland ecosystems cover different successional stages up to a climax as do forest and aquatic systems. The energy cost of biomass production varies greatly. Grasslands have a moderately simple structure often controled by large herbivoures or man. It seems that the ratio of total herbivoure biomass to the mass of primary production is higher in grasslands than in other terrestrial ecosystems. Mineral cycles are rather closed and animals like rodents, by activities such as burrowing can influence mineral cycling especially in dry conditions. Detritus food chains are very well developed.

Forests, with a complicated structure, modify the climatic factors, have high water storage and mineral retention is well developed. The retention of animal biomass is probably the highest of all terrestrial ecosystems.

The direct influence of herbivoures on plants /consumption/ in land ecosystems, except in outbreak situations, is smaller than in aquatic ecosystems especially oligotrophic ones.

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FACTORS INVOLVED IN DYNAMICS OF ALGAL BLOOMS IN NATURE

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One of the factors that must be taken into account when determining productivity of an aquatic ecosystem in eutrophic conditions is the dynamics of algal populations.

The effect of intensification of agriculture and the ever increasing release of urbane and industrial wastes on the eutrophication of water bodies makes this factor central. Algal blooms, especially of blue-greens, considerably damage the ecological balance and the quality of waters for human use. Such blooms produce foul taste and odors in water and are known to cause intoxications in animals and extensive fish mortalities. Perhaps even more important, the wax and wane of algal blooms in nature produce, in turn, tremendous fluctuations oxygen contents. The bloom first produces oxygen excesses leading in certain conditions to photooxidative death of the algae, whose disintegration leads to excessive oxygen deficits causing catastrophic die-off of aquatic organisms.

Thus there is extreme ecological significance in the understanding of questions related to mass development and bloom formation, the dominance and succession of certain species, and the mass die-off of blooms.

My discussion will deal specifically with three mean points. First, there are the factors which favor excessive blue-green growth and their dominance and succession over other algal growth. This is explained by the unique ability of many blue-green species to tolerate, survive and grow in extreme environmental conditions; these relate to temperate, salt concentration, low light, low nutrient and high H_2S concentrations and anaerobiosis.

Second, there is the nutritional versatility of the blue-greens, many of which are now known to be capable of mixotrophic, as well as chemoheterotrophic growth, in addition to their traditional photoautotrophism. We are gradually beginning to understand the role of organic substrates in the growth of blue-greens which often occur in dense growth in environments containing high concentrations of dissolved organic matter.

Finally, in understanding the kinetics of blooms in different environments, it is important to consider the agents and conditions which are involved in their mortality. Counteracting factors which enhance growth and cause blooms to appear, there are continual predations, antibiotic killing, lysis by bacteria[1] and cyanophages[2] and damaging physical and chemical conditions. Of special importance is the phenomenon of lethal photooxidation to which different blue-greens in dense populations seem extremely sensitive. A characteristic feature observed with dense blue-green populations is the rapid depletion of CO_2 and tremendous oxygen enrichment during active photosynthesis, following a diurnal cyclic pattern. Experiments[3] with pure cultures of of Anacystis nidulans and Synechococcus cedrorum under conditions of CO_2 depletion showed that these organisms are rapidly killed at physiological temperatures (35°C) under the photooxidative conditions of elevated O_2 and light. The photooxidative effect prevailed and is even more pronounced at a low temperature (4 C) even in the presence of CO_2. We tried to determine whether lethal photooxidation is related to the sudden die-out in summer blooms of blue-greens in Israeli fishponds where this phenomenon is commonly observed. Since it is impossible to test this with the natural blue-green population in the ponds, axenic Anacystis cultures in dialysis tubing were suspended in pond waters. The field observations fully supported the laboratory results indicating that photooxidation prevails in the natural conditions and could well play a key role in die-off and the seasonal appearance of blue-greens.

Continuation of all these studies, and especially tests of laboratory strains in the field conditions as described, may well lead to a more complete understanding of the kinetics of algal blooms and to better management and control of these blooms.

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COMPARATIVE PRODUCTIVITY OF TERRESTRIAL ECOSYSTEMS IN JAPAN, WITH EMPHASIS ON THE COMPARISON BETWEEN NATURAL AND AGRICULTURAL SYSTEMS

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Summary

As the result of recent intensive studies in production ecology, a fairly comprehensive collation can now be made between various types of terrestrial ecosystems with respect to their productivity. The annual net and gross production and the efficiency of solar energy utilization within the growing season are compared between forests, native and man-made grasslands, and crop fields in Japan. The highest net productivity was found in evergreen broadleaf forest in warm-temperate region. On the annual basis, paddy fields exhibit by year-round culture of rice and winter crops (wheat or barley) net productivity as high as 19 - 21 ton/ha. The efficiencies of solar energy utilization by natural forests in Japan range from 0.7 to 1.1 %, while those in native grassland are usually around 0.5 %. Fertile crop fields exhibit higher efficiencies of net production as compared to forest ecosystems.

Introduction

During past fifteen years, intensive studies on primary production of various types of natural and agricultural ecosystems have been made by Japanese investigators, especially under the framework of IBP/PT and PP. These terrestrial ecosystems include natural and artificial forests, ranging from subarctic conifer forest of Hokkaido to tropical rain forest of Thailand, as well as various types of grasslands and crop fields in many localities of Japan. Since the Japanese Archipelago extends some 1000 km from north to south, temperature climate of the investigated ecosystems differ markedly. However, vegetations in these localities hardly suffer from extreme drought during the growing season, thus exhibiting relatively high productivity.

The present review is primarily intended to compare net primary productivity and efficiency of solar energy utilization of different types of vegetations, with emphasis on the comparison between natural and agricultural ecosystems in Japan.

Primary productivity

Forest ecosystems

Since 1955, many studies on primary productivity of forest ecosystems have been published by Japanese authors. These studies were made mostly based on the harvest method (Kira & Shidei, 1967; Newbould, 1967). The data obtained from more than three hundred stands were reviewed recently by Kira & Shidei (1967), Tadaki & Hatiya (1968) and Satoo (1968, 1970, 1971). Since many of them lack information on biomass and productivity of roots, the total net productivity data for forests are rather limited.

The net primary productivities of coniferous forests in subarctic and subalpine regions range between 6 to 24 ton/ha.yr, with a peak of 10 - 15 ton/ha in frequency (Kira & Shidei, 1967). Tadaki & Hatiya (1968) gave an estimate of 13.5 ± 4.2 ton/ha.yr for the average productivity, based on data from 46 stands of this forest type in Japan.

The net productivity of pine forests in temperate zone are comparable to those of subarctic coniferous forests, having the peak at 10 - 15 ton/ha.yr. Tadaki & Hatiya (1968) also gave a value of 14.8 ± 4.1 ton/ha.yr for the net productivity of pine forests on the basis of data from 52 stands.

Deciduous broadleaf forests in cool temperate zone produce less organic matter as compared with coniferous forests and evergreen broadleaf forests. The available estimates on the net aboveground production of temperate deciduous forests in Japan range mostly between 5 to 10 ton/ha.yr, although the productivity of the whole community including undergrowth may be somewhat greater (Satoo, 1970). Average net productivity of deciduous broadleaf forest in cool temperate regions of Japan was estimated to be 8.7 ± 3.0 ton/ha.yr based on data from 64 stands (Tadaki & Hatiya, 1968).

The annual net production of evergreen broadleaf forest(laurel forest) in the warm temperate zone falls in the range from 10 to 30 ton/ha, the average value of 21 stands investigated being 18.1 ± 4.9 ton/ha(Tadaki & Hatiya, 1968). Satoo (1968) estimated net aboveground production of a 48-year-old plantation of Cinnamom camphora as 15 - 16.6 ton/ha (13.4 - 15.0 ton/ha by the tree layer

Table 1. Net and gross prductivities and efficiency of solar energy utilization by various types of forests in Japan and Thailand.

	Location	D	PN (t/ha)	R (t/ha)	PG (t/ha)	Eu (%)	Reference
Tropical rain forest	Thailand	1 y.	28.6	94.6	123.2	0.85	Kira et al, 1967
Laurel forest	Kagoshima	1 y.	20.6	52.4	73.1	0.8	Kimura, 1960
Beech forest	Niigata	V-X	16	24	40	0.84	Maruyama, 1971
Abies forest	Nagano	VI-X	11.1	29	40	1.1	Kimura, 1968
Abies veitchii	Yamanashi	IV-X	14.5	33	47	0.7	Tadaki et al, 1967
Castanopsis cuspidata*	Kumamoto	IV-X	22.7	29.0	51.7	1.1	Tadaki, 1968
Cryptomeria japonica*	Ooita	IV-X	18.8	35.6	54.4	0.9	Tadaki et al, 1967
Chamaecyparis obtusa*	Kumamoto	IV-X	15.4	25.5	40.9	0.8	Tadaki et al, 1966
Pinus densiflora*	Chiba	1 y.	15.8	38.1	53.9	0.5	Satoo, 1968

D = growing season, PN = net production, R = respiration, PG = gross production, and Eu = efficiency of solar energy utilization. * Artificial forest

and 1.6 ton/ha by the undergowth) and 17 - 19 ton/ha including roots.

Particularly interesting is the high net productivity of Cryptomeria japonica plantations in the temperate region, which generally range from 10 to 30 ton/ha.yr with the average of 18.1 ± 5.6 ton/ha.yr (based on data from 92 stands). According to Kira et al (1967), the net production by the tree component of a tropical rain forest in Thailand was 28.6 ton/ha.yr, although real net productivity of the entire community might be more than 30 ton/ha.yr if the losses by death of roots and grazing consumption are taken into consideration.

The data on the gross primary production of forests so far available is very limited, because of difficulty in estimating the total respiration of trees during the whole growing season. The available estimates of the annual gross production of forests are summarized in Table 1.

The annual gross production in a tropical rain forest of Thailand is 123.2 ton/ha, but about 77 % of this enormous amount is consumed by tree respiration (Kira et al, 1967). In a laurel forest of the warm temperate region of Japan, about 70 % of the gross production (73 ton/ha.yr) was estimated to be consumed by community respiration (Kimura , 1960). The PN/PG ratio, or the ratio of net production to gross production in various types of forests range mostly between 0.3 to 0.5. These values are rather small as compared to the values of 0.5 - 0.6 observed in European beech forests in Denmark by Möller et al (1954). The results in Table 1 also suggest that the annual gross production by forest seems to be greater with decreasing latitude, so far as the primary production by forest is not reduced by limited water supply. Kira & Shidei (1967) noted that both the increase of leaf area index and the elongation of growing period are probably responsible for this latitude-dependent increase of productivity, showing the fact that the annual gross production is more or less proportional to the product of leaf area index and duration of growing period in month.

Grassland ecosystems

There are rather many reports on the productivity of native grasslands in Japan, but most of which are only concerned with the net production of the aboveground parts, mainly because of difficulties in determining the annual increment of roots and rhizomes. Some of the data on the total net productivity of native and cultivated herbaceous communities in Japan are shown in Table 2.

The aboveground standing crop at its seasonal peak of semi-natural grasslands dominated by Miscanthus sinensis ranges from 4 to 8 ton/ha. Since the underground production of M. sinensis was equivalent to about 40 % of the peak aboveground standing crop (Iwaki & Midorikawa, 1968), the total net production was estimated to range from 5 to 11 ton/ha.yr.

Oshima (1961) reported extremely high value of the shoot biomass amounting to 77 ton/ha for a dwarf-bamboo (Sasa kurilensis) community in Hokkaido, the northernmost part of Japan. Since the culms of this grass is perennial, the shoot biomass cannot be regarded as a measure of net primary production. The estimated value of the net production of this community was 16.0 ton/ha.yr.

Some herbaceous communities developed in wetland are found to be very productive. The peak shoot biomass of Miscanthus sacchariflorus community on floodplain was 11 ton/ha and the net production was as high as 20 ton /ha.yr (Mutoh et al, 1968). The net primary production of a naturalized herbaceous perennial, Solidago altissima, community developed in a floodplain meadow was 17.8 ton/ha.yr and the peak shoot biomass was 12.3 ton/ha (Iwaki et al, 1969).

Relatively high productivity was also found in some native tall-herb communities in subalpine regions of northern Japan. The aboveground standing crop of Cirsium nipponicum community and Cacalia hastata community was 16.1 and 10.4 ton/ha, respectively (Hogetsu et al, 1954). Midorikawa (1959) reported the values of shoot biomass amounting to 10 ton/ha for an Aconitum japonicum community and 12 ton/ha for a Polygonum sachalinense community on Mt. Hakkoda. It is noteworthy that the net production of A. japonicum community is rather high (14.5 ton/ha.yr) in view of relatively short growing period (150 days) for this herb.

There is only limited information available on the annual gross production of herbaceous perennials. Gas analysis revealed that the total respiration and the gross production for a Solidago altissima community was 17.8 ton/ha and 40.0 ton/ha, respectively (Iwaki et al, 1966); the PN/PG ratio being 0.45. Similar values of the PN/PG ratio were obtained for other herbaceous perennials; about 0.5 for artificial communities of Helianthus tuberosus (Hogetsu et al, 1960), 0.57 for a subalpine tall-herb Aconitum japonicum community (Midorikawa, 1959), 0.53 for an old-field broomsedge community in South Caroline (Golley, 1965), and 0.35 for a dwarf-bamboo (Sasa kurilensis) community (Oshima, 1961). These values of the PN/PG ratio are comparable to those obtained for some annual crops in Japan (0.53 - 0.58), but relatively large as compared with those estimated for some forests of the Western Pacific (Kira & Shidei, 1967).

The net primary productivities including root production of some forage crop species in man-made grassland are presented in Table 2. The annual net production (PN) of orchargrass sward at Kawatabi in northern Japan was estimated to be 17.9 ton/ha, which was 2.5 times as large as the dry matter yield (Y) by four cuttings (7.2 ton/ha)(Sakai et al, 1969). Beneficial effects of nitrogen fertilizer application appeared both in the net production and in the ratio of yield to net production. Annual net productivities of orchardgrass swards with high and low nitrogen fertilizer application were 22 ton/ha and 16.5 ton/ha, respectively (Sakai et al, 1969).

Alfalfa sward at Chiba produced 15.6 ton/ha of dry matter during the whole growing season (Okubo et al, 1970). The dry matter yield by four cuttings of this sward was 10.6 ton/ha, thus the PN/Y ratio being 2.2. Kawanabe et al (1969) has estimated the annual net production of ladino clover swards in Japan to be 12 ton/ha in moderate productivity and 18 ton/ha in high productivity, based on the data of dry matter yield and on the assumption that the PN/Y ratio being 1.5. The data in Table 2 represent relatively high productivities of

Table 2. Net productivity and efficiency of solar energy utilization by natural and cultivated herbaceous communities in Japan.

Species	Location	Growing season (days)	PN (t/ha)	Eu (%)	Reference
Sasa kurilensis	Hokkaido	170	16.0	1.0	Oshima, 1961
Aconitum japonicum	Aomori	150	14.5	1.1	Midorikawa, 1959
Miscanthus sinensis grassland	Miyagi	185	10.4	0.52	Iwaki et al, unpublished data
" "	Nagano	185	5.6	0.37	Iwaki & Midorikawa, 1968
M. sacchariflorus	Ibaraki	215	20.0	0.80	Mutoh et al, 1968
Zoysia matrella	Ibaraki	245	16.6	0.60	Iwaki, 1968
Solidago altissima	Ibaraki	215	17.8	0.71	Iwaki et al, 1966
Perennial ryegrass	Chiba	77	7.6	1.23	Okubo et al, 1969
Orchard grass	"	"	7.7	1.17	"
Alfalfa	"	"	5.9	1.01	"
Ladino clover	"	"	4.1	0.72	"
Alfalfa	"	1 y.	15.6	0.78	Okubo et al, 1970
Orchard grass	Miyagi	223	17.9	0.98	Sakai et al, 1969
Ladino clover	Miyagi	215	12.0	0.68	Kawanabe et al, 1969

Table 3. Net productivity and efficiency of solar energy utilization by crop plants in Japan.

Crop	Location	Growing season (days)	PN (t/ha)	Eu (%)	Reference
Wheat	Saitama	226	16.81	0.86	Iwaki et al, unpublished data
Barley*	"	217	14.48	0.82	"
Barley**	"	217	13.79	0.78	"
Oat	"	241	20.04	0.97	"
Rye	"	241	20.41	0.99	"
Rape	"	234	14.12	0.72	"
Rice	Akita	130***	14.49	1.08	JIBP/PP, 1969
	Saitama	115***	15.80	1.34	"
	Fukuoka	131***	18.30	1.23	"
Soybean	Hokkaido	143	8.06	0.69	"
	Iwate	122	8.01	0.82	"
Maize	Iwate	127	17.65	1.43	"
Sugar beet	Hokkaido	197	17.12	1.17	"
Sweet potato	Saitama	150	14.03	0.95	Tsuno & Fujise, 1965

* Two-rowed barley, ** Six-rowed barley. *** Days from transplanting to maturity.

forage crops obtained in experimental plots under good management. On the basis of the average dry matter yield of mixed pasture of Japan (5.1 ton/ha in 1972) and assuming that the PN/Y ratio was 2.0, the average net production of mixed pasture of this country was assessed to be about 10 ton/ha.yr.

Agricultural ecosystems

Since 1967, much information about the net productivities and efficiencies of solar energy utilization by crop plants has been accumulated by Japanese IBP researchers. The 'Maximum Growth Rate Experiments' carried out by the Local Productivity Group of Japanese IBP/PP included 4 crop species (rice, soybean, maize and sugar beet) and 16 experimental stations throughout this country.

The net production during the growing season and grain yield of paddy rice in the 1967 experiment carried out at 7 stations ranges from 12.5 to 18.3 ton/ha and from 5.6 to 7.2 ton/ha, respectively. The ratio of the net production to the yield ranges from 2.40 to 3.17, the average being 2.79. Since the average grain yield of paddy rice in Japan was 4.56 ton/ha in 1972, the average net production within the growing season was estimated to be 12.7 ton/ha.

Relatively high productivities were observed for maize and sugar beet; the net production of the former ranged from 11 to 26.5 ton/ha and those of the latter from 15.5 to 17.1 ton/ha. Dry matter productions of soybean grown at 5 experimental stations are about one-half as much as those of paddy rice, ranging from 5.9 to 8.1 ton/ha.

The net productivity values of winter crops measured at experimental station in Saitama are comparable to those for summer crops (Table 3), although the growing season of the former is much longer than the latter. However, grain yield of wheat was so variable among different localities and the average yield was as low as 2.5 ton/ha (in 1972) that the average net production of wheat in Japan was assessed to be about 7.3 ton/ha, or about 60 % of the average net production of paddy rice.

The growing-season net productivities are usually less in grain crops as compared to those of forest ecosystems, especially of laurel forests or Cryptomeria japonica plantations. However, when the net productivities are compared on the annual basis, agricultural ecosystems sometimes surpass forest ecosystems in productivity. In paddy fields of Saitama, central Honshu,the net productivity of paddy rice in summer cropping of 1971 was 9.7 ton/ha in average, while those of wheat and barley in winter cropping was 9.5 and 11.4 ton/ha, respectively. Thus the annual net production of paddy field by year-round culture of two crops may be 19 - 21 ton /ha in average, which is comparable to those of laurel forests in warm-temperate zone.

Efficiency of energy utilization

In the preceding section are compared the estimated values of the net productivity among different ecosystems. Strictly speaking, however, these values cannot be compared with each other, since they were obtained under different lengths of growing season. Thus efficiency of conversion of incident solar energy to net production is often used as an measure of comparison of the photosynthetic productivity among various plant communities. Efficiency of net primary production is defined here as the calories of organic matter produced over the growing season divided by the calories of total solar radiation, although some authors (Loomis & Williams, 1963; Botkin & Malone, 1968; Moir, 1969; Cooper, 1970) defined the efficiency based on the energy of solar radiation in wave-length that can be utilized in photosynthesis (0.4 - 0.7 μ), which is about 45 % of total solar radiation. In order to assess the energy captured in different plant material, the net production in g/ha has been multiplied by 4 kcal/g for herbaceous species and by 4.7 kcal/g for tree species, when energy values were not measured.

The efficiency (Eu) of solar energy utilization during the growing season by various types of natural forests in Japan varies from 0.7 to 1.1 % (Table 1). The maximum efficiency was recorded for Abies forest in subalpine region of central Honshu. This forest exhibits the lowest net productivity mainly due to the short growing season of about five months. It is interesting that the efficiencies for various types of natural forests are comparable to that recorded for tropical rain forest in Thailand, although the values of net production and the length of growing season are significantly different among these forest types. The similar efficiencies (0.8 - 1.1 %) are also exhibited by some plantations in warm-temperate regions of Japan, except for a Pinus densiflora stand in Chiba, which showing the lowest efficiency (0.5 %).

The efficiency of energy capture in semi-natural grasslands dominated by Miscanthus sinensis ranges from 0.37 (Nagano) to 0.52 % (Miyagi), which is comparable to the efficiency (0.54 %) in tallgrass prairie in North America (Moir, 1969),but is lower compared to those in forest ecosystems in Japan. The efficiencies as high as 1 % are exhibited by dwarf-bamboo (Sasa kurilensis) community in Hokkaido and by tall-herb (Aconitum japonicum) community on Mt. Hakkoda in northern Japan (Oshima, 1961; Midorikawa, 1959). Herbaceous communities in floodplain meadow exhibit relatively high efficiencies; 0.8 % for Miscanthus sacchariflorus grassland (Mutoh et al, 1968), 0.7 % for Solidago altissima community (Iwaki et al, 1966). These values indicate that native grasslands in Japan usually exhibit the efficiency of around 0.5 % and seldom as great as over 1 %.

On the other hand, the efficiencies of net production for forage crops and agricultural crops are relatively high as compared with native grasslands. The efficiencies within the whole growing season of alfalfa and ladino clover swards were 0.78 % (Okubo et al,1970) and 0.68 % (Kawanabe et al,1969) respectively, while the efficiency of orchardgrass sward was as high as 1 % (Sakai et al, 1969). Cooper (1970) reported efficiencies ranging from 0.9 to 1.5 for temperate forage grasses with high fertilizer application.

Fertile cropland in Japan also gave considerably high efficiencies of net production. The efficiency within the whole growing season was 0.93 - 1.43 % for paddy rice, 0.95 - 2.18 % for maize, 1.15 - 1.80 % for sugar beet (JIBP/PP, 1969), 0.95 % for sweet potato (Tsuno & Fujise, 1965) and 0.72 - 0.99 % for various winter crops (Table 3).

Efficiency of energy utilization by crop plants varies seasonally in accordance with the variations in leaf area index and in the level of solar radiation. The seasonal maximum efficiencies observed in 1967 were 1.6 - 2.8 % for paddy rice, 2.6 - 4.3 % for maize, 1.3 - 2.5 % for soybean, and 2.3 - 4.5 % for sugar beet (JIBP/PP, 1969). The highest seasonal maximum value was 4.63 % attained in maize grown in Tokyo in 1969.

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DYNAMICS OF NET PRIMARY PRODUCTIVITY OF GRAZINGLAND AND FOREST ECOSYSTEMS IN WESTERN INDIA

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Summary

The present investigations deal with dynamics of net primary production of grazingland and forest ecosystems in Western India. The entire area, except the forest district of Dangs (represented by Ahwa and Waghai), experiences arid to semiarid climate and is mostly occupied with grazinglands. Again, most of the area is sandy. With the help of multivariate and bivariate regressions, it has been concluded that total net primary production (TNP) can be predicted with the help of simple ecoclimatic parameters. Further, a new index of water status has been evaluated from simple climatic data and it has been found that TNP is a trapezoid function of this index, with optimum values at medium water status. Optimum TNP has been accounted as due to C_4 pathway adaptation of plants to high thermal and medium water stress conditions with lower transpiration.

Introduction

Depending upon the magnitude of driving variables, potentiality of primary productivity differs in Western India from place to place. Primary production is the accumulation of net assimilation over a period of time. Net assimilation, which is maximum relative growth rate, is the function of a large number of driving variables and abiotic state variables, which also regulate the primary processes and translocations, senescence and death. In its finer aspect, primary production may in itself effect net assimilation to a smaller degree. In system's context, dynamic simulation models are being prepared of grazingland ecosystems, elsewhere (Swartzman and Van Dyne, 1972). Many of these models have been validated and found correct for predicting net primary production.

In the present communication, attempts have been made to understand dynamics of net primary production of grazinglands and forest ecosystems in Western India. With the help of stepwise and multiple regression analysis, predictive mathematical models have been prepared for assessing net primary production in the entire Western India. Predictions have been based on simple ecoclimatic parameters.

Site characteristics

Physiographic features:

With the help of three dimensional graph, figure 1 gives the physiographic features of entire Western India.

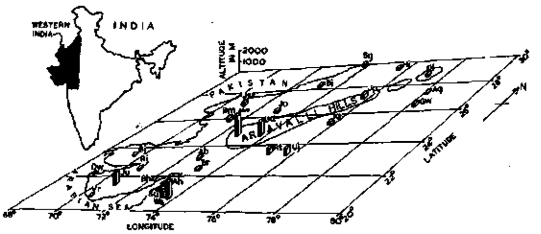

Fig. 1 - Physiography of Western India. Full names of the abbreviations of the localities are given in table 1

Latitude and longitude of each research site can also be made out from figure. The entire tract can be divided into two unequal halves along Aravalli chain of hills running obliquely from near Udaipur and extending upto Delhi. Ahwa (Centre of Dangs Forest) is the northern most extension of the western ghats. East of Aravalli chain of hills, which averages in altitude from 200 to 1000 m a.m.s.l. is semiarid and the western parts of the chain is arid. Again, around Baroda, Ahmedabad and Mehsana (Gujarat Plains) the climate is semiarid and around Rajkot it is arid. Dangs forests experience humid climate. Parts, west of Aravallis and Gujarat Plains are sandy flats. The sandy flats extend northwards into the States of

Punjab, Haryana (Hissar), Delhi and Uttar Pradesh, represented in the diagram by Agra.

Lithology

Aravallis are made up of Dharwar gneissic complex, schist and gray granite rocks; Jhansi has granites and gneissic complex and the Malwa plateau (Ujjain and Indore), Sagar and the area around Rajkot (Saurashtra) have outcrops of basalt (Deccan trap). The entire sandy flats, which constitute 70% of the area under consideration, are occupied with deep old alluvium, belonging to Eosine to Pleistocene period.

Soil

Several types of soils occur in the area. Sandy plains have sandy loams of varying thickness. It's a matter of interest that in Rajasthan sandy plains (The Great Indian Desert), west of Aravallis have generally a bed of calcium concretions at a depth varying from 1 to 2 m. In the Gujarat Plains, below a depth of about 50 cm, there is a silty thick black layer. The most conspicuous advantage of this black layer is that the water always remains suspended even during the prolonged summers. In other hilly areas (Aravallis and parts east of it) and Saurashtra have generally 3 types of soils, depending upon the drainage pattern. Soils on tops are generally coarse and gravelly, those on slopes are again coarse and due to washings, transported soils on foot hills and lowlying areas are thick clayey loams (black-cotton-soil). High degree of salinity has been recorded around Agra, Delhi, Sriganganagar and in few other localities of Rajasthan.

Observations made on soil texture, field capacity and water holding capacity (WHC) can be synthesized thus:

Clayey loams of whatever origin they may have high WHC. All soils of basalt origin have more clay and higher WHC. Sandy plains have low WHC.

Ecoclimate

It is not intended to give here detailed ecoclimatic description of the various localities examined. In Fig.3, water status (WS) of each locality has been given in three dimensional graph. For each station, mean temperature for the 4 growing months has also been given in front of the abbreviated names. WS is a new index conceived in this paper. It is the water budget of a place calculated as per the following equation: $WS = P - PE + St$, where, P is mean annual precipitation in mm, PE is total potential evapotranspiration in mm, St is water storage in mm

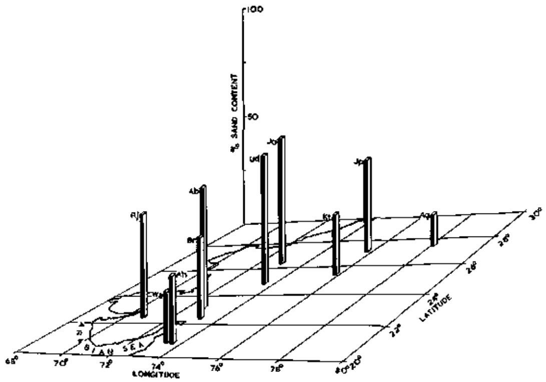

Fig.2 - Percent sand content of the different localities

All these calculations are as per the method of Thornthwaite-Mather (1957) model.

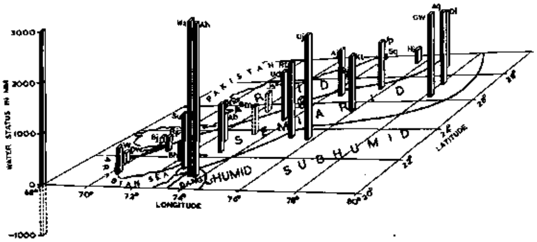

Fig.3 - Water status (WS) of the various localities. Localities with -ve WS have been shown with broken columns and are inverted (base of the locality is on the top)

Taking the overall view of the ecoclimatic conditions, Western India experiences arid to semiarid tropical monsoonic ecoclimate, extending into humid climate of Dangs. Minimum precipitation was recorded at Jaisalmer, being 217 mm and maximum at Dangs, being 1,800 mm. Monsoons are generally set in during the month of June-July and continue for about 2 to 3 months, depending upon the locality. In the grazinglands, active growth is setin during the month of June-

July with the onset of monsoons, senescence starts by end of August/ September and aerial parts dry up by September/October. Whereas, live belowground biomass is present during nongrowing season in the grazinglands of the semiarid tract, in the arid sandy plains, west of Aravallis the species are ephemerals. Dangs district has teak (Tectona grandis L.) dominated deciduous forests.

Synthesis of data and Discussion

Peak aboveground biomass (AGB) and total biomass (TB) are given in table 1:

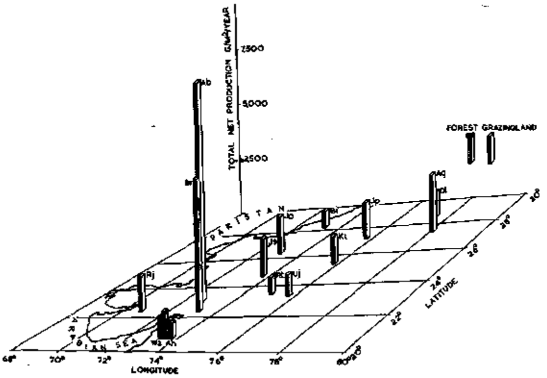

Fig.4-Total net annual production of the grazinglands and of forest in Western India

Locality	Abbreviation	Mineral status (%)	Water holding capacity (%)	Mean temp. °C for growing months (%)	Efficiency of energy capture (%)	Peak above-ground biomass (g/m²)	Peak total biomass (g/m²)	Dominant species
Ahwa (Forest)	Ah	0.114	54.3	21	0.887	-	-	Tectona
Waghai (Forest)	Wa	0.142	47.9	24	1.007	-	-	Tectona
Ahwa (Grazingland)	Ah	-	-	-	0.796	-	-	Themeda
Waghai (Grazingland)	Wa	-	-	-	1.294	-	-	Themeda
Rajkot	Rj	0.139	63.7	29	1.830	365	1314	Sehima
Jaipur	Jp	0.233	33.6	30	2.496	252	1831	Cenchrus
Agra	Ag	0.063	35.6	31	3.962	467	2587	Cenchrus
Kota	Kt	0.585	43.2	30	1.929	202	1511	Cenchrus
Udaipur	Ud	0.410	34.3	28	2.642	114	1844	Cenchrus/ Themeda
Ahmedabad	Ab	0.324	40.4	30	11.104	441	3887	Cenchrus
Baroda	Br	0.392	43.4	29	6.901	480	3432	Cenchrus
Bikaner	Bi	0.128	25.9	33	1.051	328	920	Cenchrus
Jodhpur	Jo	0.403	34.4	30	2.543	221	1636	Cenchrus
Delhi[1]	Dl	-	-	31	1.466	770	1100	Heteropogon
Ujjain[2]	Uj	-	-	28	1.063	457	1067	Dichanthium
Ratlam[2]	Rt	-	-	27	0.848	363	1086	Sehima

Abbreviations of other stations and temp.: Ajmer-Aj-29; Gwalior-Gw-31; Surat-Su-28; Veraval-Vr-28; Bhavnagar-Bh-30; Dwarka-Dw-28; Hissar-Hi-32; Sriganganagar-Sg-33; Bhuj-Bj-30; Jaisalmer-Js-32; Barmer-Bm-32; Junagadh-Ju-28.

1 - after Varshney (1972); 2 - Mall et al. (1973)

The locality variations are clear from the table. Yearly net production was calculated by subtraction method and attempt was made to evaluate the same as the function of and interrelations with the driving variables and abiotic state variables (soil characters).

Of the above named data following multivariate correlations were made:

1) Production as function of water surplus minus water deficiency (S-D) and PE
2) Production as multivariate function of mineral status (quantities of all exchangeable elements added together) and WHC
3) Separate bivariate regressions of total phytomass, net production and percentage efficiency of energy capture as functions of water

status (WS)

The results of these computations (done on computer IBM 360//44 - FORTRAN) are summarized below:

Independent variables	Dependent variables	Value of r	Significance at P level	Types of slope/ curve	Worked out equation
I MULTIVARIATE ANALYSIS					
i) S-D, PE	TNP	0.51	0.02	Dome	$Y = (-7459.73) + 1.04 X_1 + 7.40 X_2$
ii) Mineral status, WHC	TNP	0.33	NS	-	$Y = 1670.28 + 4877.35 X_1 - 14.45 X_2$
II BIVARIATE REGRESSION					
i) WS	TNP	0.40	0.10	Quadratic	$Y = 2527.12 + 0.46 X - 0.00034 X^2$
ii) WS	% Efficiency	0.47	0.05	"	$Y = 3.21 + 0.00065 X - 0.00000048 X^2$
iii) WS	TB	0.46	0.10	"	$Y = 1584.69 + 1.57 X - 0.00098 X^2$

NS = Not significant

Multivariate analysis

It is a matter of interest that total net production (TNP) is a significant function of S-D and PE at $P < 0.02$, $r = 0.51$. This is a very important conclusion with high predictive value with time, and it thus becomes a dynamic model (Fig. 5).

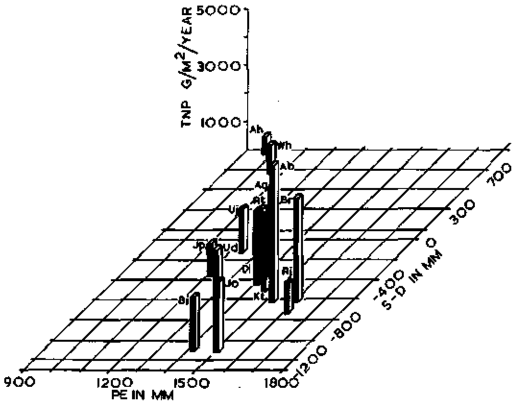

Fig.5 - Multivariate regression of TNP as function of S-D and PE. The resultant slope is dome shaped with the peak at Ahmedabad (Gujarat Plains)

In an earlier communication, Pandeya et al. (1974) have obtained similar multivariate correlation with AGB and TNP as significant function of five driving variables, when considering only the grazinglands in arid and semiarid Western India.

The multiple regression of TNP as the function of mineral status and WHC has not come out to be significant, indicating that it is not the deficiency of minerals which effects the net primary production but perhaps water is a more important factor.

Bivariate regression

Both TNP and total biomass have been worked out as significant functions of WS. The bivariate analysis, therefore, supports the functional curve (Fig.6) which is a trapezoid function

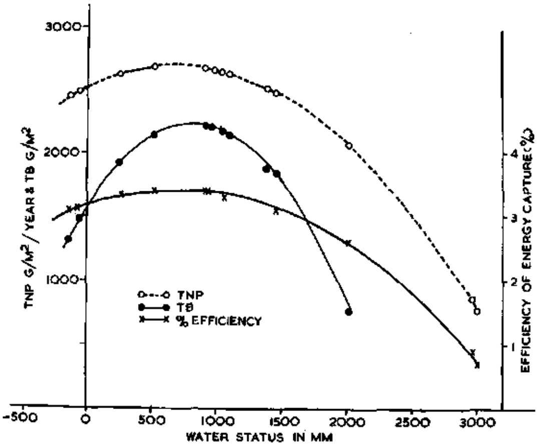

Fig.6 - Bivariate prediction curves of TNP, total biomass and efficiency of energy capture as functions of WS

defined by minimum, optimum and maximum values. The optimum has been obtained at WS 500 to 1,000 mm, which thus becomes almost a flat optimal platform.

Likewise, % efficiency of energy capture has been worked out as significant bivariate function of WS. It may be pointed out here that since WS in itself is a multifactorial index the whole computation thus becomes multivariate.

Thus, two significant conclusions have been drawn in the present investigations: (1) Highly predictive multivariate regressions have been obtained to understand TNP. This will serve as a validated dynamic model. (2) TNP, as also total biomass and % efficiency of energy capture have been found to be a trapezoid function with optimum values at medium WS. Thus localities like Waghai and Ahwa having higher water status under humid ecoclimate have lower TNP both in forest and in grazinglands. Optimum values have been obtained in the grazinglands of Gujarat Plains. The values are again lower with lower water status at Jodhpur, Bikaner, etc.

Of the two main conclusions given above, the second point deserves some discussion:

With respect to the amount of TNP, the values in the grazinglands per m^2/year are far higher in Western India than respective values in the temperate areas, elsewhere. Further, intercomparing some known studies from India in the grazinglands from humid and subhumid localities, TNP has been found to be much higher in the grazinglands of Gujarat Plains, where WS is medium. In understanding the dynamics of TNP, therefore, this becomes an important point. Gujarat Plains are characterized by medium precipitation (800 to 950 mm/annum), higher temperature during the four monsoon growing months of June to September and with the soil which has a silty subsoil below a depth of about 50 cm.

Referring to subsoil moisture conditions in the Gujarat Plains having maximum TNP, it was found that even during summers when top 20 cm of soil was dry, their was enough moisture in the subsoil with finer roots of the grazingland plants reaching into it and thus capable of holding live belowground biomass. Similar results were obtained by Björkman et al.(1972) while explaining growth of plants under less severe water stress. They have further pointed out that under such conditions the plants are adapted to high rates of photosynthesis under high temperature attributable to presence of C_4 pathway of photosynthesis with unusually high thermal stability. Björkman (1970) and Hatch (1970) have given strong evidence that C_4 pathway serves in effect as a mechanism for concentrating CO_2 for carboxylation steps in the Calvin Benson cycle resulting in high rates of CO_2 uptake under conditions of high irradiance, high temperature and limited water supply. Similar anatomical and physiological conclusions were drawn by Woolhouse (1971). Thus Black (1971) has shown that plants which make efficient use of water, may be expected to grow more in period of water stress than those which do not. Intercomparing high and low photosynthetic capacity plants, he observes that the former type requires about half as much water as the latter type to produce one unit of dry matter. Most of the plants in the grazinglands of arid and semiarid Western India belong to C_4 high photosynthetic capacity ones. Thus El-Sharkawy and Hesketh (1965) and Osmond et al. (1969) have found that higher photosynthetic rates are not accompanied by high transpiration rates. Downes (1970) has shown high photosynthesis upon transpiration in maize plant under high temperature conditions.

In light of the above understandings, as a theortical consideration, it can be said with apparent certainty that in the Gujarat Plains maximum TNP is found because of the conditions of soil and adaptation of plants in the grazinglands to fix more CO_2 under medium water stress. Conversely low TNP in Dangs forest can be accounted as due to low photosynthetic plants under high moisture condition. Present study also may reason out the fact that the forested areas with high humidity, and also temperate areas with low temperature bring about adaptation of plants which belong to low photosynthetic capacity type.

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CARBON BALANCE AND PRODUCTIVITY OF TWO COOL DESERT COMMUNITIES DOMINATED BY SHRUBS POSSESSING C_3 AND C_4 PHOTOSYNTHESIS

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Summary

Two adjacent cool desert communities in nearly identical physical environments, dominated by shrubs possessing the C_3 and C_4 photosynthetic pathways were compared with respect to productivity and carbon balance. Although, Ceratoides lanata (C_3) exhibited greater maximal leaf CO_2 fixation rates than did Atriplex confertifolia (C_4), the community dominated by Atriplex exhibited greater annual carbon fixation, standing biomass, and above- and below-ground productivity. This is largely attributable to the tendency of Atriplex to support greater quantities of foliage most of the year and to maintain a low but positive CO_2 balance for a greater proportion of the year. Both communities exhibit a heavy commitment of carbon to the below-ground plant system as indicated by very high root/shoot ratios and annual root system turnover rates. The higher productivity of the Atriplex-dominated community is not necessarily linked to the C_4 photosynthetic pathway.

Introduction

Leaf photosynthetic rates of agronomic species possessing the C_4 photosynthetic pathway have been indicated to often be much higher than rates of plants possessing the normal C_3 photosynthetic pathway at least under conditions of high irradiation intensity and high temperatures (Black, 1973; Mooney, 1972). Based on such laboratory studies and a few field studies of C_4 species (Björkman et al., 1972) the speculation has been often advanced that plants possessing C_4 photosynthesis should be much more productive -- especially in warm and arid environments (Black, 1971). Although this may be true in many agronomic situations, a review of community standing crop and productivity studies for a wide range of arid ecosystems did not indicate that communities dominated by C_4 plants were necessarily more productive or would sustain greater plant biomass than communities dominated by C_3 species (Caldwell, 1974). Rarely, however, are non-agricultural communities dominated by plants possessing C_3 and C_4 photosynthesis to be found in identical environments for valid comparison. One such comparison is, however, depicted in this study.

The salient aspects of the carbon budget of two adjacent cool salt desert communities dominated by Atriplex confertifolia (C_4) and Ceratoides lanata (C_3) are summarized in this portrayal of productivity by the primary producers at the community level. Both communities are nearly monospecific with respect to the perennial species which make up most of the community plant biomass. These communities exist in nearly identical physical environments which are characterized by an annual precipitation of approximately 200 mm, an annual temperature range of -30 to +40°C, and very saline and reasonably homogenous silty soils of lacustrine origin.

Methods

Carbon dioxide and water vapor gas exchange was measured for shoots of both species over a six-month period in 1970 by cuvette systems (Koch et al., 1971) measurements were carried out in the field with the cuvette temperature and humidity programmed to track ambient conditions. These measurements formed the basis of the shoot carbon fixation and respiration estimates for 1973 in Figures 1 and 2. Shoot litter data were provided by N. E. West (unpublished data). Carbon dioxide efflux from the soil surface in 1973 was measured by the common inverted pail technique with absorption of CO_2 by alkali (McFadyn, 1970). Sterile soil controls were also employed in these determinations. Above-ground shrub biomass and new shoot growth were determined by harvest and root biomass was determined by sampling with a soil auger and extraction of roots by flotation. Percentage carbon of various plant parts of these species was taken from N. E. West (1972). For the annual root turnover estimate, a radiocarbon dilution technique for root structural carbon was employed. This yields a realistic though conservative estimate of annual root turnover, i.e, below-ground productivity.

Results and Discussion

A depiction of the amount of biomass and standing carbon pool in these two communities based on July, 1973 harvest data are represented in Tables 1 and 2.

The differences in biomass of the two communities reflect in large part the

Table 1. Biomass and standing plant carbon pool for Atriplex confertifolia-dominated community.

Plant Component	Biomass gm^{-2}	Carbon Pool gm^{-2}
Current year's shoot growth	154	62
Previous year's shoot growth	121	64
Total Shoot System	275	126
Tap roots	48	13
Lateral root system		
5-30 cm depth	875	242
30-50 cm depth	547	172
50-70 cm depth	401	107
Total Root System	1871	534

Table 2. Biomass and standing plant carbon pool for Ceratoides lanata-dominated community.

Plant Component	Biomass gm^{-2}	Carbon Pool gm^{-2}
Current year's shoot growth	64	29
Previous year's shoot growth	82	39
Total Shoot System	146	68
Tap roots	67	22
Lateral root system		
5-30 cm depth	643	212
30-50 cm depth	518	160
50-70 cm depth	381	99
Total Root System	1609	493

different growth forms of the respective dominant shrubs. Ceratoides is a suffrutescent plant maintaining a minimal amount of perennial woody material. Atriplex is a somewhat larger shrub with a greater investment of carbon in perennial woody tissues.

Although the fixation and allocation of carbon is in part reflected by the amount of biomass supported in each community, it is the annual flux rates which are of paramount interest. These are summarized for the two communities in Figures 1 and 2. None of the quantities in this budget sheet have been derived by subtraction. By the same token it is also clear that our current estimates do not yield perfectly balanced schemes. The annual input of carbon by photosynthesis is probably underestimated. This may be in part an underestimation of community carbon fixation during the warmer months of the year. However, it may be also due to insufficient estimation of a low level of carbon fixation during the cold half of the year since both shrubs do maintain a certain quantity of photosynthetically active foliage throughout the year. The degree of underestimation of carbon fixation by both species is probably on the same order of magnitude.

Although species possessing C_4 photosynthesis are often reputed as necessarily having very high rates of leaf CO_2 fixation this was not the case in the field measurements taken in this study. Carbon dioxide fixation rates of both species were usually quite low (under optimal field conditions these rarely exceeded 18 mg $dm^{-2}hr^{-1}$) for both species (Caldwell, 1972). This is roughly one-third of maximal rates reported for several C_4 species of agronomic interest (Bull, 1969) and some exemplary warm desert species such as Encelia farinosa (C_3) (Cunningham and Strain, 1969) and Tidestromia oblongifolia (C_4) (Björkman et al., 1970) both of which exhibit unusually high rates. These maximal rates for Atriplex and Ceratoides are, however, in the same range as reported for a variety of arid land shrubs in Israel by Whiteman and Koller (1967) and in western Australia by Hellmuth (1971). In terms of daily carbon gain, Ceratoides (C_3) was usually found to exhibit much higher rates of daily carbon fixation during the most favorable months of the year, April and May, than Atriplex (C_4). However Atriplex maintained a positive carbon dioxide balance into the autumn months of September and October whereas Ceratoides would cease to maintain positive CO_2 balance by late July and early August depending on the precipitation patterns. This may in part reflect the greater net photosynthesis/transpiration ratios exhibited throughout the entire season by Atriplex, although other factors such as the proclivity for Na^+ ion accumulation by Atriplex and the consequent tendency towards greater succulence during the drier portion of the year (Moore et al., 1972) may play a role. Despite higher maximum daily rates of carbon fixation by Ceratoides, the longer season of positive carbon balance for Atriplex combined with maintenance of a greater quantity of foliage per unit ground area resulted in nearly twice as much annual carbon fixation by this community.

As with primary production in most arid regions, an episodic fluctuation from year to year of producer biomass is to be expected in this area. Earlier biomass determinations in these same communities by Bjerregaard (1971) indicate variations on the order of 30% for both above - and below-ground biomass over a consecutive three-year period. Shoot

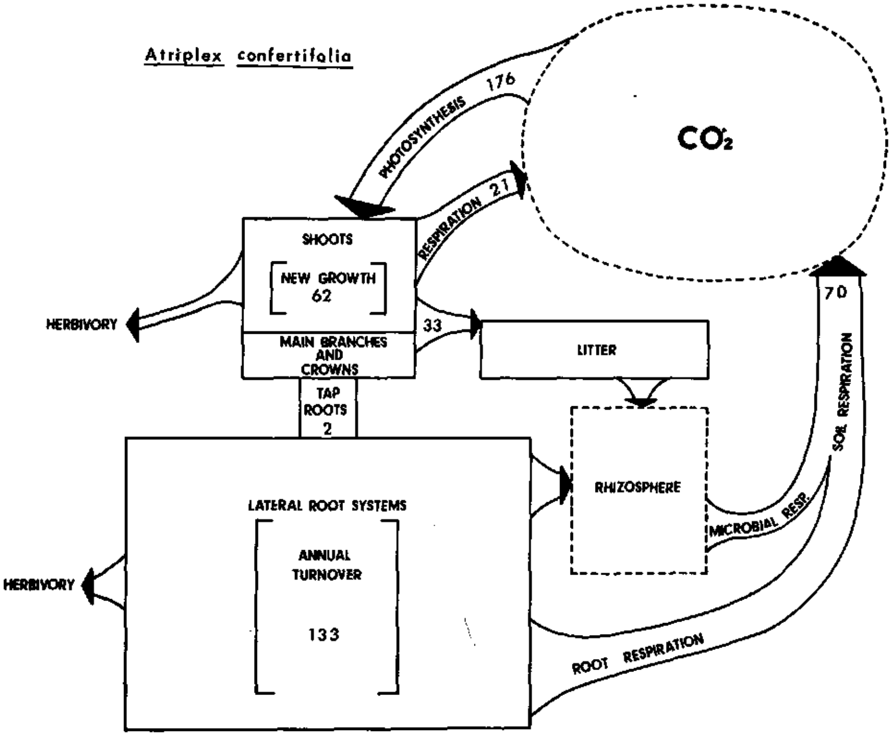

Figure 1. Carbon balance for an *Atriplex confertifolia*-dominated cool desert shrub community. Carbon fluxes are shown for the year 1973 in g carbon m^{-2} yr^{-1}.

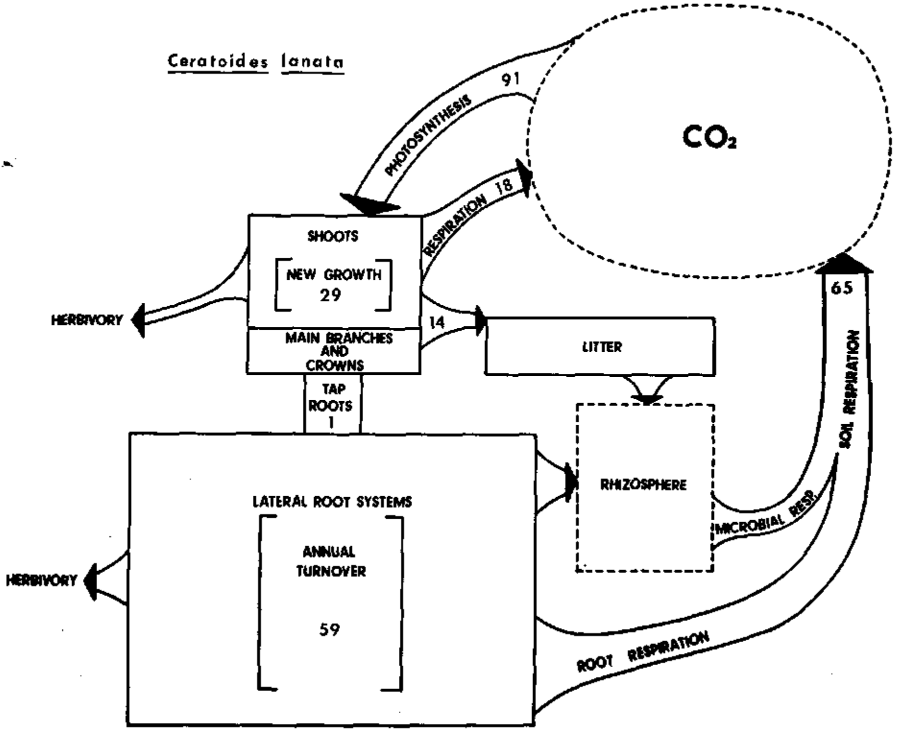

Figure 2. Carbon balance for a *Ceratoides lanata*-dominated cool desert shrub community. Carbon fluxes are shown for the year 1973 in g carbon m^{-2} yr^{-1}.

litter fall apparently varies much more from year to year than does biomass and new shoot production. Over a four-year period litter fall in these communities varied by as much as a factor of 10 (N. E. West, unpublished data). Therefore, it is not expected that annual shoot production and litter fall should necessarily be equal in any given year. It is not then surprising that the carbon in 1973 annual litter fall represented in Figures 1 and 2 was considerably less than the amount of carbon invested in new shoot production for that year. Some herbivory, probably less than 10% of above-ground biomass (Westoby, 1973), was undoubtedly also involved. In years of less favorable moisture balance, annual litter fall may well exceed annual shoot production.

Both communities exhibited a heavy commitment of carbon to the underground plant system as indicated by very high root/shoot ratios and annual root system turnover rates.

The relative importance of the below-ground system for these arid shrub-dominated communities becomes apparent in a simple comparison of plant standing carbon pools with those of a mesic hardwood-forest ecosystem in Tennessee, U.S.A. (Reichle et al., 1973). For example, whereas the *Atriplex*-dominated community has only 2% of the above-ground plant carbon pool of that of the hardwood forest, it maintains 82% of the below-ground plant carbon pool. Since the estimated annual carbon fixation rate of the *Atriplex* community is only 7% of that of the hardwood forest, the relative carbon costs for maintenance of this system are proportionately quite high.

In addition to maintenance respiration costs of these relatively large root systems, carbon investment in annual reconstruction of a portion of the root systems is also a significant component of the total carbon budget. As with shoot systems, elements of the root system have a limited longevity, especially for the fine root system. The turnover coefficients represented for these root systems are perhaps somewhat conservative but indicate, for example, in 1973 that 1/5 to 1/4 of the lateral root system was replaced in the *Atriplex* community. When these turnover coefficients are applied to the underground biomass, carbon investment in annual turnover, i.e., below-ground productivity, is indicated in Figures 1 and 2. Although the *Ceratoides* community maintained approximately 60% greater root/shoot standing carbon pool ratio (see Tables 1 and 2), the annual turnover rates were much lower and total carbon investment in this turnover was consequently only about half that of the *Atriplex*-dominated community.

The costs of root system maintenance in both communities seems excessive. However, because of very negative water potentials of these soils, often less than -60 atm over the dry portion of the year (Moore and Caldwell 1972), a continual exploration of the soil system by profuse but ephemeral root elements may be necessary for maintenance of these species. Although the root/shoot ratio of *Ceratoides* was somewhat greater than that of *Atriplex*, a greater turnover of the *Atriplex* root system may in part explain the prolonged activity of positive CO_2 balance in the drier portion of the year for this species.

An estimate of carbon investment in maintenance respiration of these root systems, is not possible because CO_2 efflux from the soil surface includes a substantial microbial respiration contribution from the rhizosphere.

If the soil-plant systems were in complete carbon equilibrium in these communities, it would be expected that the annual CO_2 efflux from the soil surface should be roughly equal to the annual carbon investment in root system turnover, the shoot litter fall, and an additional quantity representing maintenance respiration of below-ground plant parts. This is clearly not the case, it is, however, very unlikely that these systems are in carbon equilibrium since (1) until 1967 these communities were grazed by domestic livestock and are probably experiencing a slow adjustment period which may include some increase in both above- and below-ground community plant biomass and (2) these soils are reasonably young having only been exposed from the receding Great Salt Lake for a period of approximately 7,000 years (Eardley et al., 1957) and are probably accreting soil humus carbon.

The importance of a quantitative consideration of the total plant community carbon dynamics becomes apparent in studies attempting to evaluate the ecological importance of plant physiological phenomena such as photosynthetic pathways. Although in this case the community dominated by the shrub possessing C_4 photosynthesis supported more plant biomass and exhibited greater above- and below-ground productivity, an advantage conferred solely by C_4 photosynthesis is questionable. Although the superior photosynthesis/transpiration ratios may have abetted a prolongation of a positive CO_2 balance in the driest portion of the year for *Atriplex*, maximal daily rates of CO_2 fixation per unit leaf material were much lower than that of *Ceratoides*. Other factors such as differences in plant growth form, a proclivity for Na^+ accumulation, or greater root turnover activity by *Atriplex* may be of greater importance than the C_4 photosynthetic pathway.

Acknowledgments

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LIFE FORM, SURVIVAL STRATEGY AND CO_2-EXCHANGE

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Summary

Interception and use of solar energy are studied in various types of vegetation in the Mediterranean region. Results are discussed within the context of current evolutionary theory.

Introduction

As a result of its evolutionary history, the biosphere has differentiated itself into a rather small number of biomes such as forests, grasslands, etc.,each characterized physiognomically by the life form of its dominant plant species. How this differentiation came about is still not well understood. The problem is here considered in the light of current evolutionary theory using as a basis for discussion data on interception and use of solar energy by different types of vegetation exposed to similar climatic conditions.

Characteristics of climate and plant cover

The climate of the region surrounding Montpellier (43°36 N, 3°53 E) is subhumid Mediterranean with summer drought. Annual solar energy received amounts to 5 400 MJ m^{-2} with 2 740 hours of sunshine on an average. Large areas of the region are covered with a sclerophyllous vegetation, mainly on dry soils, representing different stages of degradation of the original Quercus ilex forest. Salt marsh vegetation is predominant in the coastal area, in particular in the Rhône Delta, where also most grassland vegetation is located. Extensive surfaces have been transformed into cropland. The region thus comprises good examples of the main types of biomes which caracterize the plant cover of the planet.

Life form and energy relations

The dominant species of four types of vegetation were studied in their natural habitat. Results obtained made it possible to quantify certain variables related to radiant energy interception, photosynthesis, respiration and growth. They also served to illustrate how different life forms balance energy gains against energy losses, emphasis being laid on the energy costs associated with the different survival strategies involved. A sunflower crop was used as a reference.

Salicornia herbacea L. subsp. emerici Duv.-Jouve (therophyte) is found on bare saline soils in the Camargue. A fugitive species according to Harper's terminology (Harper, 1967), its survival strategy is based on its mobility enabling it to invade unstable, unoccupied sites. A considerable fraction of photosynthates, instead of being allocated to photosynthetically active organs, are used in the formation of seeds. The resultant reduction in the energy fixing capacity is the price paid by the plant for the advantages accruing from the strategy adopted.

Salicornia fruticosa L. (chamaephyte) is also found on saline soils in the Camargue but in much less disturbed areas. A low shrub, it is the dominant species of a mature ecosystem, in many respects ressembling an old forest in miniature, in which old trees are gradually eliminated by younger trees. In terms of growth rate of the principal stem (Grouzis, 1973) and light response of photosynthesis per unit dry matter, young plants of the two Salicornia species behave in an almost similar way. In Salicornia fruticosa, however, increasing with age, respiration of ligneous organs become more and more important exceeding even photosynthesis in the oldest individuals during the hot dry summer. If the costs associated with the strategy of a colonizing species are high, so are those associated with the strategy of a dominant ligneous species in a mature ecosystem (Eckardt, 1972).

Quercus ilex L. (phanerophyte), an evergreen tree, is the principal species of the climactic vegetation, the Quercetum ilicis, which once covered an important part of the Mediterranean region. Compared with Salicornia fruticosa, which keeps its chlorophyll bearing organs for less than eight months, its rate of photosynthesis per unit green dry matter is lower. As for Salicornia fruticosa, respiration of ligneous organs is very important, in particular in summer, but in winter it becomes almost nil, i.e. much lower than would be expected from the mere drop temperature. In order to expose its leaves high above the ground, well protected against for example the large herbivores, Quercus ilex must pay a very high price, the high rate of respiration in summer. To balance its energy budget, it strongly reduces respiration in winter and prolong photosynthesis over the whole year (Eckardt, Heim, Methy & Sauvezon, submitted for publication).

Arrhenatherum elatius (L) Mert. et K. (hemicryptophyte) is the dominant species of meadows with very stable species composition occupying naturally humid and irrigated soils in the Crau. Exploited commercially, they are cut three times during the summer. In late spring, CO_2-absorption increases with the increase in standing crop until shortly before flowering, then decreases. If the vegetation is cut, the same behaviour can be observed again with, however, a somewhat smaller yield of hay each time. If the vegetation, instead of being cut three times is only cut once during the summer, the yield is reduced to about 50 per cent. The survival strategy of this grassland vegetation consists in producing large quantities of green biomass when grazed so as constantly to secure a sufficient photosynthesis (Eckardt, unpublished data).

Helianthus annuus L. is an annual crop widely grown in the Mediterranean region. Photosynthesis per unit green dry matter is fairly high, but the vegetative period does not exceed three to four months, at the end of which are formed seeds rich in lipids representing in terms of energy up to 44 per cent of the total annual production. In addition to serving as a reference, the crop made it possible to test the different methods used for assessing CO_2-exchange, i.e. the energy balance method, the cuvette method, growth analysis and mathematical modeling,and the ratio between CO_2-exchange and energy fixation in dry matter production (Eckardt, Heim, Methy, Saugier & Sauvezon, 1971).

Diversity of survival strategies

Considered together, results obtained in the different types of vegetation show the striking diversity of structural and functional characters which, combined in the right way, enable plants to balance energy gains against energy losses.

All the different types of vegetation studied, except the annual vegetation, intercept radiant energy in the photosynthetically active part of the spectrum (PHAR) quite efficiently, leaving only few per cent of incoming radiation to the least favourably exposed leaves. This is achieved, however, by leaves with different optical properties, oriented and distributed very differently in space. In the same way, annual net production does not vary much from one type of vegetation to the other. The fixation of radiant energy in dry matter produced takes place with an efficiency of the order of 0.3 - 0.6 per cent if calculated per PHAR unit in most vegetation types. Higher values are found only in meadows when regularly cut. The similar production is obtained, however, by plants maintaining very different quantities of standing crop - i.e. with very different rates of respiration - and characterized by very different photosynthetic performances. Maximum photosynthesis per unit green dry matter in Helianthus annuus exceeds 6-7 times that of Salicornia fruticosa and 9-10 times that of Quercus ilex. The length of the photosynthetically active period, on the other hand, is about 3, 7 and 12 months respectively.

Energy and genetic constraints as basic factors in evolution

To what extent are these results consistent with current ideas in evolutionary theory ? To what extent do they contribute to explaining observable facts such as the differentiation of the biosphere into plant communities or biomes each comprising numerous species ? To answer these questions four aspects of the problem can be considered separately : 1) PHAR interception 2) dry matter production 3) actual versus potential production and 4) diversity of solutions adopted by plants to balance energy gains against energy losses.

The highly efficient interception of radiant energy by leaves in the photosynthetically active region of the spectrum is in agreement with the view that conservation of genetic information is based on the maintenance of structures capable of trapping the energy necessary for their proper maintenance. To survive plants must place chlorophyll containing tissues in the pathway of the flux of radiation emitted by the sun so as to ensure the interception of energy required for the acquisition of other resources and the proper functioning of vital processes.

The similar performance with respect to annual dry matter production found in the different types of vegetation - similar anyway if compared with the variability of structural and functional traits involved in the process - suggest that selection pressure for growth is very strong indeed and that a major factor for survival is the acquisition of space at least to the extent that it does not interfere with other essential functions. It should be noted that Kira (1974) has recently suggested that the efficiency of solar energy fixation in dry matter produced is roughly the same all over the planet at least in the absence of major environmental constraints.

The considerable discrepancy between actual and potential production gives some idea of the cost of maintaining the functional structure of the plant under the prevailing conditions. One reason for the discrepancy is the strikingly high price which it is necessary for the plant to pay for the upkeep of defense systems for the protection against herbivores. This price is high even if compared with the lost opportunities for energy fixation during periods of drought due to the afternoon depression in photosynthesis. To this can be added the high price for adaptability, in particular when involving sexual reproduction. Losses due to unsuccessful germination of seeds are most significant.

The diversity of solutions adopted by plants in order to balance energy gains against energy losses lend support to the idea that evolution is based on the maximum use of already acquired genetic information (Hochachka & Somero, 1973). Instead of strictly following the direction imposed by selection pressure, evolution tends towards better adapted forms indirectly. In the process of adaptation, the plant cannot in fact give up essential functions developed in the past. It is prisoner of previous strategic choices. Exposed to the same selection pressure, for example, phyla with different evolutionary history may diverge, not converge (Stebbins, 1974), as each to survive will adopt the solution which imply the smallest genetic change. This process of evolutionary channeling (Dobzhansky, 1970) has undoubtedly contributed to the differentiation of plants into different life forms. It is likely that it has also been responsable for the general tendency of plant species to group themselves into plant communities. Adaptation to the same environment through different evolutionary channels will result in plants exploiting differently the resources of that environment, interspecific competition becoming inferior to intraspecific competition.

Conclusions

Little is known about the evolutionary history of the plant cover of the earth and current theories are highly speculative. Channelling of evolution probably played a major role in species diversification and so did strong selection pressures, often due to herbivores, forcing plants to allocate a considerable part of energy fixed in photosynthesis to the building up and maintenance of various specific defence systems. Results here presented are in agreement with this theory.

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COMMUNITY PRODUCTIVITY AND OPTIMUM EXPLOITATION OF BIOLOGICAL RESOURCES

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Summary

While investigating the productivity of populations and communities one must evaluate both biomass B and specific production C. Production P may be considered as product B and C.

The C level depends on the life span and body size of animals. Correlation of C and B exist in relation to environment capacity and level of food resources.

The efficiency of exploitation is dependent on C and B of exploited population. Intensive industrial cultivation of small invertebrates is considered as possible way to increase basically the output of the animal protein.

Introduction

Comprehensive investigation of both population and community productivity allowed to specify some facts on the structure and functioning of the particular chains of natural ecosystems. So it became possible to work out the well-founded strategy on exploitation of valuable organisms.

Some years ago the biomass of the population have been considered as productivity index. Later in a number of approaches to productivity problem there was a tendency to discriminate the biomass data. But both biomass and production are equally valuable in connection with the productivity problem (Edmondson, 1961).

In this report some interrelation are discussed between production, biomass, and level of food resources in the cases where food resources are limiting the environment capacity.

A trophic level consisting of one or a number of species populations predating the same type of food is considered as basic unit of community.

Quantity of food as a factor limiting the environment capacity

Any locus of a natural environment may be characterized by some capacity in respect of any inhabiting population or total community. Quantification of the environment capacity can be based on the biomass of inhabiting organisms. The capacity depends on a number of factors, one of them limits the biomass. In unstable environment there is a reason to quantify an average and a maximum capacity in respect of particular population.

The maximum steady-state biomass of a trophic level TL in any food web is limited often by the available total material that it can convert into its own biomass. Let us consider such situations where food resources are limiting the biomass.

If living organisms are served as a food, two trophic levels TL_I (prey) and TL_2 (predator) are under consideration with biomass B_I and B_2 respectively.

In a steady-state TL_2 is consuming such maximum quatity of food I_2 that B_I is not lowered. Hence, the rate of food elimination is equal to the rate of food recovery.

Some basic remarks about productivity (after Zaika, 1972)

The productivity of population or TL is an ability of producing organic matter. Production P is a total amount of organic matter produced for a time unit by the given biological system irrespective of the fact whether it is within the system at the end of the period under study or is eliminated partially or completely. Specific production C is an amount of production for a time unit per unit of the biomass B.

Hence, it follows useful relation

$$P=CB \tag{I}$$

Value of C in the population is related strongly to the biothic potential of the species and to the turnover rate, and C is much more stable than B. In community total value of C is more variable, alteration of C is possible by means of changing of biomass ratio for the species with different C.

High C-values have species with a short lifetime, most of them having small individual weights.

Another useful relation is:

$$P=A-R, \tag{2}$$

in which A - the food absorption and R - expenditure on metabolism, both A and R in the same units as P.

Equations (I)-(2) are equally applicable to individuals, population and TL consisting of a number of populations.

Food resources, productivity and biomass of TL

If the food resources are limiting the consumption in steady-state system, then amount of food eaten I_2 is equal to production of food organisms P_I. In any case P_I may be considered as maximum I_2. Assuming proportionality between I_2 and A_2, and between A_2 and R_2, it follows from (2) that I_2 (and B_I) is limiting P_2.

It was mentioned above that the main regulator of P is B while value of C is rather stable in natural populations in which number and biomass of organisms are closely related to their growth and reproduction rates in foregoing years. But in agricultural systems where density if individuals is man-made, the value of C is limited by the environment capacity first of all.

Let us consider two predators with different values of C in separate environment with equal capacity. If food is limiting then higher biomass appears to be in species having smaller C. Indeed, some cultivation data indicate that populations of larger animals with longer lifetime reach higher biomass in a comparable conditions (Shpet, 1968).

In succesive trophic levels a decrease of food resources take place, as from (2) it follows:

$$P_2=u_2P_I-R_2,$$
$$P_3=u_3P_2-R_2, \qquad (3)$$
$$\dots\dots\dots\dots$$

where u_2 and u_3 are coefficients of absorption of food ingested by organisms of TL_2 and TL_3 ($0<u<I$). Hence P is decreasing in succesive TL. But if C is decreasing, too, inverted pyramid of biomasses can take place. If value of B is a measure of environment capacity then inverted pyramid is evidence of increasing capacity in relation to successive TL. Thus capacity is not function of environment only but depends in a sense on C value of population or TL.

It is well known that consumption of food depends strictly on food concentration (Ivlev, 1955; Zaika, 1973). The rate of consumption is not depending on food production as such. But production of TL_I influences on consumption of TL_2 indirectly; the production of prey organisms is determining whether food concentration alters as the result of the consumption.

Biomass, specific production and population stability

A greater stability is typical to the populations of long living large organisms. Such species have usually stable high value of B. But on the other hand these organisms have low C.

A short living organisms have higher C but any change in environment even of short duration caused a great fluctuation of B. Such fluctuations are usually in many times greater than level of elimination by predators.

Optimum exploitation

The traditional catching is based on large organisms with relatively stable and high biomass as it is more profitable economically. The biomass itself is very important for the catching while values P and C are taken into consideration mainly under the threat of overcatching and in agricultural systems.

If the ratio: output/biomass is close to C in its value then the amount of biomass equal production is removed. Such regime of exploitation usually undermines population. Besides catching natural elimination exists and it can't be completely excluded that is why total elimination exceeds production in this case.

Decrease of biomass as a result of catching is very dangerous for long-living large organisms as reneval of the population demands much time. It is desirable to compare output with B, P and C for these species not only for total population but for individual age groups as well.

One of the main obstacles in exploitation of short-living organisms is unstability B in space and time. Overcatching is less dangerous for the species with short life duration (2-3 years) than for long-living organisms. In this case output equal production is permissible. The closer TL is to the primary producers the higher is the production. So it is advisable to intensify exploitation of initial chains of food web it biomass of corresponding population and individual size assume organising of economically profitable catching.

Culture of short-living animals of low trophic chains can give the highest values for harvest per unit of area. High value C of such species account for this.

To obtain high and stable production high and stable environmental capacity must be artificially created and maintained in particular in relation to food resources.

That problem involves at least three tasks:

1. The elaboration of industrial cultivation technology. All environmental factors must be strictly regulated, and a farm method is not applicable.
2. The junction of animal cultivators with a small algae or yeast cultivators, or another effective decision of the forage problem.
3. The elaboration of economically profitable technology of the utilization of the animal biomass.

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Diversity, stability and maturity in natural ecosystems

DIVERSITY, STABILITY AND MATURITY IN NATURAL ECOSYSTEMS

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The belief, that ecosystems become more diverse and, hence, more stable with time since disturbance is analysed from the perspective of current knowledge of (a) the adaptations of organisms to fluctuating physical environment, (b) resource exploitation and the results of interspecific competition for resources, and (c) the proximate and evolutionary results of predator-prey interactions, assuming that selection at levels higher than individuals is not operative.

The concepts of species richness (number of species) and species diversity (species weighted by their relative abundances) have reasonably clear meanings in the current ecological literature but the term stability is regularly used in at least six ways.

These meanings include simple lack of change (constancy), resistance to perturbations (inertia), speed of return to a stable state following a disturbance (elasticity), the zone from which the system will return to a stable state (amplitude), stable limit cycles (cyclic stability), and trajectory stability.

Since these aspects of community stability are not necessarily positively correlated, it is important to specify the kind of stability being discussed and to understand in greater detail, how these properties are influenced by the underlying interactions among individuals in the community.

The theory of adaptation of organisms to fluctuating environments is based on consideration of (a) the probability that a given environmental state exists, (b) the effects of an environmental state on the fitness of the organism, (c) the cost to the organism of improving its fitness in that state, measured in terms of energy committment and loss of fitness in other states, and (d) the predictability or regularity of occurrence of a state.

The fact that it is impossible to have a high fitness in many different environmental states is the prime reason for the richness of natural ecosystems, but little progress has yet been made in measuring the real costs in adapting to varying environments.

Optimal foraging theory shows that predators should rank potential prey according to their energy per unit time yield and should add or subtract them from their diet strictly in accordance with the abundances of higher ranked prey. Exceptions occur when it takes a great deal of time to discriminate a prey type or when there is considerable risk in attacking a prey type, i.e. the prey is actually dangerous to the predator or the encounter occurs in a situation where it is risky for the predator to pursue.

This type of theory sets limits to the kinds of foraging behaviors that should be possible in environments where resources are not so abundant that it doesn't matter how they are harvested or where competing uses of time favor minimazing the time devoted to foraging.

The mathematical theory of competition suggests that there is a fairly constant limit to the amount of overlap between competing species in all environments that fluctuate more than minimally. A species may be eliminated in an environment, or prevented from entering it, by diffuse competition from many species as well as by intense competition from one or two very similar species.

The stability properties of predator-prey interactions are inlfuenced by the existence of tresholds below which it is difficult for a predator to utilize a prey and by other processes that prevent the predator from becoming more abundant, such as territoriality or its own predators.

Nevertheless, probably the most important generator of stabilities in these systems is the patchy distribution of prey in space and time so that predators have difficulty in locating groups of prey.

Predators also affect the properties of ecosystems by their evolutionary effects on the aspect richness of the prey, that is by causing divergence in the phenotypic traits of prey living together in the same environment.

This determines the ease with which various prey can be found in featured environments and, possibly, how many prey species can live together in an environment.

Though all of these theories are still in need of further development, verification and certain modification, they represent our best current understanding of the processes taking place in ecosystems.

Therefore we can do no better than to use them fully while recognizing their imperfections.

Some of the kinds of stability are probably positively influenced by the same factors. For example, inertia and cyclic stability are increased by environmental heterogeneity and greater phenotypic diversity of prey, while others, such as elasticity and amplitude, while being enhanced by high migration and dispersal rates and generalized foraging, are oppositely influenced by the degree of density-dependence in birth rates, length of life cycles and phenotypic heterogeneity of the component species. Since the inertia of ecosystems seems to depend primarily on temporal and spatial heterogeneity, including intraspecific heterogeneity and aspect richness, there is some support for the classical dictum that diversity generates stability, but generalizations at the level usually cited in the ecological literature are so broad as to convey very little about real ecological processes.

Though tropical wet forests are the richest of the world's ecosystems and are often regarded as being the most stable, a closer examination of the properties of the component species and their patterns of interaction suggests that these forests may be highly sensitive to many kinds of perturbations because the species evolved under conditions of relative environmental constancy, have in general low reproductive rates, little or no seed dormancy, low average dispersal rates, and tend to be more specialized in their range of utilization of habitats and, possibly, prey types.

Our current knowledge about how ecosystems properties are influenced by the characteristics of their component species can be of great help in understanding the probable impacts of different kinds of perturbations on the six kinds of stabilities.

We may have to decide which kinds of stabilities we wish to maximize in different ecosystems and should be aware that we may simultaneously reduce other kinds of stabilities in the process.

In nearly every case, however, the preservation of heterogeneity in natural and modified ecosystems is probably the most important goal if we wish to achieve a rewarding long-term relationship with the ecosystems that support us.

DIVERSITY, STABILITY AND MATURITY IN NATURAL ECOSYSTEMS

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Diversity, stability and maturity, like niche and competitive exclusion, have been at the center of much discussion. As covers for a rather large spectrum of meanings, they have been useful in stimulating -and also in muddling- thinking. As one approaches them, several problems and even concepts evaporate; but something behind the words does not evaporate, and in essence I think runs more or less to the following.

In the course of our individual life, we are bumped and kicked around, we learn and this experience or information can be used to change the probability of being further kicked and bumped. The same folk wisdom can be applied to species and to ecosystems, to living systems in general: A system receives unpredictable inputs, at random; the alternative to be whipped away means to react appropriately, and this implies to preserve a minimum of organization and memory. A condition for the survival of an organization is a high reactivity, and it needs a sufficient flow of energy. History goes on: The selection of a genetic system, and/or of a set of species, leads the species or the ecosystem, respectively, to the eventual assimilation and internalization of change: Events that are unpredictable over a short term, fall into a regular law of probability if taken over years. Events unpredictable on the square centimeter, may become predictable over the acre. Food is largely assured if different foodstuffs are acceptable or if the behaviour of the preys is adequately incorporated in the mechanisms of the own behaviour. The strategy of life is to combine events and resources over time and space, or else anticipate change. Are we allowed to refer to such strategy as stabilizing? It involves more than simple habitat selection. Even if achieved, success takes time, and the properties of certain environments are harder to internalize than those of others. Not many routine responses anticipating change can be internalized in strongly fluctuating climates, exploited populations, turbulent water and mowed lawns. Under such conditions, systems are kept rather simple, building again and again, at a high thermodynamical cost if measured against the supported biomass. But as such systems succeed in keeping a place, they are "stable". All the continuous trying, failing or succeeding, goes along a certain axis, and I would use "maturity" to qualify the position of a system along such axis: At low maturity a system remains reactive and has to cope continually with new and unpredictable inputs, that mean information to be acquired and perhaps to be used later. In a mature system a larger proportion of inputs have been anticipated, or they can be ignored, because an appropriate reaction to them is no longer essential for survival, if survival is assured by other reasons. Mankind is so powerful that it can indulge in a lot of nonsense behaviour. Life is always processing information that is used to block further inputs of information. But this means prediction, reflection and combination of possibilities over space and time.

There must be a material basis in which time is bridged and events combined. Organization consists of hierarchical couplings between subsystems of necessarily different turnover. Such kind of structure places constraints in any division of sets into subsets, no matter of the adopted criterium of classification. I understand "diversity" as any useful measure of how sets fall into subsets. It is less important as an expression of some statistical average, and more important as a measure of intensity of interactions going on in a small space. Biotic diversity should approach the interest of a set of ratios between concentrations of reactants in chemical systems, where they characterize a dynamic state and measure the distance from an eventual steady state.

Measures of diversity refer to an instant of time, and stability refers to a sequence of states. If the individual is the unit, the species (the subset) the team in the game, and the whole community (the set) represents all the partners engaged in the game, then, both diversity and stability have a demographic and taxonomic interpretation. If interest is focussed on other properties, as may be energy flow, things may look differently. A system, highly unstable in species composition, may be stable concerning energy flow. It seems of common occurrence that the kind of relations that allow for a high diversity, consent as well a high stability in taxonomic composition: Nature tends to turn baroque. And this is done along a path of increasing maturity.

STABILITY IN ECOSYSTEMS: SOME COMMENTS.

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The variety of meanings that can be attached to "stability" in ecological contexts have been discussed by Lewontin, Holling, May, and others. Orians has given a crisp and insightful review of this material. Rather than attempt to gild his lily, I shall confine my remarks to a few particular points, namely: (1) the need for models to be structurally stable; (2) stable cycles in populations; (3) the relation between dynamical stability, complexity, and environmental predictability.

(1). Commonsense requires that models in population biology be structurally stable, in the sense that their predictions are not qualitatively dependent on the details of the mathematical functions used to describe the interactions between species. This is very different from physics, where the analysis frequently hinges upon special (structurally unstable) symmetries and conservation laws.

(2). In the nonlinear equations of population biology, stable limit cycle solutions are as pervasive and natural as are the stable equilibrium points so familiar from elementary mathematics courses on linear systems. Examples are to be found in predator-prey systems, in single populations with time delays in their regulatory mechanisms, in single populations with nonoverlapping generations (difference equations), and in systems with three or more competitors.

Moreover, even the simplest nonlinear difference equations can manifest further complications. As $\underline{r}$ increases, the stable equilibrium points give way to well-defined stable cycles, which at yet larger $\underline{r}$ give way to a regime of chaotic behavior, where the system can show cycles of arbitrary period, or even totally aperiodic behavior, depending on the initial population values. Such behavior, in simple and deterministic models for single populations with discrete growth, has disturbing implications.

(3). A wide variety of mathematical models, ranging from particular to general ones, suggest that as a community becomes more complex (in the sense of more species, and a more richly connected food web) it requires a very much more rigidly circumscribed set of interaction parameters if it is to be stable. That is, broadly speaking, complex systems are more fragile dynamically. On this basis, it follows that a highly predictable ("stable") environment will, by putting less stress on the system, permit the evolution of a complex (but dynamically fragile) ecosystem. Conversely, an unpredictable ("unstable") environment will require the ecosystem to be dynamically robust, and therefore relatively simple, if it is to persist.

Notice that this inverts the naive, if well-intentioned, view that "complexity begets stability", and its accompanying moral that we should preserve, or even create, complex systems as buffers against man's importunities. To the contrary, it is the complex ecosystems, currently under seige everywhere around the world, that are least able to withstand large perturbations.

I shall also make two subsidiary points here, namely:

(3a). I have gloomy doubts as to the feasibility of providing any simple recipe whereby practical people may characterize the "resilience" of an ecosystem.

(3b). As Givnish has documented, although environmental unpredictability may make for structurally simpler ecosystems, it may on the other hand be conducive to a greater diversity of reproductive strategies.

"STABILITY" IN PLANT COMMUNITIES

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Only incipient understanding of population function in plant communities is yet possible. That function should be both like that of animal communities in some principles, and quite different in other aspects (Harper & White, 1974).

Community steady states

A minority of forest communities appear stable, with relatively continuous replacement in dominant populations. This relative stability may be maintained in part by competition in the use of germination sites and the resource flows on which growth and reproduction depend. Rates of flow of plant individuals from the pool of seeds in the soil to the juvenile age class in different species may be governed by (1) availability of sites of different characteristics in the microhabitat mosaic, with sites differing in allelochemic and fungal, as well as soil and light, characteristics, (2) loss to predation (and pathogens), and (3) chance in the dispersal of seeds to sites that may leave some unoccupied at a given time, and may permit two or more species to use the same or closely similar sites in a stable balance (Skellam, 1951; Levin, 1974). Populations may thus be governed by balances between seed and site availability, and loss to predation and environmental fluctuation; but seed availability itself is part of a closed steady-state cycle from seed germination, through survival of hazard and growth limited by resources, to adult reproduction and contribution to the seed pool, which is filtered into germination by availability of unoccupied sites. Conventional models of plant-herbivore-predator interaction may need to be extended downward to consider the populations of microhabitats and the resource flows supporting plant populations.

Fluctuation and buffering

For fluctuating populations the major question may be not density-dependent control of population maxima, but the manner in which the population is buffered against extinction in adverse periods. Buffering devices include long-viable seeds, wide dispersal from locally unstable populations, genetic heterogeneity, and relations to habitat and microhabitat heterogeneity (cf. Smith, 1972). A model (by Daniel Goodman and the author) considers the population as forming a Gaussian curve along a microhabitat gradient, the integral of this curve from most to least favorable sites is a sigmoid, error function. Along this curve a unit change in environment external to the community (e.g. climatic effects on microhabitat moisture) may produce a larger population response in the steep, middle part of the curve and smaller response in the tails. Some plant populations may be relatively stable because (1) increase with more favorable environment is limited by occupation of microhabitats by the same and other species or (2) decrease with less favorable environment is limited by survival of some genetically adapted individuals in most favored microhabitats. Simplified as the model is, it predicts behaviors resembling those of many real populations.

Conclusion

Species diversity tends to increase through evolutionary time by the accumulation of species that are buffered against extinction and that differ in niche. "Stability" in the two senses of relative population constancy, and species survival, does not appear to depend on species diversity. Our limited observations suggest that population function differs widely in different kinds of communities, but within each kind may be much the same in rich communities and poor. This reasoning on plant communities converges from different models (and stability criteria) with May's (1973) conclusion that increasing diversity does not produce increasing stability.

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STRUCTURAL ANALYSIS OF AQUATIC COMMUNITIES[1]

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Summary

Community structure results from system processes analysable at several hierarchical levels of ecological organization. Microsystem observables, reflecting events at the individual and population levels, affect community structure in various ways, as exemplified by the use of a growth model based upon the "metabolic niche" to project the sizes of organisms in a fish production system. For several reasons, microsystem analyses are necessarily incomplete and thus unavoidably subject to compromise by unanticipated emergent phenomena. Emergent macrosystem properties, variables observable at the community level of organization, therefore must be explicit components of community analyses. Current ecological theory is relatively weak at the macrosystem level. Comprehensive understanding of the basis for community structure awaits the development of an ecological equivalent to thermodynamics.

Introduction

When we examine natural associations of organisms we find familiar regularities, in the form of recurrent patterns. We call this "structure". A principle goal of ecology is to arrive at a general understanding of the factors governing community structure. It is an important goal, partly because the ability to manage community structure intelligently is its practical correlate, and our present record of interventions in natural systems is of course not an admirable one.

This paper adopts a non-typological approach to aquatic communities as hierarchical systems, and examines the implications of this view for analysis of community structure. Specifically, I describe a general method (the metabolic niche) for systematizing functions of individual community components, discuss why this approach cannot in itself provide a sufficient basis for analysing community structure, and indicate the kinds of community properties that are required for comprehensive structural analyses.

Microsystem properties

Traditionally, community analysis has been approached from the perspective of individual organisms or populations. These I designate "microsystems". Numerous approaches to microsystem analysis have been developed. For present purposes I describe one such method that contributes directly to the analysis of observed size compositions in aquatic communities.

Initially, we require some common method to order the properties of individual organisms. Hutchinson (1957, 1965) has provided a useful conceptual approach which we need to modify only slightly for present purposes. The Hutchinsonian niche consists in the abstract hypervolume generated by Cartesian ordering of all the factors affecting the existence of an organism. Admittedly, the niche thus formulated does not allow us to compare the influence of one particular conjunction of parameters relative to another. Slobodkin (1961) has suggested that the hypervolume might be conceived of as shells of "survival probability", an idea that has conceptual appeal but lacks easy applicability. Alternatively we can contour the niche hypervolume in what Fry (1947) has called the metabolic "scope for activity", thereby defining a "potential metabolic niche". The metabolic scope is itself defined as the difference between the maximum sustained level of metabolic expenditure and the basal or standard rate, both determined under similar conditions. As such, the metabolic scope provides a common measure of the abilities of organisms to support internal or external activity beyond that required to preserve immediate bodily integrity.

It is useful to distinguish two measurements of metabolic scope, the "potential" metabolic niche which is defined in terms of the maximum possible metabolic rate, and the "realized" metabolic niche calculated from the actual metabolic expenditure dissipated by the organism at a given time. The potential niche provides a common measure of the theoretical potential of organisms to sustain activity (what an organism "can do"), the realized niche measures that portion of the potential niche which is actually expended at a given time (what an organism "does"). Without detailed evaluation, I adopt the intuitive view here that, on average, organisms with relatively large metabolic scope under given circumstances are more likely to fare better (survive, grow, reproduce etc) at that point in time than are competitors of the

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same or another species with less niche potential.

Among other possibilities, the metabolic niche can unify our approach to individual growth patterns, which in turn affect the resulting size composition of the community. It can be shown that growth efficiency is proportional to metabolic scope (Kerr, 1971 a), which is itself determined by the various factors, prey size and density for example, that serve to define the metabolic niche. This niche definition therefore provides us, in theory at least, with an unequivocal index of the production potential of individual organisms for any given circumstances.

A microsystem analysis of fish growth serves to illustrate the prey-predator interactions which influence size composition in a trophic system. The growth model that I use has been described elsewhere in detail (Kerr 1971a, b). For present purposes, I have broken the published equations into a "diagram of immediate effects" which shows the interactions among parameters more readily than do the original equations. Fig. 1 depicts the general structure of the model by relating the several variables found adequate for description of lake trout growth. A considerable measure of detail has been lost, but two essential points are immediately clear from the general structure of the figure. First, the equation system, and by implication the growth process, is a circular causal system with positive and negative feedbacks that are modifiable by niche parameters such as prey size and density. Second, these niche parameters determine the ensuing growth pattern by affecting the realized niche, the portion of metabolic scope which is actually expended on foraging activity for prey.

Figure 1. Schematic representation of circular causal system regulating fish growth. An arrow leading from a box indicates that the enclosed component affects the component(s) enclosed in box to which arrow leads. Based on Kerr (1971a).

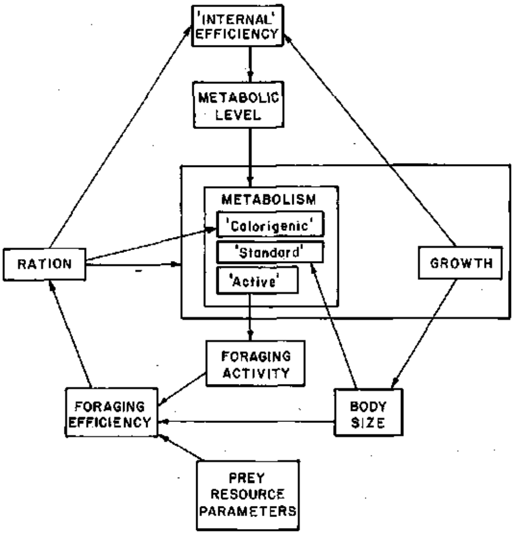
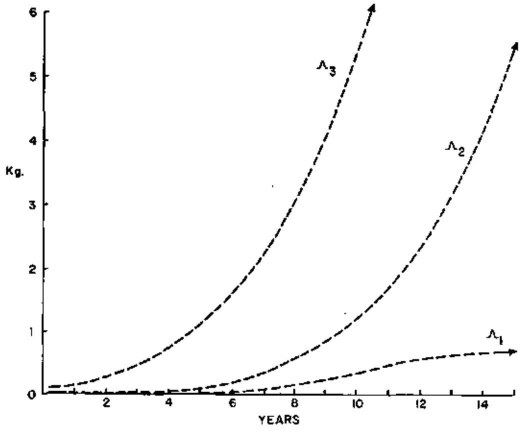


Figure 2. Growth trajectories for a fish community composed of three trophic levels, all physiologically identical to lake trout. Curves were generated by coupling three growth models of the type shown in Fig. 1, and providing the lowest trophic level, Λ_1, with a zooplankton resource of fixed density and particle size. For further clarification see text.



Because prey size is an important parameter of the metabolic niche used in the calculation system, it follows that the sizes of the various members of a food chain are determined in part by size-dependent interactions between trophic levels. This view is depicted in Fig. 2. I generated these curves by coupling a series of growth systems of the type shown in Fig. 1, to simulate a food chain. The calculation system was provided with a basic zooplankton resource of fixed size and density which was exploited by a lake trout initially ten times larger than the crustacea. In turn a second lake trout, initially larger again by a factor of ten fed on the first one, and so on. The relative sizes of predator and prey were coupled with growth. In these curves the size structure of the three terminal trophic levels has therefore been determined in large part by the size composition of the primary consumers. From this exercise, the suggestion is that explicit definitions of the metabolic niche can provide appreciable understanding of the resulting size structure in a food web. A food chain made up of physiologically identical species, as in this example, is not realistic; but Kerr and Martin (1970) have found that similar considerations apply in natural communities. There is considerable variation in mean size and other characteristics of lake trout in Algonquin Park lakes, differences that Martin (1966) showed were associated with the various diets characteristic of the different populations. Further analysis of these observations, using the growth model I have just described, indicated that the size of individual prey items was the principle factor governing the growth rates and sizes of the trout (Kerr, 1971a, b).

Undoubtedly, the growth model I have used is grossly incomplete to the extent that it does not incorporate all of the relevant parameters in the metabolic niche. There is no a priori reason why suitably comprehensive models could not be constructed on this principle. But in fact, these few factors sufficed for the lake trout. Incorporation of additional parameters did not appreciably improve the fit, perhaps because the lake trout communities seem to be relatively simple. Nevertheless, even if incomplete, a model of this kind suggests a number of ways in which the size structure of community elements can be understood, and usefully managed.

Emergent surprises

But it would be a very serious error to mistake a micromechanistic network of such models, however intricate and comprehensive, for an integral community model. As Paul Weiss (1969) has pointed out, in dissecting a community into its component parts we have lost essential information concerning the integral organization of the intact community. It could be argued that the Weiss interpretation is inappropriate if the dynamical system is decomposable into non-interacting subsystems, but Rosen (1972a) is persuasive that ordinary methods of system dissection are unlikely to achieve that happy result. It follows that micromechanistic models are unlikely in general to possess the fidelity we would like, unless satisfactory methods to preserve or restore the necessary organizational information can be found.

Current practice offers a choice between two methods for incorporating the necessary organizational information. Speaking generally, these are the so-called "holist" and "reductionist" approaches to ecological systems. The reductionist aims to restore the necessary organizational information, while the holist prefers to avoid dissection and deals primarily with the emergent properties, the macrosystem properties, of intact systems. Clearly, there is little formal distinction between these approaches because a holist explanation framed at one hierarchical level of organization becomes reductionist when preceived at a higher level. The distinction is entirely operational and depends upon the view that is taken of emergent phenomena.

It is therefore useful to discuss the concept of the emergent property, the macrosystem ecological property in the present context, because it is sometimes misunderstood. There is an extensive literature on systems theory, much of which has a bearing upon the emergence phenomenon. It suffices here to touch upon a few considerations that are relevant to emergent surprise at the macrosystem level.

Using an example provided by Gilbert, Slobodkin (1965) describes the problem vividly. In his words "...as the theory is developed for any population, a point is reached at which the organism plays what might best be described as a trick... For example...a (certain) species of rotifer...when in the presence of predatory rotifers...develops enlarged spines which make them inedible!" Slobodkin points out that no mathematical theory can be reasonably expected to predict such emergent properties, and concludes that the "incompleteness" of ecology seems to be based on empirical facts, and must be explained in empirical terms". That is, no subsystem model can be complete in itself without some provision for external reference to the remainder of the system of which it is an integral part.

The need perceived by Slobodkin for empirical reference by biological models is reminiscent of a general constraint borne by all logical systems. At its most parsimonious, reductionism approaches the method of axiomatic logic. As is well known, Gödel provided rigorous proof that all propositions that are true of any sufficiently complex logical system cannot be reached by formal deduction from the axioms of the system, nor can the axioms themselves be shown to be consistent (Nagel and Newman, 1958; Bronowski, 1966). Most ecological systems are certainly "sufficiently complex" to qualify for indeterminacy in Gödel's terms. It follows that no axiomatic system can be devised which provides a complete model of an ecological system, there will always be gaps which must be filled empirically. Ecological models must therefore be built, implicitly at least, to answer some subset of all possible questions that we might like to ask of the system. There can be no such thing in ecology as a general system model.

Apart from this ultimate constraint, there are more proximate limitations to consider. If Elsasser (1972) is correct in arguing for an essential biological indeterminacy, then appeal to empirical observation may also be insufficient to permit determinate predictions of emergent properties.

Further limitations on the predictive capacity of ecological models are apparent if we consider the formal basis for construction of system models. Following Ashby (1956) it is clear that we must make a distinction between the "system" in its totality, and its representation to the ecologist. Whatever the empirical approach, information about a system can consist only in an observed series of inputs and outputs, chosen by the investigator from among an infinite number of potential variables. Rosen (1972b) outlines the serious constraints inherent in deducing dynamical structure on the basis of system observables. It follows that our models reflect natural dynamics only to the uncertain extent that our "insight" or "imagination" allows (Bronowski, 1966).

For several reasons it therefore seems that our methods of thinking about ecological systems contribute several possible sources for indeterminacy, which are unrelated to the dynamics of the systems themselves. I am unaware of any means to assess the practical importance of these analytical limitations in any specific case.

Analytical limitations also exist at an operational level. Much current systems ecology is apparently predicated on the view that if a complete set of canonical representations exists for all the constituents of a given system, then the coupled subsystems can hold no surprises or emergent properties that cannot be predicted (Ashby, 1956). Indeterminacy, the ubiquity of emergent surprises in observation of ecological systems, stems by this reasoning from the unavoidable incompleteness of our representations of them. Knowledge of ecological systems is sought from incomplete representations because the "real" systems are themselves too large or complex to be tractable in any comprehensive sense. Accordingly, it is a partial system that is analysed, hopefully with the aid of an adequate representation of the inputs and outputs that are relevant to the question being asked. If so, then the representation may constitute an isomorphic model of the system of choice, but clearly, it will be the case in ecology that the model system is at best incomplete with respect to the "real" system. Thus even if the view is taken that the behaviour of the parts together with the details of their coupling completely determine an ecological system, practical considerations nevertheless indicate that emergent surprises are unavoidable.

Taken together, the preceding analysis suggests that theoretical and operational limitations prevent us from constructing comprehensive ecological models based solely on microsystem properties. It follows that emergent properties cannot be reliably predicted by incomplete models of their generating mechanisms. In general, the microsystem approach is incapable of providing for emergent phenomena, unless explicitly designed to do so in specific circumstances. Dickie and Mann (in press) support this point of view, on the basis of an interesting analysis of the properties of natural systems. Their documented contention that different predictions result as the system model becomes more broadly defined at a higher hierarchical level is particularly noteworthy. Accordingly, macrosystem properties themselves also warrant our attention at the appropriate hierarchical level.

Macrosystem properties

We have not done well at observing macrosystem properties, despite the necessity of doing so. But some apparently significant examples can be identified. Production uniformity is one such community property illustrated by the lake trout communities described earlier. Despite the great variability in trout size and trophic level among lakes, variation in trout yield did not depend on community structure, but was predictable from morphological and edaphic characteristics of the lakes themselves (Martin, 1966). Trophic-dynamic theory predicts, other things being equal, that the planktivorous trout feeding on small food particles should have been more productive than piscivorous trout. Kerr and Martin (1970) concluded that the smaller energy resource available to piscivores was used more efficiently because the large prey sizes for piscivores permitted a higher growth efficiency. It is noteworthy that the overall uniformity of trout production among lakes was not immediately obvious from the microsystem properties, but had to be observed directly as an emergent community property.

In more general terms, Ryder (1965) has shown that average fish yield in lakes is predictable with reasonable accuracy from morphometric and edaphic factors (mean depth and total dissolved solids), independently of the species composition and trophic structure of the exploited systems. Primary production in these circular causal systems is often nutrient limited, as is implicit in Ryder's model, but the primary producers can be thought of as energy transformers whose controlling input is some nutrient. If so, then uniform production is an energy conservatism observable at the macrosystem level. We can reasonably expect in consequence that certain kinds of structural constraint, as was observed with the trout populations, will result from the effects of energy conservatisms imposed as boundary constraints.

A related macrosystem property of potential generality is the remarkable observation by Sheldon, Prakash, and Sutcliffe (1972) that roughly equal concentrations of material occur at all particle sizes in marine pelagic communities, measured over a range of some six orders of magnitude variation in logarithmic intervals of particle diameter. It is not immediately obvious why bacteria, for example, should occur in roughly the same concentration as tuna or whales, although an explanation could be offered. But the specific reasons for such uniformities neet not concern us for the moment so much as the observation of conservatism in itself.

Emergent properties are not necessarily conservative, even in the loose sense of "uniformity" used here. For example, Woodwell (1970) has noted that ecosystems exposed to exogenous stress exhibit a general tendency to reduced average size of the component organisms, a view supported by Kerr and Vass (1973) for pesticide stress, and by Kerfoot (1974) and Regier and Loftus (1972) for fishery stress in aquatic communities.

Dickie and Mann (in press) provide and evaluate other examples of emergent properties in ecological systems. At the moment, it is difficult to determine which of these and similar observations represent generalizeable system properties, in the sense that they result as a consequence of closed, single-valued transformations (Ashby, 1956). But it does seem inescapable that macrosystem constraints do exist and that they are not necessarily obvious from the individual properties of community members. The implication for community structure is that size composition, for example, is determined by interactions observable at two or more hierarchical levels of organization. In the present instance, it appears that both the concentration and yield of energy are conserved within any particular size fraction of an unstressed community. If so, it follows that the possible spectrum of structural configurations open to a community is much more restricted than consideration of individual community members would suggest.

Community structure

In short, understanding the factors governing community structure requires our recognition that the interaction of events observable on at least two levels of the organizational hierarchy controls structure. In terms of the jargon I have been using, we must consider both microsystem and macrosystem properties.

Our record at the microsystem level is good, to the extent that in terms of size structure for example we can unify many of the essential factors in conceptual schemes such as the metabolic niche, and construct useful but limited models of specific ecological mechanisms. But our ability to reconcile microsystem and macrosystem properties is hampered by the present inability of ecological theory to provide appropriate methods for observing community properties.

An analogy may clarify this contention. Rosen (1969) pointed out that physicists surmounted the difficulties imposed by the hierarchical nature of physical systems by elaborating appropriate theory. Thus quantum theory is appropriate to microsystem properties, thermodynamics accounts for the emergent macrosystem properties, and statistical mechanics reconciles the two hierarchical levels. We have no well-developed counterpart to this in ecological theory.

Apart from the paucity of thermodynamic analogues, we also lack the conceptual equivalent to statistical mechanics, with some notable exceptions. One clear exception was provided by Kerner (1957), who applied conventional statistical mechanics to the predator-prey system embodied in the Lotka-Volterra equation. He found a conservative element, analagous to the total energy of physical systems, that eludes ready identification with an ecological system property. Goel et al. (1971) consider the behaviour of Kerner's conservative entity for modifications of the basic equation, including a Verhulst term. It can be suggested that if the Lotka-Volterra equations had been initially stated not in terms of numbers of individuals but as the associated metabolic equivalents, then the conserved entity derived by Kerner might be identifiable as community metabolism, a view convergent on other energy conservatisms tentatively identified earlier in this report for other reasons.

Although I have used an example closely related to physics, I have done so for clarity; I am not urging an exact mapping of ecological theory on physical theory. But I do insist that satisfactory elucidation of community structure entails understanding the boundary constraints imposed by the total system, in addition to the relevant microsystem properties. Thus despite decades of concerted effort by capable investigators, the microsystem approach of conventional fishing theory has been unable to predict or satisfactorily explain any of the major series of changes in the fish community structures of the Laurentian Great Lakes ecosystems. System models that explicitly invoke macrosystem properties, such as the model proposed by Dickie and Mann (in press), promise to enrich our methods for analysing such community events. At the moment, our success appears limited by our lack of good observations and robust theory at the macrosystem level.

Perhaps our poor record with macrosystem properties is because we as observers are ourselves microsystem elements of ecological communities. One wonders if the observations that led to thermodynamics could have been easily made by suitably intelligent gas molecules. Rosen argues that observation and theory at the highest organizational level necessarily precedes general synthesis at the subsidiary levels. By this reasoning, we remain some distance from a general understanding of the factors governing community structure.

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THE VALIDITY OF THE DIVERSITY-STABILITY HYPOTHESIS

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Summary

Shortcomings in the formulation of the diversity-stability hypothesis help account for the absence of critical experiments unambiguously confirming or refuting it. Examination of the rationale for the hypothesis suggests that it is not a useful generalization.

Introduction

When faced with an intractably complex system, science may at times make useful progress by treating the matter at a level of higher organization--using a description of the system that collapses its manifold details into an aggregate index, which, it is hoped, will reveal some regularities in its relationships to other, perhaps better understood, measurable properties of the system or external variables. Of course, the hoped for regularities will not miraculously materialize from nowhere. At some point they must be explicitly phrased as hypotheses, and then tested.

When such an hypothesis is articulated in advance of the substantiating data which otherwise might prompt it, there are a number of conceivable modes whereby the hypothesis might have occurred to the investigator. The hypothesis might originate in a wholly mysterious, intuitive leap. The hypothesis might be suggested by analogy with some other, currently more predictable, system. It might be suggested by the behavior of some simple case of the system under study. Or finally, the hypothesis might be suggested from the theoretical results of employing simplifying assumptions concerning the coupling of analytical descriptions of some of the components of the system.

Of intuitive leaps, nothing more will here be said. The other three described modes of hypothesis formation stand in a useful logical relation to the hypothesis, in that they involve factual assertions beyond the simple prediction made in the hypothesis itself. These assertions, respectively, are that the system in question is functionally similar to some other system; that the effects, if any, of complexity of the system, relative to the simple case, tend to cancel out; or that the assumptions regarding the integration of the system's components are correct, at least for practical purposes, and that these components are sufficient to account for a large measure of the system's behavior. If, ultimately, the hypothesis is empirically confirmed, these corollaries, implicit in the rationale of the hypothesis, can be instrumental in the interpretation of the new theory. If, for a while, the available data are insufficient to substantiate or refute the hypothesis, the reasonableness of these claims implicit in the rationale then constitutes the only real grounds, beyond wishful thinking, that the hypothesis should be seriously entertained. In the latter instance, to the extent that these claims are accessible to independent assessment, they permit an indirect means for partial validation or rejection of the hypothesis.

These remarks introduce a convenient perspective from which to judge what is probably the most perplexing theory in ecology, the diversity-stability hypothesis. Large ecological systems surely warrant the epithet intractable. They comprise many individuals of many species, each different, and all involved in a variety of qualitatively different interactions which do not yield to simple mathematical descriptions. Thus, in an attempt to develop an account of a community-level property--relative stability--having both theoretical and practical import, it was natural to cast about for a relation to some aggregate, community-level index, rather than embark on the seemingly hopeless enterprise of erecting a theory of population stability for each and every species, in relation to every other, and then summing the resultant predictions of population stability to obtain a prediction of community stability.

One appealing intuition was that the very cause of ecological systems' intractability, their complexity, might be the source of a general stabilizing influence, such that the more species of more different kinds that are present in a community, the more stable it would be (Odum, 1953; Elton, 1958; Pimentel, 1961). Four major sorts of observations were first marshalled in support of this notion:

1) Anecdotal comparisons of the natural history of species-rich tropical biota and species-poor arctic biota tended to portray the former as stable while the latter were thought typified by the documented fluctuations of some of its animal populations.

2) Some artificially simplified communities, such as extensive agricultural monoculture, seem unstable in the face of

successional processes, and are vulnerable to episodic population eruptions of some species.

3) It has proven extremely difficult to establish relatively stable, or for that matter persistent, few-species predator-prey systems in the laboratory.

4) Simple mathematical representations of few-species predator-prey interactions do not yield stable equilibrium solutions.

Accepting the presumed association between stability and some measure of community complexity, MacArthur (1955) reasoned that the primary interaction between species might be expressed in the flow of energy in a trophic web, so that a precise mathematical description of the complexity of this energy flow would be a likely candidate as the community-level index for which a regular relation to stability was anticipated. The proposed mathematical definition, borrowed from information theory (Shannon & Weaver, 1949), required knowledge only of the topology of the trophic web and the proportion of the community's total energy flow in each trophic pathway for the calculation of a single scalar quantity which described the trophic diversity of that particular community, and which could be used in making comparisons with other communities. This argument was widely mistaken by subsequent authors for a mathematical proof of a relation between diversity and stability.

The "Shannon-Weaver diversity" index has seen extensive use in ecology both as a measure of trophic diversity and as a measure of species diversity, in which latter case it is a function of the number of species, and their relative abundances, in the community.

Noting that the Shannon-Weaver diversity statistic could be construed as a measure of the information content of an assemblage of organisms, and that information has an energy equivalent [indeed, the Shannon-Weaver formula is of the same form as the expression for entropy in the Clausius formula (Brillouin, 1962)], Margalef (1957, 1963) conjectured that this information, or energy, which is somehow bound up in the community, may be a manifestation of the community's regulatory apparatus. Thus, the introduction of the Shannon-Weaver measure of diversity increased the explicitness of the diversity-stability hypothesis, by more narrowly operationalizing the term "diversity", and also gave rise to a fifth kind of support for the hypothesis:

5) Diversity can be measured as information, or entropy; therefore, by analogy with cybernetic or control processes, we may envision a community <u>using</u> its diversity for its own stabilization.

Leigh (1965) and Goel et al. (1971), by applying techniques of statistical mechanics to a system of Volterra (simple predator-prey) equations, were able to develop mathematical proofs consistent with some special cases of the explicit form of the diversity-stability hypothesis. For "food webs" with a given total "energy flow," a measure of stability was shown to be maximized, when all the interactions were of the same magnitude (this corresponds to maximizing the "evenness" component of trophic diversity); and, for similar systems in which all "populations" were of about equal size, the stability measure was shown to increase with the number of "trophic links" per species (this corresponds to increasing the "richness" component of a perfectly "even" trophic web). This limited success provided the sixth, and for purposes of this review final, major kind of argument corroborating the diversity-stability hypothesis:

6) Statistical properties of systems of very simple mathematical representations of trophic interaction concur with some special predictions of the diversity-stability hypothesis.

<u>Direct evidence</u>

The diversity-stability hypothesis has not been subjected to unambiguous, direct empirical test. In part this may be due to the difficulty of coaxing out of ecological systems enough data even to allow proper determination of the relation between aggregate indices. The two most readily available kinds of data which have been brought to bear on the hypothesis are comparisons of the respective diversity and stability of various geographic regions and observations on the stability of systems whose diversity has been recently reduced, either experimentally or as a result of some unplanned event.

Geographic comparisons are systematically confounded by local environmental differences. It is generally thought that environmental instability, increased rigor, and short community history (since some major upheaval, like glaciation) tend to depress species diversity, (e.g., Southwood, 1961; Connell & Orias, 1964; MacArthur, 1965; Pianka, 1966; Slobodkin & Sanders, 1969) thus making it impossible to tell whether an observed tendency to reduced community stability in such regions is attributable to the reduced diversity or is a consequence of the environmental conditions. These same objections may apply even when the geographic distance between the areas compared is quite restricted (e.g., Brewer, 1963; Witkowski, 1973). Interestingly, in the two available studies where the environmental conditions in the areas compared at least seemed the same (Murdoch et al., 1972; Hurd et al., 1971), and in two studies in which the units for comparison were populations classified according to their trophic relations rather than geography (Zwölfer, 1963; Watt, 1964), the less diverse systems for the most part appeared more stable.

Studies on the effects of relatively sudden reduction in diversity indicate an associated, short-term decrease in stability. When a consumer species is removed from a community, there often ensue local extinctions of other species in lower trophic levels, and occasionally in the same trophic level, in addition to the expected consequences for organisms preying on the species removed (Paine, 1966; Harper, 1969; Dodson, 1970). This class of study, employing some perturbation of the system to reduce diversity, fails to discriminate between general effects of perturbation and consequences mediated specifically by lowered diversity. Yet it seems true that any serious perturbation can cause extinctions and other seeming manifestations of instability (Whittaker & Woodwell, 1973); in fact, addition of a species (i.e., a temporary increase in diversity) can have this effect (Maguire et al., 1968; Harper, 1969; Zaret & Paine, 1973).

We see than even if the first two types of observations adduced in support of the diversity-stability hypothesis are factually correct (and there is reason to question this, too), they are not persuasive.

When experimental protozooan communities of different diversities were established contemporaneously in the lab, thus subjecting all to the same "history," environment, and perturbation, no clearcut relation was detected between their diversities and respective stabilities (Hairston et al., 1968). So, while observations of type three, concerning the instability of simple experimental systems, may be correct, we have no evidence that more diverse, but otherwise comparable, systems would be more stable.

Further difficulties in obtaining interpretable direct evidence are due to vagueness about the definition of stability (Lewontin, 1969), and to the absence of precise methods for measuring diversity when organisms are distributed nonrandomly with respect to the sampling scheme and when effective community boundaries are not known (Lloyd & Ghelardi, 1964; Pielou, 1966; Lloyd, 1967; Fager, 1972).

Indirect evidence: reasonableness of argument

The possibility of the use of thermodynamic vocabulary in the statement of the ecological hypothesis does not necessarily argue in its favor. Negentropy in a thermodynamic system is recoverable as energy only when the system decays to a less ordered state. The inherent stability of a particular state is explained by its relative free energy, not its relative entropy.

Information-theoretic analogies are similarly unpersuasive. There is no present theory that can predict the functional significance, or "relevance," of structural information (Johnson, 1970; Theodoridis & Stark, 1971). Moreover, the quantity of information represented in ecological diversity is surprisingly small compared with, say, the genetic information present in the same community. For example, the diversity information content of all the insects in the world is estimated at less than fifty bits per individual, while the information content in the DNA of one E. coli cell is more than a million bits.* Unless we can find some special reason to believe that diversity information is many orders of magnitude more relevant to the function of a community than the genetic information carried by individual organisms, the fact of a diversity-information-entropy-energy equivalence has no bearing on the validity of the diversity-stability hypothesis.

The Shannon-Weaver diversity statistic is actually a peculiar probability measure: it expresses the negative logarithm of the geometric mean of the probability per individual of correctly guessing the species identity of each individual, in sequence, in a random ordering of an assortment of individuals whose relative species frequencies are given by their respective frequencies in the sample, when the "guess" is carried out by picking some arbitrary ordering of this assortment of individuals. This imaginary ordering of individuals seems not to correspond closely to any important biological process, so it is doubtful that there is any deep significance to this specific form of diversity index.

There remain the arguments citing the instability of few-species predator-prey models and the claimed correlation between stability and special cases of diversity in systems of Volterra equations. The "statistical mechanics" derived for Volterra systems employs a linear approximation for the behavior of the system near its equilibrium composition. As the equilibrium point in these systems is not a stable one, there is no reason for expecting the composition to be near equilibrium, nor does the system tend to stay near equilibrium once there. So, the results obtained from the statistical analysis of Volterra systems do not validly describe the anticipated trajectory of the community composition in general, nor do they provide admissable predictions of the frequency of large scale fluctuations.

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*Some arguments, which owing to space constraints may appear cryptically presented here, have been developed more fully in monograph form (Goodman, 1974).

Various other sorts of mathematical analysis of very simple representations of species-species interaction have either failed to show any relationship between diversity and stability, or indicated a decreased probability of locally stable equilibrium as the diversity increased (May, 1973). Computer models of systems of simple representations of species-species interaction also indicate that increased diversity decreases stability in the sense of the system's increased sensitivity to the removal of density dependent terms (Garfinkel, 1967), the increased difficulty of adjusting the model to achieve persistence (Smith, 1972), and the diminished range of parameters for which the system could be stabilized (Hubbell, 1973).

The failure of either direct or indirect tests to substantiate the diversity-stability hypothesis arouses suspicion that the unexamined preconceptions of the model may have been faulty. It seems to have been taken for granted that stability, somehow, is a "good thing" which evolution will tend to maximize. In the sense of maximizing persistence this almost certainly is true, but in the sense of minimizing fluctuations, i.e. tending toward numerical constancy, this is very questionable (Slobodkin, 1967). For example, selection for an optimal life table, depending on the circumstances of the individual species, may result in demographic properties which tend to damp out the effects of environmental fluctuation, or it may result in life-history characteristics which accentuate fluctuations (Goodman, 1974). At times, population synchronization of a markedly discontinuous life-history (also coupled, perhaps, with environmentally mediated, longer term population instability) can be fairly clearly interpreted as a consumer avoidance strategy (Ward & Larkin, 1964; Lloyd & Dybas, 1966; Janzen, 1967); and this strategy, in turn, may induce selective pressure for adaptive instability on the part of the consumer species which are attempting to "track" the populations of their now fluctuating resource base. When a shared resource fluctuates in availability, competitors may subdivide the resource in time by exaggerating their life-history differences in a form of demographic character divergence.

An alternate view, and conclusions

The very posing of the diversity-stability hypothesis entailed the presupposition that community stability could be meaningfully treated as an aggregate property without reference to the population stabilities of individual species. This would seem to imply either that individual species were all, in a sense, mimicking the regularity anticipated in the aggregate behavior, being selected for stability and taking advantage of some potential inherent in diversity for enhancing such stability, or that the aggregate stability was an essentially higher order phenomenon which was a result of interactions strong enough to mask the complicating influences of irregular behavior exhibited by individual populations.

Evolutionary reasoning, as we see, supports neither presupposition. Species populations are using whatever tricks they can to achieve survival, and this involves a wide variety of quite different strategies, including adaptive instability. So, we have grounds for belief that the eccentricities of population stabilities will obscure whatever higher order consequences might accrue from diversity, rather than the other way around, inasmuch as no cogent rationale was established in support of plausible mechanisms for a diversity-stability relationship. In other words, diversity-stability theory appears to have been an attempt to find, at an aggregate, system level, a pervasive regularity of behavior which simply wasn't there.

Some problems which formerly were subsumed, in part, under diversity-stability theory, which still remain valid and important questions in their own right, warrant the ongoing development of independent theory. Foremost among these, I believe, are the theoretically intriguing challenge of deducing community stability from knowledge of environmental properties such as spatial heterogeneity and temporal instability, and the pressing practical need to understand the reactions of stressed ecosystems--specifically to predict how much disruption of a coevolved system is possible before its integration of function decays to a point at which the primitive mode of species-species interaction contemplated in diversity-stability theory becomes a fair approximation of biological reality.

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STRUCTURAL AND FUNCTIONAL RESPONSES OF AN OYSTER REEF COMMUNITY TO A NATURAL AND SEVERE REDUCTION IN SALINITY[1]

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Summary

A major freshet occurred during a year-long study of the benthic macrofauna associated with the oyster reefs of the James River, Virginia, U.S.A. The effect of the freshet, as measured by changes in numbers of species and individuals, was more dramatic at the relatively diverse downestuary sites than at the upestuary sites which normally exhibit low diversity. Although a classification analysis based on species abundance data indicated that a basic structural dissimilarity was retained between the upestuary and downestuary sites after the freshet, a classification by life form abundance data showed that, in regard to the distribution of individuals among life forms, the downestuary sites became more similar to the upestuary sites after the freshet. These results support Copeland's (1970) hypothesis that low diversity systems are more likely to resist changes than those adapted to relatively constant environments.

Introduction

While the scientific literature is replete with documentation of the effects of floods and other natural catastrophes on marine organisms (see Brongersma-Sanders, 1957), few studies reliably capture the dynamic aspects of biotic responses for lack of pre-catastrophe data. On June 21, 1972 Tropical Storm Agnes passed over the Chesapeake Bay drainage basin, dropping well over 30 cm. of rain in many areas, which resulted in flooding in the James River, Virginia, exceeded only by the storm of 1771. A comprehensive description of the flood and its immediate effects can be found in Andersen et. al. (1973).

This was a very destructive storm, but the timing and location of its occurrence was fortuitous from the standpoint of the amount of scientific information that could be collected on it. Chesapeake Bay and, especially, the James River estuary are relatively well known (Barrick et al., 1971) and are actively being studied by several estuarine laboratories. Due to the many research projects in progress at the time of the freshet, and the speed at which specially designed major projects were mounted, knowledge of the nature of such disturbances has been significantly advanced.

A study of the fauna associated with the mesohaline (5-18 o/oo salinity) oyster reefs of the James River was in progress at the time of the Agnes freshet. The sudden and drastic reduction in salinity throughout the estuarine segment under consideration, with background information from three previous sampling periods, allowed the freshet to be treated as a large scale field experiment on the response of the oyster assemblage to a major natural disturbance. This brief communication describes the response of the assemblage to the freshet and, within that context, discusses the relationship between diversity and stability.

Methods

Eight oyster reefs along the James River estuarine gradient were selected for study (Fig. 1). The normal and freshet modified salinity distributions are presented in Figs. 2 and 3 respectively. As the years 1971 and 1972 were much wetter than "normal" the iso-

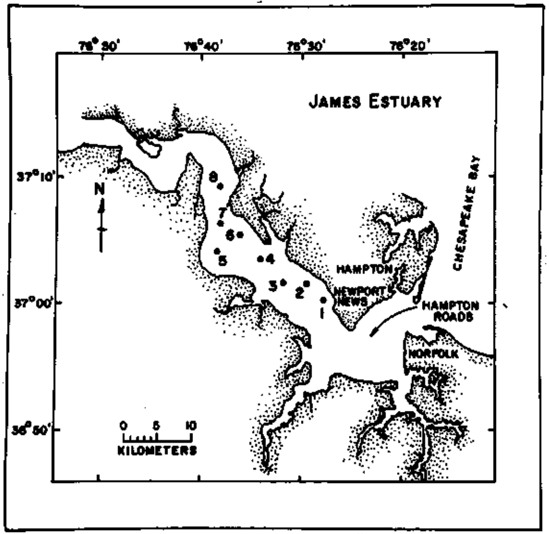

Fig. 1. The James River Estuary, Virginia, U.S.A., with locations of sampling sites.

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[1] Contribution No. 615, Virginia Institute of Marine Science

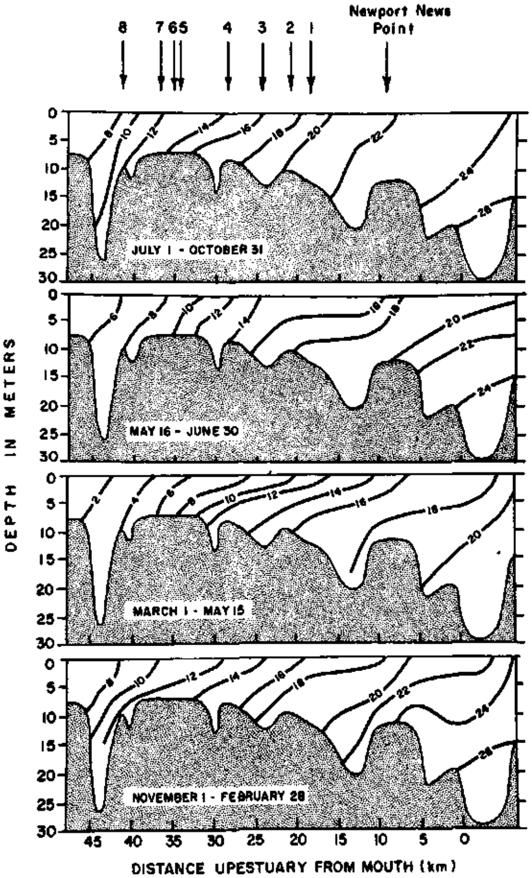

Fig. 2. Normal seasonal salinity distribution of the James River Estuary. Average from 1944 to 1965. Modified from Nichols (1972).

halines in Fig. 2 are somewhat further up-estuary than they were in the immediate pre-Agnes period. Six replicate samples of 0.0126m^2 each were obtained from each site, with a surface operated suction sampler (Larsen, 1974), in December 1971 and March-April, June and September 1972. The June sampling period ended five days before the passage of Tropical Storm Agnes and the September samples were taken about 11 weeks after it. Samples were treated with a $MgSO_4$ solution to relax the organisms, preserved in formalin, and sieved on a 1.0mm screen. Organisms were picked, identified and enumerated using a dissecting microscope.

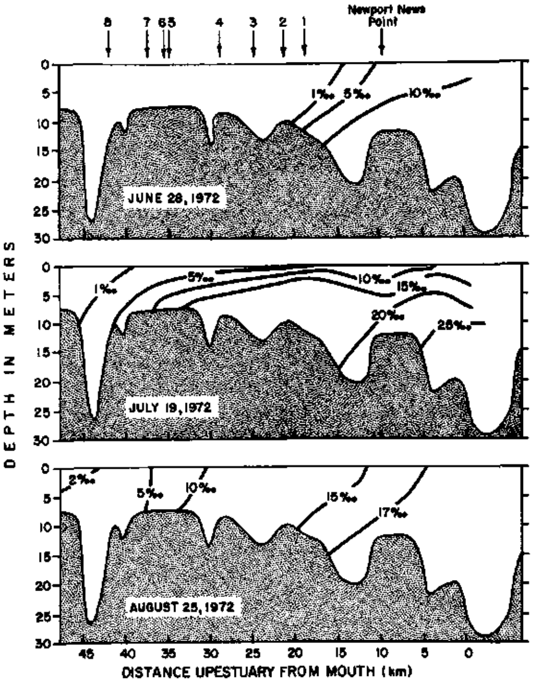

Fig. 3. Alteration of salinity distribution as a result of Tropical Storm Agnes. Modified from Andersen et al. (1973).

A classification of the 32 stations (eight sites in each of four sampling periods), using species abundance data as attributes, was accomplished using the Canberra metric dissimilarity coefficient (Stephenson et al., 1972) and a flexible sorting clustering strategy (Lance & Williams, 1967) with $\beta = -0.25$. Results of this objective procedure for determining interstation relationships are presented in dendrograms; the lower on the dendrogram that fusions between station-groups occur the greater is the similarity between them. See Williams (1971) for a complete discussion of the underlying principles.

Each species was coded based on its feeding type, purchase type (relationship to the substrate) and dispersal type, in the manner of Phelps (1964). All species with identical codes were considered as one "life form" and the classification of stations was repeated using life form abundance data as attributes.

Shannon's formula (Pielou, 1966) was used to calculate informational species diversity, $H' = -\Sigma\, p_i \log_2 p_i$ where p_i is the proportion of the ith species in the collection. The evenness and species richness components of diversity were computed as $J' = H'/\log s$ for evenness (Pielou,1970) and $SR = (s-1)/\ln N$ for species richness, where N is the number of individuals and s the number of species in the collection (Margalef, 1958).

Results

The 192 samples yielded 142 recognizable taxa, 121 of which would be identified to the

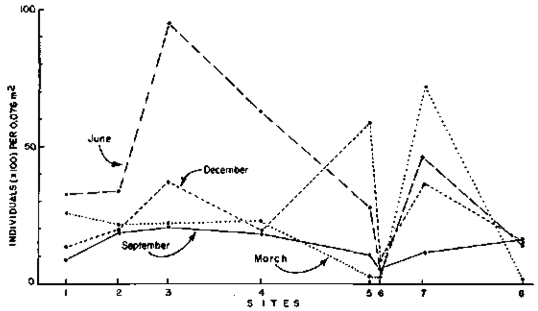

Fig. 4. Temporal and spatial patterns of density of organisms.

species level. Of the 11 phyla represented in the collections, the richest were Arthropoda, Annelida and Mollusca, in that order. These three phyla accounted for 76.7% of all species and 87.9% of noncolonial species. The noncolonial species represented 30 life forms.

Density Changes

The fauna assemblage was characterized by large, seasonal density changes. The very high densities found at sites 1-4 and 7 in June decreased to their lowest levels of the year in the post-Agnes period (Fig. 4). High September population levels of the tunicate Molgula manhattensis at sites 1 and 2, and the bivalves Brachidontes recurvus and Congeria leucophaeta at sites 2,3,4 and 6 and sites 5-8 respectively, offset some density reduction of this period. Indeed, slight density gains were noted at sites 6 and 8 between June and September.

Diversity Changes

Sixty-three species were collected in all pre-Agnes sampling periods. Forty-eight, or over 75% of that total survived the freshet, or recolonized the area after extinction, and were taken in September.

Fewer species were found at sites 1-4 in September than in any previous sampling period (Fig. 5a). However, further upestuary at sites 5,6 and 7 more species were collected in September than in any sampling period since the preceding December, and more species were taken at site 8 than during any previous period.

Increases in the levels of informational species diversity were noted at sites 3-8 between June and September. In fact, yearly highs occurred in the post-Agnes period at sites 3,5,6,7 and 8 (Fig. 5b). Slight drops in diversity were registered at sites 1 and 2 between June and September. Diversity changes followed closely changes in evenness at sites 3-8 whereas at site 2 the effect of the September evenness increase was counteracted by a species richness decrease, and at site 1 both evenness and species richness decreased slightly (Fig. 5c, d).

Classification

The classification of stations by species indicated a relatively low similarity between

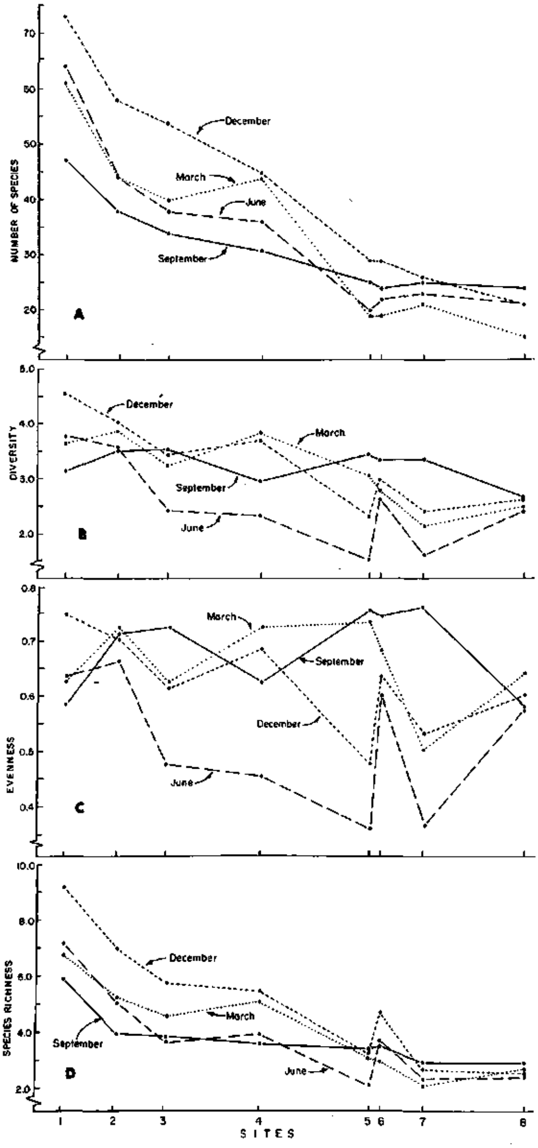

Fig. 5. Temporal and spatial patterns of: A) number of species, B) diversity, C) evenness, D) species richness.

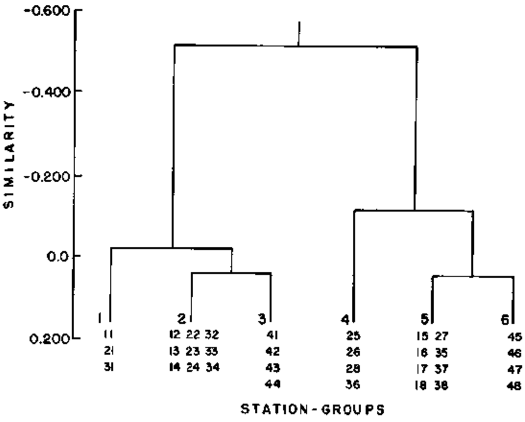

Fig. 6. Dendrogram of classification of stations by species taken to the six station-group level. Station code: first number represents sampling period, 1-December, 2-March-April, 3-June, 4-September; second number represents site.

the downestuary sites 1-4 and the upestuary sites 5-8 (Fig. 6). Stations at sites 1-4 were allocated into three station-groups: the site 1 pre-Agnes stations (Group 1); the sites 2-4 pre-Agnes stations (Group 2); and the downestuary post-Agnes stations (Group 3). Three station-groups were also formed from the stations at sites 5-8: the March stations, except site 7, and site 6 in June (Group 4); the December stations, site 7 in March and three June stations (Group 5); and the upestuary post-Agnes stations (Group 6). Several obvious changes in occurrences and abundances of species were responsible for the isolation of Group 3 from 1 and 2, while, except for the dominating presence of the bivalve C. leucophaeta in the September samples, reasons for the separation of Group 6 from 4 and 5 were more subtle.

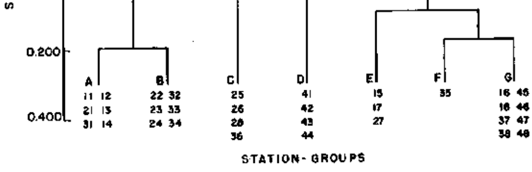

Fig. 7. Dendrogram of classification of stations by life forms taken to the seven station-group level. Station code as in Fig. 6.

The downestuary pre-Agnes stations were fused with the upestuary and post-Agnes stations in the final fusion of the classification of stations by life forms (Fig. 7). Life form station-groups are designated by letters. The left side of the final fusion contains two station-groups: the pre-Agnes site 1 stations and December stations of sites 2-4 (Group A); and the March and June stations of sites 2-4 (Group B). Five station-groups were formed on the right side of the final fusion: one identical to Group 4 (Group C); the downestuary post-Agnes stations (Group D); stations from December at sites 5 and 7 and site 7 in March (Group E); site 5 in June (Group F); and stations at sites 6 and 8 in December, sites 7 and 8 in June and the upestuary post-Agnes stations (Group G). Referral to the original data indicated that the separation of Groups E, F and G was based upon differential dominance of several life forms.

Discussion

Variations in the community structure of the James River oyster reef faunal assemblage, as measured by changes in occurrences and abundances of species, occurred throughout the year of study. The most notable changes occurred between the June and September sampling periods. Unfortunately, data are not available from the previous September but it is assumed that the most drastic of these changes were in excess of normal seasonal variation and were caused or accentuated by the Agnes freshet.

Modifications in community structure were most noticeable at sites 1-4 where both numbers of species and densities of individuals were at yearly lows in September. The species loss was apparently due to the elimination of species intolerant of the low salinities caused by the Agnes freshet. Whether the species collected in September survived the freshet or were able to recolonize from downestuary populations after the severest part of the freshet was over, cannot be determined from the data available.

The classification of stations by species indicated structural differences between the pre- and post-Agnes faunal assemblages. The greater similarity of collections at site 1 to those at sites 2-4 after the freshet than before it reflects, in part, the downestuary population expansions of such species as the crustaceans Balanus improvisus and Corophium lacustre, and the pronounced seasonality, probably accentuated by the freshet in 1972, of the tunicate M. manhattensis. The most noteworthy feature of this classification is, however, the retention of the basic dissimilarity between the upestuary and downestuary sites after the freshet.

The life form classification indicated that functional changes occurred in the downestuary assemblages between June and September. The distribution of individuals among the life forms, based on feeding, purchase and dispersal types, became more similar to those exhibited by the upestuary assemblages than by the downestuary pre-Agnes assemblages. Referral to the original showed that, in September, sites 1 and 2, which had been least similar to sites 5-8 in regard to life form distributions, both registered large relative gains in suspension feeding attached epifauna, the dominant form at the upestuary sites. These gains were caused by population increases of the tunicate M. manhattensis, the amphipod C. lacustre and the bivalve B. recurvus, in combination with population decreases of many species in different life form categories. Several slight shifts in the relative distributions of individuals among life form categories occurred between June and September at sites 3 and 4, resulting in their increased similarity to the distributions exhibited at sites 5-8. Carnivores were significantly more abundant at sites 1-4 than at sites 5-8 before the freshet but were uniformly uncommon in September.

Copeland (1970) proposed a hypothesis on the responses of estuarine systems to disturbances. He states: "Those systems already subjected to energy-requiring stresses are more likely to resist changes than those (such as tropical systems) adapted to relatively constant environments". His reasoning is that species with a long evolutionary history in constant environments have become specialized and lost much of their ability to acclimate to unpredictable physical disturbances. He predicts, based on the differing responses of temperate and tropical systems to the same magnitude of pollutional disturbance, that if an energy-requiring stress is applied to such a community, the more specialized species will be eliminated, resulting in a community of low diversity. Boesch (1972) supported this hypothesis noting that in a Virginian estuarine area affected by pollution the "'typical' benthic species were replaced by more eurytolerant species characteristic of lower salinity and lower diversity habitats".

Estuaries represent natural stress gradients. The number of species declines progressively up the estuary from the sea (Wells, 1961) until the fauna is characterized by eurytolerant species, the "organisms capable of wide adaptations" in the sense of Copeland (1970). In fact, some of the abundant species at the upestuary sites in the present study, such as the polychaetes Nereis succinea and Heteromastus filiformis, have been found to be exceptionally pollution tolerant (Wass, 1967). Estuarine faunal assemblages may be described in terms of Sanders (1968) stability-time hypothesis as ranging from more physically controlled in the oligohaline zone to more biologically accomodated in the polyhaline zone.

Copeland's hypothesis would predict that the more diverse sections of the estuary would be more seriously affected by a physical disturbance of a given magnitude. This is indeed what happened during the present study when the downestuary sites lost their less euryhaline species. The upestuary sites showed less change because a larger percentage of their species had greater adaptabilities.

These results indicate that the widely held belief (Hedgpeth, 1973) that species diversity, however it is measured, and structural stability, in the sense of resistance to or recovery from disturbances, are positively correlated must be questioned. The correlation between high environmental stability and high species diversity is well established (Sanders, 1968) and the increasing diversity in a downestuary direction evidenced in this investigation is further support for this relationship. What is questioned is Odum's (1971) supposition that high species diversity, with its resulting complex food webs, instills into a faunal assemblage a greater power to resist change when the environment is disturbed. Further evidence in support of the opposing view is provided by Andrews (1973) who states that the lower polyhaline regions of the Chesapeake Bay estuaries, regions of high species diversity (Boesch, 1972), exhibited the most dramatic reductions in abundance of epifauna and predators following the Agnes freshet.

The results indicate further that, whereas changes in informational diversity may be a sensitive index of the effect of pollution (Boesch, 1972), it added little to the assessment of the impact of the Agnes freshet. Increases in the evenness component between the June and September sampling periods caused, in part, by the largely density independent stresses associated with the freshet resulted in rises in informational diversity at six of the eight sites studied. Data on the number of species and abundances of individuals, especially when analyzed by classificatory techniques, and interpreted with a proper appreciation of normal seasonal variation, gave the most meaningful summary of the effect of the Agnes freshet on this faunal assemblage.

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THE OVERGRAZING CYCLE AS A CHARACTERISTIC OF TROPICAL SAVANNAS AND GRASSLANDS IN AFRICA

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The preservation of wildlife and wilderness is a tropic of global interest. But wilderness is indeed a rare commodity in the world today. Areas which may be considered to be remaining in a more or less natural state are rapidly becoming fewer, both in numbers and size.

Many of the world's remaining wild areas are designated as national parks. Although there are other considerations, a principal objective of national parks and nature reserves is the maintenance of wilderness conditions. Preserving samples of the earth's natural ecosystems with the indigenous flora and fauna interacting with each other and with the physical forces of nature is important to mankind from cultural, scientific, educational, recreational, economic and other standpoints (Petrides 1955, 1963). It is the hope of many people to keep at least a few portions of the world as living museums, displaying the earth as it was before man became dominant.

Yet just what were the original conditions which now should be preserved in their natural state? "Originally", was there a widespread stability in nature where, at least in the popular view, predators and prey were in balance and herbivores did not overutilize their forage resources? Or did today's conditions always exist, wherein areas sometimes became heavily overstocked by herbivores with consequent degradation of vegetation and soils? And did those depleted areas then recover so that their original animal inhabitants could return to begin the cycle anew?

An alternating abundance of tundra vegetation and microtine rodents has been demonstated in the arctic (Schultz 1973: 90-91). While there are no indications that tropical ecosystems are as periodically cyclical as the lemming-tundra cycle in the far north, yet perhaps the possibility should be considered that, at least in some tropical savannas and grasslands, periods of ungulate increase and consequent floral degradation could have occurred between times of dwindling herbivore numbers and vegetative recovery. Like the arctic ranges (Schultz 1973: 84-85), tropical pastures probably did not all become overutilized simultaneously. It would seem likely that rather extensive regions of heavily-utilized and degraded vegetation were interspersed with large tracts in process of recovery. Plant and animal species adapted to overgrazed habitats would increase in depleted districts while areas of recovery would serve as refugia for species adapted to less-disturbed sites.

It is the purpose of this paper to suggest the hypothesis that alternating periods of heavy consumption by large herbivores and then of vegetative recovery may have been characteristic of tropical grasslands and savannas and may have prevailed through the ages. Discussion of this possibility might (1) encourage other investigators to seek evidence for or against the concept and (2) enable the consideration of a different outlook for wilderness-preservation policy in tropical grasslands.

Concepts of ecological balance

It is my feeling that many ecologists tend to be ambivalent with respect to the dynamic aspects of ecological balance. In a recent report by a highly-competent ecologist, for example, it is stated that "most ecosystems were at natural equilibrium when civilization entered or began" and that the "natural equilibrium . . . of the North American grassland . . . was destroyed before its marvelous complexities were . . . studied." A goal of the American National Park Service, he reported further, is to remove the disturbing influence of man and to restore the parks "to pristine conditions."

While his large paper is mainly a discussion of the dynamic interactions within an extensive biotic community, there still seems to be an instinctive belief that prior to the development of modern man "nature's balance" was a stable and prolonged one. Preston's (1969: 7) statement that "whatever stability there is in the modern world is not a static

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equilibrium but a fluctuating or dynamic one, and normally a highly fluctuating one" perhaps needs to be recalled frequently by all of us.

Fluctuations in ungulate abundance

The prospect does not seem to have been considered that ungulate populations through the ages may have alternately depleted their food resources and then have become restored in abundance as the vegetation upon which they depended recovered. There seems to be no reason why a pattern of areas could not have existed in which individual districts varied in conditon from undergrazed to moderately-overgrazed to severely-overutilized, much as was observed in Uganda (Table 1), though on a somewhat vaster scale.

The evidence in support of this viewpoint is not overwhelming. But neither does there seem to be much to prove otherwise. The survival in large numbers of such a successional species as the warthog and its extremely widespread distribution over Africa, however, would seem to support the idea that overgrazed landscapes have themselves been widespread in the past. Of the ungulates in the southwest Uganda biotic community (Table 1), those which showed the greatest tendency to increase as overgrazing intensified (that is, the elephant, waterbuck, warthog, and Grimm's duiker) have the widest distribution on the African continent. While these species and especially the warthog seem to be associated with overgrazed landscapes in Uganda, they may have first evolved in some semiarid region where the mature vegetation resembled that of overgrazed grasslands or savannas. Their distribution and survival almost throughout the African continent, nevertheless, seems to indicate a rather general overgrazed-habitat availability over a long period of time.

Looking about the world, too, it seems evident that diverse ungulate faunas occur only on large land masses. Few islands areas support more than one or two species of native hoofed mammals. It seems to be at least a possibility that competition between herbivore species can only be sustained in areas of considerable size and vegetative diversity. Much of that diversity may be induced by the consuming animals themselves, through alternate periods of intensive use and habitat recovery. In addition, however, it may well be that space for dispersal is required by populations increasing in density. Such space may be used for indeterminate movements or for longer migrations. Even if only unfavorable environments are found by most wandering animals, some individuals may be more fortunate and overall mortality thus may be reduced both at the original site and in newly penetrated areas.

Perhaps it is not relevant with certainty, but in the Antarctic as well, it was evident on transects by ice-breaking ships through the Bellingshausen and Amundsen Seas made in 1973, that the common crabeater seals of the ice pack were not distributed evenly throughout the area, even where the same ice type was widespread. Instead these seals, and the less common species too, were clumped. There were vast regions where crabeaters were absent or nearly so, and other, more restricted, areas where they were abundant. No direct evidence was available there, but it seemed to be at least a likely possibility that the seals were concentrated where their principal food crustacean, the krill, was easily available. While the empty areas could have been places of low inherent krill productivity, they also (at least in part) could have been areas which had been "overeaten" and were in process of recovery. In this vast wild region of at least surface uniformity, no steady-state type of equilibrium seemed likely and alternating areas of intense food-depletion and recovery seemed to be a good possibility.

Does overgrazing occur now?

The communities of large mammals on African grasslands and savannas have been studied scientifically and intensively now for over twenty years. Following the 1953-54 studies in Kenya (Petrides 1956), there have been numerous researches undertaken on biomass densities, population carrying capacities, primary and secondary productivity and related matters affecting the spectacular ungulate populations and their grassland and savanna habitats. Observations made in Kenya (Petrides 1956; Glover 1963), Uganda (Petrides & Swank 1958, 1963; Buechner & Dawkins 1961), South Africa (Pienaar et al. 1966), Zambia (Brown 1969) and Botswana (Riney 1967) are among many which have determined that overgrazing and overbrowsing have caused and are causing serious effects throughout much of Africa on the vegetative, faunal, and often on the soil components of essentially wild ecosystems.

In Queen Elizabeth (now Ruwenzori) National Park in southwest Uganda the effects of overgrazing by hippopotomi on both vegetation and other large mammals were made strikingly evident (Table 1). On the most degraded and eroded portions of the "severely-overgrazed area", all palatable grasses were depleted and in consequence buffalo and kob were complete-

Table 1. Composition and numbers of large grazing mammals per square kilometer in Queen Elizabeth (now Ruwenzori) National Park, Uganda (adapted from G.A. Petrides and W.G. Swank, 1963).

	Undergrazed area	Moderately overgrazed area	Severely overgrazed area	Animal population-response to overgrazing of *Themeda* grasslands	
				Short-grass stage	Shrub-invasion stage
(Square kilometers in area)	(30.6)	(14.5)	(23.3)		
Elephant (*Loxodonta africana*)	1.5	1.4	3.4	Decreases	Increases
Hippopotamus (*Hippopotamus amphibius*)	1.1	0.7**	14.9	Increases	Decreases
Buffalo (*Syncerus caffer*)	12.4	18.2	4.0	Increases	Decreases
Waterbuck (*Kobus defassa*)	0.2	0.6	3.4	Increases	Increases
Kob (*Kobus kob*)	0.1	18.5	0.5	Increases	Decreases
Bushbuck (*Tragelaphus scriptus*)	0	*	0.5	Increases	Increases
Reedbuck (*Redunca redunca*)	*	0.1	0	Increases	Decreases
Warthog (*Phacochoerus aethiopicus*)	*	0.9	2.7	Increases	Increases
Duiker (*Sylvicapra grimmia*)	0	*	*		
Total numbers	15.4	40.5**	29.5		

* Less than 0.05 animals present per square kilometer.

** Nocturnal use of this area by hippos could not be calculated and is omitted; total biomass supported doubtless is therefore considerably higher than indicated.

ly eliminated. On the other hand, elephants, waterbucks, bushbucks and warthogs became more numerous as overgrazing, and hence bush density, increased.

In Tsavo National Park, Kenya, elephants have been important in the clearing of bush from large areas. Where in 1953-54 I took photographs of dense shrubs crowding against the roads, in recent years extensive grasslands are only sparsely and occasionally interspersed with bush clumps. Even large baobab trees have been totally destroyed in this and other areas by increasing densities of elephants. In Tsavo, there has been a widespread substitution of ungulates characteristic of the open plains for those which formerly lived in the dense bush. This is the opposite effect of the bush-encroachment induced by hippos in Uganda.

The causes of overgrazing

When overgrazing or overbrowsing becomes evident in an area, it is frequently assumed that large predators are abnormally scarce. Yet in most African national parks, many species of large predators frequently occur together. These may include lions, leopards, cheetahs, hyenas and wild dogs, plus the lesser species such as servals, caracals, jackals, foxes, numerous civets and mustelids, various eagles, hawks, vultures, and perhaps crocodiles. Although there is no certain way of knowning whether carnivores are more or less abundant than was true "originally", nowadays they seldom appear to be rare and are often numerous both in species and individuals.

Still further, among the herbivores which commonly initiate the overutilization syndrome, hippos and elephants are seldom captured by predators, even as juveniles. Furthermore, though as individuals the large cats and canids typically reproduce considerably more rapidly than their prey, the much greater abundance of ungulates means that the population of carnivores cannot be expected to outbreed the population of herbivores. Finally, as might be expected from studies of predator populations on other continents (for example, Errington 1946; Schaller 1969), recent findings of Rudnai (1973) reveal that lions tend to be limited by prey abundance (rather than the reverse) and by behavioral adaptations. In summary, it does not seem that carnivores can be counted on to prevent ungulate overpopulation. There is no evident likelihood, either, that even man with primitive weapons could have had more serious effects than other predators and yet have survived through earlier ages as a component of the ecosystem.

Certainly predation is not the only factor which could have maintained herbivores in balance with their habitats. Krebs (1973) has found that wild Microtus populations restricted within a low fence increased to overgrazed and starvation levels, whereas adjacent unconfined populations with dispersal opportunities did not do so. It may well be that large herbivores within nature reserves act similarly since such areas nowadays essentially are "islands". Some of these areas actually are fenced, at least in part (Kruger and Nairobi, for instance), but all of them are restricted by surrounding adverse land use (see beyond).

Factors ranging from climate to ungulate behavior to disease also could be responsible for ungulate overgrazing. But the evidence from North America (Wodzicki 1950; Petrides in press) indicates that, in general, populations of hoofed animals tend to outgrow their available food supplies. It may be true generally, with respect to hoofed animals everywhere, that a shortage of forage resources tends to be the factor which limits their population growth.

The precise causes of ungulate tendencies toward overabundance should be learned but, until they are, the fact that hoofed herbivores do tend to become overstocked wherever they occur must be considered in land management. This is especially important with respect to wilderness preservation policies in restricted areas of tropical grassland.

Preservation of wilderness

There are divergent schools of thought extant regarding the maintenance of surviving natural areas. Both are sincere in wishing to preserve the wilderness and its fauna and flora under "natural and original" conditions, but there is uncertainty as to what conditions were the original ones and how best to preserve them. One viewpoint is that nature if left alone will take care of itself. Advocates of this policy say to keep "hands off". Regardless of what happens, they believe, nature eventually will balance itself. (Members of this school of thought nevertheless almost invariably also wish to control extensive fires, epidemic diseases, and other large-scale catastrophies). The second says that wild lands may require management in order to preserve their character (Petrides & Swank 1958). This is not to imply that management must be undertaken in all situations. By all means, areas which are not endangered by either natural or man-induced factors should be held without alteration.

As was stated some years ago (Petrides & Swank 1958), however, it is quite proper for people to wish to preserve some forests somewhere which do not show the marks of an axe or saw. Somewhere stands of tress of representative types should be allowed to grow, mature, and die, without concern that lumber is being wasted. These areas substitute cultural and other values for their timber assets. There are many people who feel that nature similarly should be allowed an unmanaged course for some animal populations. If animals destroy their food supplies and die, they say, let them do so. The cycle eventually will repeat itself and habitat and animal life will recover.

But the overgrazing problem does not parallel the forest situation. Dying trees enrich the soil and tend to perpetuate at least the climax vegetation. In contrast, overabundant herbivores may destroy the vegetation and often important soil conditions. Presumably through the years such a completely-affected area would recover slowly, but even assuming that some animal life survived there to see that day, can we afford, in a crowded world, the destruction of limited wild lands? Will lands so destroyed be saved for a comeback perhaps a hundred years or more in the future, or will it be taken during that time for other purposes?

Looked at in another way, national parks nowadays often exist as islands in a sea of land used or planned for other purposes. Like all island biotas, those of isolated natural areas are more susceptible to destruction than are the biotic communities of extensive lands.

No longer is it possible, even in the largest reserves, to have the assurance when environments are disturbed by a natural force that some large portion of that biotic community will be preserved elsewhere in the area. With decreasing wild land availability, it is becoming evident that the ones remaining should be protected from destruction from any cause, natural or not.

Some of the largest national parks in the world are in Africa and several are in the 20,000 square kilometer class.Yet there are extensive and serious problems with overabundant herbivores even in Tsavo, Kruger, and Kafue National Parks, which are among the largest existing natural areas. Even tracts of this size cannot be assumed to be capable of survival without management. It seems to be especially true in areas which are set aside for the preservation of nature, that both flora and fauna are disturbed by biotic interactions which may have natural origins but which nevertheless may lead to the permanent destruction of the few and isolated remnants of wilderness which remain on earth. Though overhunting is well understood as a potential cause of population depletion, overprotection is becoming almost universally an even more serious cause of destruction and it is one which often affects entire biotic communities.

Heavy grazing may not only threaten some herbivore species, it also may endanger the survival of those plant species which are the most highly preferred foods of a common herbivore. Under especially severe grazing, even some plant species with lower food preference ratings may be eliminated by grazing or browsing animals. Yet the total prevention of all fires and all heavy grazing or any form of natural disturbance may reduce the numbers of plant species which are adapted to areas so disturbed. It seems frequently to be overlooked that national parks and nature reserves are established to preserve characteristic plant species and communities and the small fauna, as well as large mammals.

Management for wilderness preservation

It is evident that the problems of nature conservation are complex.

It seems to be increasingly necessary to adopt a policy of zoning within national parks and reserves similar to that in force in Kruger National Park in South Africa. There, certain portions of that 20,000 square kilometer tract are designated for the preservation of particular habitats and species, both plant and animal. Consequent land management policies are varied in efforts to preserve designated habitats, faunas and floras.

As a part of such a program, it may be essential in all national parks and similar reserves where there are important herbivores of any kind, that a number of tightly-constructed and durable exclosures be established in major vegetation zones. Comparisons of vegetation within and outside such exclosures (properly located and constructed so as to sort out the effects of rodents, insects, and the larger herbivores) enable consumer-induced changes in vegetative composition and density to be detected.

At the other extreme, entire reserves may serve as exclosures. A small but viable Cedars-of-Lebanon grove has been preserved in northern Lebanon, for example, by a stone fence around church grounds. If that remnant of once-extensive forest had not been saved from goat-grazing almost by accident. Probably it would be thought that a changing climate and not human mis-use of the land was responsible for the vast alteration of the landscape which was occurred there since King Solomon's time.

Conclusions

National parks and nature reserves are established not only to preserve animal life, but also to maintain native floras and plant communities.

Wilderness conditions in tropical grasslands and savannas may well have involved varied sets of biotic communities which replaced one another, perhaps alternately in some cases, as a variety of large ungulate species increased, recuced the available forage, and then died off and allowed the range to recover.

If so, then a varied set of natural environments should be encouraged in grassland national parks and nature reserves under a system of zoning. Where overpopulations of large ungulates develop within a reserve, it is suggested that some portions of the area be allowed to be altered through their selective feeding but that other significant tracts be protected against overuse. Under both management programs, continuing appraisals of environmental trends should be maintained. Suitable management policies should be implemented, though always with care, in order to preserve the wilderness from the dangers inherent nowadays in their isolated condition.

It is hoped that ecologists will seek

evidence for or against the possibility that tropical grasslands characteristically undergo repeated periods of ungulate overgrazing and vegetative re-growth. It is also hoped that over-protection will become more widely recognized as a principal threat to wilderness preservation in many areas.

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Diversity, stability and maturity in ecosystems influenced by human activities

DIVERSITY, STABILITY AND MATURITY IN ECOSYSTEMS INFLUENCED BY HUMAN ACTIVITIES

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I. It is customary to argue that man's major effect on ecosystems is interference with balanced natural situations, thereby reducing inherent stability mechanisms and decreasing the diversity of species and/or environmental parameters. A number of assumptions are implied in this argument: (1) Most natural, undisturbed ecosystems are in a more or less mature stage of succession which is stabilized and equilibrated by complex feedback machenisms in a co-evolved web of causal interrelations. (2) Mature, balanced systems are more diverse than unbalanced systems. (3) Maturity is the final state of developing ecosystems, i.e. a natural decay of ecosystems is regarded as unusual. (4) Man is not so much an integrated part of natural ecosystems but rather an unnatural, external force. - The questionable nature of these implications will be discussed at various points of the paper.

II. Diversity as used in this paper includes the two components of richness (see paper of Orians) and evenness of abundance. Both components of richness to species, to other groupings of organisms, or to any other quantifiable units in the ecosystem. - The term stability is used either as the capacity of selfregulation, implying stable equilibrium mechanisms, or in the descriptive sense of persistence of a given state. - The term maturity applies to the successional stage and includes the possibility of coevolution during succession. -

For the discussion to follow, some points have to be kept in mind: (1) The positive correlation of diversity, stability and maturity is partly due to tautology: The mature state of an ecosystem is usually identified by its relative constancy or persistence in a descriptive sense reached after various transient stages. As cause of this constancy, stable equilibria and high inertia are usually invoked, either by deductive reasoning, or by the empirical documentation of the asymptotic approach to constancy in the course of succession, or after disturbances. Thus maturity and equilibrated stability define each other. - Since succession from tabula rasa to maturity implies an increase in number of species, diversity will increase automatically during succession. Both species richness and evenness are involved. - (2) In spite of the automatic linkages just indicated, there are cases where diversity is lower in mature than in young stages of succession. This may apply to both components of diversity. - (3) Maturity is a relative notion, climax situations do not stay constant over indefinite periods.

III. An attempt to classify human activities with respect to their effects on diversity, stability and maturity reveals a wide spectrum. One may distinguish (1) temporary, reversible changes of the abiotic or biotic environment; (2) permanent shifts of environmental parameters which influence tolerance or preference relations of organisms; this includes structural changes of the abiotic and biotic environment; (3) changes of nutrient levels; (4) changes of the potential of species to immigrate and emigrate, and to colonize; (5) import and export of energy, or structural and other elements of high information content.

All mentioned types of activities may increase or decrease stability and diversity, with the exception of the first which will probably only cause decreases. New successions may be initiated, the natural decay of mature systems are be accelerated (e.g. drainage of swamps) or delayed (e.g. measures against erosion). The same individual factor (e.g. fertilizers, or the introduction of a species) may increase or decrease diversity and stability, depending on quantity or quality of application and the previous state of the affected

ecosystem.
There appears to be no effect on ecosystems that could be called typically or exclusively human, none of the above activities are restricted to the human species. However, the quantity and intensity of human activities reaches in many instances such high values that quantity appears to switch to quality.

Three divergent examples will be discussed to emphasize the complexity of human effects: (1) The influence of eutrophication on diversity in aquatic ecosystems. (2) Structural changes that create new ecosystems (water reservoirs; the heterotrophic urban ecosystem). (3) Conscious management of ecosystems. The last example will serve to stress the viewpoint that no ecosystem is closed, and that man, whether living in the system or outside, has to be regarded as an integrated component: In systems of intensive monoculture there is low species and structural diversity but surprisingly high stability. This seeming deviation of manipulated systems from the accepted rule is largely attributable to an arbitrary restriction of the measurement of diversity. The stabilizing effect of human management derives ultimately from the highly diverse and well-buffered structure of human society. If it is accepted that all factors involved in the structure of ecosystems should enter the measurement of diversity, then the intraspecific diversity of human society must not be excluded whether man lives inside or outside the system. In managed systems there is a displacement of diversity from interspecific and structural relations to the semi-external human subsystem which feeds its stabilizing power through the channel of manipulation.

IV. The creation of more homogeneous agricultural land to supply food for the hungry, the application of pesticides and fertilizers to increase harvest efficiency, the need to develop industries in underdeveloped countries which will produce harmful waste products, the necessity to change undisturbed areas into cities for the increasing population, are in direct and perhaps irreconcilable conflict with the interest of conscientious conservationalists who wish to minimize disturbances and to prevent irrevocable damages to ecosystems. The notion of quality of life, the recreational and spiritual values of undisturbed landscapes, are often at odds with other, equally fundamental needs. The maintenance of natural equilibrium (or a tolerable compromise) between the socially responsible desire to save ecosystems, and the social need to disturb or destroy ecosystems, are diminished every year by the increasing density of the human population.

RESPONSE OF NATURAL MICROBIAL COMMUNITIES TO HUMAN ACTIVITIES

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Microorganisms are of enormous importance to the functioning of terrestrial, freshwater and marine communities. As major agents of photosynthesis, the algae play a key role in aquatic ecosystems. By virtue of their capacity to regenerate nutrients required by higher organisms and their focal position in destroying natural organic products and synthetic chemicals, heterotrophic bacteria and fungi are essential for the continued existence of green plants and for the degradation of substances potentially harmful to the well being of animals and humans. Nitrogen fixation, nitrification, denitrification and other steps of the nitrogen cycle are solely effected by microorganisms, and various parts of the sulfur cycle and transformations of phosphorus, oxygen, iron and many other elements important to biosphere function are largely or entirely under microbiological control.

Because of the significance of microbial communities to natural ecosystems and to the maintenance of environmental quality, the influence of stresses imposed by human activities has been extensively evaluated, at least for certain of the disturbances created by society. These effects have been measured on microbial communities, the dominant species in the habitat or on particular biochemical transformations. The reactions of chief concern include photosynthesis by aquatic algae, respiration and carbon and nitrogen mineralization by terrestrial heterotrophs, nitrogen fixation, legume nodulation and nitrification. Particular attention has been given to the communities in agricultural areas, and some research has been performed in aquatic habitats; however, essentially nothing has been done in uncultivated land.

The area of human activities which has been explored most thoroughly in terms of impact on microorganisms is agriculture and farm-related operations. The disturbances arising from cultivation, fertilization, plowing under of crop residues and use of pesticides have been well defined. By contrast, the impact of industrial effluents on the aquatic microbiota has scarcely been tested so that the possible hazards of the countless compounds discharged into waterways cannot yet be described.

The impacts of pesticides, polychlorinated biphenyls, soil-derived nutrients, and acidic mine wastes on freshwater and marine inhabitants and of air pollutants on certain terrestrial populations have also been the subject of some scrutiny, the extent of disturbance varying from none to catastrophic.

Owing to the scanty literature and the key role of microscopic organisms in ecosystem function and in maintenance of human environments of acceptable quality, further work is required to define more adequately how the actions of society alter microbial populations and communities and the biochemical processes they bring about.

STRUCTURAL AND FUNCTIONAL PROPERTIES AS THEY INFLUENCE ECOSYSTEM STABILITY

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Summary

Data on old-field succession collected over 20 years are used to explore the relationships between stable and unstable ecosystems. Three community attributes are considered essential for stability: mass, functional options, and response time. The data suggest that these attributes are operative at different phases of the sere. The immediate response to disturbance is reestablishment of the production capacity of the system. Mass and options are optimized much later.

Introduction

The object of this paper will be to examine the concept of terrestrial ecological (secondary) succession as it relates to ecosystem stability. The data on which the discussion is based have been collected over the past 20 years at the AEC Savannah River Plant (SRP), Aiken, South Carolina, U.S.A. In most instances the data were collected for specific studies and therefore have been recalculated and reinterpreted for this report.

The subject of ecological succession has had a long history, receiving special impetus from the work of Cowles (1899) and Clements (1916). This emphasis on succession has partly been due to the fact that land use in the U.S.A. has been constantly changing and abandoned land is relatively common in all parts of the country. However, more interesting from a theoretical point of view than the ubiquity of the phenomenon has been its repeatability. For example, in the southeastern United States, succession proceeds through a series of physiognomic stages which include a forb dominated phase, followed by grass, pines and then a mixed hardwood forest (Oosting, 1942). The hardwood forest persists over long periods of time and was the vegetative cover first observed by European man (Bartram, 1791). The various stages form a continuum blending into one-another, but the order of the sequence can be observed repeatedly over a variety of soils, topographies and local climates. The time of the appearance and development of each phase is not predictable, however, and the first studies at SRP described the temporal dynamics of succession. Later studies were directed at the mechanisms causing the change from one community to another. And still later studies were made of the response of the sere to disturbance by plowing, and by gamma radiation. These studies do not form a complete sequence with equal emphasis on all aspects of the problem; rather they reflect the interests of the investigators present at the Laboratory at a particular period. Thus, the present interpretation is imposed on a diverse data set in which many lacunae occur. Nevertheless, the length and variety of studies at one place are unusual and warrant examination as a whole.

System Stability

Ecosystem is used in this report in the sense of Odum (1953), as a complex of living plants, animals and microorganisms interacting with each other and the physical-chemical environment and forming a system. Ecosystems have a specific structure, physiology and history. For example, a forest ecosystem consists of many thousand of individual organisms, arranged into characteristic species with a specified mass and chemical content, and with a characteristic input of energy and turnover of mineral elements. This system can be observed repeatedly over space and time under a given set of environmental conditions.

Ecologists often describe these ecosystems as stable or unstable. Stability has a variety of definitions, but these can be grouped into two fundamentally different categories. First, stability may refer to the constancy of ecosystem characteristics over time. The dimension of time is arbitrary, and may refer to weeks, seasons, or years. Since in certain terrestrial ecosystems the life span of some of the dominant organisms might exceed several hundred years, a time which exceeds a human life or even the period between the development of scientific study of ecosystems and the present, we do not know if ecosystems can remain stable in this sense indefinitely, become senile over time or exhibit some other dynamic behavior.

The second definition of stability concerns system response to external forces. Stability is defined as constancy of ecosystem properties after the system has been perturbed. In other words, a stable system is one that can resist a disturbance. The decision of whether an ecosystem has been disturbed and therefore deviates from an earlier state can be extremely difficult due to the relatively large variance in ecosystem properties. Further, it is difficult to determine what is and is not a disturbance, especially since environment is not a constant and the interaction between individual organisms entails feedback processes with time lags. When we realize that most ecosystem studies have been based on a single, albeit aerially large, sample, it is clear that conclusions about stability or nonstability must be preliminary.

Given these definitions, our interpretation of succession varies depending upon the level of organization we have focused upon. Considering community ecosystems in a time frame of interest to man, successional communities are classed as unstable since they change over time and replace one another in sequence. The sequence terminates in a stable community which does not change into another physiognomic type. On the other hand, if our focus is at the level of biome or landscape then succession can be viewed as a series of states tending toward steady states which are a function of the physical-chemical-biological environment and the genetics, history and geography of the biota. In the first case we see linear series of communities or physiognomic stages over time. In the second, we visualize a field of dynamic patterns over space. The limited data restrict us to considering only the former case.

These models are very general, of course, and we would expect the details to vary over time and space. For example, stable systems include in addition those mainly held stable by management and energy-material subsidies such as a pasture or field of wheat, and by physical-chemical forces, such as a rocky intertidal ecosystem. Successional communities occur where the physical-chemical or man-generated control of the ecosystem can be overcome by biological control. The fundamental character of successional communities which distinguish them from the other types of communities is that they exhibit a sequence of states that appears directional toward a stable state at which time biological control becomes more important and the system becomes decoupled to an extent from the physical-chemical environment.

Stability in the context developed above has been discussed by many modern theoretical ecologists, however, because of space limitations I will not test succession against their formulations. Rather, my strategy will be to explore the nature of several of successional communities' attributes as they form a basis for stability. These attributes are mass of the system, the number of functional options and the time response of the system to environmental forcings.

First, the mass of biological material which comprises the system has at least two aspects. A large biomass can be thought to damp oscillations of the environment because it has inertia, as well as an associated zone of influence around it. Mass is particularly important in mineral cycling because a large proportion of the pool of elements in the community are stored and conserved in the highly refractory mass of stems, roots and branches. Analog computer studies have shown that increase in the input of potassium to the system six times the equilibrium level in a tropical forest (Golley, 1972) had essentially no effect on the stem mineral pool. Further, free behavior of this system was controlled by the stem compartment. In addition, mass can have a strong impact on the local climate. The composition of the mass is significant since highly refractive material can exaggerate its primary effect.

Second, the number of functional options in a community refers to the variety of tasks and opportunities in a system. Option may be a function of the overlap in structure and function of units or in the breadth of the structural and functional attributes of the units or both. Species diversity studies concern option in a sense, but they do not provide direct information on either flexibility or overlap in function. Option can influence stability by providing alternative components and/or pathways in the event of a disturbance to the system.

Finally, stability involves the timing of the various interactions between the members of a community. The timing of response may be exceedingly important in stability since feedback between units can amplify or damp an oscillation. For stability a community requires a repertoire of responses which fit the timing of environmental disturbances and the time lags of the unit interactions. For example, a rapid response of a unit might reduce time lag in response of other units and result in overall system adjustment.

We suspect that these three features, mass, option, and response, have what E. P. Odum calls performance curves, in that there is a point where they have a maximum effect and another where too great a mass, option or response results in lowered stability or perhaps instability. Since all three may be operative in a community and may have different optima depending on the system, the causal explanation of stability of a community might be extremely difficult and complicated. Certainly we would not expect to find a single causal explanation, except in a few rather unusual cases.

Ecological Succession at SRP

Data are not equally available on mass, option and response from the SRP. Most data pertain to structure of communities and populations and are therefore pertinent to mass and option. Response data are very limited. Odum (1969) has utilized this information to develop his strategy of ecosystem development. My students and I have examined his list of 24 community attributes in depth and have concluded that while the trends are likely, in most instances they can be subsumed under the attributes proposed here.

One final introductory comment is necessary before we examine data on mass, option and response. Most data on succession have been collected on an annual basis (Odum, 1960; Golley, 1965). However, in this paper I have used successional stages (forbs, grass, pine, hardwood forest) rather than age of the community in years because the former are the repeatable phenomenon. We expect to find grass replacing forbs, pines replacing grass, etc. Second, our studies have indicated that size of the disturbed area, presence or absence of disseminules or desseminating agents and other factors influence the time at which one stage replaces another. Thus, time in years since disturbance does not correlate well with the stage of succession.

Mass

The total mass has not been determined for the forb, grass, pine and deciduous forest communities. Most data represent only vegetation mass. Therefore, it is first necessary to determine the relationship between the mass of plants and animals in a community. Data on the mass of plants and animals is most complete for the forb stage of succession (Table 1). In this community the total biomass is between 551.065 and 553.065 g m^{-2}; plant material makes up 550 g m^{-2}, and animals comprise 1.065 to 3.565 g m^{-2}. While the census of all animal taxa is not complete (some soil fauna, large mammals and breeding birds are missing) it is clear that animals make up a very small percentage of the biomass. In this sere we suspect that mass comparisons between communities may be based on the vegetation alone without serious bias.

Table 1. Peak biomass in g$\cdot m^{-2}$ in the forb stage of old-field succession.

Ecological group	Biomass	Authority
Living plants	300	Odum (1960)
Litter	250	Odum (1960)
Arthropods in vegetation	0.345	Cross (1956)
Cryptozoa	0.103	Tarpley (1967)
Small mammals	0.012	Golley et al. (1965a)
Harvester ants	0.089	Golley and Gentry (1965)
Savannah sparrow	0.016	Odum et al. (1962)
Nematodes	0.5-3.0	Coleman (1971)

The vegetation mass has been calculated for five different communities, representing an agricultural field, three seral stages, and the deciduous forest which is the undisturbed vegetation in the region (Table 2). The data express the average peak values obtained over an annual cycle and have been rounded from the original data. They support the well known fact that the mass of the community increases with succession toward a forest type. Not only does total mass increase but the mass persists over a longer period and thereby has a greater influence in the community. In a sense the mass creates a predictability to which species can adjust over time.

Table 2. Average peak biomass of total vegetation in g m^{-2} for five communities, including tree trunks, roots and litter.

Corn field	670	Golley & Gentry (1965)
Forb stage of succession	600	Odum (1960)
Grass stage of succession	1,000	Golley (1965)
Pine stage of succession	10,000	Wiegert & Monk (1972)
Deciduous forest	19,000	Golley et al. (1965b) Monk et al. (1970)

There are few data on the chemical content of the vegetation biomass over the sere. Comparison of the structural biomass (stems, roots, branches) with the chlorophyll biomass shows that at the grass stage about 2000 to 4000 grams of structural material is required to support one gram of chlorophyll A, depending on the season. In contrast, at the forest stage the ratio is near 10000 to 1 (Golley, 1965). The structural mass is largely cellulose and lignin and is highly refractory to decomposition. There is little question that in the communities we are concerned with here, mass increases from the disturbed to the stable state--the increase being about 300 x.

Options

The evaluation of options in these communities is more difficult than the evaluation of mass relationships. In this case we want to trace the number of pathways for, say, a molecule of calcium to travel from the soil, through the community, back to the soil. Such an analysis entails a foodweb study in which the importance of each link between populations is evaluated. While we have made many studies of trophic relationships, we do not have the data in the form required for a definitive study of pathways in the different seral communities. Even the use of radioactive tracers (Odum and Kuenzler, 1963; de la Cruz and Wiegert, 1967; Wiegert et al., 1967) has not permitted us to determine foodwebs for these communities. For this reason we are left with the counts of taxa as indices to numbers of functional options. Taxa are unsatisfactory because they represent function only very crudely.

A species list or species diversity index does not measure the degree to which species can replace one another functionally, nor their ability to change functionally if there is an alteration in their environment. Nevertheless, in the absence of data, we are left with species lists as a basis for speculation about this feature of stability in relation to succession.

The species lists in the forb community can be organized into an approximate foodweb (Figure 1). In this community the number of taxa feeding on plants is much larger than the number of plant taxas while the taxa feeding on herbivores is about one-half of the number of herbivore taxa. The number of options in the sense of increase in food chain length is limited physically by the decrease in available energy transferred from level to level. Even though the length of food chains is limited the number of chains can be increased through biological evolution and through colonization. Further, functional options can be increased by cross linking between food chains. Finally, the decrease in material transfer through the food chain can magnify the effect of increasing the variety of pathways at higher trophic levels. The data from the forb community suggest that the greatest multiplicative tendency occurs at the herbivore level. In this community about 15 species of plants set the initial possible pathways, but there are about 100 different herbivore taxa.

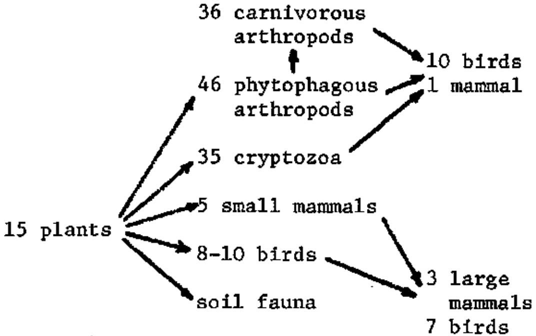

Figure 1

These relationships are certainly not constant across communities. Menhinick (1963) studied a lespedesa community at SRP which is a variant in the old-field sere and found that this essentially monospecific community contained about 125 species of adult insects per 2500 sweeps (460 m^{-2}) of which about 80 percent were herbivores. Further, in the grass stage (Table 3) the number of plant taxa doubled, yet the number of animal taxa remained approximately equal. If there is a rule describing the variety of taxa in trophic levels it may be specific to a particular life form and habitat as well as to successional stage.

The species diversity of successional vegetation has been intensively observed by Nicholson (1970) on the Georgia Piedmont near Athens and his data probably apply to SRP at least at the level of detail we are using here. Numbers of species increase from forb to hardwood stages of succession (Table 3), although certainly not at the same rate as the increase in biomass. Further, the total number of taxa depends on the area sampled. Monk (1971) shows that we would expect about 100 species on one square kilometer of Eastern Deciduous Forest. Nicholson analyzed these data according to the conventional methods for describing species diversity and showed that successional trends in diversity were similar for different strata of vascular plants and that diversity initially increased sharply, then at some point in succession abruptly diminished. The major break came at 20 to 40 years when all strata and life forms appeared in the community; that is, when the forest canopy first closed. The animal taxa do not show consistent trends across all groups (Table 3). These data suggest that numbers of functional options or pathways increase in succession and that the greatest variety within any one community occurs in the primary biophage or primary saprophage groups.

Table 3. Numbers of taxa of groups or organisms in a sere in the southeastern U.S.A. Taxa do not represent numbers of species in arthropod or cryptozoa groups.

	Stage of sere			
	forb	grass	pine	hardwood
Plants[a]	15	38	47	60
Arthropods[b]	87	93	--	--
Cryptozoa[c]	35	28	--	--
Small mammals[d]	6	7	1	4
Lycosid spiders[e]	4	4	3	5

[a] Nicholson (1970)
[b] Cross (1956)
[c] Tarpley (1967)
[d] Golley et al. (1965a)
[e] Kuenzler (1958)

Response

Response refers to the ability of the system to react to a disturbance. Thus, responce concerns both the speed and appropriateness of the internal signals between species but also the timing of system function.

Response may be explored as reactions to a set of disturbances by the species populations which compose the community. Data of this sort are available from a series of experiments involving plowing fields or the radiation of natural communities with a portable gamma source (McCormick and Golley, 1966). Golley and Gentry (1965) plowed an 11 year-old grass field, planted a crop of maize and then followed succession over five years after the maize was harvested. The net production and mass of vegetation were similar in the two sets of communities (Table 4), while the number of species was quite different. We concluded that the standing crop and net primary production of the community was probably repeatable and predictable, while the numbers of species may not be. Not all species are equally able to invade and colonize the field, but apparently those that do operate at about the same functional rate.

Table 4. Experiment to test repeatability of old-field succession. The initial observations represent community attributes in old-fields studied by Odum (1960). The experimental observations represent the same old-field disturbed one year by a crop of maize and then abandoned.

	Year after abandonment				
	1	2	3	4	5
Peak standing crop					
initial	500	320	180	250	200
experimental	290	220	190	240	230
Net primary production					
initial	490	330	280	--	300
experimental	580	410	360	290	380
Numbers of species					
initial	5	6	13	--	15
experimental	45	--	38	37	50

The radiation experiments have shown that with high levels of radiation the dominant plants are killed or their growth is altered (McCormick, 1967). If the dominants are trees, acute radiation results in an increase litter fall, a drastic change in the microclimate and rapid growth of forbs. However, within one year recovery is underway. Reestablishment of trees will then depend upon growth rate of the trees. The impact of the radiation was not merely death of the pines or change in growth rate, although pine is especially sensitive to radiation, it also involves a decline in plant diversity (Monk, 1969).

These studies suggest that response to disturbance can be extremely rapid. The first stage in the recovery of the community is development of the vegetation canopy since satisfaction of the power and material requirements of the system is dependent upon the leaves. Reestablishment of the canopy may occur almost immediately after disturbance with the consequence that net primary production of the community reaches a relatively high level the first year and then is relatively constant from stage to stage although a peak is achieved at the pine stage (Table 5). Following this rapid response there is a slower development of mass and functional options. In my judgement, it has been this character of very rapid recovery of the energy flow and material cycles that has allowed man to convert succession into agriculture and forestry by stabilizing a successional stage through the input of labor, energy, or fertilizer.

Table 5. Net primary production (g m^{-2} y-1) of four stages of old-field succession.

Stage	Production	Authority
Forbs	300-500	Odum (1960)
Grass	550-650	Golley (1955)
Pine	1000	Wiegert and Monk (1972)
Hardwood	600	Monk et al. (1970)

In summary, these observations on old-field succession suggest that constancy of the hardwood forest over time is a function of its large mass and the richness of functional options, which are crudely represented by the numbers of species population. If this system is disturbed, stability is reestablished by a sequence of events that involves first, the rapid response of the vegetation with reconstruction of the production machinery of the system. A great variety of possible combinations of species occurs at this early stage. With development of adequate power and materials, the recovery takes on a more directed form and the biomass damps oscillations in mineral cycling and in local climate conditions. Finally, the interconnections and pathways between species and functional groups are fully developed.

These conclusions conflict with those of Odum (1969) and Drury and Nisbet (1973). Odum stresses the importance of system properties in controlling the successinnal process, while Drury and Nisbet conclude that succession can be interpreted as differential growth, survival and dispersal of species adapted to grow at different points of the stress gradient. They state that "a complete theory of vegetational succession should be sought at the organismic, physiological or cellular level, and not in emergent properties of populations and communities." In my view both of these points of view are necessary for a full explanation and understanding of this process. Explanation of the mechanisms of succession will be obtained through study of the subunits of the community and understood in the context of the relationship of the successional community with other communities over space and time.

The analysis of stability in terms of succession is disconcertainly difficult in several regards. First, we do not have data on a mature or stable community over sufficient time to determine the degree of variation in community parameters from year to year so that stability can be expressed as a dynamic process. Second, we do not know if the successional trends we observe and interpret as development toward stability are actually artifacts of man, representing mixtures of species responding to widespread human disturbance in the landscape. Possibly disturbance of the Great Forest before the advent of European man was point disturbance and recovery was largely replacement of small sets of species in a limited area. And finally, it is probable that communities are in a constant dynamic process of adaptation to environment with the result that there is continuous interaction between species populations, with development and evolution of species in concert with one another under the constraints of resources and environment. And thus, stability is entirely a construct appropriate to our limited powers of observation in time and space.

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RELATIONS BETWEEN DIVERSITY AND STABILITY IN EXPERIMENTAL PLANT SYSTEMS

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Summary

The used variables of diversity and stability (of production) being defined, the relations between them are considered and compared for a set of few systems. The plant material includes grass, legume cultivars and populations collected in a plant community (mountain grassland). The lay-out of the experimental designs allows to compare systems of varied complexity (mono to plurispecific cultures which are diversifying or not by establishment of other species). The experiments have been conducted in greenhouse or outside (in the original community or not). The experiments established "in situ" are in observation from many years. The interest of such a type of research on simplified systemps is underlined, specifically for the study of communities after a man's slight intervention. In such a vegetation "in situ", submitted to contrasting treatments, an example of variation is given. In conclusion, the limits of such an analytical approach in system ecology are indicated.

Introduction : variable definitions

A plant system may be defined as the union of three sets of variables :

1. the resource variables (R) ;
2. the habitat variables (H_t), as pH or temperature ;
3. the biotic variables (B_i), including the whole set of the community organisms.

These last may be subdivided in :

a. structural variables, characterized by the species or genotypical unit numbers, the numbers of individuals per species or units. Synthetically they are expressed by the diversity ("sensu stricto" diversity and equitability),

b. functionning variables (biomass,..).

The relation between structure and functionning shows the neighbouring or group effects.

The articulation between these three sets makes the organization.

In a plant community, the functionning may be measured in terms of :

1. biomass (the whole of the living material) ;
2. production (biomass increase by cycle) ;
3. productivity (yield).

The structure is characterized by diversity indices, the most simple of which is the specific diversity (species number). Some measures of diversity are based on the information theory. That application is founded on the "entropy" of information. If the "entropy" is a measure of the level of degradation for a physical system, the biological systems are characterized by "an order" the analysis of which is possible by means of the information.

The structure may be also expressed by the concept of dominance, which measures" the appropriation of... space of certain... species by others..." (Mc Naughton & Wolf, 1970). An equitability component may be calculated. Ares (1972) has used that component to verify that the interspecific competition would determine a reduction of the niche overlapping (sec also Ares & Leon,1972). A method for measuring the niche width may be derived from it.

The distribution of the individuals, their disposition, determines a pattern ; this spacial diversity is a part of the structure but subsequently this aspect will not be treated.

With respect to the stability, three types may be defined :

1. the sociological stability, which expresses the ability of a species to tolerate the pressure from environmental species (Jacquard & Caputa, 1970) ;
2. the cenological stability expressing the variation of a community in relation to the environment ;
3. the ecological stability which reflects

a concept akin to the previous two, but in terms of turn-over of the biomass in an ecosystem.

The first two characterize the homeostasis and may be evaluated by the coefficient of linear regression of the species or community performances on the mean performances of the sample of species or communities studied (Jacquard, 1970). The third type of stability indicates that the greater the biomass is in relation to productivity, the less the community would maintain unvarying its amount of living matter.

The relations between diversity and stability have been described for some biological systems , with sometimes an extension of the statistical mechanics to ecology

Material and methods

Subsequently the results of two types of experiments realized by the Centre d'Etudes Phytosociologiques et écologiques are used

Experiment laid out in Montpellier

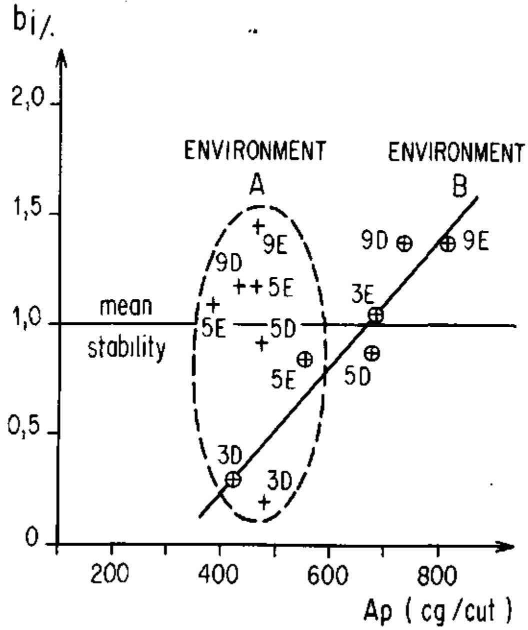
It was intended to collect informations about the structure of the biomass and its functionning (Donadieu, 1970) for systems built by cultivars of Trifolium repens L., Lolium perenne L., Dactylis glomerata L., Phleum pratense L., Festuca elatior Schreb., or by **commercial** lots of Lotus corniculatus L Trifolium pratense L., Poa pratensis L., Festuca rubra L. Systems with 3,5 and 9 species has been sown, some with an equidistribution of individuals between species (E), the others exhibiting a dominance (D), of 1,2 or 3 species respectively, and observed in two environments (A & B).

Experiment laid out in the Cantal

It is designed to study the neighbouring relations between five plant species (Agrostis vulgaris With., Festuca rubra L., Lolium perenne L., Poa pratensis L., Trifolium repens L.) from a closed herbaceous community (Poissonet, 1972). Pure stands and binary mixtures of these species have been established in the original vegetation. The diversification of the experimental plots, following the establishment of other species is measured from 1969.

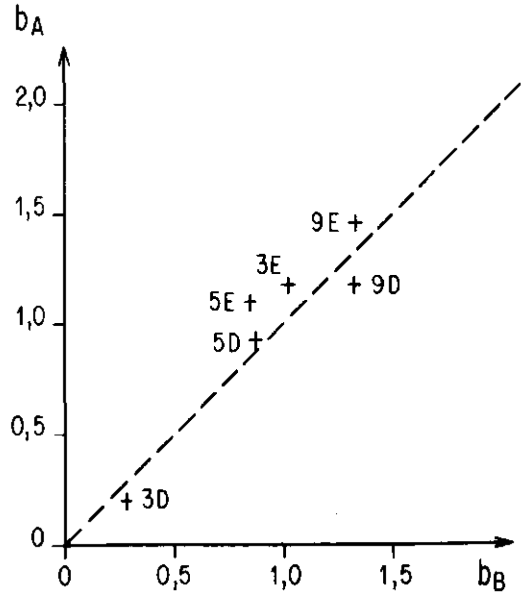
Results and discussion

Figure 1. Relation between the production (Ap) of a plant system and its cenological stability ($b_{i/.}$).



In Montpellier, it has been possible to study the relation between production and **cenological** stability (Figure 1). The production is different for each environment, but the stabilities of each system, in A and B, are very similar (Figure 2).

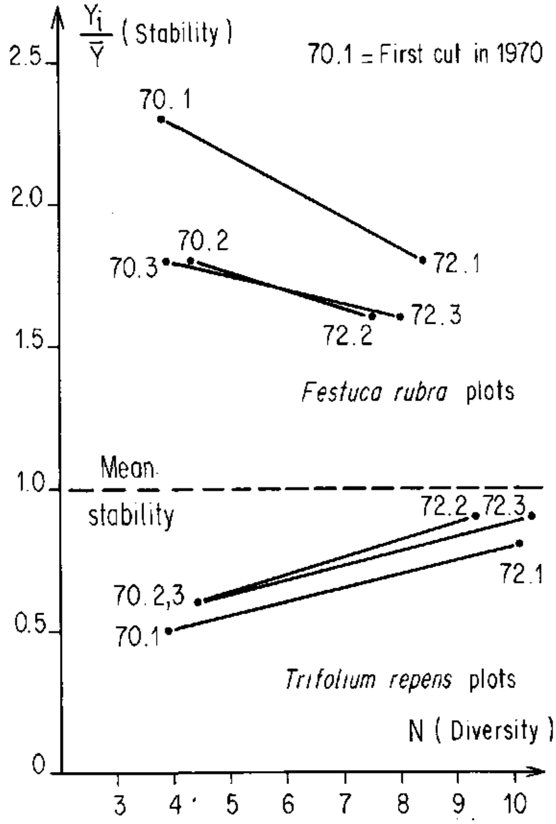
Figure 2. Comparison between the stabilities of six plant systems in an environment A(b_A) and in an environment B(b_B) b = coefficient of linear regression.



For the environment B, the calculated relations are shown with their significance on the figure 3 (following page). The production-stability relation is redrawn in 3 a, on the basis of mean data. Although the stability indice calculated is different from that of some authors, it may be verified, as them, that a community is all the more stable as it is less diversified (3e) and less equidistributed (3d), in the fixed experimental conditions. All the results agree to show clearly that when the community becomes more rich in species, the trend of the biomass to concentrate in a limited number of categories decreases (3 f). Here, the diversity is a favourable factor to production (3e) ; in the same way, this latter increases when the dominance indice decreases (3b).

In the Cantal, some of the obtained results allow to bring together the diversity evolution, expressed by the species number, and that of the stability. The figure 4 give an example of the relation for two types of treatments. It is clear that the experimental plots, during the process of diversification, following the invasion by new species, show a tendency to express stabilities more and more closed to the mean stability of the design.

Figure 4. Evolution of the relation between the diversity (N = species number) and the stability (Y_i = mean production of a plot type ; $\bar{Y}_i$ = mean production of the whole design).



Comparison with not very disturbed vegetations

Trouvat (1972) have analysed micro-plots from a Norman permanent grassland, submitted to two cutting systems (during two successive years) : unfrequent and frequent. The analysis of their stability by the regression method shows that their coefficients are never different from 1.0 ; in contrast (Figure 5) some unstability

Figure 5. Relation between the diversity (N : species number) and the stability (standard deviation from linear regression).

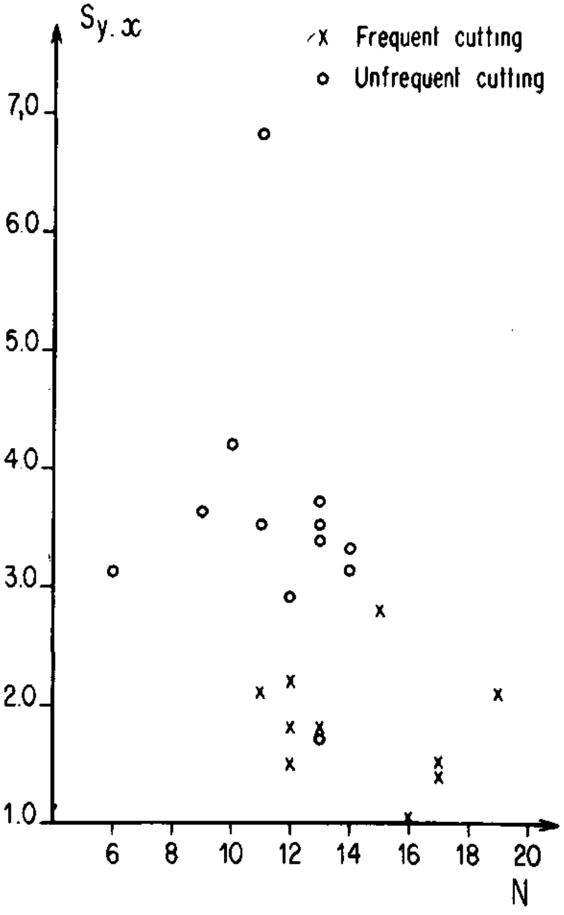
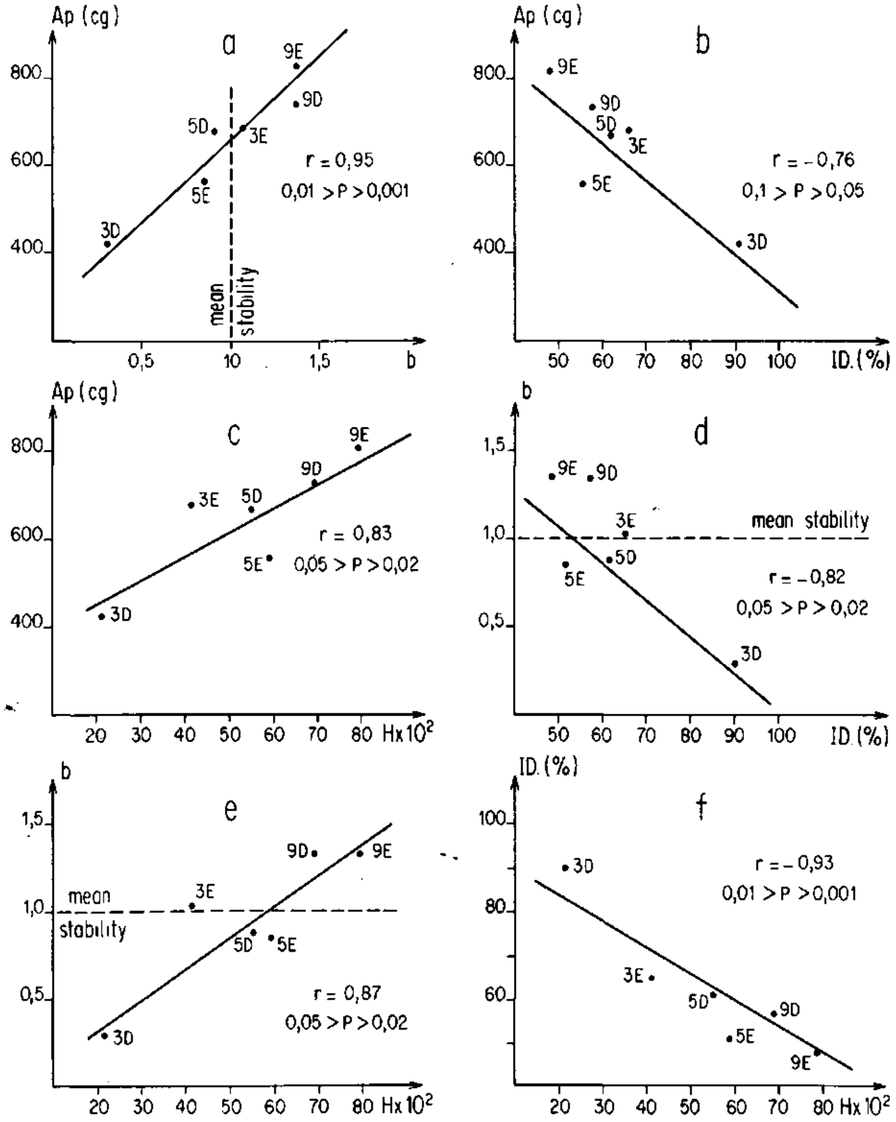


Figure 3. Relations between the production (Ap), the stability (b), the dominance (ID. %), the diversity (H). Ap= mean production of six cuts ; b = coefficient of linear regression ; ID. % = per cent contribution of the dominant species ; H = information/individual or diversity.



can be revealed in it ; it is an inverse function of the diversity (species number). Here, the stability is studied by means of the variation of the standard deviations from linear regression.

Conclusions

The question of the structure (diversity "sensu stricto", dominance or equitability, pattern) may, in fact, be approached under different points of view. It is very linked to the theory of ecological niche (Mc Naughton & Wolf, 1970).

The fitting to a linear regression allows to analyze the relation between that structure and the stability, as well in simplified systems as in not very disturbed communities.

If in an oligotrophic environment (as a permanent grassland), the diversity is maximal because the totality of the reactions to competition counterbalances in it the totality of competition effects, the eutrophization (intensive agriculture is an example of which) affords to express only to the potentially dominant species, and in the distrophic environments (pollution) only the few adapted species are expanding.

The studies bearing on the diversity evo lution relative to time, as that initiated in Cantal, for a system of primary producers are, just now, more speculative than experimental (Loucks, 1970).

In the "natural" vegetations in equilibrium, the populations of each species are hierarchically ordered each other (Daget & Poissonet, 1970). To test that dominance, Mac Naughton et Wolf (1970) compare the observed and calculated frequencies. Indeed, if the most part of the models for the analysis of neighbouring or group effects (charactèristics of the linkage between structure and functionning) are of satisfactory use for binary systems (Jacquard & Caputa, 1970), they are with difficulty suitable for the systems of a higher order.

Finally, the opposition between the mechanisms of the production efficiency (adaptation) and of the stability (adaptability) probably is only a semblance at the ecosystem level (Figure 6).

For the populations, it should be verified the hypothesis according to which the increase of diversity leads to homogeneous populations of heterozygous individuals and the increase of dominance to heterogeneous populations of homozygous individuals (Mc Naughton & Wolf, 1970).

Lastly if the studied stability more often is that of functionning, it should be studied the stability of structure, too.

Acknowledgment

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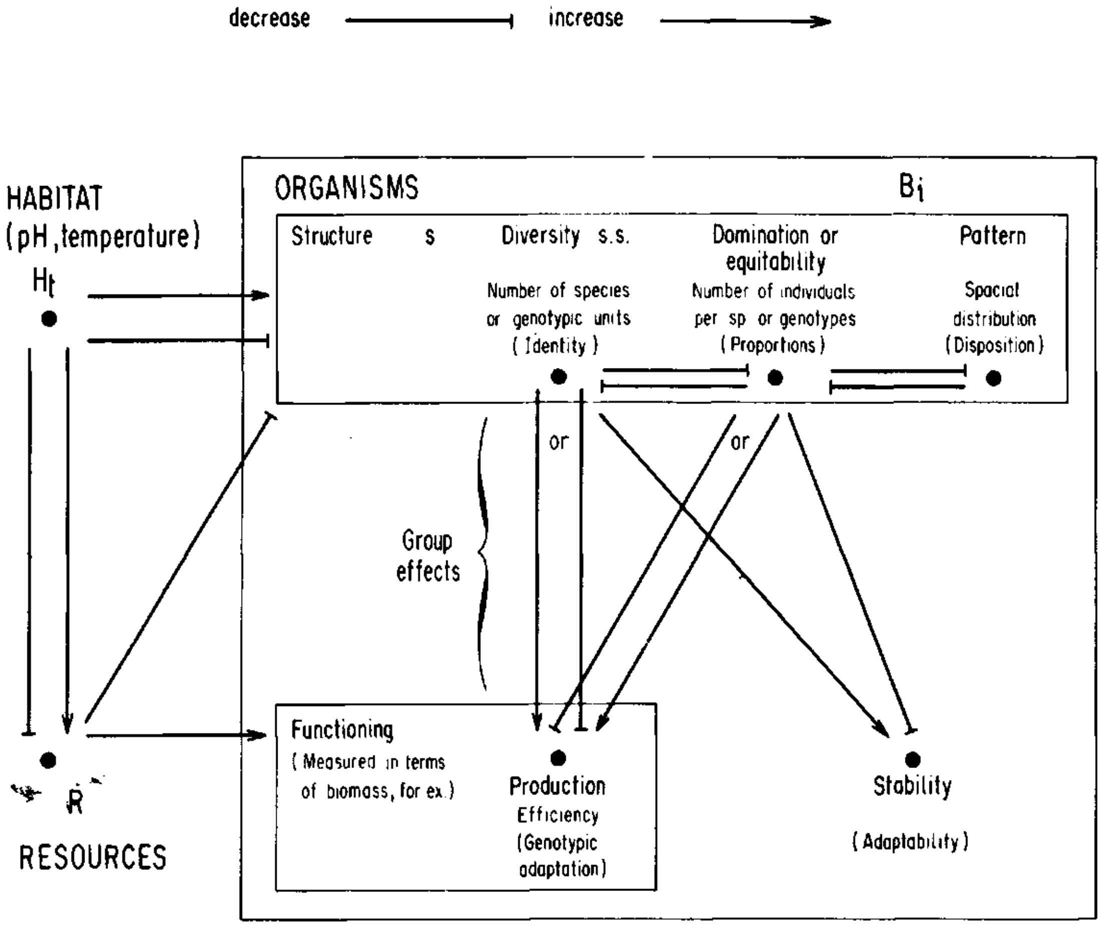
Figure 6. Graph of the relations between components of a biological system (ecosystem and its subdivisions).



DIVERSITY, STABILITY AND RESPONSE TO HUMAN DISTURBANCE IN ESTUARINE ECOSYSTEMS[1]

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Summary

Estuarine ecosystems are characterized by low species diversity attributable to low environmental constancy and predictability. Although estuarine communities lack persistence in the sense of constancy of species populations, they are stable to perturbation because of their high resistence and resiliency. The vulnerability of estuaries to human disturbance is not a result of biological instability but of the concentration and irreversibility of disturbances.

Introduction

It is widely known that estuarine ecosystems are typically of low species diversity compared with most marine and freshwater ecosystems. The oft-reproduced diagram of Remane (1971) depicts the number of species of organisms declining gradually from the sea into brackish water, then percipitously to a low point in that section of an estuary in which the water is only slightly salty (typically about 5 o/oo), and steeply rising upon entering permanently fresh water. However, the "stability" of estuarine ecosystems is much less studied.

Lack of agreement in the usage of the term stability in ecological discussion has caused confusion in the application of ecological theory concerning diversity and stability. Firstly, the term as used by Sanders (1968) and others in explaining the relationship of species diversity to constancy of abiotic factors is easily separated from those concepts related to biotic dynamics and is here termed environmental constancy. Biological stability, however, is harder to define (see Margalef, 1969). Most biologists have used the term to imply persistence of a community in time with little fluctuation in species populations (Margalef, 1968; Frank, 1968; Lie and Evans, 1973). To remove ambiguities I will call this simply persistence (alternate terms suggested by Margalef (1969) are conservatism and endurance). The term stability as used here is that derived from thermodynamics, i.e. the ability of a system to maintain or return to its initial state after external perturbation (Hurd et al., 1971). This is inherent in the stability concepts of Lewontin (1969) and May (1973), who further distinguish between neighborhood stability, the ability of a system to return to an equilibrium point following small perturbations, and global stability, the ability of a system to converge to an equilibrium following any degree of perturbation. Although the former is more theoretically tractable (May, 1973), the latter is of greater practical importance and will be implicit in this treatment.

Two facets of stability are important in understanding the effects of perturbations on ecosystems: resistance, or the ability of the ecosystem to withstand stress without change, and resiliency, or the speed at which the ecosystem returns to an equilibrium state following perturbation. Although perhaps correlated, these two characteristics are obviously distinct and deserve separate treatment in the discussion of stability.

The relationships of stability to ecosystem complexity and species diversity is relevant to the understanding and prediction of the effects of human disturbance in coastal ecosystems, which are often heavily stressed. This paper seeks to describe the general trends of species diversity in estuarine communities and relate them to trends in persistence and stability. These trends will be illustrated by benthic macrofaunal communities which, because of the longevity, immobility, and broad taxonomic representation of their constituent species seem most appropriate as examples.

Diversity

The subtidal, soft bottom macrobenthos (>1 mm) of three large estuaries was sampled using comparable techniques. These estuaries were: (1) the estuary formed by the lower Chesapeake Bay and York River (Virginia, U.S.A.), (2) the nearby James River estuary, and (3) the Brisbane River estuary (Queensland, Australia). The York and Brisbane estuaries were sampled up to the usual limit of salinity intrusion and the entire tidal James River, including a long section of permanently fresh water, was sampled.

The average patterns of within-habitat species diversity (Shannon's formula, H') and species richness (number of species

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[1] Contribution No. 618, Virginia Institute of Marine Science

found on about 0.2 m^2 of bottom) for each of the three estuaries are shown in Fig. 1. There is a sharp drop in species diversity along each of the three estuaries. In the Chesapeake-York and James estuaries, in which salinity at any given location usually does not fluctuate much over the course of the year (homeohaline), this sharp drop occurs at the transition from polyhaline (30-18 o/oo) to mesohaline (18-5 o/oo) salinity regimes. Minimum diversity is experienced in the oligohaline (0-5 o/oo) zone and the increase in diversity into fresh water is much less than suggested by Remane (1971).

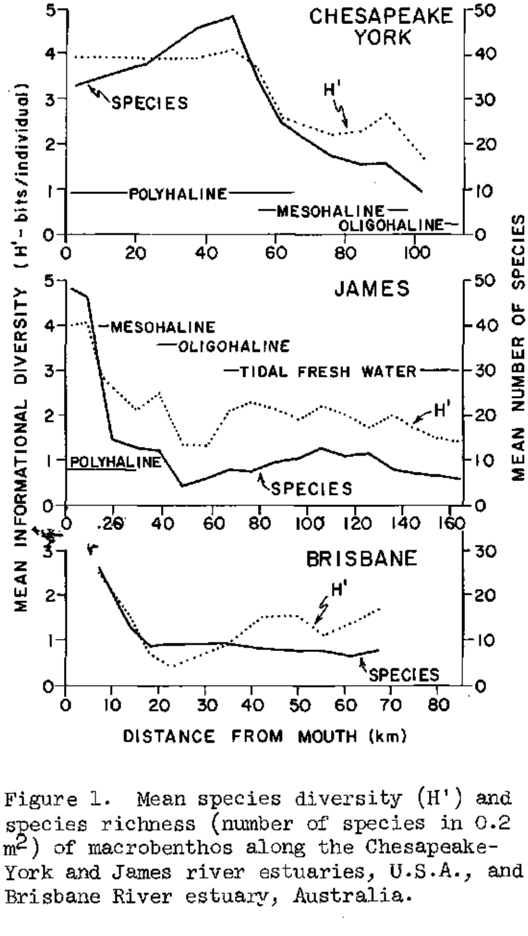

Figure 1. Mean species diversity (H') and species richness (number of species in 0.2 m^2) of macrobenthos along the Chesapeake-York and James river estuaries, U.S.A., and Brisbane River estuary, Australia.

The Brisbane estuary is strongly influenced by heavy summer freshwater discharge, often resulting from cyclones, such that although polyhaline salinities (>18 o/oo) are found as far as 40 km above the mouth during low flow conditions, freshwater conditions often prevail to within 10 km of the mouth during high discharge. As a consequence, diversity is rapidly attenuated in the lower reaches of the estuary and is uniformly low over most of the length of the estuary. Thus, the constancy as well as the level of salinity affects diversity, allowing more species to penetrate farther up homeohaline estuaries and restricting the inhabitants of more poikilohaline estuaries (those seasonally or tidally variable in salinity) to a few species with broad physiological tolerances (Slobodkin and Sanders, 1969).

As measured by the information function (H'), the trends in species diversity along the estuarine gradients are predominantly reflections of the patterns of species richness rather than changes in species evenness. Wolff (1973) has also noted the decline of diversity upestuary is a result of a decline in between-habitat diversity as well as within-habitat diversity. Furthermore, hierarchical partitioning of informational diversity, which successively considers the diversity of phyla, classes, orders, families, genera and species (Pielou, 1967), shows that for the Chesapeake-York estuary a decline in diversity of families within orders is responsible for about 70% of the decline in diversity from polyhaline to oligohaline zones. That is to say, although the diversity of orders and the diversity of genera and species within families declined relatively little, the orders present were represented by far fewer families. This suggests that selected families (or more exactly sub-familial groups) of benthic invertebrates are more disposed, either because of physiological preadaptations or habitat restriction, to evolve into true estuarine species. This is supported by the high degree of familial similarity of estuarine endemic taxa throughout the world. For example, representatives of the annelid families Nereidae, Spionidae and Tubificidae, the mollusc families Mytilidae, Tellinidae and Hydrobiidae and the crustacean families Gammaridae, Corophiidae, Spheromatidae, Anthuridae, Mysidae and Acartiidae are found in low salinity habitats throughout most of the world (Green, 1968).

It has been variously held (e.g. Sanders, 1968; Wolff, 1973) that benthic communities in tropical estuaries are more diverse than in temperate estuaries, thus paralleling the well established trend in fully marine environments. Yet, diversity in the lower reaches of the Brisbane estuary, subtropical at 27°30'S, is lower than in the homeohaline Chesapeake Bay. Sanders (1968) bases his conclusions on diversity in tropical estuaries on two collections from the mouths of Indian estuaries. The salinity range of these stations is not reported and, as we have seen, this is a critical consideration in comparisons of diversity. Nonetheless, comparison with Sanders' rarefaction curves shows that polyhaline communities in the Chesapeake Bay system are at least as rich in polychaete and bivalve species as those in the Indian collections. Furthermore, a thorough examination of the taxonomic and faunistic literature on estuarine-endemic peracarid crustaceans, a diverse and important taxon in estuaries, shows no obvious latitudinal trend in diversity. On the other hand, the diversity of intertidal decapod crustaceans (MacNae, 1968) and calanoid copepods (Tranter and Abraham, 1971) in estuaries is considerably higher in the tropics. The former are more controlled by atmospheric conditions (much less rigorous and variable in the tropics), and the latter because of their short generation time are able to reestablish in estuaries after monsoonal flooding. However, for sedentary longevous animals constancy of salinity rather than constancy of temperature is the overwhelming distributional determinant and tropical estuaries are generally very poikilohaline.

Persistence

Data on the persistence of benthic communities are conspicuously sparse--few communities are ever studied for over a year. M. L. Wass (unpublished data) sampled the community of a sandy-mud site in the polyhaline portion of the York estuary over a six year period from 1960 to 1966. During the first three years, samples were taken monthly or bimonthly. Quarterly sampling at that station was recommended in May 1972--just before floods resulting from Tropical Storm Agnes, the worst floods in 200 years, struck the Chesapeake drainage basin--and continues to the present. Fig. 2 depicts the fluctuations in the populations of several common species in the community. Populations of the polychaete Nephtys incisa and the ophiuroid Micropholis atra were relatively persistent, although Nephtys populations showed strong seasonal pulses. Populations of the shrimp Ogyrides limicola became much less dense after mid-1963 when at the same time populations of the gastropod Acteocina canaliculata increased. Several other species became more or less abundant during around mid-1963 suggesting a subtle habitat change had taken place. Populations of Ogyrides were depressed by low oxygen conditions resulting from the tropical storm of the summer of 1972 (Boesch, Diaz and Virnstein, in press) and remained low until November 1973, however, Acteocina increased sharply at the end of 1972. Population fluctuations of the bivalve Mulinia lateralis show an eruptive pattern characteristic of the fugitive strategy of this fast growing and fecund species. Large populations of Mulinia develop during the cooler months of some years, but not others, and quickly perish during the summer. The success of the Mulinia eruptions following the 1972 perturbation suggests that Mulinia is only successful after some disturbance in the community. The polychaete Paraprionospio pinnata is another eruptive opportunist which has continued to be more abundant following the 1972 storm than previously, when it had been usually abundant only in the mesohaline zone. Finally, the polychaete Pseudeurythoe sp. has been much more abundant throughout the lower Chesapeake Bay system in recent years than in the early 1960s, but the cause of this mysterious "species shift" is unknown.

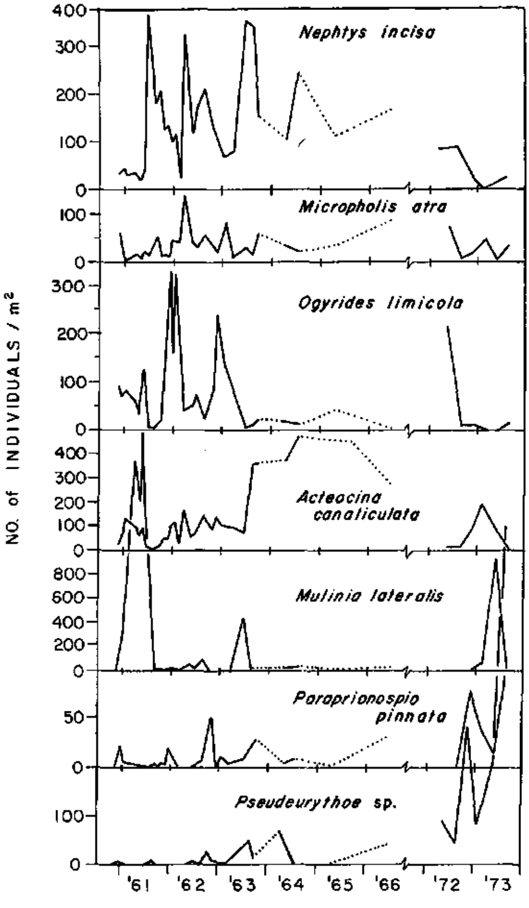

Figure 2. Temporal variation in abundance of some common species at a site in the lower York River, Virginia, U.S.A.

It is difficult to draw conclusions about the relative persistence of benthic communities because of the lack of comparable data. Ziegelmeier's (1963, 1970) data on benthic populations in the German Bight during the period 1949 to 1965 show the presence of persistent species as well as eruptive opportunists. For example, the unusually severe winter of 1962-1963 eliminated the mussel Angulus fabula, allowing the development of unusually large populations of other species, particularly the polychaete Spiophanes bombyx, the larvae of which would have otherwise been prevented from settling on the sea bed by the intense suspension feeding of Angulus. Lie and Evans (1973) concluded that there was high persistence of benthic infaunal communities in Puget Sound, U.S.A., over a six year period. This was based on the observation that although relative dominance among the numerically important species varied somewhat, the species composition of the assemblage did not change. This brings us to the difficult question of what constitutes community persistence--is it constancy of constituent populations, constancy in species composition or constancy of similar "structure" to the point of allowing the exchange of species, shift in their proportions and alteration of trophic webs (Margalef, 1969)?

Stability

A major problem in determining the relative stability of communities in the real world is the difficulty in finding or performing comparable perturbations to disparate communities. Although my evidence is highly circumstantial, it indicates that the low diversity communities of the meso- and oligohaline zones are more resistant to perturbation than higher diversity polyhaline ones. Firstly, multiple pollution stress in polyhaline portions of the harbor of Hampton Roads, Virgina, has caused alterations to communities by eliminating or reducing populations of several benthic species and has favored more eurytolerant species characteristic of lower salinity and lower diversity communities (Boesch, 1973), suggesting that communities upestuary would have fared better with respect to alteration given an equivalent degree of pollution stress. Secondly, although salinity reductions resulting from Tropical Storm Agnes were comparable, polyhaline benthic communities in the Chesapeake Bay system were substantially affected while the mesohaline and oligohaline communities were little affected by this disturbance (Boesch, Diaz and Virnstein, in press).

Estuarine organisms are inherently resistant creatures and assertions that they are living exceptionally close to the limit of their tolerance range, and thus are more vulnerable to alteration (e.g. W. E. Odum, 1970) are unfounded. Stenohaline marine species may be living just as close to the limits of their narrower tolerance range. Fisher et al.'s (1973) experiments on PCB sensitivity of diatoms show that estuarine clones are more resistant than oceanic clones. Euryhaline organisms are generally eurytopic in other habitat dimensions. There is much to support Slobodkin and Sanders' (1969) observation that in the hypothetical case "a perturbation that would have little effect on physically controlled communities (e.g. estuarine communities) may be catastrophic when applied to biologically accommodated ones."

Circumstantial evidence also indicates that low salinity benthic communities are more resilient than polyhaline or marine communities. The polyhaline York estuary community discussed above has not yet fully recovered from the low dissolved oxygen stress of almost two years ago. On the other hand, Hanks (1968) found that man-made ponds developed a community similar to that of the surrounding mesohaline habitat within one year at an upper Chesapeake Bay location. Estuarine species are generally "r-strategists" with high reproductive potential (rapid growth and high fecundity) adapted to quickly recover from local extinctions caused by the environmental inconstancy. Thus, estuarine communities must be more resilient than those in physically benign marine environments.

Relationship of persistence and stability to diversity

Although it is a widely held and seemingly soundly based generalization (Sanders, 1968) that high diversity, biologically accommodated communities are more persistent than physically controlled communities such as in estuaries, conjecture on the relative persistence of estuarine ecosystems is not extensively documented. I am struck, when on returning to a sampling site in the low salinity portion of an estuary, by the high predictability of the composition of collections compared with those from more marine environments. Similarly, Murdoch, et al. (1972) found old field insect communities of low diversity more persistent, as measured by percentage similarity from one year to the next, than those of higher diversity. Is this attribute persistence or is it merely an artifact of the low diversity or the spatial homogeneity of these environments? Aside from these observations I have no evidence to dispute the conventional wisdom that somehow estuarine ecosystems are not very persistent in terms of constancy of populations.

However, there is a body of thought with which I must take exception, that low diversity systems, such as those in estuaries, are relatively unstable (not resistant to stress or resilient from perturbation). The hypothesis that diversity confers stability had its roots in the intuitive argument that food web complexity should stabilize a community by providing alternate pathways of energy flow. It was formally expounded in a model by MacArthur (1955) and gained wide acceptance in ecology. The hypothesis was incorporated into E. P. Odum's (1969) "strategy of ecosystem development" in which he characterized low diversity "developmental stages" of succession as having poor stability, defined as resistance to external perturbation, and high diversity "mature stages" as having good stability.

The diversity-stability hypothesis has recently been empirically challenged by the results of perturbation experiments on old field communities by Hurd, et al. (1971). Herbivore and carnivore populations were less resistant to an equivalent perturbation at the producer level in the older, more diverse field community than in the younger field community. Furthermore, May (1973) has shown that mathematical models of trophically complex food webs are less stable than those for trophically simple ones.

Part of the confusion over the relationship of diversity and stability stems from the long-ambiguous usage of the term <u>stability</u>. Margalef (1969) asks whether a system is stable (a) if it survives many changes but preserves similar structure (<u>stability</u> in the sense used here) or (b) if it remains much the same and its presumed stability is never tested (my concept of <u>persistence</u>). He suggests that nothing is gained by imagining the effects of hypothetical perturbations if the capacity of a persistent system to return from a far different state is never needed or realized. However, the distinction does become important and practically relevant when ecological theory on the relationship of diversity and stability is applied in resource management and in weighing the environmental impacts of alternative human activities.

For example, the authors of a series of reports (e.g. Offshore Oil Task Group, Massachusetts Institute of Technology, 1973) assessing the potential impact of petroleum-related developments to the coastal marine environment of the United States reason that while a mature (diverse) ecosystem may contain a larger number of individually vulnerable species, because of its diversity it should be better able to absorb stress than less mature (less diverse) systems. Imagine the potential for misapplication of such ecological dogma by unquestioning bureaucrats! On the other hand, Copeland (1970) offers for application the quite opposite hypothesis that systems adapted to "energy requiring stresses" (low diversity systems) are better able to resist disturbances of a given magnitude than those adapted to relatively constant environments (high diversity systems). The information assembled in this report supports the validity of Copeland's "response to disturbance" model.

Estuaries and human disturbance

I conclude that estuarine ecosystems are characterized by low species diversity attributable to low environmental constancy and predictability and, although they may lack persistence, they have high resistance and resiliency. Thus, given a hypothetical stress of a given magnitude, estuarine ecosystems should be disturbed less and recover faster than marine ecosystems of higher diversity. Contrary assertions appear unsupported and their use detracts from arguments stressing the relative vulnerability of estuaries. Rather, the argument for preservation or careful management of estuaries should concentrate on other facets of environmental alteration (W. E. Odum, 1970), including (1) the confined and restricted nature of most estuaries; (2) the concentration and multiplicity of human disturbances in many estuaries; (3) peculiarities of estuarine circulation; (4) the large role played by sediments (e.g. in the concentration and transfer of pollutants) and (5) man's propensity for irreversible geological changes in estuaries.

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THE STABILITY OF CANADIAN BOREAL FOREST ECOSYSTEMS

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Summary

The increasing demands made upon the extensive boreal forests in northern Canada have resulted in practices which do not always duplicate the natural processes of renewal. Basic questions concerning the long-term stability of forest ecosystems arise as a result of these practices. Particular attention is drawn to questions concerning organic matter decomposition, nutrient exports and loss of genetic material.

Introduction

Canada's boreal forest stretches across an immense area of land and water, from Newfoundland to the Alaska border. It is characterized by conifer forests of spruce, fir and pine, and pure and mixed stands of birch and aspen, long cold winters. The region has slow rates of organic matter decomposition and podzolic soil processes which have developed in soils of glacial origin during the last 10,000 years (Rowe 1959). The general characteristics of northern coniferous ecosystems have already been reviewed by Tamm (1973a).

The forest stands are relatively simple in structure, composed of few species and are usually even-aged, usually originating from large scale forest fires. The fate of the forest stands up until recently were to be blowndown, killed by insect and disease epidemics, or more likely, to be burned by wildfires (Heinselman 1971). Nearly all of these forests are under public ownership with resource control vested in provincial government departments.

With increasing human demands on these forests and increasing forest protection against fire, insects and disease, as well as rapidly increasing mechanized logging operations (Place 1973) some questions arise as to whether the stability and continuity of these virgin forest ecosystems will be maintained (Holling 1973, Tamm 1973b, Carlisle and Maini 1974).

The purpose of the paper is to provide some perspective on these problems, in terms of current thinking and scientific study about Canadian boreal forests.

Parallelism of natural and human disturbances

Older methods

Extensive human exploitation of these forests has mainly developed since World War II. It originally involved primitive forest management on these public lands in which licensees clearcut all marketable trees in mature or, more often, over-mature stands. Most cutting schedules were largely dictated by a need to normalize age class distributions and to cut or salvage stands affected by, blowdown, fire or insect or disease epidemics.

The trees were removed using manual and horse power methods to rivers, usually over snow during the winter months. Utilization standards were low, all logging slash was left *in situ*, and ground disturbance was minimal. It became apparent many decades ago, that this logging method did not appreciably reduce the nutrient reserves of the site, since only nutrient-poor logs and bark were removed, did not duplicate the seed release mechanism of forest fire in breaking the resin bonds of serotinous cones (as in jack pine, *Pinus banksiana*) and did not prepare seedbeds as receptive to forest tree seeds as those produced by wildfires in mature stands.

Initially the reduction in forest productivity of these latter two problems were allowed for by the acceptance by forest managers of young trees established prior to cutting in over mature stands and by the acceptance of regeneration periods and associated long rotation ages, often around 100 years. As these solutions became less acceptable due to rising demands for wood, techniques were developed using various types of pushed or pulled mechanical equipment to scarify the humus covered soil surfaces in order to provide receptive seedbeds and enough heat at the ground surface to break resin bonds of the cones. Attempts to prepare seedbeds by the use of prescribed burns met with little success. Since forest inventories were largely designed to locate merchantable forests, little attention was paid to growth rates. Consequently, very old forest stands which had commercially operable timber volume accumulations in spite of slow growth rates on poor forest sites, were often, and still are, cut. Kimmins (1973,1974) has pointed out that the ecologic rotations may be longer on such sites than economic rotations, and thus such cuts are not suitable.

Also during this period some workers expressed concern that over-enthusiasm for fire and forest protection and thus the removal of the natural agencies for stand renewal might lead to accumulations of poor quality stands with low timber and wildlife productivity and also might lead to long term successional trends towards peat accumulation on wet sites which could not be arrested, and further, the older stands might result in epidemic populations of insect and disease organisms. For example, spruce budworm (Choristoneura fumiferana) the natural agent for removal of old balsam fir (Abies balsamea) stands, has persisted at near epidemic levels following annual pesticide spraying for over 10 years instead of collapsing following the mortality of the trees (Baskerville 1971).

Newer Methods

Starting in the 1960's with the desire of the provinces for increased economic returns from unused forests, and with rising labour costs, a new wave of forest exploitation started using chain saws, logging machines and trucks. Concern rapidly developed over the ecological consequences of these new methods.

Concern focussed on the size and ugliness of clearcuts necessitated by efficient use of expensive machines well adapted to the even-aged stands, the destruction of established forest regeneration, water quality problems associated with soil disturbance, the silvicultural implications of the new need for shorter rotations, and rapid restocking and the ecological implications of nutrient removal in full-tree harvesting systems, in which the branches and needles are also removed to roadside.

These concerns coincided with the environmental movement in North America and the presence of increasing numbers of recreationists in the forests.

Attempts to duplicate the required natural seedbeds by the use of cheap powered machinery and the required natural seed source by modified cutting have had a limited success. The exigences of the new economic climate have increasingly indicated the use of planted trees on cutover forest lands which have been mechanically and chemically prepared to reduce vegetative competition. Whenever the topography and stone content of soils are suitable the approach has been increasingly agronomic with all the ensuing ecological implications. Forest lands unsuitable to these new treatments may be abandoned following cutting. Production is tending to be concentrating on more productive lands, often using fertilizers and trees of selected genetic origin.

The new situation is giving rise to forest surveys which are ecologically based and in which priorities for the various forest uses are established (Jurdant 1969, and Jurdant Belair 1973). Most of the more accessible forest lands in Canada have already been mapped and ranked for timber, wildlife, recreation and agriculture production. Unfortunately, such maps are not suitable for ecological planning. Environmental impact studies are now often required for major timber sales and there is increased public and professional concern and scrutiny of forest operations. There is growing realization that by replacing natural disturbances of the boreal forest by human disturbances less stable and less diverse forest ecosystems may develop and careful ecological planning is now required.

Specific Problems

Handling Organic Matter Accumulations

The tendency for organic matter to accumulate in wet boreal forest sites has been studied by Siren (1955) in Finland and Heinselman (1963) in Northern Minnesota. The development of sphagnun mosses and the associated deterioriation in soil drainage in wet black spruce (Picea mariana) stands following cutting has been noted often. On upland drier conditions there has been speculation about the lowering of site fertility under ericaceous dwarf shrub vegetation. Damman (1971) has shown how Kalmia heath land formation on non-regenerated black spruce stands in Newfoundland can lead to increasing immobilization of nutrients in the unincorporated humus layer and to pan formation and paludification of the site.

The presence of the raw humus layer has long been known to be associated with shortages in available nitrogen supplies to trees. This situation has led to the practice of forest fertilization with urea in order to stimulate tree growth. Urea is rapidly converted to ammonium nitrogen via the action of urease and the nitrogen deficiencies are temporarily alleviated. The temporary nature of this response has led to studies of the operation of nitrogen cycle and the role played by decomposers in this cycle, with a view to discovering ways to make the appreciable reserves of organic nitrogen in the humus layer more available to tree growth. Concern has also been expressed on the effects of fertilizer additions on the functioning of forest ecosystems particularly the decomposer activities (Weetman and Hill, 1973). The role of epiphytic feather mosses (eg Hylocomium splendens and Pleurozium schreberi) in acting as traps for incoming nutrient supplies in dust and precipitation has been recognized (Tamm 1953, Weetman and Timmer 1967) and has led to a realization of their value in building fertility on shallow rocky sites. Steps are now being made to protect this moss layer from dessication by modified strip cutting operations on such sites.

On most boreal forest sites, following large scale clearcutting, the temporary removal of vegetative competition for nitrogen and other nutrient supplies leads to lush development of pioneer vegetation and the lack of a need for fertilization of young trees. The discovery of active nitrification, not normally suspect as present in such conditions, following herbicide killing of all vegetation on a watershed study in a temperate forest in New England (Likens and Bormann 1970) has led to speculation that nitrate contamination of water supplies might occur following cutting. However, to date, studies indicate that nitrate ion release due to organic matter decomposition following cutting is mainly taken up by pioneer vegetation (Gosz et al. 1973, Marks 1974) and serious contamination of water supplies appears unlikely.

With the advent of radical mechanical disturbance of the humus layer following cutting due to ploughing, rolling, chopping, discing and scarification activities for site preparation, further study of long term consequences of such actions is needed.

2. Nutrient Losses in Logging

With the removal of needles and branches to roadside in full-tree logging appreciable quantities of potentially readily available nutrients may be lost from the site. The reductions in forest site fertility due to the ancient practice of litter raking in Europe are due to the same nutrient export problem. The problems associated with the dynamics of the nutrient cycle on different forest sites must be considered, particularly the turnover rate of organic matter and the proportion of the total nutrient reserve in the living biomass. While preliminary calculations indicate that on medium quality sites, such losses may be modest (Weetman and Weber 1973) much more attention is now being paid to potential losses from drier, shallow and welter sites with modest nutrient reserves (Kimmins 1974). Full-tree logging operations are now often not applied to such sites. This potential problem points to the need for careful evaluation and identification of fragile sites which would have long periods of nutrient recovery following such logging operations.

3. Loss of Genetic Material and Preservation of Ecosystems

The relatively uncontrolled forest exploitation of virgin boreal forest ecosystems has, in some cases, led to the removal of all trees of all species of superior form and quality. Forest geneticists have speculated about whether or not such practices are disgenic or not. In many cases it is considered that enough advanced growth has been present at the time of cutting to avoid this problem. The cutting of many high quality virgin stands over large areas has led to concern that certain gene pools have been lost or endangered (Maini 1971). For this reason tree breeders have been quick to support efforts to set aside representative and unique examples of forest ecosystems in the IBP-CT survey programs. Desirable locations for ecological reserves or natural areas have been located throughout the boreal forest, although the coverage is very spotty in some regions. A national registration system for such areas is now operative and the provinces of British Columbia and Quebec have passed special legislation to set aside public lands for this purpose.

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Strategies for mangement of natural and man-made ecosystems

STRATEGIES FOR MANAGEMENT OF NATURAL AND MAN MADE ECOSYSTEMS

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Ecosystems contain a diversity of living organisms, these organisms display in their life processes a complex pattern of interdependance and interaction with one another and with their environment. There is evidence that increasing ecosystem complexity confers some degree of stability.

Virtually all ecosystems have been modified by man, either deliberately or accidentally. Man induces ecological change by altering the abundance, activity and species composition of the living organisms present and by modifying the environment as when he drains marshes or adds mineral fertilisers to infertile soils.
Besides affecting ecosystem structure such activities bring about associated changes in the nature and magnitude of the four dynamic processes whereby ecosystems function as integrated biological units.
These processes are organic production and breakdown, energy flow, nutrient circulation and water movement.

Whilst some terrestrial ecosystems, particularly in remote places, can still be regarded as essentially natural, such others as commercial forest plantations, agricultural crops and cities are highly artificial with their flora, fauna and environment greatly modified and usually are less diverse biologically than the preceding more natural ecosystems.

With his large numbers and advanced technology modern man has acquired a new capacity for massive and rapid modification of ecosystems and landscapes. Currently, large areas of tropical forest are being cleared to provide land for agriculture or to obtain foreign capital quickly.
Where such exploitation leads to widespread vegetation destruction and soil erosion there can be an unjustifiable disruption of ecosysten processes with loss of biological capital on which man's future depends.

Because of growing public concern with environmental matters entrepreneurs are being increasingly constrained in development projects and government and international agencies are being required to take a broader more integrated approach in allocating land as between alternative forms of use.

Land use decisions are complicated because they often require a coordinated assessment of potential social economic and ecological repercussions taking into account both short and long term implications. The difficulty is further compounded where aesthetic considerations and sectional community interests are involved and by an inadequacy of information with regard to new scientific techniques such as the use of pesticides, the effects of which may be difficult to contain both in terms of time and space. For any ecosystem a choice of management strategies is available, and it is necessary to decide which strategy is most suitable for a particular land use at a specified time.

Despite inherent problems in deciding whether a particular form of management is good or bad, it is possible to identify certain underlying ecological principles applicable to ecosystem management and utilisation on a continuing basis. Gradually a body of experience has accumulated, which combined with ecosystem simulation technology, now permits more precise forecasting of the response of ecosystems to different strategies of management. In this way more rational land use decision with minimum ecological risk can be made and local and regional viewpoints be reconciled into overall schemes of natural resource use and development.

FAIL-SAFE OR SAFE FAILURE?

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The past management of ecosystems has implicitly presumed that the consequences of an incremental action will be quickly detected. If the intervention produces higher costs than benefits, then a revised incremental action can be designed. It is this trial-and-error strategy that has succeeded in producing phenomenal increases in production of the food and fiber needed by man. Little knowledge of ecosystems was required so long as the consequences of an erroneous trial were minor and alternate trials remained possible.

But now, incremental acts seem to be producing more extensive and intensive consequences, consequences which resist further incremental solutions. And other consequences are emerging from the accumulation of past incremental decisions. Our remedial responses to these new emergencies are as shortsightedly ad hoc as their original causes.

Trial-and-error seems to be an increasingly dangerous strategy for coping with ignorance. And yet the solution cannot be to withhold action until we have sufficient knowledge. We need a new strategy for dealing with the unknown.

Four major classes of uncertainties and unknowns may be identified. We have incomplete, although growing, knowledge of the functional relationships within ecosystems -- of their number, kind, form, and intensity. Also, we have limited knowledge of the social objectives for ecosystem management. These two sources of ignorance -- the descriptive and prescriptive -- are important but manageable. Present techniques can identify and hedge against these sources of uncertainty in inputs, parameters, functions, and alternate values.

But what of the qualitative unknowns inevitably dealt us by 'fickle fortune?' The basic rules underlying linked economic-ecological systems can change, and new species, economic dislocation, and changes in perception all leave society committed to policies and systems that cannot themselves shift to meet these new needs.

Few systems which have persisted for extensive periods exist in a state of delicate balance, poised precariously in some equilibrium state. The ones that are, do not last, for all systems experience unexpected traumas and shocks. The ones that survive are explicitly those which have been able to absorb these stresses. They exhibit an internal resilience. Resilience, in this sense, determines how much disturbance -- of kind, rate, and intensity -- a system can absorb before it shifts into a fundamentally different behavior.

Historically, ad hoc management approaches have succeeded specifically where applied to highly resilient systems. The potentially disastrous consequences of an ill-informed trial can be absorbed by the resilience of the system. But the price often paid is reduction of the resilience so that an unexpected stress which previously would have been absorbed now is not.

Our goal for a new strategy of ecosystem management must therefore be to develop approaches that maintain or expand resilience while still achieving economical production of resources for man. Such a strategy must not be based on the presumption of sufficient knowledge but the recognition of our ignorance; not the assumption that future events are unexpected, but that they will be unexpected. In short, not a fail-safe strategy, but one that is 'safe' in failure.

A resilience strategy can accommodate this shift of perspective, for it does not require a precise capacity to predict the future, but only a qualitative capacity to devise linked ecological/management systems that can absorb and accommodate future events in whatever unexpected form they may take.

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MANAGEMENT STRATEGIES IN SOME PROBLEMATIC TROPICAL FISHERIES

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Abstract

The need to develop national fish resources for food in tropical countries has resulted in increased fishing effort throughout the tropical world and re-assessments of production potentialities from all available sources. Comparatively few regulatory measures previously existed in such regions. Those which were applied have not been based on completely satisfactory data. In many cases of newly emerging fisheries no controls existed. The era of speculative or "logical" management tools is giving way to the rationalisation of some systems and in new fisheries measures are being introduced which are conservative and based on gradually accumulating data. A dilemma of choice is however posed for many developing countries in specific areas of inland and marine fisheries which are being heightened by political global decisions and strategies, as well as population and employment pressures.

Specific management problems are illustrated in the natural systems of floodplain fisheries in Guyana and the Niger River in Mali as well as the explosive growths of tropical aquatic weeds in relation to fisheries, public health and general water usage. Certain man-made lakes in Africa and aquaculture systems in South East Asia provide examples of the challenges and constraints of man-made eco-systems on a macro- and micro-scale.

Regarding marine fisheries, the rapidly growing multi-species fishery of the East Central Atlantic presents a management problem of great biological and political complexity while the demersal shrimp fisheries off the Guyanas present an economic dilemma for rational cropping. Human intervention causing imbalance in tropical estuaries and reef fisheries are described and beneficial developments re mangrove oysterculture and mariculture of molluscs and aquarium reef fishes are illustrated.

The current effectiveness of management machinery is briefly reviewed. The various international commissions which now function are seen to offer an opportunity for the unified application of management strategies. Additionally the specific programmes of governments may be aided by systems which seek to crop resources "evenly" until adequate data is gathered to justify regulatory measures which are internationally acceptable and practically applicable for rational cropping.

The development perspectives and strategies which seem to be evolving in the areas cited are summarised and projected. The need is stressed for a flexible but reliable system which continually and objectively reviews, assesses and refines any management measures applied to attain the objectives. These must realistically satisfy both human needs as well as tropical fishery eco-systems which are now coming under exploitive pressures if they are to be mutually viable.

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MAN-MADE NATURAL ECOSYSTEMS IN ENVIRONMENTAL MANAGEMENT AND PLANNING

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Abstract

Ecosystem management is considered as a set of human activities within the interaction system human society - environment. This system may be called geosphere; it involves the various spheres operating at the surface of the earth, including cosmosphere,atmosphere, hydrosphere, lithosphere, biosphere, and noösphere -ranked according to increasing dependence.

Ecosystem management, environmental management, environmental conservation are defined, related to each other and placed within the framework of physical planning.

The terms natural ecosystem and man-made ecosystem are considered. Classifications of ecosystems according to their degree of naturalness or man-madeness are discussed. Naturalness of an ecosystem is defined in terms of the spontaneous development of native species within that ecosystem.

Biological management and nature conservation are defined in relation to more or less natural ecosystems.

Man-made natural ecosystems are defined ad hoc as ecosystems consisting largely of spontaneously developing native species but showing a structure that is determined by human influence.

Man-made natural ecosystems can be considered as replacements of particular types of potential natural ecosystem and their structural and functional properties can be considered in relation to the corresponding potential natural ecosystem.

Environmental management and planning are supposed to profit from an increase in the extent of man-made natural ecosystems as well as from an increase of our knowledge of these systems.

Various man-made natural ecosystems ,including grasslands, swamps, fens, scrubs, heathlands, coppices and open woodlands, are discussed in terms of exploitation, regeneration, diversity and stability (constancy in environment, management and species composition).

The relation between composition and structure of man-made natural ecosystems and the gradient structure of the environment is discussed. Implications of gradient theory and its application to small-scale patterns of variation in complexes of ecosystems of varying degrees of naturalness are shown.

Possible perspectives of gradient theory for the establishment of man-made natural ecosystems and their subsequent management are discussed.

Attention is paid to the procedure of the so-called biological evaluation of ecosystems in terms of their maturity, irreplacebility, various types of diversity and ecosystem and species rarity.

Various factors causing devaluation and various possibilities for revaluation of ecosystems are mentioned.

Ecological qualities of ecosystems are considered in terms of functions of ecosystems for society. Interactions between'ecological'functions and other functions of the environment as studied in interaction matrices are discussed.

The special values of man-made natural ecosystems are summed up and their role in environmental planning is emphasised.

Finally some attention is paid to the use of environmental planning models.

ECOLOGICAL CONSIDERATIONS IN THE MANAGEMENT OF SEMI-ARID ECOSYSTEMS IN SOUTH-CENTRAL AFRICA

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Summary

There are four significant ecological characteristics of semi-arid ecosystems in south-central Africa which have an important bearing on their management. i) They have a low and erratic rainfall which is closely correlated with primary production. ii) The rate of water infiltration is critical and is determined by the percentage litter cover and herbaceous basal cover. On sandy loam soils it is nine times faster through soil under litter than through a bare soil surface. iii) Species composition varies markedly according to the proportions of perennial and annual grasses, the palatability of the perennials, and species diversity. Annual grasses increase inter-seasonal variation in production. Seasonal production is positively correlated with an increase in species diversity. iv) There is evidence that clearing woody vegetation can lead to increases of up to 400% in grass growth, but this must be balanced against a number of benefits derived from the presence of trees.

Five management principles are discussed. i) The ratio of grazing to browsing should approximate the ratio of grass to available browse. ii) Area selective grazing should be overcome by five suggested means. iii) Cattle should be managed using multi-paddock, short duration grazing systems. iv) The use of fire, especially on lithosols, should be avoided. v) In National Parks and game reserves, animal numbers and fires should be controlled, but the introduction of artificial water supplies into characteristically dry areas should be avoided.

Introduction

The semi-arid ecosystems of south-central Africa evolved under light and probably intermittent utilization by mixed communities of wild herbivores. In these ecosystems permanently resident species such as kudu (Tragelaphus strepsiceros) and duiker (Sylvicarpa grimmia) invariably occur singly or in small groups and are relatively few in number. In terms of vegetation impact, the dominant wild herbivores are herd species such as buffalo (Syncerus caffer), eland (Taurotragus oryx), zebra (Equus burchelli), wildebeeste (Connochaetes taurinus), etc., and under natural conditions they generally migrate according to local rainfall and vegetation conditions. In the past, they would usually have been forced to move before their impact on the vegetation became serious, owing to lack of water.

Apart from the areas set aside as game reserves, present systems of land use now include game ranching, cattle ranching on a more or less planned basis, and communal grazing by peasant owned cattle, goats and sheep. The rapidly increasing human and cattle populations have forced a year-round animal pressure and there is a general trend of widespread, retrogressive change throughout this extensive region. Although the tribesmen persist in attempts to cultivate land, dryland crop production is generally not viable and land use is still dependent on the natural vegetation.

The aim of this paper is to describe the more important ecological characteristics of this ecosystem and to discuss these in terms of management principles.

Ecological characteristics of the ecosystem

There are, in particular, four significant ecological features of these semi-arid ecosystems which distinguish them from other more mesic areas in the region, and which have an important bearing on management procedures.

1. Rainfall is low (300-500mm p.a.) and occurs in summer, from November to March, when temperatures are high. Maximum daily temperatures are frequently in excess of 40°C. Within this period the rainfall is very unevenly distributed, both temporally and spatially, and generally occurs in high intensity storms of short duration. Large fluctuations also occur between seasons (e.g. at Nuanetsi in south eastern Rhodesia, from 150mm to 1000mm). Primary production is closely correlated with rainfall, particularly on the heavier-textured soils, and the availability of forage therefore varies considerably between seasons (see Fig. 1).

Soil moisture is rapidly depleted after periods of rain and may drop below the wilting point for periods of up to several weeks during the growing season. The most successful herbaceous species, the perennial climax grasses, are able to go dormant during these periods and resume growth with the next rain. However, the annual species and most other perennial grasses die.

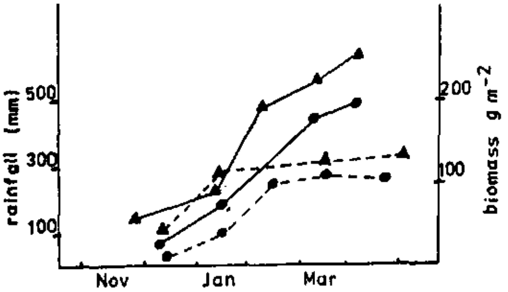

FIG. 1. Average rainfall and mean maximum above-ground seasonal biomass of the herbaceous layer from four sites in southeastern Rhodesia (data from Kelly 1973). ---------- = 1971, ——— = 1972, ▲= rainfall, ● = biomass.

2. The rate of water infiltration into the soil is critical and on any particular soil type it is a function of two factors; the percentage of the ground covered by litter, and the basal cover of caespitose, perennial grasses. On sandy loam soils the ratio of infiltration under a litter cover and on bare surfaces, as measured with a double-ring infiltrometer (Kelly 1973), is of the order of 9 : 1 (Fig. 2). The low rate of infiltration on bare areas is due mostly to the presence of a soil cap, and the effect of this cap is frequently intensified by the development of an algal crust, mainly composed of blue-green algae. During dry periods this crust forms a hydrophobic, impermeable surface, and observations on crusts in petri dishes have shown that it takes up to two hours or longer for the surface to soften and absorb water. This is considerably longer than the average duration of a rain storm.

According to Volk and Geyer (1970), a further cause of reduced infiltration on bare areas in these arid ecosystems is the presence of a layer of small vescicles near the surface of the soil, which effectively prevent water from percolating through. In the vegetated areas, water infiltration through the base of a tuft is very rapid and the perennial, caespitose tufts funnel water into their own rhizospheres (Glover et al. 1962).

3. Composition of the grass sward varies considerably with respect to, firstly, species diversity and the proportion of annuals and perennials, and, secondly, the palatability of perennials. The proportion of perennials is important because perennial grass growth varies much less between seasons than does the growth of annuals (Fig. 3) and the higher the proportion of annuals the greater, therefore, is the inter-seasonal variation in available grazing. This causes considerable management difficulties where constant numbers of livestock have to be maintained from year to year.

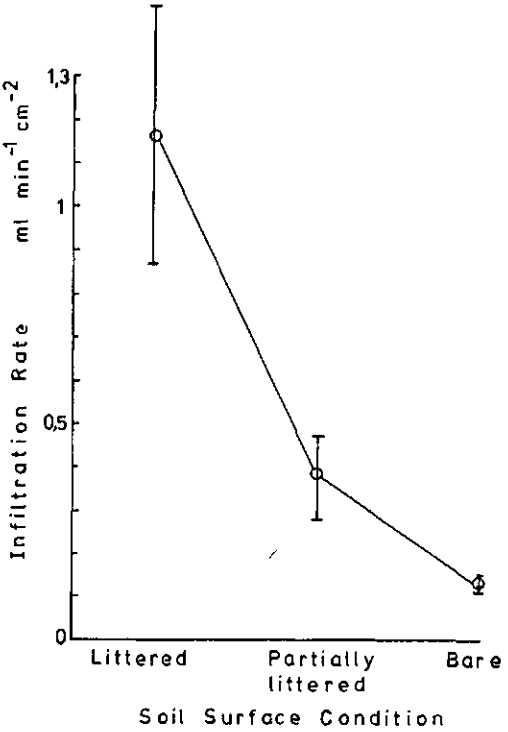

FIG. 2. Rate of water infiltration, using a double-ring infiltrometer, on littered, partially littered and bare soil on a sandy loam in southeastern Rhodesia. Two standard errors are shown on either side of the mean.

As opposed to the findings of workers in some temperate grasslands (e.g. McNaughton 1968), Kelly (1973) has shown that an increase in species diversity in this semi-arid ecosystem corresponds to an increase in seasonal production (Fig. 4). Species diversity tends to reach a maximum in swards that are lightly to moderately grazed. It decreases slightly in unutilized swards and drops sharply under intense utilization.

Some perennial grass species, such as the aromatic Bothriochloa radicans, are relatively unpalatable to stock and are seldom grazed if other food is available. Once left for more than a season these swards become increasingly unattractive to herbivores (especially cattle) and in a few years become moribund. Selective grazing by herbivores can be on two levels. Firstly, it can be for particular areas, and secondly, within an area, it can be for particular species. In a comparison of an adjacent game and cattle ranch, Taylor (1974) has shown that whereas a mixed population of wild

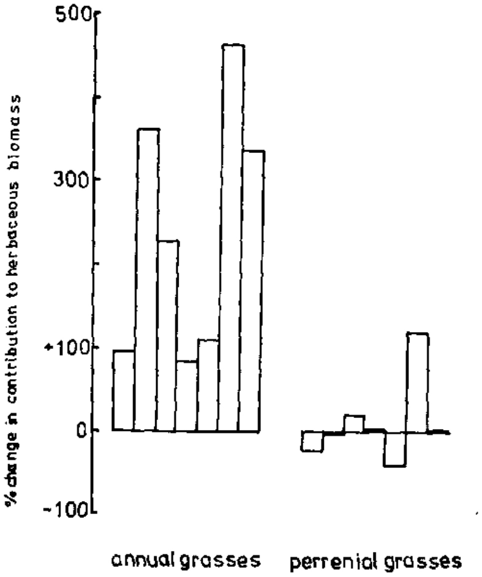

FIG. 3. Seasonal changes in the contribution of annual and perennial grasses to the total herbaceous biomass of eight protected sites in southeastern Rhodesia. The values represent the contributions in 1971 expressed as a percentage of the contributions in 1970. (After Kelly, 1973).

herbivores makes more even use of all the grass species within a particular area, on an inter-area basis they are more selective than cattle. Forty sites were examined on each ranch and the percentage utilization of the grass sward in each site, regardless of species, varied between 4% and 60% under cattle, and between 8% and 95% under game. Part of this difference is due to an improved distribution of water supplies on the cattle ranch, and to the fact that cattle distribution is to some extent controlled by fencing. Nevertheless, despite this difference in management, game animals appear to be inherently disposed towards particular, preferred areas, some of which are not related to watering points, and they will continue to utilize these sites considerably beyond the point at which cattle will move to other, less utilized, sites. This phenomenon is associated particularly with impala (Aepyceros melampus) and wildebeeste.

With respect to selection of grass species, it was found that, in the same community-type, the two most preferred species in the cattle section contributed 80% to the total grass diet, whereas on the game section, these species contributed 60% and there were two further species which contributed significantly (>10%) to the total grass diet. In addition to the more even use of grass species, the game utilized considerably more of the available browse (19%, as opposed to 8% on the cattle section).

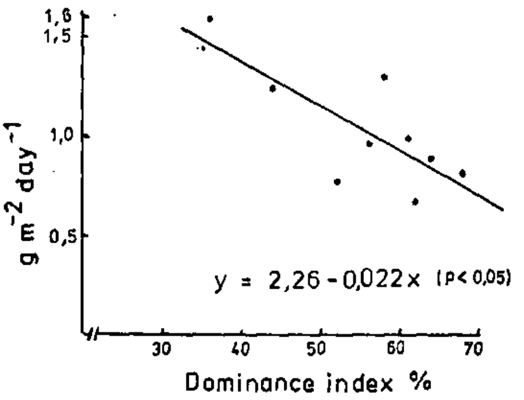

FIG. 4. The relationship between species dominance and production of above-ground biomass of the herbaceous layer in southeastern Rhodesia. The dominance index is that of McNaughton (1968). (After Kelly, 1973).

4. There is a complex relationship between herbaceous growth and tree cover. Experimental evidence from woodland areas has shown that where trees and shrubs are completely removed, up to fourfold increases in grass growth occur (Barnes 1972, 1973). Some of these are accompanied by desirable changes in species composition towards stable perennial swards of palatable grasses, but in other cases undesirable changes have occurred. It has been a general finding in tree-clearing experiments (Barnes op.cit.) that the adverse effects of woody plants on grass growth are particularly severe in dry years, and that cleared areas have a smaller inter-seasonal variation in grass production.

If the herbivore community contains both grazers and browsers, the loss of browse must be taken into account, and Kelly (1973) has shown that the production of leaves and new twigs from the shrubs and trees is at least equal to that of grass. It was also shown in this study that at low tree densities, where total canopy volume was less than 10 000m^3 ha^{-1}, herbaceous biomass was up to 50% greater than where there were no trees. Under dense canopy volumes (c. 40 000m^3 ha^{-1}), herbaceous growth was reduced. Accepting that competition from tree roots beyond the edge of the canopy may reduce grass growth in the open, there nevertheless appears to be a beneficial effect from a sparse tree cover in this environment.

The benefit from trees is at least partly due to the modifying effect which the trees have on the very high temperatures which occur in exposed areas (over 70°C on the soil surface). Interim results from a trial using shade cloth to investigate the effects of artificial shading are presented in Table 1. The experiment consists of a control and four levels of shading using nylon shade cloth, viz. 53, 45 and 27% of full sunlight. Each treatment consists of two 9m x 9m plots. The centre 1m strip of each plot, in an east-west direction, receives shade during all seasons between c. 9am to 3pm, and the three 1m^2 quadrats in this strip were measured separately. Data for the densest shade plots have been omitted since the shade cloth concerned altered the normal distribution of rainfall by funnelling it towards the centre of the plots. The experiment was set up in 1970 and the differences between treatments in that year are largely a result of differences between sites. Since then, herbaceous production has increased under increasing shade. Observation of the sites also shows that, under shade, the sward remains green for considerably longer in the dry season than it does in exposed sites.

Table 1. Maximum seasonal biomass of the herbaceous layer under various degrees of artificial shading in southeastern Rhodesia. S.E.'s are given in parentheses.

Year	Percentage of full sunlight 100	53	45
	biomass in g m^{-2}		
1970	421(33)	358(12)	311(28)
1972	198(15)	266(21)	362(46)

In the northern Transvaal bushveld of South Africa, Bosch and Van Wyk (1970) have demonstrated that the soil under trees has a higher nutrient status than soil in open areas, owing to enrichment from stem flow. Furthermore, Kennard and Walker (1973) have shown in Rhodesia that the loose, organic surface under trees, together with reduced temperatures, favours the germination and seedling survival of round-seeded (non-awned) grasses such as Panicum maximum, which is a preferred, palatable species. There is a strong association between species such as this and tree canopy cover in these arid ecosystems, which is not apparent in the more humid areas.

Finally, in terms of herbivore food supply, the woody component of the vegetation supplies high protein browse during the dry season when the food value of perennial grasses is minimal (Table 2).

Management principles

Apart from the areas set aside as game reserves, the three main systems of land use in this type of ecosystem all have some undesirable aspects. On the game ranches the distribution of water points is generally inadequate and the animals tend to congregate around these points and on a few other preferred areas, with a resulting degradation of local areas of vegetation. Inadequate census techniques makes the determination of correct culling intensities of each species difficult, and frequent imbalances in species composition occur.

Table 2. Crude protein content in the dry season of leaves from various browse species (Anderson 1973) and of perennial and annual grass swards (Kelly 1973), in semi-arid areas of Rhodesia.

Species	Crude protein %
Browse	
Diplorhynchus condylocarpon	9,7
Combretum mossambicense	15,7
Acacia robusta	9,2
Grewia flavescens	15,7
Acacia nigresens	7,0
Colophospermum mopane	10,5
Grass	
perennial grass sward	4,3
annual grass sward	9,5

On the cattle ranches the marked inter-seasonal variation in herbaceous growth results in over-grazing in some situations, and in the accumulation of moribund grass in others. Over-grazing leads to an increase in the proportion of annual species, and this further increases the inter-seasonal variation. Extensive areas have already degenerated to a predominantly annual sward, but where stock numbers have been controlled, and where an even distribution of water has been achieved, the herbaceous vegetation is generally in good condition. On all cattle ranches there is an under-utilization of browse and this is coupled with problems of scrub or bush encroachment. Under very similar stocking rates, based on total biomass of the herbivores, the percentage browsing on a game ranch has been shown to be between 14 and 19% as opposed to between 7 and 8% on an adjacent cattle ranch, where some game animals were also present (Taylor 1974).

In the tribal areas the two main problems are over-stocking and a very uneven distribution of animals. Cattle and sheep are traditionally penned at night and their movements are thus restricted to the vicinity of the pens. Areas more than 2-3 km from a homestead are generally under-utilized, while in the vicinity of the homesteads the herbaceous cover has invariably been reduced by intensive grazing to a sparse cover of annual and micro-perennial grasses. Litter cover is practically eliminated and therefore effective rainfall is reduced. A lack of adequate fencing around arable areas ensures that during the growing season the animals are herded well away from the lands and considerable areas of grazing are therefore left untouched by livestock until the dry season, when their nutritional value is far lower. This problem with arable lands occurs in spite of the fact that in most years the low rainfall results in a crop failure.

A consideration of the land use systems in relation to the ecological characteristics of the ecosystem leads to a number of management principles which should be incorporated into whatever strategy of land use is adopted.

1. The ratio of grazing to browsing should be approximately the ratio of grass to available browse. Seasonal changes in diet preferences of all herbivores (including cattle, which make use of browse in the dry season) render this a difficult problem, but examination of vegetation utilization indicates the direction and extent of any imbalance. The effect of man on this ratio has been to shift it towards relative overgrazing, firstly by increasing the proportion of grazing animals and, secondly, by decreasing the relative abundance of grass owing to scrub encroachment. At present, there is a general need to incorporate more browsers into the system, usually at the expense of some of the grazers rather than merely in addition to the grazers already present. Where cattle are the only significant herbivores it is advisable to thin trees and shrubs to a sparse, open woodland. In the absence of conclusive evidence complete clearing is considered unwise.

2. Area selective grazing is a major contributor to degeneration of the grass sward, and to overcome this problem the following points should be included in any management plan. i) Cattle should not be penned at night. In the hot, dry season they do a considerable proportion of their feeding at night and, if they are not penned, their distribution will be much more even. ii) Available water should be evenly distributed. The lack of evenly spaced water points is the single most important cause of vegetation deterioration in the areas occupied by peasant farmers. iii) Considerably more fencing is required, both to separate the grazing and arable areas, and for the reasons given in 3. below. iv) Attractants, such as salt-licks, should be placed in non-preferred areas. v) Any regular culling of natural game populations should be centred in preferred areas.

3. In order to achieve optimum growth and development of the grass sward, grazing by domestic livestock should be controlled by the use of multi-paddock, short duration grazing systems (Roberts 1969), to complement the growth pattern of grasses and to minimize species selective grazing. The number of paddocks and rate of rotation, which will vary according to season, should be such that the following two requirements are met. i) The animals must not be in any one paddock long enough for a grass plant to be defoliated and re-grow more than once in a grazing period, or to allow severe selective grazing of preferred species. One or two severe defoliations (to below 5cm) results in a greater decrease in vigour of the grasses in the following year than several light defoliations (Anon. 1972). ii) The times between grazing periods should be sufficient to allow perennial grass root reserves to be replenished but not long enough for the grasses to develop too far into the reproductive phase - when leafy material is proportionately less, low in protein, and the tufts become fibrous and unpalatable. With respect to the ungrazed portion of the sward, the concentration of stock in smaller areas tends to increase the ratio of litter : standing dead grass, which in turn increases overall infiltration of rainfall.

4. On upland sites, especially those with thin, lithosol soils, the use of fire should generally be avoided. In this dry, rather low-production ecosystem, it has an overall deleterious effect, mainly through the removal of litter. It should be used only to remove accumulated, moribund growth which herbivores will no longer utilize, and burning should then be practised in the spring. Only large, lowland sponge areas (vleis, dambos) can be burned in the winter to provide green grass. Unlike the higher rainfall savannas, the use of fire to control scrub encroachment in semi-arid regions has limited success and frequently does more harm than good.

Under certain circumstances, where small scrub plants have increased in density, fire may be beneficial in restoring the area to a more open grassland. The difficulty in these circumstances is that there is usually insufficient dry grass fuel to produce a fire hot enough to kill the scrub. In the tribal grazing areas it has not been possible for a fire to take hold for many years.

5. In the National Parks and game reserves the main management considerations are the regulation of herbivore population numbers, the control (or non-control) of fire, and the development of water supplies. Owing to the restrictions which the reserve boundaries place on migration, and because the rapidly expanding human population has forced more animals into the game reserves,

some control of animals numbers is necessary. Likewise, the obvious impact of man on the frequency of fires in and around the reserves calls for some policy on fire control. Since it is not possible to establish the "normal" frequency of natural fires, or the pre-civilization densities of the various animal species, it is necessary to base manipulation of these factors on recorded changes in permanently located stands of vegetation. In both cases the aim should be to allow a rate of change in the vegetation which is neither excessive nor so slow as to amount to a policy of preservation.

Extensive areas in these ecosystems are characteristically dry and are therefore used by herbivores for only a short time during the rains. Where permanent water supplies have been introduced they have resulted in a rapid degeneration of the vegetation and soil, mainly through overuse by elephant and buffalo. Certain tree species, such as Colophospermum mopane, are adapted to intensive use and coppice profusely when broken or pushed over by elephant. The introduction of artificial water supplies into areas dominated by these species, which are normally on heavier soils, results in a change in the structure of the vegetation, usually from a woodland to a hedged scrubland, but the changes in species composition are less marked. The water relationships of sandy soils in this semi-arid environment are far more suitable for tree growth and the sandy soils consequently support a higher diversity of larger trees, including species such as Pterocarpus angolensis and Sclerocarya caffra. Mature trees of these species are easily killed by bark stripping and other elephant damage, and the introduction of artificial water supplies into these areas may lead to drastic changes in both structure and species composition. Anderson and Walker (1974) have described the differences between the present and recent past orders of importance of tree species, according to measured basal areas, in the Sengwa wildlife research area in Rhodesia. In contrast to the trees, the herbaceous layer on sandy soil is able to withstand the effects of over-grazing and trampling better than on soils of heavier texture, and the grass sward recovers from damage much sooner.

The introduction of artificial water supplies into an area where water was previously a limiting factor to population numbers must be accompanied by carefully planned and monitored population reduction programmes. However, where the objective of the National Park or game reserve is to maintain the ecosystem in as natural a state as possible, artificial water supplies should be prohibited or kept to an absolute minimum in these semi-arid areas.

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REGIONAL ENVIRONMENTAL SYSTEMS ANALYSIS: AN APPROACH FOR MANAGEMENT[1]

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1. Summary

This paper documents procedures developed for the evaluation of environmental consequences of spatially distributed activities. The strategy has been to develop integrated analyses of cultural and natural systems. The research is directed toward a 7,000-square-mile, 16-county urban/rural region in the southeastern quarter of the United States centered on Knoxville, Tennessee. An important aspect of this research is the ability to interrelate and to show the cumulative effects of different changes to the environment. The decision maker can begin to interact with the system and see the results of different management decisions.

2. Introduction

The primary objective of regional environmental analysis is to aid decision makers and managers as they try to cope with existing problems and plan for the future. Such an effort should:

(1) forecast and simulate future changes,
(2) evaluate the consequences of alternative plans,
(3) determine the optimal solution to given problems,
(4) provide the user with information and computational tools so that he can develop solutions subject to his own criteria.

To develop these capabilities within a total management context requires that many complex issues be considered simultaneously: economic alternatives, environmental effects, political processes, etc. For such a comprehensive effort to be successful, the following set of capabilities is required:

(1) a multidisciplinary team that is structured so that each issue may be attacked individually, yet the solutions be combined to meet the overall need.
(2) integration of each area of expertise so that the models developed in each area may interact and affect one another as happens in the real world.
(3) research methodologies that are common to, and can be used by, all members of the multidisciplinary team.

The purpose of this paper is (a) to present the structure of a multidisciplinary team, (b) to examine a series of modeling results which exemplify the integration and research methodologies developed by the teams, and (c) to examine applications of the system to particular management problems. The capabilities presented represent the essential phases of a management approach rather than an implied total capability. The focus of the proceedings demands a concentration on natural systems. However, as this is only a part of a total methodology, an overview is presented.

3. Results and Discussion

The multidisciplinary team is made up of five basic components:

Basic Components	Primary Function
Socioeconomic	The socioeconomic analysis must be capable of making base-line and conditional forecasts of aggregate regional activity in terms of population and employment.
Land allocation	The land-allocation analysis must be able to spatially allocate the predictions of land-use changes.
Sociopolitical/ policy	The sociopolitical/policy analysis must develop management strategies in response to fiscal impact and public reaction.
Natural systems	The natural-systems analysis must be capable of predicting the effects of patterns of change on the regional natural environment.

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Cultural systems The cultural-systems analysis must be able to predict the consequence of alternatives to man, his welfare, and institutions.

Further subdivision of each team is possible based upon the region being studied and the processes that take place within the region.

Various types of research methodologies are needed to provide the capabilities outlined above. These include:

(1) data collection, which includes data measurement (e.g., remote sensing) and data capture (digitization and inputting into an information system);
(2) data storage, retrieval, and manipulation, which may be sufficient to solve some of the regional analyst's problems without using complicated simulation models and statistical techniques;
(3) statistical analysis techniques such as regression, factor, and cluster analyses;
(4) analytical models, which traditionally are used by science in attempting to solve problems by understanding and describing in mathematical form the basic processes that are taking place;
(5) optimization models, which attempt to find the best solution to a given problem, subject to the user's criteria and constraints;
(6) simulation models, which predict or simulate a series of activities that take place over time.

The East Tennessee Development District (ETDD) was chosen as a study region (Figure 1). It is a 7,000-square-mile portion of eastern Tennessee, U.S.A., and encompasses 16 counties centered around the city of Knoxville. The area was chosen because of the diversity of the region in both cultural and natural systems. It contains approximately 700,000 people, with a slowly increasing population. The area is in the greater Appalachian range including the Cumberland Plateau on the west, the ridge and valley province in the center, and the Great Smoky Mountains on the east. To an extent the region dictates the management approach (Voelker et al., 1974).

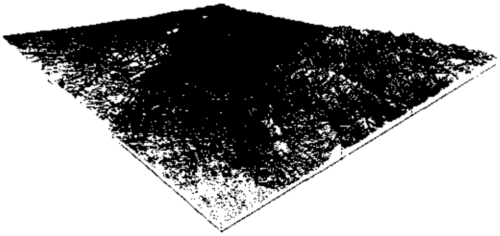

Figure 1. Computer Generated Three Dimensional Relief of East Tennessee

The results presented in this section come from a flow of analyses, beginning with economic projections for the ETDD region and progressing through the land-allocation process to a consideration of natural system effects. In many cases, cumulative effects elicit response from various agencies and interest groups which may result in policy changes. By understanding analyses such as these, the decision maker is better prepared to develop and implement total management strategies.

Economic projections are created by disaggregating national forecasts of population and employment into functional economic areas of the United States. This disaggregation is accomplished by determining the relative "attractiveness" of each area in terms of measures such as market accessibility, labor conditions, natural and amenity resource availability, and financial resources and subsidies. The analysis provides "regional export employment" data that are then combined with demographic, labor participation, and locally oriented employment analyses to predict changes in population, labor force, types of employment, and unemployment rate. These predictions are subdivided into specific standard industrial classifications (SIC) such as retail services, chemical industries, and recreation services (Olsen et al., 1974).

These activities are spatially allocated in a two-step process. First to subregions within ETDD and then to cells within each subregion. The model (Meyers et al., 1972) allocates industries initially and then associated land uses (residential, recreational, etc.). The subregional allocation is based on the construction of indices that describe subregional characteristics such as labor force skill and availability, proximity to support services and supplies, transportation availability, and land availability. These indices are combined with suitable weights to construct attractiveness scores for each type of industry for each subregion. The cell assignment is made in a similar manner, except that different indices and weights are used to reflect the change in scale.

The types of employment, the number of employees, the spatial location, and the associated development can be predicted at this point for any area within ETDD. This prediction gives a decision maker/manager a base line from which specific alternatives can be examined in terms of the effects to the natural system and of the resultant policy questions. Because of the length restrictions on this paper, only a few examples can be presented. As a hypothetical flow of alternatives, the following questions might be asked by a decision maker interested in the ETDD region.

(1) Given predicted increases in employment and urbanization, what will be the landscape pattern over the next 15 years?
(2) Given the landscape pattern change, what would be the effect on privately owned woodlots of increased forest harvesting by the Tennessee Valley Authority (TVA)?
(3) If TVA harvests a large number of woodlots and private land owners harvest their own land due to economic pressure, could this affect water quality of the streams in the area?
(4) If water quality of the streams in the area is affected, would biota of the reservoirs of the area be affected?
(5) If reservoir quality is changed, how will various regional publics react through the political system?

For the purpose of display, the area selected is only a portion of the total ETDD area. Land-use change, categorized as urban build-up and residential, is simulated over time by the land-allocation model as described above. A land-cover model recognizes the following vegetative communities: (1) hardwoods, (2) pine hardwoods, (3) pines, (4) cedar hardwoods, and (5) old fields. The model simulates the natural successional changes by considering categories of land cover as states in finite Markov chains.

As the simulation proceeds, the land-allocation model overrides the natural change in some cells with man-induced perturbations. This causes the land-cover model to project changes into neighboring cells where applicable, thus creating a new vegetative pattern in the natural system. Figure 2 shows the 1987 land-use distribution as predicted by both land-allocation and land-cover models. Figures 3, 4, 5, and 6 illustrate the changes from 1940 to 1987 of two categories of land cover. Figures 3 and 4 illustrate the increase in hardwoods from 1940 to 1987; Figures 5 and 6 display the decrease in old fields for the same period.

The following summation gives the predicted change in the five natural land covers over the 47-year period:

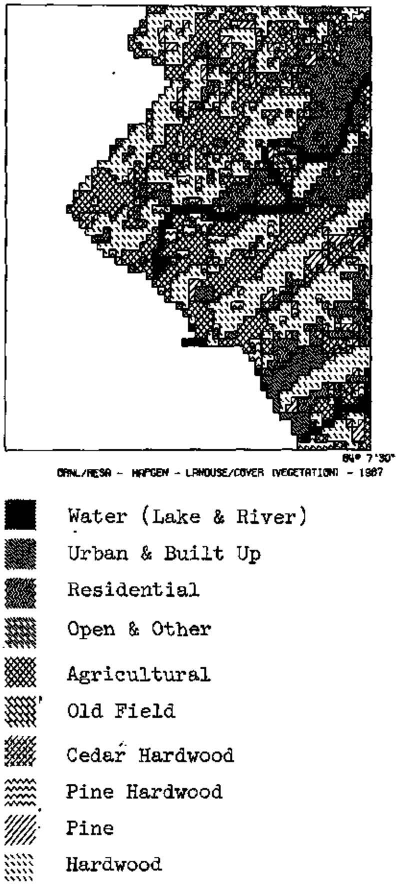

Figure 2. Computer Map Showing Predicted 1987 Land Cover.

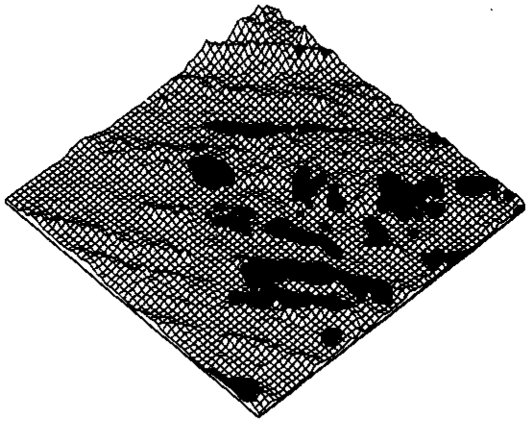

Figure 3. Computer Plot of Forest Cover (1940 Hardwoods) Superimposed on Relief Map

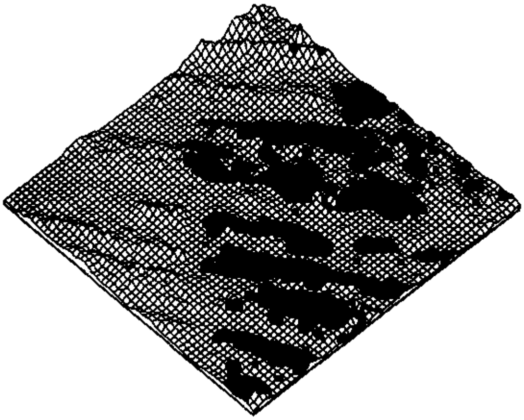

Figure 4. Computer Plot of Forest Cover (1987 Hardwoods) Superimposed on Relief Map

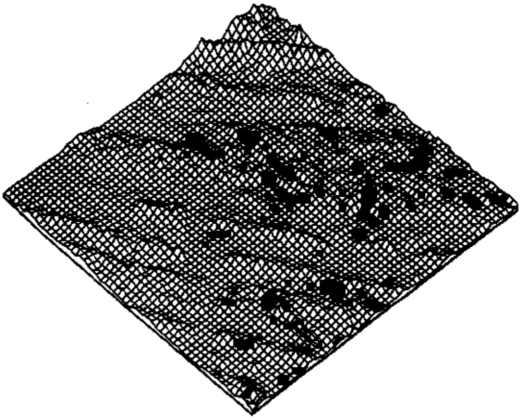

Figure 5. Computer Plot of Land Cover (1940 Old Fields) Superimposed on Relief Map

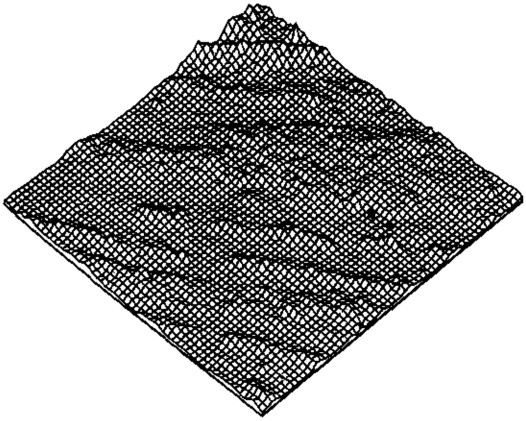

Figure 6. Computer Plot of Land Cover (1987 Old Fields) Superimposed on Relief Map

	Hard-woods	Pine hardwoods	Pines	Cedar hardwoods	Old fields
1940	417	563	0	21	209
1972	772	78	119	15	21
1987	738	85	87	10	2

Note: The figures above are the number of 10-acre cells in each category.

Inferences can be made on vegetation and wildlife states from dynamic land-cover patterns. Indices of diversity, biomass dynamics, productivity, and stability can also be applied to different management strategies. The change of patterns over such a period (30 years historical, 15 years simulated) is the sort of information that should be brought to the attention of decision makers in assessing what type of landscape is desired. Obviously, the composition of the example area is greatly affected by changes in both cultural and natural systems.

Large TVA land holdings lie north of the example area presented above. The second question concerns optimizing the area of prime forest harvesting. Decision makers can be helped by knowledge of the amount of land owned by TVA in this area and where profitable forest harvesting could take place. Figure 7 is an example of a composite map created from forest cover type, stand size, volume/acre, and slope along Norris Lake. This map may be used to determine sites suitable for harvesting medium to heavy hardwood sawtimber. The cells on the map are 2.68 acres. Forest stands in categories 1 and 2 could be harvested using conventional techniques; category-3 stands would require special techniques such as uphill skidding; due to soil erodability, stands in categories 4 and 5 would require buffer strips before harvesting to help prevent runoff into streams.

The third question addressed the effect on water quality of increased forest cutting. Regional water-transport modeling by TVA (1972, 1973, 1974a, 1974b) can be used for both water-control management and prediction of changes in water quality caused by practices such as increased forest harvesting. A continuous streamflow model using stochastically generated rainfall and geologic data as input has been used to predict selected water-quality constituents (total dissolved solids, NO_3, etc.) and to model the transport of such constituents. Use of this model has made possible predictions of the effect of forest cutting on streamflow and water quality. Figure 8 shows representative simulated and observed results of the effect of cutting on streamflow.

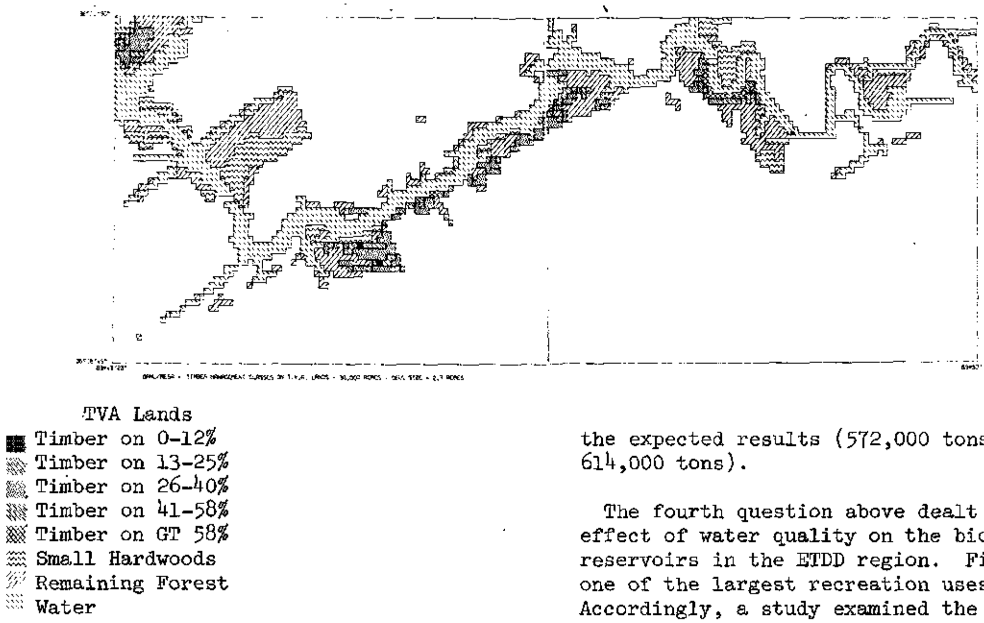

Figure 7. Computer Map of Timber Management Classes

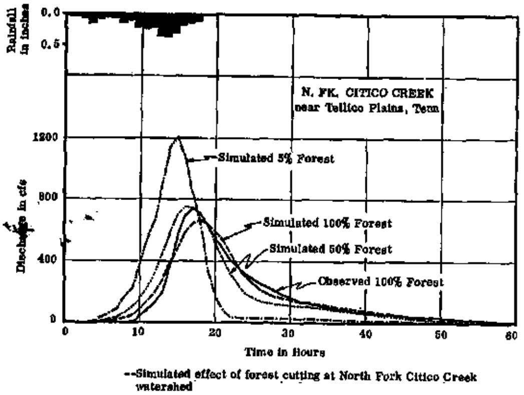

Figure 8. Effect of Forest Cutting on Streamflow

To further test the nonpoint source water-quality model, a simulation of total dissolved solids (TDS) transport was conducted for the Melton Hill Reservoir in the ETDD region. The test was not expected to be decisive because (1) the model was calibrated for only one major watershed in the drainage area, (2) only a limited number of water-quality samples were taken below the reservoir for verification, and (3) much of the TDS originates upstream at the Norris Dam Reservoir. However, by adjusting the model to account for the larger drainage area, the simulated results were close to the expected results (572,000 tons versus 614,000 tons).

The fourth question above dealt with the effect of water quality on the biota of the reservoirs in the ETDD region. Fishing is one of the largest recreation uses. Accordingly, a study examined the influences of environmental factors on the standing crops of fish in Tennessee reservoirs. Environmental parameters such as mean depth, water level fluctuation, shoreline development, total dissolved solids, and growing season were included in the study. Total standing crop of fish was considered in addition to standing crop disaggregated by species. Total dissolved solids and mean depth were found to be two of the most significant variables in explaining differences in biological productivity among the TVA reservoirs (TVA, 1974c).

Although the analyses presented here (economic projections, landscape patterns, forest harvesting, water quality, and biotic patterns) are hypotheses, they raise various types of policy questions that serve as feedback to the socioeconomic, land-allocation, and sociopolitical components of the multidisciplinary analysis. From this feedback information, alternative policies and management strategies are developed and cycled through the decision system. For example, the fifth question bove related to the response of agencies and interest groups to the aesthetic and water-quality changes induced by the TVA forest-management scheme. The initiation of increased cutting may precipitate a conflict situation in which numerous regional interest groups would place divergent demands on the resource base. Thus while wilderness preservation groups may oppose a management scheme because of its impact on the aesthetic or natural quality of a region, local commerce groups may support it for the resultant benefits to the regional economy.

These divergent viewpoints are reflected in the regional political system. If a powerful coalition of opponents to the management scheme can develop, the scheme may well be deleted from the list of feasible alternatives. If this happens, the manager has lost valuable planning time and resources due to a lack of consideration of the political realities of an issue. Thus, managers must explicitly consider interest group variables in their analyses. In the approach documented in this paper, a political interaction simulation program (PISP) (Bulkley, 1970) is used to forecast political feasibility of various management options. In the harvest strategy case, the PISP analysis indicated that clearcutting would be an unacceptable approach in a number of areas in the region. This negative result forces the manager/planner to search for additional alternatives or conflict-mitigating measures. One such measure for the harvest issue may be to guarantee the inclusion of untouched buffer zones at points of visual access to the management area. The inclusion of such zones raises further questions that must be addressed by natural-system, socioeconomic, land-allocation, and additional sociopolitical analyses. Thus, the policy-analysis segment of the pproach is a feedback mechanism to the multidisciplinary component teams.

It is through the iterative, interactive, and interdisciplinary nature of the Regional Environmental Systems Analysis approach that the objectives of regional analysis - forecasting, evaluation, optimization, and information - are met.

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DEVELOPMENT OF STRATEGIES FOR MANAGEMENT OF MARINE AND ESTUARINE SANCTUARIES IN THE UNITED STATES OF AMERICA.[1]

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Summary

In 1972 the Congress of the United States of America passed two laws relating to sanctuaries. The Coastal Zone Management Act contained a provision for establishing estuarine sanctuaries which would be natural field laboratories for study of natural and human processes in the Coastal Zone. The Marine Protection, Research, and Sanctuaries Act contained provisions for establishing marine sanctuaries for preserving or restoring areas for conservation, recreational, ecological or esthetic values in the region from the edge of the continental shelf landward to as far as the tide ebbs and flows and in the Great Lakes.

For the purpose of establishing a management policy for both marine and estuarine sanctuaries, a series of sanctuary purposes was envisioned. These purposes were habitat preserves, species preserves, research areas and recreational/esthetic preserves. Each sanctuary unit would have its management plan oriented around one or more of the primary purposes. This paper considers sanctuary management strategy in context with existing state, federal and private sanctuary programs.

The management strategy which permits the maximum number of non-destructive compatible uses is recommended for all but a research area designated for manipulative research.

Introduction

During the late 1960's events such as the Santa Barbara oil spill, the Torry Canyon disaster, controversy over dumping of toxic wastes in ocean waters, and an increasing public awareness of the necessity, productivity and fragility of the nation's estuaries and coastal areas spawned a series of major federal, state and private studies related to the development, utilization and preservation of marine and estuarine ecosystems (see Laird & Patton, 1974).

General conclusions arrived at by these studies were that certain activities had the potential of being detrimental to the marine environment and therefore required close regulation; wide data gaps existed in our present knowledge of marine and estuarine ecosystems; some form of coastal zone management was imperative; and that some areas needed a degree of protection over and above that afforded by routine regulation of activities.

The result of these events and intense activity was two major pieces of legislation enacted by the 92nd Congress in 1972. The Coastal Zone Management Act (Public Law 92-583) established a program of development and management grants to encourage the coastal states to exercise their full authority over the resources of the coastal zone through comprehensive state Coastal Zone Management plans. In addition, the Act authorizes the Secretary of Commerce to make grants available to the Coastal States:

> "....of up to 50 percentum of the costs of acquisition, development, and operation of estuarine sanctuaries...."

Under the Act an estuarine sanctuary is defined as:

> "[A] research area which may include any part or all of an estuary, adjoining transitional areas, and adjacent uplands, constituting to the extent feasible a natural unit, set aside to provide scientists and students the opportunity to examine over a period of time the ecological relationships within the area."

In this legislation the term estuary is defined to include estuary-type areas of the Great Lakes. For purposes of Coastal Zone Management planning, the Great Lakes states are considered to be coastal states.

The Marine Protection, Research and Sanctuaries Act (P.L. 92-532) consists of three titles:

I. Ocean Dumping
II. Comprehensive Research on Ocean Dumping
III. Marine Sanctuaries.

Title III provides that the Secretary of Commerce, after consultation with heads of appropriate Federal agencies and with the approval of the President, may designate as marine sanctuaries:

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[1] Contribution No. 606 of the Virginia Institute of Marine Science.

> "[T]hose areas of the ocean waters, as far seaward as the edge of the continental shelf, as defined in the Convention on the Continental Shelf (15 U.S.T. 74; TIAS 5578), of other coastal waters where the tide ebbs and flows, or of the Great Lakes and their connecting waters, which he determines necessary for the purpose of preserving or restoring such areas for their consideration, recreational, ecological, or esthetic values."

Where the proposed sanctuary would lie within the territorial or seaward boundaries of a state, as defined by the Submerged Lands Act of 1953, the Secretary is required to consult with and consider the views of the responsible officials of the State involved. A designated sanctuary becomes effective within 60 days after publication unless the Governor of the state involved declares the sanctuary or any portion of it unacceptable. The state may subsequently withdraw its objection in which case the designation, if still pending, will become effective immediately. The intent of this provision is to protect State title ownership in lands beneath navigable waters and within their seaward boundaries.

When the area of the proposed sanctuary is outside of U. S. territorial jurisdiction, the Secretary of State is directed to take appropriate action to obtain those international agreements which may be necessary to protect the purposes of any sanctuary which includes waters lying outside the contiguous zone.

Existing programs

Although no national designated programs of marine and estuarine sanctuaries existed in the U.S.A. prior to enactment of these two laws, there were a number of Federal, State and Local programs which contained elements closely related to preservation of marine and coastal areas (Lynch, et al, 1974). The major federal programs are the National Park System which contains some 49 coastal units classified as natural, recreational or historic areas, and the National Refuge System which contains many large areas of coastal wetlands managed primarily for waterfowl production. Although both these programs have significant coastal holdings including aquatic areas, the major management strategies have been land oriented. Two marine areas have been given specific recognition and protection from mineral exploitation activities, the Key Largo Coral Reef Preserve in Florida and the Santa Barbara Ecological Preserve and Buffer Zone in the waters off California. The Key Largo Coral Reef Preserve is actively managed for recreation by the state of Florida in conjunction with adjacent John Pennekamp Coral Reef State Park but management of the Santa Barbara area for the present is limited to non-leasing of oil and gas drilling rights.

A few states have enacted specific marine or estuarine sanctuary laws. These state coastal sanctuaries fall into six general categories. These categories, however, are not mutually exclusive in that a given sanctuary or regulated area, other categories may occur to a greater or lesser extent.

1. Recreational areas: Florida's John Pennekamp Coral Reef State Park.
2. Natural areas: Hawaii's Natural Areas Reserves and Marine Life Conservation Districts.
3. Esthetic areas: Some of Florida's Aquatic Preserves.
4. Scientific areas: Wisconsin's Scientific Areas; Some of Florida's Aquatic Preserves.
5. Species preserves: State Waterfowl Refuges; Virginia's Blue Crab Sanctuary.
6. Multiple-use management areas: California's oil sanctuaries; Massachusetts' Ocean Sanctuaries.

Within the private sector, two groups have substantial acquisition and preservation programs: The National Audubon Society and the Nature Conservancy. The Audubon Society manages or owns just under 30 coastal areas. The Nature Conservancy has just recently begun an active island and coastal acquisition program and now is developing a management plan for a substantial area of wetlands and barrier islands off the mainland of Virginia.

Although not formally included in the marine and estuarine sanctuary programs, the presence of these Federal, State and Local areas can be considered in overall sanctuary program design and management strategy, particularly in view of funding limitations within the programs and the extremely high cost of coastal lands.

Classification

Four major classification or sanctuary types appear suitable for establishing management strategies; habitat preserves which are established for the purpose of preservation, protection and management of essential or specialized habitats utilized by rare or endangered animal species or representative habitats of outstanding quality; species preserves which are intended to conserve genetic resources; research areas established for scientific research and education of both a manipulative and an observational nature;and recreational and esthetic areas established primarily to provide for public enjoyment.

Management strategies

Management strategies must be developed to fit each specific sanctuary unit. No set of management regulations will cover the diverse habitats found within marine and coastal areas. Certain general approaches may, however, be established for each sanctuary "type." Management options for habitat preserves usually will involve total preservation or severe restriction in use. It is generally agreed that the quantity and type of public access must be limited and controlled much as with wilderness areas. Constraints on species preserves, however, probably need not be as severe as with habitat preserves. The management strategy should be flexible enough to adequately protect the target species during particularly vulnerable portions of the life cycle such as spawning. An orientation towards species preservation might entail protection of migratory pathways, spawning grounds, nursery grounds, etc. which might be separated in time and space, adding another dimension to the management considerations for this type sanctuary.

Development of management strategies for research areas pose a major conflict between two conflicting concepts of research areas, that of a research natural area in which research and educational activities are restricted to essentially non-destructive observation and data collection and that of a field laboratory area which may be subject to manipulation ranging from removal of species to possible severe modification to study impacts of stress and/or restoration processes. A consensus is difficult to reach even among scientists as to degree to which manipulative studies should be sanctioned, particularly in fragile coastal areas which are under stress from many sources other than science. I personally advocate the establishment of manipulative areas in which specific problems of concern to coastal area managers may be studied under carefully controlled conditions.

Recreational area management strategies again may differ widely. A management plan emphasizing maximum recreational use of shore and aquatic areas will differ in almost all respects with a plan to protect the recreational pleasures associated with a wilderness type experience. Experience with attempting to manage National Sea Shores, which are specifically designated as recreational areas has proven that increasing recreational opportunities without very careful safeguards frequently creates situations that destroy or severely damage the attributes of the area which initially made it desirable for recreation. A prime example of this is the ecological havoc which can be caused by off road vehicles transporting people away from clutter of civilization.

It is unlikely that any given area, particularly if extensive, will be managed for only one purpose. As is true of presently established protected areas, some form of multiple-use management strategy will probably be developed. With the primary purpose of a given sanctuary area as the focus, conflict matrices should be developed indicating degree of compatibility between existing or projected uses and the primary purpose of the sanctuary. Where possible, a management strategy which permits the maximum number of non-destructive, compatible uses should be developed. The only sanctuary purpose for which this approach will probably not be pertinent is that of a manipulative research area. The specific management problems which will arise at each sanctuary site will be compounded by the inability to isolate, to any degree of effectiveness, that specific site from either upland influence and/or adjacent aquatic areas. The Estuarine Sanctuary provision of the Coastal Zone Management Act does recognize this in that a provision is made for purchase of adjacent uplands. No such provision is clearly stated in the Marine Sanctuary legislation. Consideration of establishing coastal sanctuaries adjacent to protected upland areas may help alleviate this problem. This consideration will also assist managers of protected upland areas with their problems of maintaining high quality adjacent waters.

Conclusion

The management of marine and estuarine sanctuaries will not be an easy task. In addition to the problems associated with preservation or protection of any area will be the ever present problem of exchange between adjacent aquatic areas or subsystems. The management strategy can be made much easier by an establishment strategy which considered such factors.

Coastal ecosystems and subsystems are often very fragile entities, and these areas are receiving increasing stresses from our expanding uses of the coastal zone. In order to maintain the attributes of this region which make it so desirable, effective management must come. Within the overall management plan for coastal areas, there is a definite need for certain areas to receive the added protection of sanctuary status both to preserve for posterity that which we value and to enable us to gain insight with regard to better management for lesser protected areas.

Acknowledgements

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ECOLOGICAL LAND SURVEY, THE BIO-PHYSICAL BASIS OF LAND-USE PLANNING. THE SAGUENAY-LAC-SAING-JEAN REGION, QUEBEC

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Summary

Population increase and economic growth demand maximum utilization of renewable resources. Also, developing a better environment is becoming a goal which must be achieved at all levels of land management policies. Integrated resource management cannot be done without an integrated knowledge of the resources of the land.

This paper describes a methodology of ecological survey developed in Quebec, Canada aiming at providing the land planners and land managers with data on the potential productions of the renewable resources and interactions between the various uses of the land. The method has been tested in the Saguenay-Lac-Saint-Jean pilot area and is now successfully applied operationally in the James Bay region, an area totalling 328.000 square kilometers.

Introduction

The ecological survey: a tool for land planners and land managers. Unless that goal is clearly realized, an ecological survey is doomed to be considered as an interesting academic exercise. It is not an easy task to translate the scientific jargon of soil scientists, ecologists and geomorphologists into practical terms useful for practicioners. Yet, so many uses of the land resources are limited by the bio-physical or ecological characteristics of the land itself that there is a need for differentiating and classifying ecologically significant segments of the land surface to serve as the ecological basis for land-use planning and environmental management.

This study attempts to illustrate the kind of information obtained by an ecological survey of an area of 23.000 square kilometers in Quebec (Canada) which has been completed in 1972 by a multidisciplinary team. (Jurdant et al. 1972). The methodology is now applied operationally in the James Bay region, northern Quebec, an area totalling 328.000 square kilometers.

General description of the area

The Saguenay-Lac-Saint-Jean region is located between latitudes North 48°00' and 49°15' and longitudes West 69°30' and 70°00'. It is characterized by a huge oval depression, called the Saguenay-Lac-Saint-Jean Lowlands, surrounded by the Precambrian Shield, or the Laurentides Highlands. The center of the depression is occupied by a lake whose diameter is about 50 kilometers and is connected with the St. Lawrence River by the deeply incised Saguenay fjord.

The bedrock geology is dominated by the Precambrian crystalline rocks except in two small areas of the lowlands which are underlaid by sedimentary Paleozoic rocks. The depression is filled with quaternary sediments of glacial, fluvio-glacial, deltaic, and marine origin. Most of the Precambrian Highlands are covered by glacial and fluvio-glacial sediments.

The relief of the Laurentides Highlands is hilly although some parts are mountainous and others are rolling; elevation varies between 180 and 900 meters. The topography of the Lowlands is undulating with a variation of elevation between 100 and 180 meters but, locally, the relief is broken by dune fields, fluvio-glacial hills, deeply incised terraces and rock outcrops.

The climate of the region belongs to the type Dfb of Koppen (1936): humid continental with cold summer and without dry season. The mean annual precipitation varies between 600 mm. in the Lowland to 1500 mm. at the highest elevations in the Highlands. The mean annual air temperature varies between 32 and 37°F. The growing season is short: the frost free period varies from 125 days in the plain to 90 days in the Highlands.

The complexity of the landforms causes a wide variation of the soils in the region. Ferro-Humic Podzol and Humo-Ferric Podzol (C.D.A., 1970) are the main soil Sub-Groups on well drained sandy loam materials. An Acid Brown Wooded soil develops on fine textured materials. The poorly drained soils belong generally to the Gleyed Humic Podzol Sub-Group on coarse textured materials and to the Humic Gley Sub-Group on fine textured materials.

The natural vegetation has been subjected to severe disturbances by fire and cultivation, particularly in the lowlands. It is practically impossible to assess objectively the nature of the climatic vegetation in the Lac-Saint-Jean lowlands, but it seems that balsam fir-yellow birch forests, containing a certain amount of white pine, did cover much larger areas than today. On the plain, jack pine, aspen, balsam fir and, black spruce are the most important species but the relatively favourable climatic conditions are expressed by the occurrence of yellow birch, white pine, sugar maple, red pine, american elm, and basswood. In the Laurentides Highlands, the major tree species are balsam fir and black spruce associated with white spruce and white birch; aspen and jack pine are abundant in the driest areas where fires have been frequent, particularly in the western part of the region.

Discovered in 1647 the region was open to agriculture only in 1871. The demographic evolution of the region is as follows:

year	population
1850	5.000
1870	17.000
1890	28.000
1910	50.000
1930	106.000
1950	198.000
1960	262.000
1966	268.000

Today, almost two thirds of the total population live in the vicinity of Chicoutimi-Jonquière, a heavily industrialized area. The economy of the region is based on the use of its natural resources: agriculture, forest, wildlife, mines, water, and landscapes.

Concepts

Land produces trees, agricultural crops, water, wildlife and aesthetic or recreational values. All these renewable resources of the land interact or compete in such a way that man can direct their productions according to his needs. Yet, both the productivity of these land resources and their interactions vary in space and in time depending on the biological and physical characteristics of the land itself. A comprehensive quantitative and geographic knowledge of the bio-physical characteristics of the land is therefore a prerequisite to land planning and management.

Such a knowledge has been obtained in the Saguenay-Lac-Saint-Jean region by means of an ecological survey which involves the description, classification and mapping of the bio-physical land characteristics as well as the interpretations of these bio-physical properties which are useful for the management of forestry, agriculture, recreation, wildlife and water yields.

In order to accomplish this inventory quickly and at low cost, a survey method has been developed whereby most of the mapping has been done by using aerial photographs.

Various concepts have influenced the methodology used in this survey. The Australian system (Christian, 1952, Christian et al., 1968; Christian and Stewart, 1962, 1968) and the Ontario system (Hills, 1960, 1961) can both claim parental rights, but the influence of many other workers is also evident, among these are the soil scientists of the Canadian Soil Survey Committee (C.D.A., 1970) and Rowe's concepts on ecosystems (Rowe, 1962). The method conforms also to the Canadian viewpoint on bio-physical land classification expressed by the leaders of various pilot studies conducted in different Canadian environments (Jurdant et al., 1974).

Method

The survey team consisted of five professionals and four techniciens; the professionals involved were: one ecologist, one geomorphologist, one phytosociologist, one soil scientist and one forester. Emphasis was always placed on the ecological whole rather than on the parts of the ecosystem components. At all phases of the survey, there had been a continuous exchange between the five specialists, whose individual contribution was centered around that one goal; the identification of the key land parameters of biological production and the delineation of their spatial and temporal distribution. Too often, so-called multidisciplinary land survey teams are created which are merely groups of scientists working parallely providing sectorial information with limited use to the ecologists who try to assemble the parts into an integrated land map; the limited use of the soil survey maps to the forestry sector is a clear example of the problem involved here.

Man has the natural tendency to group into organized units or cells which engender various government levels. In Canada one could distinguish five levels corresponding to five types of communities, i.e.:

(1) the family
(2) the municipality
(3) the region
(4) the province
(5) the country

Each of these socio-economic communities has its requirements for land planning and management. Also each corresponding territory is directly proportional to the size of the community; the basic land ecosystem is therefore smaller for a family than for a municipality and so on.

A hierarchical system is therefore needed which permits a choice of the degree of detail required to meet the purpose of a particular survey. The following five levels of ecological integration have been used:

(1) The Land Region: an area of land characterized by a distinctive regional climate as expressed by vegetation. The mapping scale is 1:1.000.000 and the average size of mapping unit is 600 square kilometers. Regional vegetation and physiographic pattern are the major differentiating mapping characteristics. Twelve Land Regions have been mapped in the surveyed area.

(2) The Land District: an area of land characterized by a distinctive pattern of relief, geology, geomorphology and associated regional vegetation. This is the level which corresponds most closely with the notion of "pays" or "terroir", or "landscape". The mapping scale is 1:250.000 and the average size of the mapping unit is 40 square kilometers.

(3) The Land System: an area of land throughout which there is a recurring pattern of landforms, soils, vegetation chronosequences, and water bodies. The mapping scale is 1:125.000 and the average size of the mapping unit is 10 square kilometers.

(4) The Land Type: an area of land having a fairly homogeneous combination of soil (e.g. Soil Series), and chronosequence of vegetation. The mapping scale is 1:200.000 and the average size of the mapping unit is 25 hectares.

(5) The Land Phase: an area of land characterized by a fairly homogeneous combination of soil and vegetation. The mapping scale is 1:10.000 and the average size of the mapping unit is 5 hectares.

The basic ecological classification was derived from an a priori integration of the knowledge on vegetation, geology, geomorphology, soils and climate obtained during four years of field and laboratory work. The classification and mapping of landforms on aerial photographs were used as the framework for a stratified sampling of 632 bench-mark ecosystems. These were selected to cover the full range of ecological conditions existing in the region. The descriptive and analytical date on soils and vegetation of these 632 bench-mark ecosystems are the basis of the classification of the Land Phases and of the Land Types.

The Land Type is the basic cell of the ecological classification; it is established on the basis of similarity in both soil and vegetation. They can be readily mapped by using large scale aerial photographs since their boundaries follow major changes in vegetation composition and/or physiography. However mapping large areas at that level is time consuming and expensive.

The survey methodology developed was designed to be applicable to large, unsettled areas for which only scanty information is available. A mapping scale of 1:125.000 seemed desirable to cover the 23.000 square kilometers area in a reasonable period of time. Land Types cannot be used at that scale. Yet the boundaries must bear ecological significance. The most convenient unit is therefore the Land System which is a distinctive and recurring pattern of Land Types.

The mapping of the Land Systems was done on aerial photographs at the scale of 1:40.000 by the multidisciplinary team. Each Land System is identified by means of symbols which express:

- a uniform regional climate,
- a characteristic relief,
- a characteristic pattern of landforms,
- a characteristic pattern of soils,
- a characteristic pattern of vegetation chronosequences,
- a characteristic pattern of aquatic ecosystems.

Interpretation for environmental management

The data collected in the course of the survey was used to evaluate the potential biological production of each mapping unit for the purpose of regional integrated resource management.

The following evaluations and interpretations were achieved.

(1) Agriculture:
  - potential production in 7 classes
  - land suitability for various crops
  - surface erosion potential

(2) Forestry:
  - potential production in 7 classes
  - timber potential production in cu. ft./acre/year
  - land suitability for various species
  - plantation difficulty
  - establishment cost of plantations in dollars per unit area
  - production cost of plantations in dollars per unit volume
  - windthrow hazards
  - natural regeneration hazards
  - trafficability
  - plant competition following harvesting
  - plant competition following fire

(3) Recreation:
  - land capability for recreation in 7 classes
  - recreation potential of water bodies
  - landscape attractiveness
  - land suitability for various recreational uses such as:
    - intensive camping and picnic sites
    - recommended species for aesthetic reforestation

(4) Wildlife:
  - land capability for ungulate wildlife
  - land capability for various plant

species important for wildlife

(5) Water:
  - water holding capacity of soil and land units

(6) Engineering:
  - land suitability for engineering use
  - suitability as source of sand and gravel
  - suitability as source of fill material
  - soil features affecting roads location

(7) Finally the level of management integration requirement within each mapping unit has been assessed, which gives the land manager information on the compatibility and complementarity of the various possible uses.

Practical applications

From the knowledge of the ecological relationships between the landscape components and the dynamics of the natural renewable resources of the studied area, the following practical application can be foreseen:

(1) The integrated zoning of the land;
(2) The delineation of the areas suited for intensive agricultural, forest, wildlife or recreational management;
(3) The determination of the land suitability for various uses;
(4) The planning of commercial and aesthetic reforestation programs;
(5) The assessment of the regional ecological problems requiring particular attention by the managers or the research institutions;
(6) The determination of areas best suited for public infrastructures such as roads, railways, power lines, pipe lines, airports, hydro-electric reservoirs etc...
(7) The determination of areas to be protected by virtue of their ecological value, uniqueness, or fragility;

Conclusion

Many soil surveys, vegetation surveys and ecological surveys have been undertaken in the past but very few of these have been used pratically by the land planners and managers. One must recognize that scientists did not bother to translate their scientific jargon into comprehensible terms for the practionner. The ecological survey methodology developed here is attempted to fill a gap. Let's hope that it will facilitate the advent of true ecological land use planning.

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MANAGEMENT OF MAN-MADE FOREST ECOSYSTEMS WITH SPECIAL REFERENCE TO THE CURRENT SITUATION IN JAPAN AND PROSPECTS FOR THE FUTURE

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Abstract

Management of ecosystems is a human activity to moderate the conflicts between ecology and economy, or to seek compromises between requirements of the laws of flow and turnover in the ecosystems and in the human society. If we were only to respect ecology human society would not survive, and if we were only to think of economy ecosystems would be desolated and, as the result, human society would also go to ruin. The role of management of an ecosystem is to find out optimum relations between the ecosystem and human society, and to keep them within their flexibility. So, in this context, under certain conditions, we may even decide that the best management of a given ecosystem is to do nothing with it.

Compared to other man-made ecosystems, such as agricultural lands, man-made forests occupy land areas for longer periods of time and human interventions are far smaller, and flow and turnover similar to natural ecosystems could be well kept, if properly managed.

In an overpopulated country like Japan, all the flat lands have to be utilized for other purposes like food production and industries, and forest can be found only on steep hillsides in remote countries. Consequently, environmental conditions in most of the forested areas are severe and there are many difficulties in management of forests, expecially from ecological point of view. The typical man-made forests of Japan are of Cryptomeria japonica and Chamaecyparis obtusa which are native conifers and of high timber values. Discussion will be limited to the problems in management of man-made forests of these conifers on the Pacific side of Honsyu, the Main Island, because there are quite large differences in climate and, accordingly, in problems between this and the other side, the Japan-Sea side.

In this zone, where most of man-made forests are on steep hillsides, heavy rains brought by typhoons and thunderstorms in the summer sometimes cause landslides, weeds grow vigorously owing to warm and moist summer, and dry and cold north-west wind prevails during most parts of the winter. All these bring difficulties in management of forest ecosystems, expecially in regeneration of them. Though clear-cutting of forests is ecologically undesirable under these circumstances, as shade-tolerance of these tree species are not high enough and weeds grow luxuriantly, adoption of silvicultural systems by use of natural regeneration is hardly practicable. For centuries, commercial forests have been managed as man-made forests regenerated by means of clear-cutting and planting.

In recent years, conversion of natural forests into man-made forests have been accelerated by increased demands of wood, and man-made forests have expanded their territories to remote sites where environmental conditions are not favorable. On the other hand, the rapid industrial growth resulted rapid move of population and, consequently, shortage of labor in forested areas, and so-called modernization of forestry had to be accelerated. Modernization was mainly promoted in harvesting of timber which, so to speak, is a technology of handling weighty materials. The system of manual works used for centuries of harvesting and transportation was changed into another system of mechanized works: hand saw into power saw, manual pre-hauling and skidding into operation with cable-cranes, and floating into truck transport. In the older system the size of clear-cutting affected merely the number of working units but not the size of them, whereas, in the mechanized system, larger areas of clear-cutting mean larger working units and the economic gains. Thus, the size of clear-cut areas inevitably became larger and larger with the progress of mechanization. In addition, to make the rapid recovery of capital invested in road constructions, many, sometimes continuous, clear-cut areas were made.

This recent trend is very hazardous in view of regeneration and maintenance of productivity of forest ecosystems, not to mention forest influences. Ecological problems raised by the large-area clear-cutting and some of trials to solve them are discussed. The only solution seems to be to intensify the degree of freedom in management.

FORMATION OF ECOSYSTEMS IN THE REGULATED PLAIN RIVERS AND FEASIBILITY OF THEIR CONTROL

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Summary

Results of the long-term investigations carried out by the Institute of Hydrobiology AS Ukr.SSR on the Dnieper river are presented. General regularities related to the formation of ecosystems of reservoirs set up on plain rivers have been formulated. The paper contains data on waterbloom resulting from the anthropogeneous eutrophication and disturbance of natural balance in the reservoirs. Measures to control the intensity of waterbloom are proposed.

Introduction

In the European part of the USSR in regulating the flow of plain rivers a number of large reservoirs were created in a short space of time (I950-I970): the Kiev, Kremenchug, Dnieprodzerzhinsk, Zaporozhye, Kakhovka on the Dnieper river, Gorkov, Kuibyshev, Saratov, Volgograd etc. on the Volga river, Tsimlyansk on the Don river. They significantly affect hydrological, hydrochemical and hydrobiological regime of the water bodies.

Results and discussion

Long-term investigations have found out a number of general regularities related to the formation of ecosystems of reservoirs set up on plain rivers. Before the effect of regulation the rivers were characterized by rich bioresources, they contained over one thousand of algae species, several hundreds of invertebrates species, tens of fish species. In the reservoirs the quantity of hydrobionts species in ecosystem is limited by the degree of the variety of abiotic factors and by the number of biotops; the monotony of biotops and abiotic factors limit variety of hydrobionts.

In the process of formation the ecosystems in the reservoirs 2 stages are observed: (1) quality variety and quantity abundance of hydrobionts; (2) progressive decrease of species variety and reduction (to a certain degree) in the abundance of hydrobionts (plankton and benthos). The first stage is stupulated by mixing in the new reservoirs the bioresources of the initial flooded water bodies and those supplied from the tributaries. The mixed bioresources develop on the basis of water mass rich in biogenic and organic matters in coming from the flooded bed and poor in oxygen as a result of its intensive chemical and biological absorbtion.

The second stage is the result of biocenosis formation under conditions of the ecosystem in the given water body on the basis of the changed hydrological and hydrochemical regime. It should be taken into account that duration and specific nature of ecosystem formation in reservoirs of different ecological zones are affected to a considerable extent by the degree of their anthropogeneous eutrophication.

In the river-reservoir system important changes occur in the dominating complexes of planktonic and benthic organisms. The principle factors here are a change of water flow speed and turnover of biogenic elements, a reduction of turbulence and oxygen content in water mass when the river-to-lake regime conversion takes place. In the latter blue-green algae (Aphanizomenon, Microcystis, Anabaena etc.) dominate phytoplankton; Steganopodous and Cladecera dominate zooplankton, larvae ofHyronomidae, Oligichaeta, Dreissena dominate benthos. In reservoirs with shallow area (I8-40% of total area in the Dnieper reservoirs) phytophilic biocenosis-phytocenosis, zoophytous, thicket plankton are diverse and rich.

In large lake-like reservoirs intensive waterbloom of blue-green algae especially increased by the anthropogeneous eutrophication appears in summer. Accumulation of the algae in clusters in creeks and littorals of reservoir promotes biological pollution (selfpollution). The latter deteriorates the water quality and makes biocenosis scanty (if fish and invertebrates kill). Considerable damage caused by the unfavourable waterbloom aftereffects has stipulated the necessity to elaborate measures on an active and purposeful control of this complex biological phenomena, especially intensified by the anthropogeneous eutrophication.

The Institute of Hydrobiology jointly with other institutions has proposed a complex of prophilactic and active measures to control the intensity of waterbloom such as (1) Reduction of the anthropogeneous eutrophication by-passing purified sewage to sewage-farm areas (for example,Bortnichy irragation system); (2) Planting protective coniferous forest-belts along the bank of reservoirs to intercept the local flow of biogenic elements from the drainage basin; (3) Use of water aeration system on local sections in littoral zones, recreational areas at water intakes, creeks, outer harbour; (4) Application of water-air protection of certain parts of water area, beaches, drainage basins; (5) Introduction of phytoplanktophagous fish Hypophthalmychtis molitrix Val. into reservoirs; (6) Melioration of shallow sections with an extensive use of higher aquatic plants (vegetable mass must be removed); (7) Removal of blue-green algae and concomitant organisms and detritus (seston) by hydrochemical methods in zones of their natural accumulation. The removed algae used in national economy. With that end in view seston removal methods have been worked out as well as the method of its separation from water, concentration and production of agriculture fertilizer, manufacture of concentrated amino acids and economical grounds of the measures proposed for their application in a number of the Dnieper reservoirs have been outlined.

An introduction of the measures mentioned above into practice will give the possibility to control the process of the water quality formation in natural waters under conditions of large hydrotechnical construction and intensive anthropogeneous eutrophication.

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B1

Freshwater, brackish and marine ecosystems, their similarities and differences at all trophic levels

PRIMARY PRODUCTION IN THE SEA[1]

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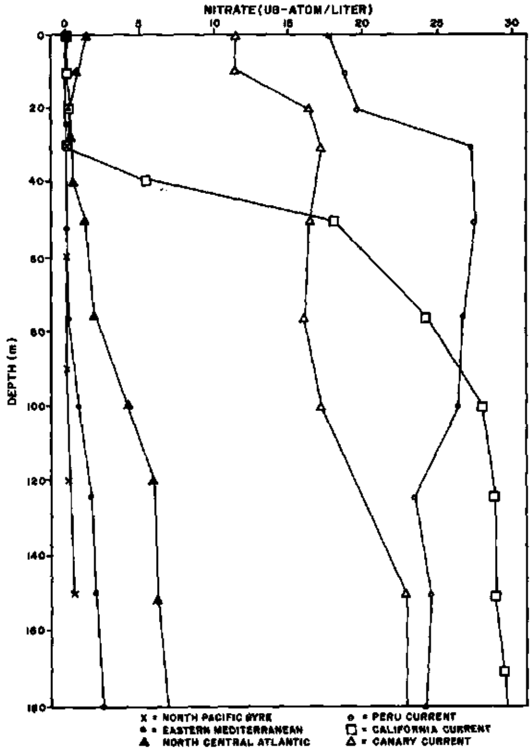
Measurement of primary production in the sea has a long history with initial attempts to estimate photosynthesis with pH in the 1920's (Atkins, 1922); since then, subsequent nutrient utilization, oxygen evolution and ^{14}C, ^{15}N, or ^{29}Si fixation techniques have also been developed, but we are still not accurately assessing the growth of phytoplankton in aquatic systems (McMahon, 1973; Gieskes & van Bennekom, 1973). While methodological problems of incubation time, filter retention, and container size or physiological problems of algal respiration, photo-oxidation, and excretion continue to be fruitful avenues of research, it is perhaps more appropriate at the First International Congress of Ecology to summarize ecological factors that might control primary production. I will further confine myself to phytoplankton based food chains and assume that productivity and biomass estimates are at least of the right order of magnitude (Riley, 1972). An attempt will be made to define in a few pages what we have learned during the IBP years since John Ryther's (1963) synthesis a decade ago, and I will briefly discuss what appear, from our US IBP efforts, to be some of the critical problems yet to be solved. I would like to acknowledge Drs. Ramon Margalef and Achim Minas for providing unpublished data from their cruises off northwest Africa, and Drs. Andrew Bakun and Warren Wooster for the use of Fig. 3.

We are aware, of course, that nutrients, light, temperature, and mixing can be very important in establishing productivity gradients in the sea. Oligotrophic areas of the ocean such as the North Pacific Gyre (30°40'N, 143°09'W), the Eastern Mediterranean (37°51'N, 17°42'E), and the North Central Atlantic (20° 0'N, 22°0'W) have much lower nutrient concentrations in the upper 200 m of the water column (Fig. 1) than eutrophic regions such as the Peru (15°27'S, 75°13'W), California (26° 40'N, 114°02'W), and Canary (16°37'N, 17°58'W) Currents. Despite a deep euphotic zone of 100-125 m in oligotrophic areas, the integrated primary productivity of these regions strongly reflects nutrient limitation with a daily production of 0.1-0.5 gC m^{-2} day^{-1} from a standing stock of 15-30 mg Chl a m^{-2} in the three regions (Eppley et al., 1973; Dept. of Oceanography, 1971; Estrada, in press). In contrast, our IBP expeditions to the above upwelling areas have indicated that intense production of 1-10 gC m^{-2} day^{-1}, involving standing stocks of usually 60-180 mg Chl a m^{-2}, occurs in 20-30 m euphotic zones within 10-20 km of the coast (Walsh, in press; Walsh et al., in press).

Figure 1. A comparison of the vertical nitrate (μg-atom $liter^{-1}$) distribution in oligotrophic and eutrophic regions of the oceans.



The ecological effect of light alone can be best inferred by comparing major upwelling regions with latitude, since previous geographic comparisons, which suggested that sub-tropical

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and boreal regions might be equally productive, involved a combination of both nutrient and light limited regimes (Sheldon et al., 1973; Walsh, 1969; Riley et al., 1949). Little data are available, however, on the seasonal and areal extent of primary productivity of upwelling systems, as quickly pointed out by fishery scientists, objecting to predictions of fish from phytoplankton (Alverson et al., 1970); it thus seemed appropriate to try to predict phytoplankton from fish in determining whether fishery statistics would support physiological evidence that photosynthesis declines at reduced light intensities (Ryther, 1956). The decreasing potential yield of fish (Gulland, 1970) with increasing latitude of upwelling ecosystem (Fig. 2) suggests that light is an important factor in controlling not only primary productivity with latitude (Brylinsky & Mann, 1973) but energy transfer to the higher trophic levels as well; a statistical analysis would be of little value, however, because of the inherent noncausal nature of regression analyses and uncertainty in the data (Walsh, 1971).

Temperature is also an important factor in algal production and the seasonal range of surface values is at least 10°C in upwelling ecosystems (Fig. 3). If the effects of nutrients, light, and mixing could be removed, one might expect a Q_{10} of about 2 (Eppley, 1972) or a twofold increase of production as a result of elevated temperatures, despite increased respiration losses (Packard et al., 1971). Such temperature-induced higher productivity or increased specific growth rate is not observed in the sea (Eppley, 1972), however, and in fact a theoretical maximum diatomaceous biomass of 300-400 mg Chl $\underline{a}$ m^{-2}, on the basis of shelf-shading light extinction (Lorenzen, 1972; Steeman Nielsen, 1962), is rarely encountered in nutrient unlimited, light unlimited tropical upwelling areas.

Figure 2. Latitudinal variation of estimated fish yield (x 10^6 tons) from eastern boundary currents and the Southern Ocean.

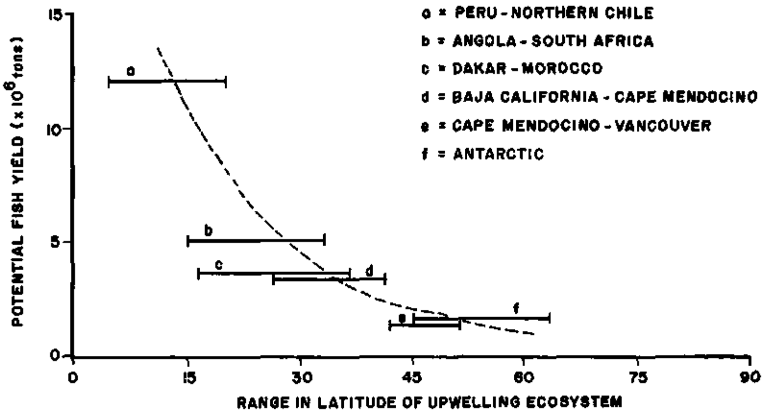
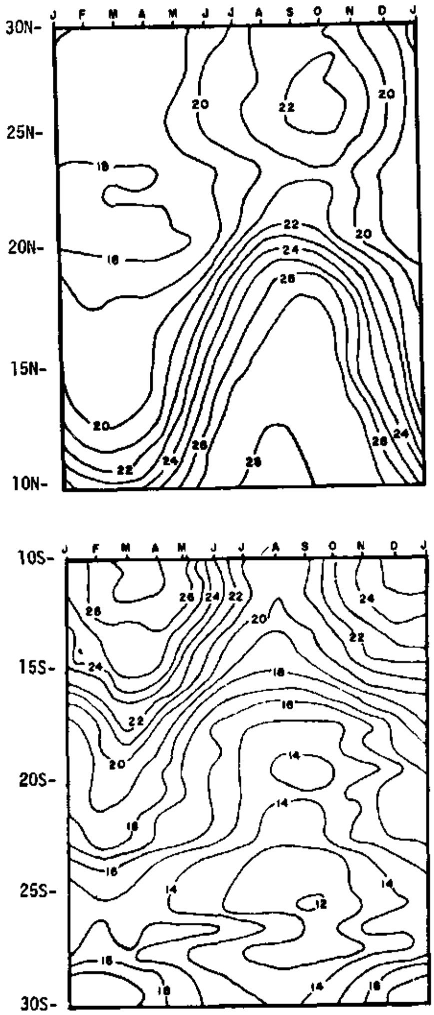


Figure 3. The seasonal range of surface temperature (°C) in one degree squares along the west coast of Africa.

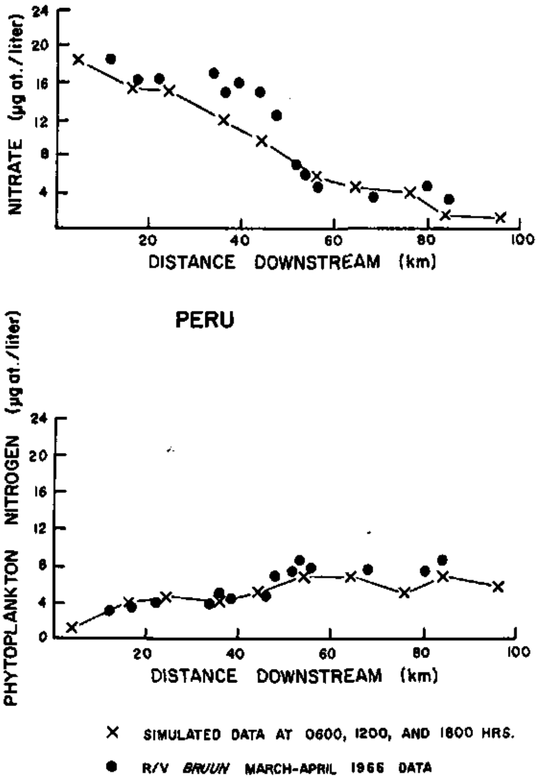


It is possible that grazing losses are sufficiently large to curtail both maximal growth and biomass of phytoplankton (McAllister et al., 1960) but unfortunately still little is known about the quantitative role of herbivore grazing (McAllister, 1970) as a control function of primary production.

Other limitation such as vitamins, chelators or trace metal toxicity (Barber et al., 1971) may explain lower biomass observations of 60-180 mg Chl a m^{-2} in most upwelling systems. Additions of EDTA to dinoflagellate blooms of up to 393 mg Chl a m^{-2} off Baja California, for example, did not increase growth rates (Walsh et al., in press) as was observed in diatom populations off Peru (Barber et al., 1971) with a mean biomass of 67 mg Chl a m^{-2}. The 5:1 particulate C:N ratio of diatomaceous phytoplankton in these systems, however, suggests that incorporation of protein may be occurring at close to a maximal rate (Walsh & Howe, in press) and therefore that losses by physical dispersion are more important in reducing phytoplankton biomass of eutrophic areas. For example, we have been able to incorporate functional relationships of nutrients, light, herbivores, and water circulation to predict the distributions of nitrate, reduced nitrogen, phosphate, silicate, particulate nitrogen, particulate carbon, and detritus over 0-50 m depth and 0-50 km offshore in the Peru upwelling ecosystem (Walsh, in press); the euphotic zone results of this simulation model are in good agreement with observations (Fig. 4) and a simulated increase of advection predicts a low biomass similar to observations of seasonal productivity off Peru (Walsh, in press). Additional correspondence of model and observations has been obtained for the Baja California and Northwest Africa upwelling ecosystems as well.

One of the goals of the International Biological Program was a comparison of productivity in different areas of the world; it appears that we have achieved such a goal for marine systems and the trends are about the same in 1974 as they were in 1963, although observations of higher productivity have been made in local areas of eutrophic systems. The main point of this short communication, then, is not that our impressions of the productivity of the ocean has changed, or that we are unaware of what may be some of its important parameters, but rather that our approach to the understanding of marine productivity has been refined over the last decade. It is not clear, for example, that just ^{14}C measurements taken every day at stations 25 km^2 apart over the whole ocean for a year, would provide any more than a marginal increase in our present knowledge. With the development of vector averaging wind and current meters, autoanalyzers, fluorometers, laser particle counters, acoustic assessment, and sea-going computers for data acquisition and reduction (Walsh, 1972), however we now have sufficient technology to attack questions of spatial and temporal variability of the parameters effecting primary production (Walsh et al., in press) in sufficient "real" time to modify the sampling plan of an oceanographic expedition while actually in the study area.

Figure 4. A comparison of the predicted and observed nitrate (μg-atom $liter^{-1}$) and particulate nitrogen (μg-atom $liter^{-1}$) over 0-10 m in a drogue study of weak upwelling along the Peru coast.



Synoptic data on the concentration and fluxes of a large number of variables allow one to specify the relevance of a single productivity measurement. It was our collective IBP intensive studies of local systems, rather than surveys, for example, that generated comprehensive data sets in space and time, allowing us to construct the above causal models of different ecosystems that reasonably mimic observations. Such tropho-dynamic syntheses are still rather crude, and are mainly concerned with steady state phenomena; but these models have forced us to the realization that understanding of causative factors affecting primary production of the sea and any implied predictability must now await additional studies of transient phenomena at all levels of temporal resolution (i.e., storms, spring overturn, or El Niño phenomena) and their role in controlling food chain structure of the sea.

We still know very little about energy transfer to the higher trophic levels (Ryther, 1969), the role of size fractionation in determining the productivity of each trophic level (Parsons & Takahashi, 1973), and the role of spatial heterogeneity as a stabilizing factor of marine systems in resisting perturbation (Walsh, 1972). A search for an intermediate level of taxonomy such as functional groups, rather than species or trophic levels, may also allow us to answer more detailed questions about the dynamics of marine ecosystems beyond inventory statements of the number of producers or carnivores summarized in a diversity index. Physiological data must thus be placed within an environmental context of temporal and spatial variability in either selected regions of the ocean, or perhaps in big enough bags to simulate most of the properties of a marine ecosystem, before we can begin to hope to advance past rather gross compare and contrast analyses.

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PRIMARY PRODUCTION IN FRESHWATER

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Summary

Annual phytoplankton production was correlated with annual phosphorus income for 47 sites where both measurements were made. Annual nitrogen income, nutrient concentration, and chlorophyll were poorly correlated with phytoplankton production.

The correlation between latitude and phytoplankton production observed by Brylinski (1974) appears to be due only in part to the influence of solar radiation. Latitudinal differences in nutrient input from precipitation, runoff and cultural sources appear to be other factors responsible for the observed correlation.

Introduction

In a recent summary of IBP results Brylinski (1974, also Brylinski & Mann 1973) found that most of the variation in phytoplankton production between IBP sites could be explained by differences in latitude. Nutrient concentrations (phosphorus, nitrogen) were poorly correlated with production. They conclude that latitudinal differences in solar radiation were largely responsible for the observed variation in production.

Other results do not agree with this conclusion. In an independent treatment of IBP freshwater results (using data which only partly overlapped with Brylinski's), Hammer (1974) found little correlation between latitude and production. Also, in studies outside IBP, major effort has been devoted to studies of elevated primary production and standing crop caused by nutrient enrichment (Vollenweider 1968; Edmondson 1969; 1972; Schindler 1974; Vollenweider et al. 1974; Fee 1974; Winberg & Lyaknovich 1965. We shall therefore attempt to offer some insight into possible reasons for these apparently conflicting results.

Light and phytoplankton production

In the two latitudinal extremes included in this analysis, annual light reaching the surface of Char Lake (75°N lat.) was only about 20 percent of that falling on Lake George (0° lat.). Annual surface light reaching Char Lake was reduced by about 50 percent in penetrating ice and snow cover, so that the light available for photosynthesis in these two extreme aquatic environments differs by an order of magnitude (Ganf & Viner 1973; Schindler et al. 1974b). Extreme latitudinal differences in annual production due to light alone should be not greater than this, and are probably less because of the high efficiency with which polar plankton utilize low light intensities (Kalff et al. 1974, Holmgren 1968).

Fee (unpublished data) used a numerical simulation model to estimate the effect of different light conditions on annual phytoplankton production in a series of 8 basins in the Experimental Lakes Area, northwestern Ontario. The pattern or seasonality of light proved unimportant to annual production. Local meteorological conditions (cloudiness) reduced light during the ice-free season to 53 percent of that expected if weather were totally cloudless, but phytoplankton production was only 26 percent lower than in could have been in cloud-free weather (Figure 1). Annual primary production in different basins varied over an order of magnitude at identical light conditions. The reason is known to be different inputs of phosphorus and nitrogen.

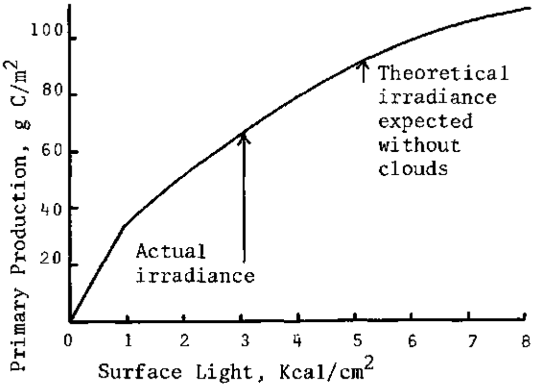

Figure 1. The relation between phytoplankton production in the ice-free season and surface light during the same period for lakes in the Experimental Lakes Area. Light data are for wavelengths of 400-700 nm.

Nutrients and phytoplankton production

On a local basis, production increases of an order of magnitude due to nutrient enrichment have been reported (Vollenweider et al. 1974; Fee unpublished). It therefore appeared worthwhile to explore this relationship on a worldwide basis. Because few IBP studies have included nutrient input data, we have combined IBP data with that available elsewhere. Results of this analysis are shown in figure 2.

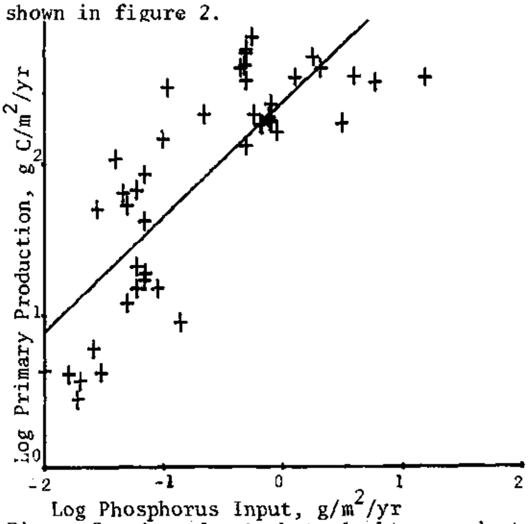

Figure 2. Annual net phytoplankton production for a number of lakes from 0-75°N lat., as a function of phosphorus input, plotted on a log-log scale. $r^2=0.84$. It is assumed that both oxygen light bottle and ^{14}C results estimate net production. A conversion factor of 0.375 was used to convert oxygen to carbon units.

Considering the inevitable technical errors involved in measuring primary production and nutrient input, the relationship is extremely good. We were, however, unable to include the most productive sites analyzed by Brylinski, because nutrient input data were not available. Also, lakes where phosphorus inputs were extremely high in relation to nitrogen (>1:5 by weight) did not fit the relationship, and it seemed logical to exclude those data points on the grounds that phosphorus was unlikely to be the controlling nutrient.

We found, as Brylinski did, that nutrient concentrations were poorly correlated with primary production. It is logical to expect that nutrient concentration and nutrient input might be poorly correlated, particularly in lakes where high loading and high water renewal rates occur.

We also attempted to adjust phosphorus input data by subtracting a correction for phosphorus flushed from the lake by water renewal. This did not significantly improve the relationship between phosphorus input and primary production, possibly because most of the lakes treated had very slow water renewal.

The correlation between phytoplankton production and nitrogen input was not significant, confirming the widespread belief that phosphorus, in most circumstances, is the nutrient controlling phytoplankton production and growth.

Discussion

The correlation between production and latitude observed by Brylinski may be due at least partly to latitudinal differences in nutrient input. Five of the areas supplying data for this analysis are remote from populous industrial areas, yet span 75° of latitude. Inputs of phosphorus and nitrogen by precipitation at the equator are an order of magnitude higher than at temperate latitudes (Table 1). Precipitation supplies still an order of magnitude less nutrient in the Arctic. It is likely that runoff, too, supplies less nutrient in polar regions, because organic acids supplied by terrestrial biota, a major influence on geochemical weathering farther south, are less abundant. Long periods when soils are frozen would also hinder solution of nutrients. Yet a third factor may contribute a nutrient bias which is apparently dependent on latitude: Cultural eutrophication is largely confined to temperate and tropical areas. Few instances are known from arctic regions (Schindler et al. 1974a, b).

The group of lakes analyzed here appeared to reach some sort of asymptotic maximum production level, at 500-700 g C/m^2/year (net). Values of this magnitude were found for sites up to 60°N lat., but always when phosphorus input was high (>0.5 g/m^2/yr). Higher values, which have been reported (Brylinski 1974, Hammer 1973), may be possible in special circumstances, based on extraordinarily efficient food chains or balances between compensation and mixing depths.

More surveys of primary production seem pointless at this time. To provide further advances in our understanding, a large body of fundamental experimental data is needed instead, providing quantitative information on the effects of nutrients, water circulation and light. Considerable attention should also be devoted to development and intercalibration of methods that may be used on a worldwide scale. Variation associated with methodology in the above studies probably is 100 percent or even more. Such data are difficult to analyze in any meaningful way.

Unless concerted efforts are made to improve our understanding of the above areas, further advancement of our knowledge of production and its management will be slow, if not impossible.

Table 1. Latitudinal trends in total phosphorus and nitrogen falling as precipitation. All locations are included in the analyses shown in figures 1 and 3. All are far from industrial or cultural nutrient sources which might obscure the relationship.

Lake	Lat, °N	P, $g/m^2/yr$	N, $g/m^2/yr$	Reference
L. George, Uganda	0	0.48	4.61	Ganf and Viner 1974
Clear Lake, Ontario, Canada	45	0.027	0.72	Schindler and Nighswander 1970
Experimental Lakes Area, Canada	50	0.035	0.67	Schindler et al. unpub. data
Kuokkel Project, Sweden	68	0.008	0.18	Limnological Institute, Uppsala, Kuokkel Proj. Rep. #3, 1973
Char Lake, Cornwallis Island, Canada	75	0.005	0.09	Schindler et al. 1974a

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PRODUCTION IN MARINE PLANKTONIC COMMUNITIES

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Introduction

The ocean is large, deep and contains a diverse assortment of habitats few of which can be considered truly isolated in the usual sense. The oceans are also very old and have evolved numerous species with a greater diversity of form and function than would be encountered in any single body of freshwater. These organisms are distributed in various non-random and unpredictable ways. This so-called "patchiness" may be associated with measurable discontinuities in the physical environment but need not be. The whole of this confused community "structure" may be altered and shifted about by water mass movement. The marine pelagic regime also has a much greater mean distance from land in all dimensions than most freshwater systems. Presumably then allocthanous materials have a smaller role to play in the sea, but it would still be a mistake to underestimate the effect of land-derived influence. To add further complications, many marine zooplankters have elaborate life cycles and often breed more or less continuously producing several to many generations a year which makes it very difficult to follow the history of an individual cohort.

Methods of measurement

I use the term "production" to mean the total amount of organic matter formed de novo (primary production) or converted from the preceding trophic level so as to be available for utilization or actually utilized by the next trophic level. Hence its direct measurement in animal populations is complicated by the fact that, for any given observational period, a portion produced will have already been cropped by the next level of consumers or lost to the decomposers. If recruitment (ie, reproduction) occurs periodically it is usually possible to follow the growth of the individuals in a population and their mortality simultaneously using the Allen-curve (Mann, 1969) or some variant. If the number of individuals lost from a cohort in a specific time interval is plotted against their mean weight or the number of survivors is plotted against their average increment of weight increase for an interval, a curve will be generated such that the area under the curve will represent the production by the cohort. In mathematical terms

$$P = \int_{W_0}^{W_t} N_t \, dW_t, \tag{1}$$

where N_t is the number of animals and W_t their mean weight at time t.

This concept of measurement has been used several times for analysis of production by certain boreal marine copepods having but one period of propagation a year, but for neritic species, especially in warmer waters, the single cohort method of graphical analysis usually cannot be used. Where breeding is more or less continuous, three basic methods have been employed to determine either a short term production rate or the turnover rate, P/B (production over biomass) for the population. (1) A modified graphical method (Greze and Baldina, 1964), requires that duration of development of the different stages be known. Growth curves are constructed for different seasons and the daily growth rate, determined from such curves for each stage or size class is then multiplied by the numerical abundance of the stage to give daily production. (2) A radioactive method was adapted by Chmyr (1967) from the standard primary production methods using C^{14}, but should be used with caution for reasons explained in Conover and Francis (1973). (3) The so called "physiological" method at first glance would seem to rely on even more tenuous assumptions than the radioactive method. Thus, Shushkina (1968) suggested that

$$P_z = R_z(K_2/1 - K_2), \tag{2}$$

where R_z refers to the metabolic use of calories derived from the familiar relationship $R = \alpha W^{\gamma}$ and K_2 is the efficiency of utilization of assimilated energy for growth. Then, the turnover rate or specific growth rate

$$C_w = P/B = dW/Wdt = P_z W^{-(1 - \gamma)}. \tag{3}$$

Once the specific growth rate (or P/B ratio) has been determined for each size or age category, i, in a population by whatever method is appropriate, production can be calculated as

$$P = \Sigma (C_w)_i \, W_i n_i. \tag{4}$$

In the case of the physiological method, it generally is necessary to assume some level of growth efficiency, K_2. However, Shushkina et al. (1968) suggested that K_2 could be calculated from the relationship

$$1/K_2 = 1 + dR_c/dW, \qquad (5)$$

where dR_c/dW is computed as the derivative (ie, slope) of the accumulated metabolic expenditure (cost of maintenance) plotted against weight as the animal grows. I will consider some of these concepts again shortly.

Table 1. Production:biomass ratios and daily production for some marine copepod species.

Species	Region	Season	Daily P/B	Production* $mgCm^{-2}day^{-1}$	Source
Calanus finmarchicus	Barents Sea	Year	0.019	7.8	Kamshilov, 1958
C. plumchrus	Georgia Strait	Feb-May	0.035-0.14	23.3	Parsons et al., 1969
C. helgolandicus	Off California	Apr-Sept	0.11-0.16	4-172	Mullin & Brooks, 1970
Acartia tonsa	Patuxent River	July-Sept	0.50	77	Heinle, 1966
A. clausi	Black Sea	Year	0.035	0.38	Greze & Baldina, 1964
A. clausi	English Channel	Year	0.034	0.72	Greze & Baldina, 1964
A. clausi	Black Sea	Year	0.040-0.175	0.92	Greze et al., 1968
Pseudocalanus elongatus	Black Sea	Year	0.104-0.203	2.57	Greze et al., 1968
P. elongatus	Ogac Lake	June-Sept	0.033	4.55-5.67	McLaren, 1969
Oithona minuta	Black Sea	Year	0.050-0.144	1.82	Greze et al., 1968
O. similis	Black Sea	Year	0.069-0.179	0.60	Greze et al., 1968
O. similis	Ogac Lake	June-Sept	0.033	2.24-3.86	McLaren, 1969

*Carbon assumed to be 5% wet weight in some instances

Estimates of Secondary production

In Table 1 I have assembled some of the data on production by certain boreal and temperate species, generally neritic, for which we have some limited knowledge concerning their life cycles. Production values range from less than one mg per day to more than a hundred but for most temperate, neritic species the values lie between one and ten. As for turnover rates (P/B), with few exceptions the values range between 2 and 20%. Cold water habitats (i.e., Barents Sea and Ogac Lake) yielded generally lower P/B values though some larger tropical forms also have specific growth rates less than 5% (Greze, in press). The warm water, neritic copepod species Acartia tonsa can replace its biomass in two days under favourable conditions (Heinle, 1966), and the luminiscent protozoan, Noctiluca miliaris, has a P/B coefficient of 1.2 (Greze, 1970). Though the data are very limited other crustacean groups like mysids and cladocerans have relatively high specific growth rates, while those for the few euphausiids studied to date are low.

Table 2. Herbivore production and production efficiency (herbivore production/ primary production) for some planktonic communities.

Locality	Season	Daily P/B	Daily* Prod. $mg\ C\ m^{-2}$	Prod. eff.	Source
English Channel	Year	0.10	75	0.30	Harvey, 1950
North Sea	Jan-June	0.08	4.9	0.14	Cushing, 1959
North Sea	Mar-June	0.10	46	0.20	Cushing & Vucetic, 1963
Ogac Lake	June-Sept	0.03	11	0.07	McLaren, 1969
Pacific, Station P	Year	0.12	35.6	0.27	McAllister, 1969
Black Sea (epiplankton)	Year	0.07	25.8	0.29	Petipa et al, 1970
Black Sea (bathyplankton)	Year	0.12	53.2	0.17	Petipa et al, 1970
Ionian Sea	Summer	0.18	22.0	1.33	Greze, 1970
Equatorial Atlantic	Spring	0.15	13.8	0.38	Greze, 1970

*Carbon assumed to be 5% wet weight in some instances

In Table 2 I have assembled some representative data on production by zooplankton communities. Often the data are even less reliable than for individual species, being based on extrapolation of the performance by one or two important ones to the whole community, or even another environment, or a best "quesstimate" made from the output of a model. Frequently, the estimate is more nearly "potential production" than actual because no attempt was made to correct for mortality. All considered perhaps it is surprising that the data show any consistency, but all P/B values are 3% or better and less than 20%. Perhaps P/B for the warmer locations, Ionian Sea and equatorial Atlantic are somewhat higher than those from north temperate environments, but we have still too little comparative data. Cushing (1971) assembled production data on major upwelling systems using "generation times: to calculate crude secondary production. His data yield daily P/B values between 1.5 and 3.6% which are probably minimal estimates.

Values for what I call "production efficiency" generally range between 10 and 40%. Only in Ogac Lake on Baffin Island, which is ice bound for most of the year, would zooplankton production seem to use less than 10% of primary production. Quite possibly the residual summer plant production goes to maintain the resident population during the period of no primary production. In contrasting warm "oligotrophic" areas production efficiency is generally highest, being even greater than 100% in the Ionian Sea in summer. Cushing (1971) also calculated production efficiencies considerably greater than 10% in many upwelling systems.

My production efficiency differs somewhat from so-called "ecological efficiency", often stated to be about 10%, which Slobodkin (1960) defines as yield to the next trophic level over that acquired from the preceding. However, Kozlovsky (1968) shows that the two types are numerically similar though ecological efficiency decreases at trophic levels greater than 2. What then of these numbers in Table 2? Are marine food chains generally more efficient than terrestrial or freshwater? Are tropical systems more efficient than temperate?

Food sources and food web structure

I do not think we can answer these questions with certainty at this time, but consideration of some of the fundamental problems of marine plankton biology may help our understanding. As a starting point, I refer again to the unlikely occurrence that secondary production in the Ionian Sea is greater than primary production (Table 2). Several plausible explanations may be put forward to account for this discrepancy all of which bear some scrutiny. I will list them first and discuss them in order: 1) Primary production measurements, particularly in tropical waters, could be seriously underestimated; 2) zooplankton are using some unmeasured reservoir of energy such as the dissolved organic matter or detritus; 3) primary production is higher at another time and/or place and transferred to the secondary producers through an intermediate or alternative link in the food web; 4) secondary production rates are seriously overestimated.

1) A discussion of the technical detail of measuring primary production is beyond the scope of this paper, but I do not believe that the average C^{14} measurement of primary production tells the amount of carbon being fixed photosynthetically at that time and place in the sea with any great degree of accuracy. Recently Sheldon et al (1973) have shown that small particles in the Sargasso Sea are apparently in nearly dynamic equilibrium, that is, they are probably eaten about as fast as they are produced, unless certain precautions are taken to exclude predators. They found a minimum doubling time of 2.5 hr for 20 μ particles in their experiments. To illustrate the probable effect of grazing on C^{14} primary production measurement let us assume that the doubling time is 3 hours and that each cell is eaten on being produced. Without grazing we could expect 8 divisions in one day or $P/B_p = 2^8 = 256$. With grazing the standing crop remains 1 but $P/B_p = 8$, the number of divisions. However, we would measure only $1 + (P/B)_p(P/B_z)$ at the end of the experiment, where P/B_z is the approximate turnover rate of the grazers, overlooking any complications resulting from excretion and respiration by both plants and animals in the bottle.

2) The two largest pools of organic matter in the sea are non-living. Dissolved organic matter can be assimilated by many marine organisms but in this form it seems of minor nutritional importance in planktonic communities, although particulate organic matter made from it will support some growth in the brine shrimp (Baylor and Sutcliffe, 1963).

The importance of organic detritus in the near shore environment has been alluded to many times, but zooplankton, for the most part, do not seem to thrive on it. In Winter, off Nova Scotia Balch (1971) found that Calanus finmarchicus consumed it only during the spring flowering when living carbon was also high. At most other times the copepods fed very little on either living or dead carbon though some faecal pellets were formed.

3) There would seem to be two alternative or intermediate pathways between primary and secondary production. The production of bacteria is stated by Sorokin (1971, 1971a) to exceed that of the primary producers in some tropical regions. He suggests that the extra organic substrate is advected or transported from some distant region where primary

production greatly exceeds utilization. Banse (1974) rather convincingly demolished some of Sorokin's ideas, but the fact remains that there is probably a significant community of microorganisms everywhere in the ocean converting dissolved organic matter to particulate organic matter.

Even if bacteria are present in significant quantities, can it be demonstrated that they are a sufficient food? Sorokin (1971a) and Pavlova et al (1973) have tested a number of species most of which will assimilate some radio-carbon from bacteria but only pelagic tunicates and the marine cladoceran Penilia avirostris would be likely to survive if bacteria were the only food available. Unfortunately, they do not seem to have examined any "microzooplankton".

The microzooplankton, including larvae of many of the macroplankton as well as colorless flagellates and ciliated protozoa, represent the other probable pathway between what we normally think of as the first two trophic levels. Their numerical abundance has been emphasized by Beers and Stewart (1971) and their greater metabolic activity referred to by Conover (1964) and many others. It has also been shown that most macrozooplankton, even the so-called herbivores, take animal food and many warm-water species prefer microzooplankton to diatoms or flagellates (Mullin, 1966).

4) Where a single cohort of a species can be studied over a period of time there would seem little possibility of seriously over estimating the rate of production. However, when a location is visited only briefly, as on an expedition, an "instant" method must generally be used. The inherent technological difficulties in the radiocarbon method have led to a greater reliance on the physiological method at least by Russian workers.

To use the physiological method one needs a measure of metabolic expenditure per unit weight and K_2, the second order growth coefficient. A measure of metabolic rate can be made in a few hours or calculated from existing size-metabolism relationship. On the other hand K_2 is generally calculated for a period of growth long enough for reliable estimates of assimilation and weight change to be measured. Shushkina et al (1968) concluded that K_2 for a freshwater copepod was constant around 0.50 although K_1 decreased with growth. In a later paper, in which the physiological and graphical methods were compared with captive populations of mysids, Shushkina (1972) concluded that K_2 did change somewhat but could be approximated by a single value of K_2.

We have just sent off a paper (Conover and Lalli, submitted) in which we show that in the specialized carnivore, the pteropod Clione, K_2 remains constant and high so long as the food supply gets progressively larger as the animal grows. In nature the prey, another pteropod, Spiratella, has approximately the same propagation time and growth rate as Clione.

Returning to intermediate steps in the tropical food chain and the general concept of food chain efficiency, I submit that each predator has an optimal-sized food particle, a concept also implicit in Parsons and LeBrasseur (1970). If the particle size eaten changes as the animal grows, it, like Clione, may be able to keep the K_2 value high, even constant. Kerr and Martin (1970) have already shown that there is no loss in food chain efficiency in lake trout when an intermediate link is inserted, which may be because growth efficiency has been raised at all trophic levels as a result of "particle size optimization". So I would say that tropical food chains, which are much more diverse than temperate ones, have a greater degree of particle size optimization and therefore greater growth efficiency at each trophic level in accord with Taniguchi's (1973) recent observations. However, we must not expect high efficiency and high production to necessarily be positively correlated. My little model of what might happen in a tropical C_{14} bottle shows quite clearly that if the right-size grazer was not immediately present there could have been 2^5 times more primary production.

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SECONDARY PRODUCTIVITY IN FRESHWATERS - ITS VALUES AND EFFICIENCIES IN PLANKTON FOOD CHAIN

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Summary

A tentative analysis of the collected data on the productivity parametres of unpredatory and predatory zooplankton in different water bodies (lakes, reservoirs) enables us to point out some general statements concerning the relationships between the production of consecutive trophic levels and their efficiencies.

When the size structure of phytoplankton is favorable for filtering capacity of filter-feeders (nannoplankton predominates in food suspension), the direct utilization of P (rimary) P(roducts) is intensive and its efficiency is high as well as the efficiency of energy transfer from producers to primary consumers is high, almost twice as high as the theoretically expected 10%. When the net forms predominate in the composition of phytoplankton and/or the fine detritus and bacteria predominate in food suspension the direct utilization of PP is not efficient and the energy transfer efficiencies are very low. The former situation occurs more frequently in oligo-mezotrophic water bodies with a low or moderate annual PP and with a negligible input of A(llochtonous) O(rganic) M(atter). The assimilation of heterotrophic bacterioplankton as an alternative primary consumer is rather low in relation to the PP. The domination of nannoplankton in food suspension stimulates the occurrence of coarse filtrators with a wide spectrum of particle size selection. The latter situation occurs more frequently in eutrophic water bodies with higher annual PP and water blooms in summer and also in water bodies with significant participation of AOM in pelagic zone. The utilization of PP by bacteria can be very high but probably the secondary products of bacetrial transformation are very efficiently utilized by fine filter-feeder communities usually dominating under these conditions. The energy transfer efficiencies in link II: filter-feeders - invertebrate predators are as a rule greater than in link I and reveal a tendency to be greater under eutrophic conditions than under oligotrophic, probably because of a more complex and saturated food web.

Introduction

The collected data (mainly in the frame work of the IBP) on the production and structure of phytoplankton in different water bodies (lakes, reservoirs) together with some assessments of the heterotrophic bacterial production and assimilation, production and consumption of unpredatory zooplankton (filter-feeder communities) and their invertebrate predators enable the tentative assessment and analysis of the general relationships and ecological efficiencies between trophic levels. The analysis was based on the data published Kajak & Hillbricht-Ilkowska (Eds., 1972); Winberg (Ed., 1973) and on the other sources. Because of the lack of space only some general results are presented here, with limited illustration and references.

Results and discussion

Y-shaped pattern of the transformation of PP in plankton food chain

The P(rimary) P(roducts) available in pelagic zone (organic matter produced by phytoplankton and A(llochtonous) O(rganic) M(atter) coming from various external sources, like littoral zone) are transformed in two parallel or alternative ways - through grazing the algae in vivo by filter-feeders and/or utilization by bacteria. The secondary products of bacterial transformation of PP are included then into the plankton food chain through the activity of filter-feeders. The rate of PP utilization in these two ways is genrally determined by the relation between autochtonous PP and AOM, size and species composition of phytoplankton and the particle selection size pressure of primary consumers.

The tentative assessments of bacteria assimilation and production in open water, expressed both in absolute numbers and in relation to PP and AOM, made for several lakes and reservoirs suggest that on the average a half to two-third of all PP can be directly utilized by bacteria as primary consumers to some extent competitive to the animal grazers. The values of annual bacterial assimilation are frequently of the same order as the annual PP in pelagic zone (Winberg, 1972a,b; Winberg, Ed., 1973). Ratio of bacterial production to phytoplankton production can be very high up to 70-80%, especially in the lakes with the heavy input of AOM (assessed or expected) and with the intensive decomposition processes in open water, sometimes significantly exceding the actual phytoplankton production rates (Winberg, 1972 a_. Even in the typical eutrophic lakes with a negligible input of AOM the bacterial production and decomposition occasionally exceed the phytoplankton production rates (Sorokin & Pavelyeva, 1972; Gliwicz & Hillbricht-Ilkowska, 1975).

Efficiency of grazing, ratio of filter-feeder (unpredatory zooplankton) total consumption to the PP

The amount of PP available for direct grazing is determined by the size composition of algae, on the one hand, and the particle size selection spectrum of consumers, on the other. Only a part of the whole phytoplankton - nannoplankton, can be grazed in vivo by the majority of filter-feeders because of the limited size selection capacity (up to 30-50 μ), (Gliwicz, 1974). As a rule, the contribution of nannoplankton to the biomass and production of phytoplankton is greater in oligotrophic waters with low or moderate PP rates and with insignificant occurrence of blue green or peridinian blooms than in more eutrophic water bodies with higher PP rates and significant occurrence of net algal blooms (Gliwicz, 1967; Hillbricht-Ilkowska et al., 1972). In oligotrophic water bodies the small algae are probably the main component of the food particle suspension, especially when the input of AOM to the pelagial zone is negligible, and there is no significant bacterial production. The same situation occurs in more productive waters in the spring periods when the contribution of nanoplankton is greater in comparison with the summer algal bloom periods (Hillbricht-Ilkowska et al., 1972). Usually, under the oligotrophic conditions the occurrence of coarse filter-feeders (like Calanoida) and some raptators (like Cyclopoida) with wide spectrum of particle size selection enable the efficient utilization of food suspension in which the alive algae dominate. That is why the assessment of the grazing efficiency (the ratio of the amount of grazed algae to the nannoplankton production or total phytoplankton production) gives greater values under the oligotrophic conditions (even up to 100%) than under the eutrophic ones (Gliwicz & Hillbricht-Ilkowska, 1972).

The same tendency is observed while comparing the ratio of the total filter-feeder food requirements to the amount of PP in different water bodies with the probable negligible input of AOM (basing on the assessments for about 30 habitats). The range of the total filter-feeder consumption values increases with the increase of PP (Table 1) but drops in very productive waters; at the same time the range of this ratio decreases. The tendency is more pronounced while comparing the range of the ratio in different types of water bodies irrespective of the absolute values of PP. In oligotrophic situations the total food requirements of filter-feeders consist about two thirds of the total PP, in eutrophic situations not more (an average) than one third.

Table 1. Range of the total unpredatory zooplankton food requirements (consumption, C_h) and its efficiency (EC_h)[1] in relation to the phytoplankton production (P_{ph}).

No. of water bodies	P_{ph}	C_h	EC_h (%)
4	<200	<70	7-50
21	200-1200	30-600	5-100
10	1200-2500	250-2000	15-80
4	>2500	50-550	3-15

[1] ratio of the total filter-feeder food requirements to phytoplankton production, in per cent. Values for C_h and P_{ph} in kcal per m^2 per year or growing season.

Thus in eutrophic habitats because of the unfavorable for grazing size structure of phytoplankton, greater part of PP is left for bacterial utilization being responsible for decreasing the efficiency of utilization PP by unpredatory zooplankton.

The above tendency is masked to some extent by the input of AOM because there is no real difference between the efficiency in oligo and eutrophic habitats (with different size composition of algae) with significant (assessed or expected) input of AOM. Generally, the efficiency is low, similar to that of eutrophic habitats. Even if the nannoplankton predominates in the PP, in the food particle suspension dominate the fine detritus and bacteria, stimulating, in turn, the occurrence of fine filter-feeders (protozoans, small rotifers and cladocerans) with a narrow spectrum of size selection (mostly 1-2μ) for which the algal cells in the food suspension consist of too big particles to be effectively grazed (Gliwicz, 1974).

Few data on the efficiency of grazing of filter-feeders on bacterioplankton exist and they suggest the higher values up to 70% of daily bacterial production (Gliwicz, 1969; Gak, 1972). It means that besides the ineffective direct utilization of PP by zooplankton, the utilization of the secondary products of bacterial transformation can be highly effective.

Efficiency of energy transfer - the ratio of filter-feeder production to the amount of PP.

The relation: the biomass production of filter-feeder communities - the PP annual values is to some extent similar to the relation of the consumption of these primary consumers to the PP values (Table 2). Higher the values of PP - higher the range of the filter-feeder production but dropping in the very productive waters. Energy transfer efficiencies are low (the ratio of production of filter-feeders to PP values) in very unproductive and very productive waters (less than 10%). The highest reported values of 25-30% were mainly found for oligotrophic habitats, or for short periods in other water bodies. They are the highest possible ones imaginable only if the total PP amount is consumed, highly assimilated and transferred into biomass by the rapidly growing or reproducing population of consumers. For most eutrophic habitats the energy transfer values lie below 10% (in most cases a few per cent). In most oligotrophic habitats, they are higher than 10% (of an average 17%). The water bodies with a significant input of AOM are generally less effective irrespective of the character of phytoplankton communities.

Thus, the oligotrophic habitats usually with lower PP rates and favorable size structure of the phytoplankton have more efficient transformation of PP in link I of plankton food chain than the eutrophic habitats usually with higher PP rates and unfavorable size composition of phytoplankton. The similar relation was observed by Cushing (1973) in the marine habitats. Bacteria are the alternative primary consumers to the filter-feeders grazing on the algae. While the amount of bacteria in food suspension is predominating the system becomes less efficient in respect to the PP transformation by zooplankton but probably it does not exclude the effective transformation of secondary products.

Table 2. Range of the unpredatory zooplankton production (P_h) and the efficiencies of energy transfer (EP_h)[1] in relation to the phytoplankton production (P_{ph}).

No. of water bodies	P_{ph}	P_h	EP_h(%)
6	<200	<50	1-10
27	200-1200	10-250	2-30
17	1200-2500	75-400	2-25
6	>2500	25-250	1-10

[1] ratio of the filter-feeder production to the phytoplankton production, in per cent. Values for P_h and P_{ph} in kcal per m^2 per year or growing season.

The changing relation between the bacterial and zooplankton direct utilization of PP accordingly to the changes in the structure of the phytoplankton is also evident in the course of the seasonal events in a typical eutrophic lake (Gliwicz & Hillbricht-Ilkowska, 1975). In the late spring the contribution of nannoplankton to PP is great and enable an effective grazing by the rapidly growing and reproducing filter-feeder community, the monthly production of which is the highest in the year; the efficiency of energy transfer is higher than 10%. On the contrary, in late summer the dying masses of large peridinians (Ceratium hirundinella) not accessible to zooplankton in vivo, stimulate the intensive decomposition processes and bacterial production; the efficiency of energy transfer from PP to zooplankton is three times lower than in the spring period, and no more than 20-30% of nannoplankton production is consumed by filter-feeders.

The efficiencies in link II - the ratio of predator production to the production of the unpredatory zooplankton

There are rather few typical obligatory predatory species in open water (hunters, like Leptodora kindtii or Chaoborus larvae) but the majority of raptators or "particle-seizers" such as cyclopids and some rotifers can be predators in most freshwater habitats (Gliwicz, 1974). According to the research on the food preference of the common predators, the basic communities of primary consumers in open water are well "covered" with the predation pressure of secondary consumers.

Table 3. Range of the predator zooplankton production (P_p) and the efficiency of energy transfer (EP_p)[1] in relation to the unpredatory zooplankton production (P_h).

No. of water bodies	P_h	P_p	EP_p(%)
16	<50	<20	5-40
18	50-150	2-50	5-40
4	150-250	30-80	15-40
5	>250	10-80	4-20

[1] ratio of predator production to the production of herbivores in per cent. Values for P_p and P_h in kcal per m^2 per year or growing season.

The assessment of the total food requirements of predator communities in absolute values and in comparison with the production of their prey communities in several water bodies suggests a very high efficiency of predation, especially in the period when the predation pressures of most active predators are overlapping (Hillbricht-Ilkowska et al., 1975). Higher the production of unpredatory zooplankton - higher the range of the production values of their predators, except in very productive waters in which the production of predators does not increase further (Table 3). Judging from about 40 water bodies, the efficiency of energy transfer in this link of the plankton food chain is rather great and averages 20%; quite frequently very high values are reported, which are hardly reliable. This is probably the effect of a gap in the knowledge of the real trophic status of so called "predators" and an overestimation of their predatory activity. But still remain a good number of data suggesting the high energy transfer efficiency in this link. There is also a small but remarkable difference in the energy transfer through this link between oligotrophic (on an average 17%) and eutrophic habitats (on an average 24%). The reverse differences were found between these two kinds of habitats in link I. More effective transformation of unpredatory zooplankton production by their predators in eutrophic habitats could be explained by the greater complexity of relations in these habitats (more species of predators and more favorable conditions for their occurrence, for instance, for L. kindtii).

In general, the available data on the relations in link II of plankton food chain suggest that the transformation is as effective as possible.

The comparison of interlevel efficiencies in plankton food chain in freshwaters suggests that in the habitats with intensive direct grazing of PP by zooplankton as well as in predatory trophic level the theoretically expected efficiency of 10% could be easily surpassed.

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COMPARISON OF FRESHWATER AND MARINE SYSTEMS: THE DIRECT AND INDIRECT EFFECTS OF SOLAR ENERGY ON PRIMARY AND SECONDARY PRODUCTION

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Introduction

While none would deny that primary production is under the influence of both solar energy and nutrients, attempts to predict the level of primary production have invariably been slanted towards either energy or nutrients as the controlling factor. Thus Walsh (this volume) and his colleagues in the U.S. IBP Upwelling Biome developed their models for primary production mainly from studies of nutrient dynamics, while Platt (1969), working in an IBP project in Eastern Canada, developed his predictions on the basis of energy and chlorophyll relationships.

In the PF programme of IBP, data were assembled from 93 lakes and reservoirs and were subjected to correlation-type analyses with a view to determining which factors, on a global scale, appeared to have the most influence on primary and secondary production (Brylinsky & Mann, 1973; Brylinsky, in press). It was found that variables related to energy availability, such as incident radiation, air temperature, length of growing season, or latitute, had stronger correlations with primary production than did variables related to nutrient availability, such as average total phosphorus concentration, average total nitrogen concentration or conductivity, in the surface waters. Correlation coefficients are shown in Table 1.

On the other hand Schindler (this volume) has shown that consideration of the input, output, and internal recycling of nutrients in lakes can be used to explain most of the variance in primary productivity, and that latitude, which is a good index of energy-related variables, explains very little more of the variance. In working towards a synthesis of IBP results in this symposium we should address ourselves to the question of whether the work quoted above, and other work along similar lines involves unresolved contradictions.

Direct and indirect effects of energy

Most references to energy flow in ecosystems are concerned with solar energy which becomes fixed in reduced carbon compounds during photosynthesis and is subsequently passed to successive trophic levels before being released in respiration. This may be viewed as the direct effect of solar energy on life processes. However, it is gradually becoming clear that the indirect effects of solar energy are also of major importance, especially in aquatic systems. As is well known, the tendency of organisms to sink in a water column and to become mineralized at lower levels leads to a spatial separation between the region of high light intensity at the surface and the region of high nutrient concentration near the bottom. Continued primary production is possible only as long as a mechanism exists for vertical transport of nutrients between the two.

Table 1. Simple correlations between phytoplankton production and environmental factors in 93 IBP lakes. Number of observations in parentheses. From Brylinsky (in press).

Variable	Correlation Coefficient	
Related to solar energy:		
Latitude	-.6787**	(93)
Altitude	.1664^{ns}	(93)
Visible incident radiation	.3564**	(93)
Daylength range	-.5219**	(93)
Air temperature	.6328**	(93)
Epilimnion temperature	.6283**	(40)
Related to water chemistry:		
Conductivity	.2902**	(65)
pH	.4570**	(82)
Total phosphorus	.1732^{ns}	(33)
Phosphate phosphorus	.1781^{ns}	(65)
Total nitrogen	.7133**	(27)
Nitrate nitrogen	.1431^{ns}	(58)
Lake morphometry and physical factors:		
Mean depth	-.1673^{ns}	(91)
Surface area	-.1079^{ns}	(92)
Volume	-.1399^{ns}	(91)
Drainage area	-.0091^{ns}	(49)
Depth of thermocline	-.1461^{ns}	(66)
Duration of stratification	-.1654^{ns}	(51)
Precipitation	-.0411^{ns}	(84)
Retention time	-.2028^{ns}	(45)

** Significant at 99 percent level

^{ns} Not significant at 95 percent level

There are three main mechanisms for achieving this: wind-induced circulation, convection and river runoff. All three are driven ultimately by the flux of solar energy, and all three influence primary production by causing the upwelling of nutrients. Hence, by this means, solar energy exerts an indirect effect on primary production in aquatic ecosystems.

Indirect effects of energy in marine systems

On the western coasts of the major continental land masses there exist regions where the prevailing, wind-driven oceanic currents cause major upwelling of nutrient-rich deep water. Examples, quoted by Walsh (this volume) are in the Peru, California and Canary Currents. The IBP studies of these areas have shown that primary productivity is of the order of 1-10g C m^{-2} day^{-1}. In mid-ocean gyres, such as the North Pacific Gyre or the North Central Atlantic Gyre, which have comparable amounts of direct solar influence but lack the upwelling currents, primary production is an order of magnitude lower, about 0.1 - 0.5 g C m^{-2} day^{-1}.

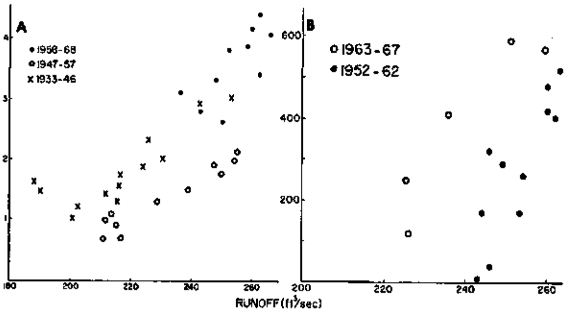
On the continental shelves where the distance from surface to bottom is less than in mid-ocean, a seasonal regime of heating and cooling of surface waters leads to vertical mixing by a combination of convection and wind influence. As a result, primary production on the shelves tends to be higher than in mid-ocean, of the order of 0.5 - 2.0g C m^{-2} day^{-1}. Thus Platt (1971) found in an IBP study that over a period of 3 years the phytoplankton productivity in St. Margaret's Bay, on the east coast of Canada was 190 ± 60 g C m^{-2} $year^{-1}$.

In the Gulf of St. Lawrence, the spatial distribution of primary production was studied in several successive years by the IBP group from McGill University, Montreal. They found (Steven et al., 1973) that primary productivity was highest in the area at the mouth of the St. Lawrence River, where entrainment by river runoff was causing upwelling of nutrient-rich water. Sutcliffe (1972) has followed this effect still further and has shown that production at higher trophic levels, in the Gulf of St. Lawrence, as revealed by commercial landings of fish and shellfish, is closely correlated with the volume of freshwater flow down the river (Fig. 1). The correlation is between landings of a species in a particular year and the flow of the river in the year when those organisms were in the larval stage. It is postulated that there is an indirect effect between the river runoff and larval survival, through its effect on primary production.

One more indirect effect of energy should be mentioned. This is the effect of tidal energy on the productivity of attached algae. In St. Margaret's Bay, Nova Scotia, it has been found that beds of the seaweed Laminaria produce about 1750g C m^{-2} $year^{-1}$, achieving rates of 10-20 g C m^{-2} day^{-1} for parts of the year (Mann, 1973). These plants grow at 5 to 20 m depth and have the unique advantage of remaining attached to rocks while a dilute solution of nutrients is moved over them on the rising and falling tide. In addition, the water at this depth is agitated by wind and waves so that they receive indirect effects of both tidal and solar energy. There is evidence (Dr. J.S. Craigie, pers. comm.) that the seaweeds are able to build up internal reserves of nitrate during the winter, when nutrient concentrations of surface waters are highest. These may help production during the summer, when nitrate levels in the water are extremely low.

Fig. 1. A. Halibut catch of Quebec (x 10^5 lbs) for 1933 to 1968 plotted against discharge of the St. Lawrence river (x 10^3 ft^3/sec) 10 years earlier. Data smoothed by 3-year running averages. Correlation coefficient r = .797. Significant at 99.9 percent level.

B. Haddock catch of Quebec (x 10^3 lbs), plotted against discharge of the St. Lawrence River (x 10^3 ft^3/sec) 8 years earlier. Data smoothed by 3-year running averages. For 1952-62 r = .934, significant at 98 per cent level. For 1963-67, r = .773, significant at 99.9 percent level. From Sutcliffe (1972).



It is thus possible to discern in marine systems a relationship, as yet not quantified, between the energy available for transporting nutrients and levels of primary production. The differences between areas of upwelling, mid-ocean gyres, continental shelves, estuaries, and the littoral/sublittoral fringe can be related to the indirect effects of solar and tidal energy. We may look forward to the day when predictive relationships can be established.

We should, however, be on our guard against assuming that the levels of production indicated by ^{14}C incubation experiments are true levels of primary production. Sheldon et al. (1973) showed that when production was determined by particle counting, using a Coulter counter, and when precautions were taken to exclude consumers, waters of the Sargasso sea had a rate of production much higher than that indicated by radiocarbon uptake. They postulated that in these waters there is a constant state of rapid production accompanied by almost equally rapid consumption which has the effect of masking the true level of production. It is possible that the productivity of oligotrophic marine areas has been seriously underestimated.

The differences in productivity of marine surface waters are reflected in the secondary production of the benthos. In general, as one proceeds from the coast to deep water there is a progressive decline in the biomass of benthos. For example, in the northern Pacific Ocean, off the coast of the U.S.A., the biomass of benthos at depths of 400 to 1200m is in the range of 20 to 200 g m^{-2} wet weight (Zenkevitch & Filatova, 1960, Filatova & Levenstein, 1961). Beyond the 200m contour it drops to an average of 1.4 g m^{-2} and beyond 400 m to 0.2g m^{-2} (Vinogradova, 1962). Average figures for the Indian sector of the Antartic Ocean are of a different order of magnitude, but the trend is the same (Belyaev & Uschakov, 1957):

Depth	Biomass
100-200 m	1397 g m^{-2}
200-500 m	239 g m^{-2}
500-1000 m	43 g m^{-2}
1000-2000 m	13 g m^{-2}

Using data of this type, Zenkevitch et al. (1960) made a tentative estimate of the total biomass of the benthos in the world's oceans and calculated that more than 80% is found on the continental shelves, at depths of less than 200m, while less than 1% occurs in the abyssal depths. This calculation did not take into account organisms in the world's intertidal areas.

There are no data for the productivity of benthic populations at a range of depths, but it is reasonable to suppose that as one moves from shallow to deep water, productivity falls off even more rapidly than biomass, since growth is probably slower in deeper, colder waters.

The productivity of benthos is presumably determined by its food supply and the efficiency with which it is used. For organisms below the euphotic zone, all food is ultimately derived from above. The amount reaching the bottom will be determined by the level of productivity in the surface waters, and by the amount of that productivity that is consumed as it sinks through the water columns. Hence, productivity of benthos in the deep ocean is low for two reasons, firstly because the primary productivity of the mid-ocean regions is lower than that of the coastal regions, and secondly because the surface production has a long way to sink and hence a high probability of being consumed and digested. In shallow coastal waters, where the time taken to sink to the bottom is relatively short and constant, Hargrave and Peer (unpublished) showed a clear correlation between the average chlorophyll concentration (March to May) in surface waters, and the biomass of benthic macrofauna. Using data from ten sites in Eastern Canada, Long Island Sound, the North Sea, and the West Coast of Scotland, they obtained a correlation coefficient of 0.89. If we assume that production is approximately proportional to biomass, it is clear that energy factors that influence primary production in the plankton also influence secondary production in the benthos.

Indirect effects of energy in freshwater systems

It was mentioned earlier, that in the IBP (PF) analysis of results from 93 lakes, energy related variables showed the highest correlation with phytoplankton production. I should like to review the reasons why this correlation is probably attributable more to the indirect effects of energy then to the direct effects.

The first reason is that the correlation with latitude (Table I) is much stronger than the correlation with visible incident radiation, suggesting that it is the diurnal and seasonal pattern of radiation, rather than its absolute amount, that has the major influence on primary production. Also, correlations with daylength range, mean air temperature and mean epilimnion temperature are all stronger than the correlation with visible incident radiation.

In Table II are shown the partial correlation coefficients of various factors previously mentioned after correcting for differences in latitude. We see that the indirect effects of solar radiation are now no longer significant, having been removed by the correction for latitude. The strongest correlation is now with total nitrogen. However neither nitrate nitrogen nor phosphate phosphorus show a significant correlation, and the correlation with total nitrogen may be a correlation with the nitrogen contained in the phytoplankton cells -- a kind of autocorrelation. This table shows additional evidence of an indirect effect of solar energy: a strong negative correlation with precipitation. One might have expected high rainfall to lead to high nutrient input to a lake, but this would have led to a positive correlation. Instead, high rainfall correlates with reduced production, caused perhaps by heavy cloud cover (reduced solar input), increased flushing of phytoplankton, or both.

Table II. Partial correlations between phytoplankton production and environmental factors after correcting for differences in latitude, in 93 IBP lakes (Number of observations in parentheses). From Brylinsky (in press).

Variable	Partial Correlation Coefficient	
Related to solar energy:		
Altitude	-.2317**	(93)
Visible incident radiation	-.2755**	(93)
Daylength range	.0910^{ns}	(93)
Air temperature	.1253^{ns}	(93)
Epilmnion temperature	.1362^{ns}	(40)
Related to water chemistry:		
Conductivity	.3718**	(65)
pH	.3669**	(82)
Total phosphorus	.3081*	(33)
Phosphate phosphorus	.0612^{ns}	(65)
Total nitrogen	.5803^{ns}	(27)
Nitrate nitrogen	.1394^{ns}	(58)
Lake morphometry and physical factors		
Mean depth	-.1434^{ns}	(91)
Surface area	-.1015^{ns}	(92)
Volume	-.0317^{ns}	(91)
Drainage area	-.1356^{ns}	(49)
Depth of thermocline	-.2094*	(66)
Duration of stratification	-.1434^{ns}	(51)
Precipitation	-.4708**	(84)
Retention time	-.1134^{ns}	(45)

* Significant at 95 per cent level

** Significant at 99 per cent level

ns Not significant

The second reason why the indirect effects of solar energy are thought to be important is that these effects are likely to be associated with the transport of nutrients. In general, within IBP (PF) a large body of data has been collected on nutrient *concentrations*, but little attention has been paid to the *supply* of nutrients to primary producers. A high concentration of nutrients in a lake may indicate rapid uptake and high productivity, but the converse situation, in which rapidly growing phytoplankton maintain nutrient concentrations at a low level, is just as plausible. It is the level of supply that is important. Mechanisms which ensure a good supply of nutrients to the euphotic zone include convective and wind-induced circulation, regeneration mechanisms at various levels in the water column, and water movements within the hydrological cycle of a watershed.

Hence, I suggest that the high correlations between phytoplankton production and energy-related variables in the 93 IBP lakes and reservoirs are in part the result of the indirect effects of solar energy on the supply of nutrients to the euphotic zone. To arrive at a coherent theory of primary productivity in aquatic systems we need to abolish the old divergence between energy limitations and nutrient limitation in primary production, and consider the total mechanism. This requires that we pay attention to the energy needed to transport nutrients within the ecosystem.

Table III. Simple correlations between secondary production and phytoplankton production in 93 IBP lakes (Number of observations in parentheses). From Brylinsky (in press).

Secondary producer	Correlation Coefficient	
Herbivorous zooplankton	.6939**	(27)
Carnivorous zooplankton	.6731**	(24)
Herbivorous benthos	.4956*	(18)
Carnivorous benthos	.4708*	(17)

Significance symbols as in Table II.

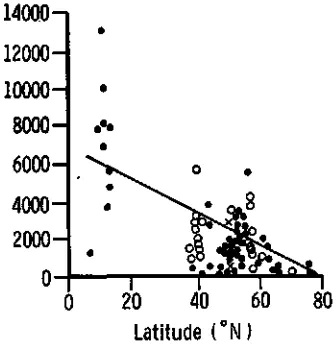
Although IBP (PF) data on secondary production in lakes are more limited than those for primary production, Table III shows that phytoplankton production is strongly correlated with zooplankton production, but less strongly correlated with benthic production. In the case of the benthos, multiple regression analysis showed that the best estimates of productivity of herbivorous benthos are obtained from a combination of phytoplankton production, mean thermocline depth and duration of stratification. In other words, it appears that indirect effects of energy as represented by stratification and mixing, affect the transfer of primary production to the benthos, in lakes just as in the sea.

Predicting aquatic productivity

Although the role of solar energy in promoting the transport of nutrients in both marine and freshwater systems is basically the same, the practical problems of predicting productivity are very different in the two types of system. As Walsh (this volume) has stated, advances in predicting production in the sea await further study of transient physical phenomena, such as storms, spring overturn, or El Nino. These are large scale processes having their origins in meteorology, so that there is a sense in which progress in predicting marine productivity awaits progress in the science of large scale meteorological prediction. Nevertheless, there exists a well recognized geographic pattern of marine phytoplankton productivity which was reasonably well understood a decade ago, and which has not been greatly modified during the period of IBP. The significant advances have been made in our ability to predict local variations in that pattern on the basis of measurements of light energy, nutrient supply and phytoplankton biomass. As was shown by Platt (1969) and others, chlorophyll concentration is often a good integrator of information on plant biomass and nutrient supply.

In lakes, the geographic pattern of productivity is less well marked because each body of water is partly or completely isolated from the next one. There is not the large scale interconnectedness of subsystems which occurs in the oceans. As reported by Schindler (this volume), information on input and output of nutrients, and on internal recycling, is required for a good prediction of primary production. Hence detailed, long range prediction depends on knowledge of rainfall, timing of stratification, and other meteorologically-based phenomena, and we are once again forced to await improvements in the science of meteoreology. Nevertheless, much can be said on the basis of average weather conditions in the past, coupled with a knowledge of the characteristics of the drainage basin of a particular lake. The regression of plankton production on latitude (Fig. 2) from Brylinsky & Mann (1973) showed that while lakes at high latitudes invariably had low productivity, those at low latitudes had a wide range of levels of productivity. In other words, solar energy availability sets an upper limit on phytoplankton productivity, but not a lower limit. Within the possible range, availability of nutrients in the drainage basin, inflow and outflow characteristics, and vertical transport phenomena determine the level of productivity in individual lakes.

Fig. 2. Regression of phytoplankton production on latitude. Production in kcal m^{-2}.



When this information is lacking, as in the IBP studies recently completed, the largest component of the variance is explained by using latitude as an integrator of energy-related phenomena and chlorophyll as an integrator of plant biomass and nutrient-supply information. The power of various combinations of variables to predict phytoplankton productivity in lakes is summarized in Table IV.

Table IV. Results of linear multiple regression analyses using both abiotic and biotic variables to estimate phytoplankton production in IBP lakes.

Variables included and percent variation explained by each	N	Percent of total variance explained	Percent error of prediction of mean
1. a) Biomass (52.4), latitude (19.6).	29	72.0	55.7
b) Chlorophyll a (60.3), latitude (18.3).	27	78.6	52.4
2. a) Chlorophyll a (59.7), conductivity (4.4)	20	64.1	69.2
b) Chlorophyll a (60.1), nitrate nitrogen (3.7)	25	63.8	67.4
c) Chlorophyll a (58.8), phosphate phosphorus (2.1).	25	60.9	68.5
3. Chlorophyll a (60.1), latitude (17.6), precipitation (12.3), thermocline depth (9.2)	23	88.4	37.7

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B2

Global geography of biological productivity

PRIMARY PRODUCTIVITY OF THE MAIN WORLD ECOSYSTEMS

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Summary

The total phytomass of I06 terrestrial soil-plant formations, grouped into bioclimatic areas and thermal belts,has been calculated along with estimates of annual productivity. The total phytomass of the land is estimated to be 2.4 x IO^{I2} metric tons dry weight. The bulk of this organic mass is in the tropical zone /56 percent/,followed by the boreal /I8 percent/,subtropical /I4 percent/,subboreal /I2 percent/and polar /I percent/ zones. The majority of phytomass is concentrated in forests /82 percent/. Regularities of phytomass distribution in the world's oceans resemble those on the land /alternation of belts with high and low amounts of phytomass;abundance and concentration in the areas of cyclonic cycling of atmosphere and waters/,but there exist some pecularities pertinent only to the oceans /maximum accumulation of phytomass in temperate latitudes and the shores. Total phytomass in the world's oceans amounts to I.7 x IO^{8} metric tons, which is about I5.000 times smaller than that of the land.

The total primary production of the land is estimated to be I.72 x IO^{II} metric tons/year. The tropical belt produces 60 percent of this total; subtropical,20 percent,subboreal,IO percent; boreal,9 percent; and polar,0.8 percent. Forests produce 49 percent of primary production of the land. The total primary production of the oceans is estimated at 4.7 to 7.2 x IO^{IO} metric tons/year /Steemann et al., I957; Koblents-Mishke et al.,I968; Bogorov,I969/. Hence,the oceans contribute approximately one-third as much primary production as do terrestrial plant communities. The total primary production of the earth is calculated as being 2.33 x IO^{II} metric tons/year of dry organic matter /Table I/.

Table I. Areas,phytomass and primary production of the Earth /dry weight,metric tons/.

TableI/continued/

Thermal belts	Area		Phytomass		Primary production	
	IO^{6}km^{2}	%	IO^{9}tn	%	IO^{9}tn	%
Polar	8.05	I.6	I3.77	0.6	I.33	0.6
Boreal	23.20	4.5	439.06	I8.3	I5.I7	6.5
Subboreal	22.53	4.5	278.67	II.5	I7.97	7.7
Subtropical	24.26	4.8	323.90	I3.5	34.55	I4.8
Tropical	55.85	I0.8	I347.I0	56.0	I02.53	44.2
Land/without glaciers, lakes and rivers/	I33.4	26.2	2402.5	I00	I7I.54	73.8
Glaciers	I3.9	2.7	0	0	0	0
Lakes and rivers	2.0	0.4	0.04	0.0I	I.0	0.4
All continents	I49.3	29.3	2402.54	I00	I72.54	74.2
Ocean	36I.0	70.7	0.I7	0.00I	60.0	25.8
The Earth	5I0.3	I00	2402.7I	I00	232.54	I00

Introduction

As the most vital of the zones enclosing the earth,the biosphere accumulates and converts the extremely powerful stream of incident solar energy into the chemical energy of organic compounds. This conversion is accomplished by an organic matrix that has constantly reproduced and perfected itself in the process of evolution over the thousands of millions of years of geological history.

Some fifty years ago,V.I.Vernadski /I926/ wrote: "Unfortunately,the data currently available still too scarce to pinpoint the exact share of green plants in the earth's total organic matter. For the present,we have to make the best of rather inaccurate figures in an effort to size up the phenomenon in hand". Today the situation has radically changed with the development of plant and soil maps,the accurate calculation of areas within particular soil-vegetation formations,and the determination of biological productivity for many of these formations. It has been shown that the earth's living organic matter /biomass/ is dominated /99 percent/by autotrophic and photosynthesizing organisms As a result of these developments it is now possible to characterize global biotic productivity based primarily upon the primary production of green plants.

Since organic matter is capable of reproduction,growth and accumulation only for a delimited period of time,it is fair to assume that phytomass reserves are correlated with annual increment[1]. Both parameters may be calculated either on a unit area of a given vegetation cover type. The geographical patterns of phytomass distribution per unit area /biomass/ for the major types of terrestrial vegetation already have been summarized and mapped /Rodin and Bazilevich,I965; Bazilevich and Rodin,I967/.

The data on geographical patterns show that each of the earth's thermal zones is associated with a particular soil-vegetation formation with characteristic biomass. Going from the polar through the boreal, cool temperate or "subboreal",to "subtropic"[2] to tropic[3] thermal zones,the range between maximum and minimum biomass increases because of an increase in absolute maximum and a decrease in absolute minimum values /see Bazilevich et al.,I97I,Table I p.295/. This phenomenon is associated,on the one hand,with changes in the efficiencies in energy fixation along pole-to-equator gradients with varying moisture supply and,on the other hand,with genetic properties and life forms of the plant communities. Within the intrazonal soil-vegetation formations these patterns are manifest with the same prominence,yet upon them are superimposed the effects of additional factors. An example is the geochemical sequence of landscapes which involves the redistribution of energy resources as well as water,nutrients,anaerobiosis, salinization,etc. Thus,in semiarid and arid regions,flood-land formations yield large quantities of biomass,while saline and alkaline areas yield very small quantities. In calculating the total global reserves of biomass,surface areas were categorized according to suitable types of soil-vegetation formations using the soil and continental vegetation maps from the Physico-Geographical Atlas of the World /I964/. These data were synthesized into I06 soil-vegetation formations which,in turn,were classed with thermal zones and hydrothermal /bioclimatic/ subzones /see Bazilevich et al.,I97I,Table 2,pp.295-302/.

Since our primary objective is to estimate the earth's biological potential, calculations of biomass and annual increments assumed that the vegetation cover existed in its precultivated or natural state /not exceeding I5 percent of the total dryland area/ or prelogging status. Besides the materials furnished by L.E. Rodin and N.I.Bazilevich /I965/,the authors used extensive new data on productivity of vegetation cover obtained during the International Biological Programme.

The total land phytomass reserves of the earth are estimated as $2.4 \times IO^{I2}$ metric tons. The bulk of this biomass occurs in the tropical zone - $I.35 \times IO^{I2}$ metric tons or over 56 percent of the total continental phytomass /minus rivers,lakes and glaciers/[4]. This phenomenon is not unexpected since the area of the tropical zone makes up almost 42 percent of the earth's total land area and almost half of this zone is vegetated by highly productive moist tropical forests /see Bazilevich et al.,I97I,Table 3,pp.304-305/

The boreal zone /I8 percent of the global reserves/ is second in biomass reserves followed by the "subtropical" /approximately I4 percent/,subboreal /approximately I2 percent/,and the polar zone /less than I percent/. It is noteworthy that the boreal,subboreal and subtropical zones are approximately equal in area. The differences in phytomass are primarily determined by the degree to which the landscape is covered with forests /which is greatest for the boreal zone/.

Within each of the thermal zones,a precipitous decrease occurs in total phytomass and average figures per unit area /biomass/ from humid to semiarid and arid bioclimatic regions,even though the latter may be more extensive in area. However, biomass values /phytomass per area unit/ for humid areas only /dominated by forest communities/ increases from north to south. This is a crucial factor responsible for the progressive increase in the biomass estimates throughout the thermal zones,moving similarly from subboreal to subtropical zones.

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[1] Hereafter figures for phytomass and annual increment will be given as dry weight.

[2] i.e.,warm temperate in customary English usage

[3] including equatorial

[4] The same holds for the total continental area of the entire earth since the phytomass reserves of inland reservoirs /rivers and lakes/ as well as the global oceans are much lower than in vegetation communities on land.

Thus, the geographic distribution of phytomass reserves over the earth's land is determined by the forest types of the different soil-vegetation formations. Indeed, the total phytomass reserves of the world's forests are I.96 x IO^{I2} metric tons, i.e., almost 82 percent of the entire terrestrial phytomass, with the total under forest cover amounting to 5 x IO^{7} km^{2} or 39 percent of the area of the earth's surface. Tropical zone forests make up half of this total /I.03 x IO^{I2} metric tons/, boreal zone forests account for some 20 percent /0.4 x IO^{I2} metric tons/ and subboreal and subtropical forests an additional I5 percent each. It is significant that the phytomass reserves of desert types of soil-vegetation formations, which occupy a total area of 2.89 x IO^{7} km^{2} /22 percent of the earth's surface/ make up only 0.02 x IO^{I2} metric tons or 0.8 percent of total land phytomass.

Oceanic phytomass

The distribution of oceanic phytomass generally follows the principles established for terrestrial environments, and yet there are some differences. The concept of the marine zonation was proposed by L.A.Zenkevich /I948/. Underlying this concept of natural oceanic zones is a combination of the same five factors that influence terrestrial productivity: light, temperature, nutrients, substrate and the interrelationships of organisms /Bogorov, I969/. Also important in the geography of terrestrial and oceanic phytomass is the effect of vertical /for land/ and abyssal /for ocean/ zonality. Similar to the land, the ocean is characterized by the alternation of zones high and low in phytomass /as well as in zoomass/. The zones of land and ocean which are relatively rich in living matter are characterized by the cyclonic regime of air and/or water circulation. Such regimes in the ocean cause mixing of water zones and upwelling of nutrients to surface phytoplankton. In areas with an anticyclonic regime, the surface waters sink and thus deprive the upper layers of nutrients. The areas poor in living matter are confined to anticyclonic regions in the center of the Pacific and Atlantic Oceans and in the southern Indian Ocean. The areas high in living matter occupy less than a quarter of the world's oceans /Bogorov et al., I968; Koblenz-Mishke et al., I968/.

And yet, in contrast to the land, the highest marine accumulation of living organic matter occurs at moderate temperate rather than tropical latitudes. This results not only from the cyclonic water currents and divergence, but also from the more intensive mixing of water layers in temperate latitudes under the influence of water-autumn temperature fluctuations. Additional factors in the high biomass of the littoral zone are sea-to-shore winds and nutrient inflow from river discharge, abrasion effects, discharge of underground waters, etc. The low amounts of biomass in high latitude and Antarctic waters are explained by the shorter growing season and lower water temperatures. The absolute phytomass reserves in the world ocean are not high, 0.I5 x IO^{9} metric tons of phytomplankton and 0.02 x IO^{9} metric tons of phytobentos for a total of 0.I7 x IO^{9} metric tons. Thus, the phytomass reserves on land exceed almost I5,000-fold those in the ocean /Bogorov, I969/. The earth's total phytomass /including 0.04 x IO^{9} metric tons occurring in rivers and lakes as calculated by Whittaker /I97I/ amounts to 2.4 x IO^{I2} metric tons.

Terrestrial annual production

The annual production of phytomass also may be expressed in dry weight per area unit by considering the areas of different soil-vegetation formations. These data have previously been published and plotted as schematic maps of the earth's terrestrial productivity /Rodin and Bazilevich, I965; Bazilevich and Rodin, I967/. These data reveal the same patterns obtained in examining the distribution of phytomass over the earth's land. Plant biomass /per unit area/ increases sharply from the pole to the equator within humid cyclonic regions and just as sharply drop to a minimum in arid anticyclonic regions /see Bazilevich and Rodin, I967, figure 2, pp.I92-I93/. Phytomass production per area unit in humid regions grows from less than 2 metric tons per hectare on the average in the polar zone to between 6 and I3 metric tons per hectare in the boreal and subboreal zones and to between 26 and 29 metric tons per hectare in subtropical and tropical zones. At the same time, the annual increment in arid regions follows a different pattern, increasing from 3 to 7 metric tons per hectare going from the subboreal to subtropic regions and dropping sharply in the arid tropics to an average of 2 tons per hectare. This is due to the wide occurrence in the arid subtropics of plant communities dominated by ephemers and ephemeroids yielding abundant phytomass.

These geographic regularities of distribution of annual increment /and also phytomass reserves/ correlate very well with climatic factors. This correlation is elucidated in the literature /Budyko, I956; Grigoriev and Budyko, I965; Budyko and Efimova, I968; Bazilevich, Drozdov and Rodin, I968/. The annual total phytomass increment of the terrestrial vegetation is put at I.72 x IO^{II} metric tons /7 percent of total phytomass reserves/. The bulk of the phytomass of I.03 x IO^{II} metric tons /60 percent of total phytomass/ is produced in the tropical zones,while the soil-vegetation formations of humid regions are responsible for 7.73 x IO^{IO} metric tons or 45 percent of the total increment of the earth's land . Second to the tropic is the subtropical zone /34.6.IO^9 tn,or 20 percent/. Being roughly equal in area, the plant formations of the subboreal and boreal zones produce much less organic matter - I8.IO^9 tn /IO percent/and I5.IO^9 tn /9 percent/ respectively. The annual increment in polar regions is the lowest: a little more than I.IO^9 /0.8 percent/.

The same as for phytomass distribution there is a sharp decline in annual increment within each of the thermal zones in the direction from humid to semiarid and especially arid regions. This pattern is the least pronounced in the subtropical zone and the most pronounced in the tropical one which is associated with the wide occurrence of arid types of vegetation largely dominated by ephemere in the former zone and vast areas practically devoid of vegetation cover in the latter. The annual total increment of desert formation fails to exceed 7.22.IO^9 tn or some 4 percent of the total land increment /the earth's area under desert makes up some 22 percent/.

Making up some 39 percent in area,forests produce almost half /49 percent or 84.I.IO^9 tn/ the annual total land increment.

It is also significant that,while occupying a very small area of some 3 percent, the soil-vegetation formations of deltas and flood-lands produce over 20.IO^9 tn /I2 percent/ of organic matter to additionally confirm their special biogeochemical character.

Oceanic annual production

The annual increment to oceanic phytomass according to the latest samplings at home and abroad is put at I.3-2.0 tn per hectare or,making a total,at 47-72.IO^{9}tn /Steemann et al.,I957 - quoted by Lieth, I964-I965; Gessner,I959;Koblenz-Mishke et al,I968;Whittaker,I97I/. Thus,the annual total increment of the World Ocean exceeds 30.000 percent of its total phytomass reserve[5]. This is all too natural since the ocean is dominated by unicellular plants with extremely rapid reproductive potentials. And yet,the annual increment of terrestrial communities is three times greater than the world's oceans /including the increment of rivers and lakes which, according to Whittaker /I97I/ produce I x IO^9 metric tons/year. It is significant that even though the ocean covers I80 times the area of rivers and lakes,its phytomass reserves are only four times as large.The geographical pattern of productive and low productive aquatoria is correctly described in the previous studies of primary production distribution over the world's oceans /Lieth,I964-I965; Koblenz-Mishke et al., I968/.

The data now available make it possible to estimate the primary production of the entire earth at 2.33 x IO^{II} metric tons/year of organic matter,with some 74 percent being produced by plant communities on land. The scanty data available in the literature on phytomass reserves both on land and in the ocean are summarized by Bazilevich et al.,I97I /see Table 4,p.3I2/. This Table also includes data on the mass of consumers and reducers for the purpose of assessing the total quantity of living matter of the entire planet. It is obvious from the Table that wide gaps between data from different sources still exist in some cases. Since phytomass data are limited, especially those from the beginning of this century,many researchers have attempted to estimate both phytomass reserves and total organic matter even though they based their conclusions on indirect information correlated only to the aboveground parts of plants.

The productivity data presented by Bazilevich et al.,/I97I,see pp.304-305/,reject the once prevalent opinion that most of the living matter is concentrated in the ocean. Recent studies have repudiated this past misconception /Koblenz-Mishke et al.,I968; Bogorov et al.,I968; Olson,I970; Whittaker,I97I/.

According to our estimates[6],the earth's total living matter is equal to 2.42 x IO^{I2} metric tons. The living matter of the land thus exceeds by some 750 times that of the world's oceans.

Conclusion

The figures of phytomass primary production in literature vary widely /see Bazilevich et al.,I97I,Table 5 p.3I4/. This is especially true of the estimated production on the continents.

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[5] Some I.700percent according to Whittaker /I97I/;since he put oceanic phytomass reserves at 3.3.IO^9; however,we relied upon a value of 0.I7.IO^9 tn in dealing with data from literature.

[6] The sequence of figures for consumers and reducers adopted in this paper is based upon the data of Duvigneaud and Tanghe /I968/.

According to our calculations, production by the terrestrial landscape far exceeds that published by most other authors with the exception of Deevy /I960/, the American workers as quoted by Duvigneaud and Tanghe /I968/, and the most recent data of Olson /I970/, Whittaker /I97I/ and Lieth /I972/. Such large differences may be most rationally explained by the fact that /i/ ones authors have relied on second hand information and have extrapolated widely in estimating primary production, /ii/ many have failed to take notice of the considerable annual increment produced by the underground parts of plants and /iii/ there has been a paucity of data of recent origin based upon modern analytical techniques.

Generalizations of potential primary productivity may best be estimated by evaluating the ratio between annual increment and phytomass of the continents. To calculate this ratio incorporating the data of those authors who fail to account for the extent phytomass reserves, it is advisable to use the value 2.4 x IO^{I2} metric tons which we have found to be the average phytomass value cited in most recent publications on the subject. These publications give ratios of increment to phytomass from 0.I5 to I.9 percent with the exception of Deevy, Lieth, Whittaker and the authors of this paper.

Yet, actual sampling of different types of terrestrial vegetation shows that there are few plant communities which yield such low ratios. Thus, the ratio between annual increment and phytomass reserves for tundra is between IO and 20 percent, for boreal and subboreal forests 2 to 5 percent; for subtropical forests 5 to 6 percent, for tropical forests 8 to IO percent, for the grass communities of steppes, prairies and savannas 20 to 55 percent, for desert communities 30 to 75 percent and for communities of annual field crops it is IOO percent /Rodin and Bazilevich, I965/. Thus, the absolute value of I.09 to I.72 x IO^{II} metric tons and the relative /6 to 7 percent/ values for annual increase in phytomass on land seem to be consistent with those of Whittaker /I97I/.

Estimates of the annual increments and reserves of land phytomass currently under discussion have been based on actual determinations. The patterns of distribution of living plant organic matter were established by a detailed calculation of the areas occupied by various soil-vegetation formations. This approach enabled us to calculate with greater precision the phytomass reserves and the relationships with the annual increment for the land. These results have been compared with our calculations of the corresponding values for the world's oceans, which illustrates the role of mineral nutrition in primary productivity. Phytomass production has been shown to be highest in the zone in which physiographic processes are most intensive due to a favourable combination of warmth and moisture, such as the tropical zone. Geographical regularities of phytomass distribution per unit area /=biomass/ for basic types of the earth's vegetation /Rodin and Bazilevich, I965; Bazilevich and Rodin, I967/ indicate that soil-plant formations with both high and low values are characteristic of every thermal belt. This is explained by a nonuniform latitudinal distribution of energy resources, different conditions of moisture supply, and by the genetic properties of primary producers.

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ENERGY FLOW AND BIOGEOCHEMICAL REGULARITIES OF THE MAIN WORLD ECOSYSTEMS

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Summary

For the first time calculation has been made of the reserves of chemical elements /sum total of N,Si,Ca,K,Mg,P,Al,Fe, Mn,S,Na,Cl and separate amounts of N,P,K, Ca/in the living phytomass,dead organic matter and in the annual production of the terrestrial plant formations of the main thermal belts and bioclimatic regions and in the World Ocean.

Green plants on the Earth play the most significant role in the cosmic energy transformation processes and in the mobilization of chemical elements contained in rocks. The geochemical work of green plants is determined by their mass and selective ability to absorb chemical substances.

Reserves of living phytomass of all plant formations on the land make up practically I00% of its reserves on the Planet /Bazilevich et al.,I97I/. The main phytomass production is concentrated in the forests. The living matter of all plants on our Planet has accumulated more than $IO \cdot IO^{I8}$ kcal. /Table I/.

Table I. Living phytomass,dead organic matter,annual production[x]and energy.

Table I /continued/

Subject	Land		Ocean		Earth as a whole	
	IO^9t	IO^{I8}kcal	IO^9t	IO^{I8}kcal	IO^9t	IO^{I8}kcal
Living phytomass	2402.5	IO.2I7	0.2	0.0006	2402.7	IO.2I8
Dead organic matter[xx]	563.8	2.84	I5IO.0	7.504	2073.8	IO.344
Land humussphere	2400.0	I2.00	-	-	2400.0	I2.000
Total	5366.3	25.057	I5IO.2	7.5046	6876.5	32.562
Annual production	I72.5	0.732	60.0	0.I94	232.5	0.926

[x] Excluding animal and microbial matter /$23 \cdot IO^9$t/

Note: in all tables the data in dry weight

[xx] Litter,steppe or desert matting/I93.8/; dry trees,standing dead /I50/;peat/220/-Land; detritus-Ocean.

The energy accumulated in the dead plant remains,including the detritus of the World Ocean /Gerlach,I97I/approximately amounts to that of the living phytomass. If this quantity is supplemented by the energy accumulated in the Earth's humus mantle /Kovda and Yakushevskaya,I97I/then the energy accumulated in the dead organic matter will by more than two times exceed that of the living phytomass.

Therefore, the modern biosphere has accumulated more than $32\text{-}33 \cdot IO^{I8}$ kcal /without taking into account the energy accumulated in the products of rock weathering/. In ancient biospheres /coal,oil,abyssal oozes, ground waters,organic matter of rocks,etc/ the amounts of accumulated energy are by several orders of magnitude greater.

The predominance of dead organic matter over the living one evidences the smaller rates of decomposition of plant /as well as animal/ remains as compared with the production of living organic matter.This, probably,reflects the climatic shifts in the geological history of the Earth/from Paleozoic to our days/towards cooler temperatures.

Especially great is accumulation of such dead plant remains as litter/about 80% of their total mass on the land/ in the plant formations of the Polar and Boreal belts /Table 2/. The reserves of litter in all the areas of the Tropical belt are low due to a high rate of decomposition of plant remains. According to Fittkau /I97I/,a complete litter-fall decomposition in the Amazon basin forests occurs in two weeks.

The annual primary production of the Planet is by one order of magnitude smaller than the reserves of living phytomass amounting to $232.5 \cdot IO^9$ tons /Bazilevich et al.,I97I/ and including that of the land /74%/where its amount is also determined by forest formations /mainly of humid tropics[x]/. The energy flow is close to $I \cdot IO^{I8}$ kcal/year /Table I/.

The living phytomass of the plant formation of the Earth has accumulated millions of tons of nitrogen and ash elements[xx] /Table 3/,practically I00% of which have been accumulated by terrestrial plant communities[xxx] mainly /more than a half/ in the humid-tropical forests /Th/ which is conditioned by their greatest reserves of living phytomass and higher content of nutrients in the organic matter.

A distinct tendency towards increasing an average content of N and ash elements

Table 2. Areas,reserves of litter,steppe or desert matting and reserves of nitrogen and ash elements.

Table 2 /continued/

Thermal belts,bioclimatic regions	Area, $10^6 km^2$	Reserves $10^9 t$	Nitrogen			Ash elements		
			total, $10^6 t$	%	content in matter, mean,%	total $10^6 t$	%	content in matter, mean,%
Polar /P/	8.05	48.11	855	25.0	1.8	1973	23.5	4.1
Boreal /B/	23.20	101.31	1763	52.0	1.7	3650	43.5	3.6
Subboreal/SB/	22.53	13.54	224	6.5	1.8	774	9	5.9
including humid /SBh/	7.39	9.08	162	5.0	1.8	519	6	5.9
including semiarid/SBs/	8.10	3.48	44	1.0	1.7	196	2	6.0
including arid/SBa/	7.04	0.98	18	0.5	1.8	59	1	6.0
Subtropical /ST/	24.26	12.70	228	7.0	1.9	681	8	5.6
including humid /STh/	6.24	6.64	112	3.5	1.8	343	4	5.5
including semiarid/STs/	8.29	4.93	87	2.5	1.8	278	3	5.6
including arid/STa/	9.73	1.13	29	1.0	3.0	60	1	6.2
Troipcal /T/	55.35	18.18	335	9.0	2.0	1345	16	8.0
including humid /Th/	26.50	13.77	228	7.0	1.7	979	11	7.4
including semiarid /Ts/	16.01	3.91	92	2.0	2.9	316	4	9.8
including arid /Ta/	12.84	0.50	15	0.5	3.0	50	1	9.7
Streams, lakes	2.00	0	0	0	0	0	0	0
Land total[x]	149.30	193.84	3405	100	1.7	8424	100	7.0
Ocean	361.00	0	0	0	0	0	0	0
Earth as a whole	510.30	193.84	3405	100	0.2	8424	100	4.1

[x] Glaciers including, $13.9 \cdot 10^6 km^2$

in the plant organic matter in the direction from plant formations of the Polar and Boreal belts to the Subboreal belt and further to the Subtropical and Tropical belts is observed. Within the belts this increase is traced in the direction from humid to arid areas. The above-stated tendency is also characteristic of litter /Table 2/ but the average contents of N and sum total of ash elements in the litter are noticeably higher than in living phytomass. These values are still higher for peats. On the contrary, the average content of nutrients in dry trees as well as in grass "standing dead" is the lowest: 0.2% and 0.7% of ash elements in 100 g of dry organic matter of terrestrial plant formations. An increase in the content of nutrients in litter and peat is conditioned by the processes of transformation of plant remains during their decomposition or conservation which are accompanied by humification and mineralization. These processes are also responsible for the changes in the composition of chemical elements, loss of the most mobile elements /Cl,Na/ and elements of the first minimum /K,P/and for a relative accumulation of less mobile elements /Ca and especially Si,Al and Fe/.

Despite a certain diversity of the leading elements accumulated in the living phytomass of various plant formations, the chemical composition of litter is comparatively monotonous /Table 4/.

The amount of nitrogen and ash elements consumed to build up the annual production of the Planet is approximately 2.5 times lower than their quantity accumulated in the living phytomass. This difference in the plant formations of the land reaches 5-6 times /Table 5/.

This regularity is stipulated by an extremely great rate of reproduction/and, consequently, absorption of chemical substances/ of the phytoplankton of the World Ocean as compared with the terrestrial green plants.

From the total amount of nutrients consumed by all plants of the Planet to build up annual production, 52% of N and 62% of ash elements are mobilized by the organisms inhabiting the Ocean, even though its annual production is almost 3 times smaller than that of the terrestrial plant formations. This phenomenon is explained by a considerably higher content of N and ash elements in a unity of organic mass of the annual production of phy-

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x/ High productivity is explained not only by great resources of energy and abundant water supply, but also by genetic peculiarities of edificators. Thus, Slack and Hatch /1967/ discovered in tropical plants a new enzyme responsible for a special pathway of the photosynthetic assimilation which increases the efficiency of photosynthetic active radiation /PAR/.

xx/ Account has been made of Si,Ca,K,Mg,Mn, Al,Fe,Ti,P,S,Na,Cl /Rodin and Bazilevich 1967; and others/

xxx/ The content of N and ash elements in phytoplankton of the World Ocean has been calculated from the data of Vinogradov (1953)

Table 3. Nitrogen and ash elements reserves in living phytomass.

Thermal belts, bioclimatic regions	Phytomass t/ha	Nitrogen			Ash elements		
		total, IO^6t	%	Content in matter, mean, %	total, IO^6t	%	Content in matter, mean, %
P	I7.I	98	I	0.7	II5	0.5	0.8
B	I89.2	I745	I2	0.4	4086	I2	0.9
SB	I23.6	I28I	9	0.5	2508	7.5	I.0
including SBh	342.0	IOII	7	0.4	I658	5	0.7
SBs	20.8	I77	I	I.0	596	2	3.5
SBa	II.7	93	I	I.I	254	0.5	3.I
ST	I33.5	I779	I3	0.6	4454	I3	I.4
including STh	366.I	I003	7	0.4	2588	8	I.I
STs	98.7	560	4	0.7	I283	3	I.6
STa	I3.9	2I6	2	I.5	583	2	4.3
T	243.3	9II5	65	0.7	22895	67	I.7
including Th	440.4	7604	54	0.7	I905I	56	I.6
Ts	I07.4	I406	I0	0.8	3503	I0	2.0
Ta	7.0	I05	I	I.I.	34I	I	3.9
Streams, lakes	0.2	2	<0.I	4.0	4	<0.I	I0.0
Land total[x]	I60.9	I4020	I00	0.6	34062	I00	I.4
Ocean	0.005	8	<0.I	4.5	36	<0.I	20
Earth as a whole	47.I	I4028	I00	0.6	34098	I00	I.4

[x] Glaciers including

toplankton of the Ocean in comparison with their average amounts in the annual production of terrestrial plant formations /Table 5/.

In the composition of nutrients consumed by terrestrial plant formations one can observe an increase in the share of Ca in the direction from the Polar to Boreal and Subboreal belts and in the share of Si, Al and Fe from the Subtropical to Tropical belts /Table 4/.

The average content of nitrogen and ash elements in the annual production of terrestrial communities increases in the direction from northern to southern latitudes and from humid formations to the arid ones, whereas an increase in the average contents of K and Ca is observed only from the Polar to the Subtropical belt and that of Ca only in the semiarid and arid areas. This is due to the leaching out of soils in the humid areas /predominantly forest ones/ and the substitution of Fe, Al, and partly Mn for Ca in the biological cycles of plant communities growing in

Table 4. Dominant elements in phytomass, litter /steppe or desert matting/ and annual production.

Thermal belts, bioclimatic regions	Phytomass	Litter /steppe or desert matting/	Annual production
P	N/Ca,K,Si/	N,Ca,Si,Al,Fe	N/K,Ca/
B	N,Ca,K	$\genfrac{}{}{0pt}{}{N}{Si}$,Ca,Al,Fe,Si	N,Ca,K
SB SBh	Ca,N,K	Ca,N,Si,Al,Fe	Ca,N,K
SBs	Si,N,Ca,K	Si,N,Ca,Al,Fe	Si,N,Ca,K
SBa	N,Ca,K/Na,Cl/	Ca,N,Si,Al,Fe	N,Ca,K/Na,Cl/
ST STh	Ca,N,K/Al,Fe/	Si,N,Ca,Fe,Al	N,Ca,K/Si,Al,Fe/
STs	Ca,N,Si $\genfrac{}{}{0pt}{}{K}{Mg}$ /Fe,Al/	Si,N,Ca,Fe,Al	Si,N,Ca $\genfrac{}{}{0pt}{}{K}{Mg}$/Fe,Al/
STa	Ca,N,Si/Fe,Al,Cl/	Si,N,Ca,Al,Fe	Ca,Si,N/Fe,Al,Cl/
T Th	N,K,Si/Al,Fe/	$\genfrac{}{}{0pt}{}{Fe}{Si}$,N,Ca,Al/Mn/	Si,N,Ca/Fe,Al,Mn/
Ts	Si,Ca,K,N/Fe,Al/	Si,N,Ca,Fe,Al	Si,N,Fe/Ca,Al/
Ta	Ca,Si,N/Fe,Al,Cl/	$\genfrac{}{}{0pt}{}{Ca}{Si}$,N,Fe/Al/	$\genfrac{}{}{0pt}{}{Si}{N}$,Ca,Fe,Al/Cl/

lower latitudes /Table 6/.

The average indices for P change insignificantly within the thermal belts since this element in the soils of the Subtropical and Tropical belts is firmly bound with R_2O_3 and is low mobile. Marine organisms play a leading role in the mobilization of P/an average content of P in phytoplankton of the Ocean is 0.6% versus 0.I% in the terrestrial plant formations/.

Thus, N and P are the typomorphic elements of the Ocean's phytoplankton; Ca is a typomorphic element of the terrestrial plant formations, and K is practically of the same significance for both.

The aforesaid enables us to conclude that despite the smaller annual production of the Ocean, the biogeochemical significance of phytoplankton in the mobilization of the most important organogens is greater than that of the terrestrial plant formations. This makes it imperative to revise once again the role of the Ocean as the main source of food resources of our Planet.

The geochemical work of living matter in various thermal belts and bioclimatic zones conditions the differences in the types of the small biological cycle and is most closely associated with the types of soil formation.

The biological cycle is not closed. Even in the arid bioclimatic zones chemical substances are removed by wind and partly by rainfall. In humid areas this is mostly done by migrating waters /surface runoff, intersoil lateral flow, removal into ground waters and subsequent trasporation of chemical substances to the Ocean with river flow/. Annual removal of various elements ranges from I0 to 40% of their amounts annually involved into the small biological cycle to create yearly annual production /Remezov, I962; Bazilevich and Djafarova, I972; and others/. The most firmly retained elements in the biological cycles of the terrestrial plant formations are N, K, Si, Fe and Al.

Chemical elements removed from a landscape are continuously replenished during

Table 5. Consumption of nitrogen and ash elements for building the annual production

Table 5. /Continued/

Thermal belts, bioclimatic regions	Annual production, t/ha	Nitrogen			Ash elements		
		total 10^6 t	%	content in matter, mean, %	total, 10^6 t	%	content in matter, mean %
P	I.6	I3	0.5	I.0	I7	0.5	I.2
B	6.5	I48	3	I.0	304	I.5	2.0
SB	7.9	226	4	I.2	580	3	3.3
including SBh	I2.6	I07	2	I.2	259	I.5	2.8
SBs	8.2	89	I.5	I.3	240	I	3.6
SBa	2.8	30	0.5	I.5	8I	0.5	4.I
ST	I4.2	5I5	9.5	I.5	I626	8.5	4.7
including STh	25.5	236	4.5	I.5	702	3.5	4.4
STs	I3.8	I72	3	I.5	550	3	4.8
STa	7.3	I07	2	I.6	374	2	5.3
T	I8.5	I620	30.5	I.6	5064	25	4.9
including Th	29.2	I230	23	I.6	4030	20	5.2
Ts	I4.I	346	6.5	I.6	9I6	4.5	4.I
Ta	2.0	44	I	I.7	II8	0.5	4.6
Streams, lakes	5.0	40	I	4.0	I00	0.5	I0.0
Land, total[x]	II.5	2562	48	I.5	769I	38.5	4.5
Ocean	I.7	2762	52	4.5	I2274	6I.5	20.0
Earth as a whole	4.5	5324	I00	2.3	I9965	I00	8.5

[x] Glaciers including.

the processes of soil formation and weathering which is preconditioned by a selective uptake of nutrients by plants from soils and rocks. Due to the denudation of the land surface /about 90μ /year; Maximovich,I955/ new and new strata of rocks are gradually involved into the sphere affected by plants. Correlations between the chemical elements removed,mobilized by living organisms and retained in a landscape are rather diverse and depend on the hydrothermal conditions as well as on the structure and composition of plant formations.

Table 6. Consumption of K,P,Ca for building the annual production.

Table 6. /continued/

Thermal belts, bioclimatic regions		K								
		total IO^{6}t	%	content in matter,mean, %	total, IO^{6}t	%	Content in matter mean %	total IO^{6}t	%	content in matter mean,%
P		5	0.5	0.4	2	0.5	0.I	6	0.5	0.5
B		82	4	0.5	I5	2.5	0.I	II6	5.5	0.8
SB		II5	5.5	0.6	20	3.5	0.I	I50	8	0.8
including	SBh	60	3	0.6	I2	2	0.I	77	4	0.8
	SBs	42	2	0.6	6	I	0.I	56	3	0.8
	SBa	I3	0.5	0.7	2	0.5	0.I	I7	I	0.9
ST		282	I3	0.8	36	6.5	0.I	35I	I7	I.0
including	STh	I30	6	0.8	I7	3.5	0.I	I56	7.5	I.0
	STs	89	4	0.8	I3	2	0.I	I2I	6	I.I
	STa	63	3	0.9	6	I	0.I	74	3.5	I.I
T		7I2	34	0.7	I05	I9	0.I	945	45	I.0
including	Th	538	25.5	0.7	73	I3.5	0.I	633	30	0.8
	Ts	I56	7.5	0.7	30	5	0.I	275	I3	I.2
	Ta	I8	I	0.7	2	0.5	0.I	37	2	I.4
Streams,lakes		I0	0.5	I.0	5	I	0.5	5	0.5	0.5
Land total^x		I206	57	0.7	I83	33	0.I	I573	75	0.9
Ocean		920	43	I.5	368	67	0.6	523	25	0.8
Earth as a whole		2I26	I00	0.9	55I	I00	0.2	2096	I00	0.9

^{x} Glaciers including

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THE REGULARITIES OF BACTERIA BIOMASS REPRODUCTION IN THE SOILS OF DIFFERENT GEOGRAPHICAL ZONES

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Summary

Abundance, biomass and productivity of bacteria in soils of different geographical zones were studied on the territory of the USSR. It was established that at a definite time of the growing season the number and biomass of bacteria become the subject of significant short-time fluctuations. The fluctuations of the greatest amplitude were noted in some tundra soils. In the direction to the South the fluctuations got a more moderate character. The periods of very intense fluctuations (when the multiplication and elimination of bacteria cells proceed at a maximum scale) were replaced by periods of relatively stable stata of microflora (when the frequency and the scale of changes decreased sharply) in all soils exluding semi-desert ones.

In semi-desert soils of Western Kazakhstan the fluctuations were observed permanently. The average multiplication rate of bacteria in summer was the greatest in some tundra soils and the lowest in some Siberian sod-podzolic soils.

The intensity of bacteria reproduction in different soils and in different months of the growing season was not equal. The raw wieght of month production of bacterial biomass varied between I.3 and 7I.0 mg per I g of dry soil. The same quantity of biomass was approximately eliminated within the same period of time.

Introduction

Microorganisms represent the more active part of the biosphere. Their special role in ecosystems results from the diversity of their biochemical features and the abilities to cause different transformations at an extremely high rate.

In accordance with V.I.Vernadsky's point of view (I967) the geochemical energy of living organisms is connected with their rate of multiplication. The greatest the multiplication rate of the organism the more important is its role in the migration of chemical elements in the earth crust.

Compared with other creatures microorganisms multiply with the greatest rate. E.Vacelet (I972) showed that the cells division of some species of bacteria took place every two minutes. However, these data characterize only the potential possibility of such rapid reproduction. Under natural conditions in soils this process proceeds at a different rate and its being so intense is doubtful. During the warm period of the season of growth the duplication of bacteria number in different soils requires usually several hours or several days depending on environment conditions (Parinkina, I972, I973; Zikina, I972, I972a; Bagdanavichene, I973).

The average time of bacteria generation in different soils and in diverse geographical situations varies from I8 to 3I2 hours in summer. Under the unfavourable environment the multiplication of bacteria proceeds more slowly and the generation time is measured by weeks (Nikitina & Sharabarin, I972).

It is quite clear that the biomass of bacteria in soil is renewed several times in the course of the growing season even in the conditions of very slow multiplication. However, the real scale and the rate of reproduction and destruction (i.e. the rapidity of bacteria biomass "turnover") of microbial cells in the soils of different geographical zones remained unstudied till recently.

During the period of the IBP investigations the estimations of the number, biomass and productivity of bacteria inhabiting the soils of different regions of the USSR were carried out by the participants of these works.

The main results of these investigations will be considered in this paper.

Material and methods

The following soils were used as the objects of investigations: the soils of tundra, of forest zone, of forest-steppe, of semi-desert ones and of maritime land.

The quantity of bacteria in each soil studied was estimated every day within a period of one month or more. Shulgina's modification of the direct count method by Vinogradsky was used. The size of cells was measured in the course of their counting and the data received were converted at first to volume and then to the weight ones (Zwiagintsev , I964). The density of cells was taken conditionally to be equal to I.

The estimation of bacteria productivity was carried on by means of the indirect method. It is known that the number of bacteria in soils is the subject of short-term fluctuations (Thornton & Gray, I930; Thornton & Taylor,I937; Khudiakov, I953). Significant increase and decrease of bacteria numbers take place every 3-5 days, even under constant conditions of temperature and moisture of the soil.

This phenomenon gives the possibility to calculate roughly the multiplication rate of bacteria and the whole production of their biomass synthesized within the period of observations.

The multiplication rate may be calculated for each period of increasing of bacteria number. The following equation may be used:

$$G = \frac{t.Lg2}{LgB-Lgb}$$

, where:

G - generation time in hours,t- time of increasing of bacteria numbers, B - maximum number of bacteria within the period, b - minimum number of bacteria.

The whole month or seasonal production of bacteris is calculated by means of summation of all reliable individual increasing of the weight of bacterial biomass during the corresponding period of investigations.

The general principles of method used had been suggested and considered by us (I972) before. A detailed description of the technique under consideration was given in the papers of O.Parinkina (I972,I973), L.zikina (I972,I972a) and of Schapova (I972).

Results and discussion

The changes of bacteria number and biomass in soils

The data obtained showed that at a definite period of the growing season number and biomass of bacteria in soils studied were the subject of significant fluctuations. The amplitude of these fluctuations was different in different soils (Table I).

The data obtained by Bagdanavichene (Lithuanian soils), Efremova (demi-desert soils), Nikitina,Sharabarin (Siberian soils), Parinkina (tundra soils), Schapova (Far East soils) and Zikina (meadow soils) are presented in tables I-3 . The fluctuation of the greatest amplitude were observed in some tundra soils. In the direction from the tundra regions to the semi-desert ones the fluctuations acquired a more moderate character.

It was noted (Parinkina,I972,I973; Schapova,I972; Zikina,I972, I972a; Nikitina & Sharabarin, I972; Bagdanavichene, I973) that the number of cells and the weight of bacteria biomass in soils decreased and increased every few days. In some tundra soils the quantity of bacteria decreased and increased a dozen,hundreds and in some cases a thousand times during I-2 days (Parinkina, I973).

The periods of intense fluctuations of bacteria number and biomass in soils (when the multiplication and elimination of these microorganisms proceed at a maximum rate) are replaced mostly by the periods of relatively stable state of soil microflora (when the scale of fluctuations sharply diminished).

As O.Parinkina nobed (I973), the most sharp fluctuations of bacteria biomass in some tundra soils proceeded in the last decade of July. In accordance with Bagdanavichene's (I974) observations more intense and frequent changes of bacteria biomass in sod-podzolic soils of Lithuanian SSR took place in May. In July the number of cells and the biomass weight decreased and no wide scale fluctuations were noted. In September the fluctuations in some cases became more intense than in July but don't reached such a great amplitude as in spring and proceeded on the background of the low content of bacteria in soils.

S.Egorova (I974) observed more significant changes of bacteria number and biomass in gray-forest soils of forest-steppe zone also in May.

T.Efremova (I974) established that the fluctuations under consideration proceeded in the semi-desert soils of western Khazakhstan in different time of thegrowing season with the same intensity approximately.

Consequently the curve of changes of bacteria number and biomass northern soils are characterized by a greater irregularity than in southern ones.

Multiplication rate of bacteria

The multiplication rate of bacteria in all soils studied was very change-

Table I.The limits of fluctuations of bacteria numbers (milliards per I g of dry soil) and biomass (mg per I g of dry soil) in upper horizons of soils.

Habitat	Observation time	Limits of fluctuations		Range of fluctuations	
		biomass	number	biomass	number
Taimyr, Dryas-carex mossy frost boil tundra, the soil of spot crust	VII-VIII	0.5-I7.0	0.05-38.75	I6.5	38.70
The same habitat, main surface	" "	–	0.07-8.90	–	8.83
Taimyr, the steep banks river, tundra soddy soil	" "	–	0.0I-32.00	-	3I.99
Karelian isthmus, meadow sod-podzolic soil, loamy sand	VII-VIII	0.I-7.5	I.5-I2.0	7.4	I0.5
	VIII-IX	0.3-2.0	0.6-2.4	I.7	I.8
Karelian isthmus, meadow sod-podzolic soil, sandy loam	VII-VIII	0.I-8.3	2.0-I5.0	8.2	I3.0
	VIII-IX	0.5-I.7	0.7-3.3	I.2	2.6
Lithuanian SSR, sod-podzolic cultivated soil, loamy sand under clover	V	0.7-4.7	3.96-25.03	4.0	2I.07
	VII	0.I-2.2	I.I7-6.75	2.I	5.58
	IX	0.2-I.9	I.02-4.93	I.7	3.9I
Lithuanian SSR, soddy calcareous soil, heavy loam	VIII	0.8-3.0	3.0-3I.0	2.2	28.0
Lithuanian SSR, sod-podzolic soil under oats, loamy sand	VI	0.6-4.5	5.0-28.0	3.9	23.0
Far East, Prikhankisky lowland, meadow podzolized glay soil	VII-VIII	–	4.I0-I0.30	–	6.20
The same habitat, cultivated soil, rice field	" "	–	4.5-I7.2	–	I2.7
Western Khasakhstan, semi-desert, dark coloured soil of depression under cereal association	V-VI	0.4-I.3	2.38-8.77	0.9	6.39
	IX-X	–	0.78-4.94	–	4.I6
The same habitat solontchak-solonetz under Artemisia and Kochia association	V-VI	0.2-I.I	2.I7-I0.29	0.9	8.I2
	IX-X	–	0.6-4.37	–	3.77

able. It varied within the wide limits depending on the period of the growing season and was the greatest during the more sharp fluctuations of bacteria numbers. This was noted by O.Parinkina (I972) in tundra soils in the last decade of July and by Z.Bagdanavichene (I974) in sod-podzolic soils in May.

The comparison of the average indices of the generation time of bacteria in the soils of different geographical zones led us to the conclusion that the multiplication rate of bacteria is the greatest in some soils of the extreme north (Table 2) The lowest multiplication rate of bacteria was noted in some Siberian soils by Z.Nikitina and U.Sharabarin (I972).

The size of biomass production of bacteria

The intensity of bacteria reproduction in different soils and in different months is not equal. The amount of the whole month production of bacteria biomass varies in summer between I.3 mg and 7I.0 mg per I g of dry soil. The same quantity of biomass is approximately eliminated within the same period of time, being eaten up by the components of soil microfauna or perished and lyzed.

Some data concerning the size of biomass production in different soils are presented in the table 3. It shows that the month production of bacteria is the greatest in the soils of tundra and the lowest in the soils of semi-desert.

Evdokimova (I973) observed the enormous month production of bacteria in the Risoplane zone of some grasses. This production reached more than I00 mg per I g of dry soil.

In the most part of soils the process of bacteria cells reproduction proceeds at an irregular rate. So, about 80 p.c. of the whole month production of biomass was formed in some tundra soils during 8-9 days in the last decade of July (Parinkina, I973). From 64 p.c. to 69 p.c. of the three months production of biomass (forming during May, July and September) were presented by May production in some sod-podzolic cultivated soils of the Lithuanian SSR (Bagdanavichene, I974).

Only in semi-desert soils of the western Kazakhstan the difference between the weight of biomass production forming in different months is not so significant (Efremova, I974).

Table 2. The average generation time of bacteria in upper horizons of soils (hours)

Habitats	Observation time	Generation time
Taimyr, Dryas-carex mossy frosz boil tundra, the soil of spot crust	VII-VIII	I7.7
The same habitat, main surface	" "	42.4
Taimyr, the steep banks of river, tundra soddy soil	" "	I8.0
Karelian isthmus, meadow sod-podzolic soil, loamy sand	VII-VIII VIII-IX	45.0 24.0
The same habitat, sandy loam	VII-VIII VIII-IX	38.0 54.0
Lithuanian SSR, sod-podzolic cultivated soil under clover, loamy sand	V,VII,IX	63.0
Lithuanian SSR, sod-podzolic cultivated soil, under oats	VI	38.0
Siberia, Low Irtish Station, sod-podzolic soil under spruce, silver fir and grasses, hor. A_0	VII	I05.0
A_I	"	IOI.0
The same habitat hor. A_0	IX-X	327.0
A_I	" "	300.0
Siberia, Onun Argunsky steppe shallow depth chernozem, freezing soil under steppe plants	VII-VIII	77.0
Western Khazakhstan, semi-desert dark coloured soil of depression	V-VI IX-X VIII	II3.6 6I.4 43.9

The different duration of the growing season in different parts of our country should be taken into account in the course of the consideration of the result obtained. This factor is of great importance for the intensity of the process under examination. In the conditions of the tundra the process of bacteria reproduction in soils proceeds with-

Table 3. Month production of bacteria biomass in the upper horizons of different soils (mg of raw weight per I g of dry soil)

Habitat	Observation time	Weight of biomass produced
Taimyr, Dryas--carex mossy frost boil tundra, the soil of spot crust	VII-VIII	54.0
The same habitat, main surface	"" ""	8.0
Taimyr, the steep bamks of river, tundra soddy soil	"" ""	7I.0
Karelian isthmus, meadow sod-podzolic soil, loamy sand	VII-VIII VIII-IX	2I.0 5.0
Karelian isthmus, meadow, sod-podzolic soil, sandy loam	VII-VIII VIII-IX	26.0 4.0
Lithuanian SSR, sod-podzolic cultivated soil	V VII IX	9.29 I.50 3.65
Lithuanian SSR, sod-podzolic cultivated soil, loamy sand	VI	4.0
Lithuanian SSR, sod-calcareous soil, heavy loam	VI-VII	3.0
Western Khasakhstan semi-desert dark coloured soil	V-VI IX-X IV-V VIII	2.7 I.9 2.3 2.4
The same habitat solonchack-solonetz	V-VI IX-X IV-V VIII	2.6 I.3 2.0 2.8

in a very short period of time and is very intense. This results in the greater scale of the month production of bacteria biomass in comparison with the production formed under the climatic conditions of middle latitudes and of southern ones.

In the direction from the North to the South the duration of reproduction process increases but its intensity decreases.

Not the month but the seasonal production should be used as a basis for the comparative evaluation of bacteria productivity in different soils independently of different duration of the growing season in divers climatic zones.

In some cases the weight of bacterial biomass formed in the course of the growing season or within a month is so high that the possibility of using the latter as the only energetical source for heterotrophes is doubtful. The existence of others available sources of energy in soils has to be supposed.

Probably the root excretions, the dead cells of plant roots and the repeatedly renewing biomass of soil algae may be considered as the underrated sources of energy in soils.

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PRODUCTIVITY AND CARBON METABOLISM OF BROADLEAVED FORESTS: A Summary of Progress from the International Biological Program[1]

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Woodland Workshops in Oak Ridge (1972) and Göttingen (1973) organized forest ecosystem data for analysis by four classes of ecosystems: tropical, other broadleaved evergreen, temperate deciduous, and coniferous forests. To stimulate interchange of data and concepts before completion of the IBP Woodland's Synthesis, this overview summarizes the major patterns of the organic carbon inventory and annual production of these ecosystems and their major structural components.

Forests are noted for their relatively large pools of organic carbon and nitrogen with relatively slow turnover coefficients, i.e., relatively long mean residence times. Non-living organic matter, which constitutes these large pools with slow turnover, still need to be functionally related to those of living biomass. New IBP forest data provide important contributions to the interrelationships between ecosystem biomass and productivity.

The large living support structures (bole, branch, roots) range from 2.67 to 4.51 x 10^4 kg dry wt/ha for boreal Picea to median values of approximately 1.45 x 10^5 kg/ha for Quercus forests and 4.14 x 10^5 kg/ha for old stands of Dipterocarpus rain forest to maxima of 9.67 x 10^5 for Eucalyptus. The maximum photosynthetic biomass (foliage) ranges from 5800 to 9000 kg/ha for tropical forests, 6880 to 10300 kg/ha for other broadleaved evergreen forests, 3000 to 4840 kg/ha for temperate deciduous forests, and 3340 to 9990 kg/ha for coniferous forests. Production/biomass ratios, net primary productivity, and ecosystem respiration will be discussed as these parameters vary among forest types and latitudinal gradients. Estimates of carbon residence times for major ecosystem components will be examined in relation to overall ecosystem metabolism.

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B3

The evolution of ecosystems and its contribution to biogeography and evolutionary theory

THE EVOLUTION OF ECOSYSTEMS AND ITS CONTRIBUTION TO BIOGEOGRAPHY AND EVOLUTIONARY THEORY: INTRODUCTION

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The first four of the papers on this symposium will be presented by persons who are participating in the "Origin and Structure of Ecosystems" Integrated Research Program, which is a component of the U.S. participation in the IBP. This project is both multidisciplinary and transnational in scope. Some 70 scientists of many specialties from 19 U.S. universities, other institutions and agencies and from Instituto Nacional de Investigaciones Agropecuarias, Instituto Miguel Lillo, Universidad de Buenos Aires, Universidad de Cordoba in Argentina and Universidad Catolica de Chile and Universidad Austral de Chile have participated in the research.

The concept of convergence at the level of individual organisms has had a place in evolutionary biology for a long time. However, this project, for the first time, examines the degree of convergence of whole major ecosystems that have evolved under relatively similar environments but on separate continents and while rather effectively isolated from one another. Two sets of comparisons are being made. One is between desert scrub systems, know respectively as the "Monte" in western Argentina and as the Sonoran Desert in southwestern North America. The other pair is comprised of the Mediterranean scrub systems as represented near Santiago, Chile and in southern California.

The basic question is whether or not the flora and fauna of two disjunct ecosystems that begin from a different basic situation must adopt the same strategy of adaptation when facing the same kind of physical environment. One consideration in comparing the disjunct ecosystems is that of just how similar are the physical environments of the two areas. The matorral of Chile and the chaparral of California occupy sites that are remarkably similar in physiography and climate, with winter rainfall, summer drought being a major climatic feature to which the system has had to adapt. The Monte and Sonoran Desert are comparable in physiography and climate, with both having generally less than 200 mm. of rainfall per year. However, differences in distribution of rainfall through the year might be expected to account for some differences in the two systems.

The comparison of the two parallel ecosystems must take into account several additional factors that have influenced their evolution. One of these is the age of the ecosystem. How long has the system been evolving? For the two desert scrub systems there is indirect evidence of various kinds that suggests xeric systems have been evolving for 25 million years or so on both continents. There is also evidence that the geographical locations of both xeric systems were shifted about under the global climatic fluctuations of the Pleistocene.

Another basic consideration is that of the availability of phylogenetic lineages from which the components of the system might evolve. If the same lineages were available down to a low taxonomic level (i.e. same genera) then it would be hard to argue that similarities in the systems represent convergent rather than parallel evolution. However, the isolation of South America from North America through much of the Cenozoic Era and the present latitudinal zonation of climate that imposes a vast belt of tropical rainforest between the two sets of arid-adapted systems account for rather major phylogenetic differences between the biotas of the South American and North American systems.

The plants of the matorral and chaparral differ largely in their taxonomy but show similar physiognomy. The dominant plants of the Monte and Sonoran Desert mostly belong to the same genera (<u>Prosopis</u> <u>Larrea</u>, <u>Cercidium</u>, etc.) and hence provide a very similar vegetational component in these ecosystems. The animals are largely different at the generic level between South American and North American counterpart systems. Vertebrates in the two desert scrub systems are illustrative. Among anuran amphibians, only one of six families and one of 10 genera are in both systems. Four of five families of lizards are shared, but only one of 17 genera is in both deserts. All five families of snakes occur in both, but only two of the 27 genera are shared. Only seven of 21 families of mammals occur in both deserts, and only seven of the 54 genera occur in both. The animals of the Chilean matorral also show major differences from those of the North American chaparral.

Similarities in ecosystem structure, and in function, as it involves plant-animal interactions, thus can be attributed in large part to evolutionary convergence in these systems that are being compared.

The final paper on this symposium takes a theoretical approach to mechanisms of ecosystem evolution and examines the possibility of natural selection operating at levels of organization higher than that of the individual.

AN EVOLUTIONARY APPROACH TO THE STUDY OF ECOSYSTEMS

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In recent years there has been increasing recognition of the importance of studying ecosystems (Evans, 1956) despite the fact that many of the earlier ecosystem studies suffered severely because insufficient information was available about the behavior of the populations within the systems (Andrewartha and Birch, 1954, p. 4). Whatever the extent of available knowledge about the component species, any model of an ecosystem requires that we make some trade-offs between reality, generality and precision (Levins, 1968). Different approaches to ecosystem studies reflect the values we place on the various objectives which might be pursued with the models and how seriously we value the loss of precision necessarily incurred when seeking generalities in such complex systems.

The approach to ecosystem studies which has dominated research during the past decade, and which has been institutionalized in the International Biological Program Biome studies, has been oriented toward ecosystem metabolism with the goal of developing energy budgets for different communities such as tundra, boreal forest, temperate deciduous forest, grassland and tropical forests. In these studies attempts are made to measure primary productivity and to determine the pathways through which this energy flows and the amounts moving through them.

There are good reasons for studies directed toward this goal. Energy is, after all, a major currency of ecosystem commerce and the patterns of energy flow are an important attribute of a community. In addition, our species is attempting to maximize production for human consumption without unalterably degrading the system. Since it is clear that we will continue to make concerted efforts to reduce the number of people suffering from malnutrition, knowledge of how far ecosystems can be bent to yield human food is of vital importance to our collective future.

Nevertheless, despite these important reasons for ecosystem studies oriented toward productivity, it would be unwise for ecosystem studies to be restricted to this one approach because there are serious limitations implicit in the goals and methods of these studies that can only be oversome by a variety of approaches. For example, the form of the question "What is the primary productivity of a grassland ecosystem?" reduces the likelihood that the answer will be generalizable. The direct answer to the question is a simple number though its determination may require years of effort on the part of many people. Once the number is obtained, there is no obvious way in which we can extend the result to other ecosystems except by repeating the laborious field work which was invested to obtain the first number. If it is generalizations we seek, a more profitable form of the question would be to ask "Is the primary productivity of a site predictable from a knowledge of the actual evapotranspiration on the area?" A positive answer to this question would strongly suggest that the ability of green plants to move nutrients through their bodies, which is rate-limited by transpiration through the leaves, is the prime determinant of photosynthesis. The importance of other factors, such as soil fertility, season of rainfall, etc., which do influence the rate of photosynthesis might then be estimated from the pattern of scatter of the regression of grass productivity on potential evapotranspiration. Once we know the slope of such a regression line we could predict the primary productivity in an area simply by an examination of the climatic data probably already available. This would save countless hours of field work.

A second limitation of the productivity approach to ecosystem problems is that the properties of the species are taken as given and the proximate consequences of these properties are then investigated. This leaves untouched the important problem of the evolution of the properties of the interacting species. This is of more than basic theoretical interest because as we intervene in ecosystem processes, we are selective agents and the properties of the species in the system change, often rapidly and usually in the direction of countering the kinds of changes in the system we are attempting to perpetuate. Some of our most dismal failures in ecosystem management have come from failure to recognize that, by entering as the most powerful selective agent in the system, we would inevitably evoke rapid responses. Thus, within three decades of the start of the use of DDT there are already over 200 species of crop pests that are highly resistant to the insecticide. New pests have appeared, and the evolutionary responses of the herbivores appear to have been more rapid than those of their natural predators. The results have been, to use Jay Forrester's phrase, "counter intuitive".

Therefore, without implying that productivity studies of ecosystems should be terminated, there is clearly a need for additional approaches with different goals that will better serve to meet the needs not adequately served by current ecosystem efforts. Several alternative approaches might be envisioned but here we describe only the approach that has been developed by the Origin and Structure of Ecosystems Integrated Research Program of the IBP.

An approach to the convergent evolution of ecosystems

As does any other approach, an evolutionary one requires decisions concerning goals and methods. Several restrictions are placed upon such studies by the very nature of the time spans of the evolutionary processes being investigated. For some ecosystem processes it is fruitful to use perturbation experiments to obtain interesting answers about proximate responses of the system to disturbance. For many other processes, however, it is simply not possible to perturb the environment and to measure a meaningful response to the perturbation within the period of several grants, not to mention the span of creative activity of individual scientists. Therefore, it is necessary to rely on a number of indirect approaches which take advantage of "experiments" which have been performed in nature and whose results are available to be measured. Our hypotheses are thus of the form "If natural selection had acted in the following way for a long period of time, then we would expect nature to have the following structure." George Gaylord Simpson (1949) suggested that this approach be designated "postdiction" since we are not predicting something that will happen in the future but are attempting to decipher the events of the past leading to present results. This is a standard technique in geology and is also widely used in evolutionary biology.

Origin and structure of ecosystems

The major focus of the Program has been to determine the degree to which the evolution of community structure and processes is predictable from a knowledge of the physical environment in which the community has evolved. This general problem has been tackled by the selection of sites of comparable climate and physical features that have been isolated from one another for long periods of evolutionary time. If this is the case, then any parallels or convergences exhibited by these separate communities can reasonably be attributed to the predictability of evolutionary outcomes in similar environments. Therefore, the initial stage of the program involved the selection of appropriate sites in the North and South Temperate Zones of the New World. The two communities selected were chaparral in California and Chile and Sonoran Desert in Arizona and Argentina. The actual study transects were selected on the basis of climatic criteria and similarity of physical factors.

The selection of sites does not, however, do more than provide a place where ideas can be tested. By itself it contains no ideas nor does it suggest methods. The formulation of hypotheses for evolutionary tests is one of the most critical aspects of the study and much of the success or failure depends upon the wisdom with which the problems are formulated. Since the focus is on the evolution of the properties of species and ecosystems, the critical problem is to determine what natural selection is expected to produce.

Our understanding of the fundamental process of natural selection is still similar to what it was when Darwin first formulated it. His version of the theory was purely phenotypic but he assumed that the traits he was dealing with had some heritability. During the past few decades there has also been developed a genetical theory of natural selection in which fitnesses are applied to alleles rather than to phenotypes (Fisher, 1958). This theory gains precision of inheritance, because genes very accurately determine their progeny, but it loses precision in measuring fitness which resides in the phenotype and not in the genotype. The genes do not directly determine phenotypes but, in turn, the phenotype provides uncertain information about the genotype (MacArthur and Connell, 1966). Which of these trade-offs is more desirable depends upon the goals of the investigation and the extent of our knowledge. Our knowledge of the inheritance of most ecological traits is meager or nonexistent, and for this reason alone we are compelled to deal primarily in phenotypic approaches to natural selection. This has been done in the present study.

The theory of natural selection as developed by Darwin, and as since refined by evolutionists and population geneticists, is based on the differential fitness of individual phenotypes (or genotypes). As emphasized by R. A. Fisher (1958) the question of the "good of the species" or the "good of the community" has no meaning in terms of the mechanisms now known to be operative, though this does not preclude the discovery of presently unknown mechanisms. This problem has been reviewed more recently by Brown (1966), Lewontin (1970), Maynard Smith (1965) and Williams (1966). For this reason our study has not posed questions such as "Why did the community evolve to put so much energy into nonphotosynthetic tissues?" Instead we have asked why plants with a particular apportionment of their resources have been effective competitors in that environment. The difference in the form of the two questions is non-trivial and leads to generalizations about community dynamics of a very different form. We attempt to understand all features of the community in terms of selection for individual organisms with attributes making them successful in that environment. These properties then combine to yield the community characteristics which are also of interest to us. Any "emergent" community properties must be consistent with selection at the level of individual phenotypes even though they need not be immediately obvious consequences of that selection.

These constraints in the theory of natural selection set the boundaries to the kinds of models we have erected and tested. Basically these are in the class of optimality models (Rosen, 1967), and our problem is to guess what natural selection has actually optimized. The hypotheses have to be stated in a form which leads to "postdictions" about some structure or process in nature which are open to verification or falsification in the study areas. Failures to obtain confirmation can then lead to the rejection or modification of the original hypotheses and may also lead to new ideas about evolutionary processes. The hypotheses may be very specific in their focus, such as the adaptive significance of the shapes of leaves, or the role of some specific chemical in anti-herbivore interactions, or they may be more general, dealing with resource acquisition over a life span or means of surviving fluctuations in weather of long periodicity. Normally the narrower the focus of the model the greater is its precision but the less applicable the results are to other aspects of the system.

The two study systems were selected because we already did have knowledge that at the gross level of vegetative physiognomy there was convergence. What was unknown, however, was the degree to which this convergence was expressed at other trophic levels and also in finer adaptations of the vegetation. An excellent example of the kind of reasoning employed to deal with this kind of problem is given by Mooney and Dunn (1970) in an analysis of the selective forces resulting in the convergence toward chaparral vegetation wherever there are wet winters and hot, dry summers. The similarities of hot (Sonoran) desert vegetation in different areas of the world are striking, but instead of converging on a rather uniform plant type, as occurs in Mediterranean climates, the desert vegetation includes a diversity of physiognomic plant types, such as fleshy stem succulents, slender stem succulents, sclerophyllous shrubs, mesophyllous shrubs with leaves only during the rains, annuals, etc.

Our project has been involved with the erection of hypotheses at all trophic levels in the community. Included are studies of the morphology and physiology of the dominant plants, pollination systems, plant-herbivore interactions and community structure among various groups of carnivores and scavengers. Which organisms have been studied and the types of questions asked about them has been determined primarily by the availability of investigators and their individual training, skills and inclinations. No attempt was made to force people into particular boxes in some organizational chart, but interchange of ideas and information was aided by regular research conferences, some of them at the field sites. We feel that if we have developed and tested models with skill and insight we will be in a better position to understand both immediate and long-term effects of our interventions in the processes of these, and hopefully other, ecosystems.

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THE ORIGIN AND STRUCTURE OF AMERICAN ARID-ZONE ECOSYSTEMS

THE PRODUCERS: INTERACTIONS BETWEEN ENVIRONMENT, FORM AND FUNCTION

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INTRODUCTION

The concept of subdividing the vegetation of the world into catagories based on the form of the plants is old, appearing in Greek literature. Early attempts classified vegetation of the basis of a static concept of vegetation form (Humboldt 1806). After Darwin, classification systems included a concept of the biological significance of the different life forms. Grisebach (1872), Drude (1913), Schimper (1898) and Warming (1895) proposed systems relating life form to climate. Raunkiaer (1934) proposed a scheme to compare different vegetation types statistically, based on the position of the overwintering buds. Clements (1916), Tansley (1935), and Braun-Blanquet (1951) began their vegetation classification schemes with divisions based on the form of the vegetation. The later schemes assumed that the form of the vegetation was causally related to climate. The functional factorial approach of Jenny (1941) and Major (1951) generalized that any ecosystem or vegetation property depends on climate, relief, parent material, floral or faunal history, and time. The repeatable patterns of form, function, climate, and soil gives ecologists the basis to generalize from one geographic area to another.

Ascertaining the essential relationships in the interactions between climate and vegetation form and function is a vital area of ecological research. This analysis can proceed by selecting two geographic areas with broadly similar climates and broadly similar vegetation forms. The degree of similarity and dissimilarity can be assessed and existing concepts of the interrelations between primary production, microclimate, and plant growth can be used to explain both the similarity and dissimilarity of vegetation form and function. The working hypothesis, in functional factorial notation, is that given similar climates, similar vegetation will occur, if topography, parent material, and recent disturbance (time) are matched, regardless of floral and faunal history. This convergence of form from different genetic stock will occur either through the evolution of genotypes or through the selection of species, in order for the plants to attain a favorable carbon balance through the year. The convergence of form should be especially apparent on those characteristics which are important in maintaining carbon balance. Mooney and Dunn (1970), Mooney and Parsons (1973) and Mooney (1973) formulated qualitative models of the diverse factors leading to convergence of form and function. They considered patterns of allocation of carbon to productive, supportive, root, and reproductive systems. The carbon costs of allocating to these systems involved costs of construction maintenance, and protection against herbivory. The carbon gain was through an allocation scheme such that photosynthesis by the productive system was least hampered by light, water, or mineral limitation in any climatic and edaphic situation.

There now exists a body of mathematical, physical, and physiological analyses synthesizing some of the details of the climate-microclimate-stand structure-water-and primary production system which can be used to analyze some of the interrelations between the climate and the form and function of the vegetation (Monsi and Saeki 1953; Davidson and Phillip 1958; Monteith 1965; DeWit 1965; Duncan et al. 1967; Miller 1969, 1972, 1973; Miller and Tieszen 1972; Lemon et al. 1971, 1973; Stewart and Lemon 1972; Anderson 1966; Gaastra 1962; Chartier 1969; Waggoner 1969; Slatyer 1970; Lommen et al. 1971; Denmead 1964; Waggoner and Reifsynder 1968; Waggoner et al. 1969; Gates 1962, 1965, 1968; Raschke 1960). If the essential aspects of the interrelations are encoded, the models should assign different relative importances to plant properties in different climates, which should correspond with the observed different life forms in different parts of the world. On the other hand, the models should assign similar relative importances to plant properties in different geographic regions which have similar climates. The plant properties of greater importance to the carbon balance should be those which show the greatest convergence of form, and plant properties of lesser importance should show the least convergence. A correspondence between the prediction based on simulation experiments and field observations will increase our confidence in both. A lack of correspondence should cause a revision of our concepts.

MEDITERRANEAN SCRUB AREAS OF THE WORLD

The Mediterranean scrub areas of the world are examples of areas with similar climates and similar vegetation, but with different genetic histories. Such areas occur around the Mediterranean Sea, on the southwest coast of South Africa, in southern Australia, in southern California, and in central Chile (Fig. 1). Aschmann (1973) defined the Mediterranean climate as having one month with an average temperature below 15°C, but not so cold that more than 3 per cent of the hours of the year are below 0°C. The arid boundary has 275 mm of precipitation per year. At least 65 per cent of the yearly precipitation must fall in the winter six months, November through April in the northern hemisphere and May through October in the southern hemisphere.

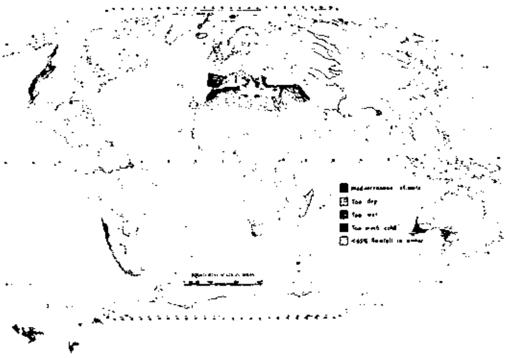

Figure 1. World map of the areas with Mediterranean climates (from Aschmann 1973).

MEDITERRANEAN SCRUB AREAS OF CALIFORNIA AND CHILE

The Mediterranean scrub areas of California and Chile are centered around 32.5° latitude. At these latitudes, climatic and vegetational differences occur between countries and within each country, providing some variation to test the predictions. The climate of California is warmer and more continental than that of Chile (Fig. 2). California experiences air masses from the inland deserts, especially in the fall, and some summer precipitation from tropical storms which develop to the south. The coastal climate in both countries is warmer in winter and cooler in summer, and has less precipitation, than the interior climate. Mean temperatures and precipitation for the two areas are similar, but extremes diverge.

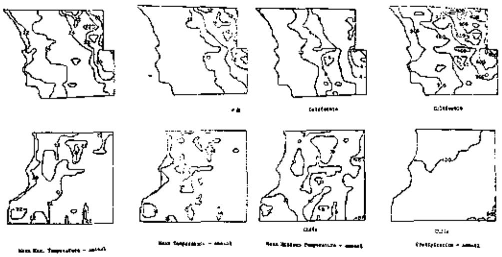

Figure 2. Isopleths of annual mean maximum, mean, and mean minimum temperature and precipitation for southern California (Between latitude 32°32' and 33°25') and central Chile (Between 32°30' and 33° 15'). Elevation range is from sea level to 2000 m (from Hynum 1974).

Solar radiation in the summer tends to be slightly less in southern California than in Chile, and in the winter slightly more in California than in Chile. This difference is because the earth is closer to the sun on December 21 than on June 21, and the difference is reflected in our measurements in the two countries (Fig. 3). Solar radiation in the summer was about 60 cal cm^{-2} day^{-1} less and in the winter about 30 cal cm^{-2} day^{-1} more in southern California than in Chile. In both countries solar radiation at the coast is about 100 cal cm^{-2} day^{-1} less than in the interior because of fog and cloudiness.

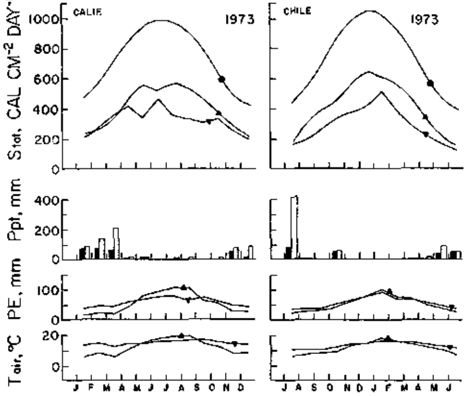

Figure 3. Seasonal courses of potential solar radiation at the top of the atmosphere (●), measured solar radiation at the inland sites (▲), measured solar radiation at the coastal sites (▼), precipitation at the inland (clear block) and coastal (dark block) sites, potential evapotranspiration inland (▲) and coastal (▼), and mean air temperature inland (▲) and coastal (▼) for 1973 in California and Chile.

Diurnal variations in air temperature of 20°C were common at the inland site in California, but variations were rarely greater than 10°C at the inland site in Chile. Air temperatures in the summer were between 10 and 35° in California and 10 and 30° in Chile. Air temperatures in the summer were between -2 and +15° in California and 5 and 17° in Chile. Soil temperatures at 2 cm depth reached 55°C repeatedly from April to August during a dry year and 37°C during a wet yeat at the inland sites in California, while at the inland site in Chile they reached 43°C. Minimum soil temperatures at 2 cm were colder in California than in Chile.

Soil moisture is high throughout the soil profile in winter and spring. As the soil dries out the spring, surface layers dry faster. At San Dimas in southern California soil moisture was above the wilting point from December to June throughout the profile and above the wilting point all year at about 1.2 m (Mooney, et al. 1973). At the inland sites in California and Chile and at the coastal sites in California, soil moisture below 30 cm depth was above -10 bars throughout the year on ridgetop sites, but below -10 bars at these depths on pole facing slopes. Soils dried earlier in the spring at the coast than at the inland site.

The drier conditions along the coast are reflected in measurements of plant water potential and leaf resistance to water loss. Dawn xylem water potentials of Heteromeles arbutifolia, a characteristic California chaparral shrub occuring at both the coastal and inland sites, were lower than -20 bars from June to mid-November at the coast and from mid-August to mid-November in both sites. Midday water potentials were lower than -35 bars from late July to mid-November at both sites. The relation between xylem water potential and leaf resistance to water loss is such that at -20 bars leaf resistances are three times the minimum leaf resistance and at -35 bars stomates are fully closed. Along the coast leaf resistances in June were low in the morning and high through the rest of the day, but from August to mid-November resistances were high throughout the day. At the inland site, resistances were low throughout the day in June and July and low in the morning in early August. Resistances were high through the day from late August until mid-November. Thus the period of water stress was about one month longer at the coast than inland, as measured by the leaf resistance, or about two months longer, as measured by the xylem water potential. It is expected that photosynthesis was suppressed by the high leaf resistances for about 90 days in the interior and 150 days at the coast.

In both countries the vegetation of the interior consists of evergreen, sclerophyllous shrubs with broad-leaves 0.2 to 3 cm wide (Mooney, et al. 1970; Parsons 1973). Towards the coast in both countires, deciduous soft leaves shrubs with leaves 0.2 to 2.0 wide, and succulents, become more common (Parsons 1973; Mooney et al. 1973). Mooney and Parsons (1973) suggested that along an aridity gradient from dry to wet, plant communities are arranged thus: coastal sage, chamise chaparral, mixed chaparral, oak woodland, and riparian woodland. Towards increasing aridity succulents become increasingly common. With increasing elevation and colder temperatures, the winter deciduous form becojes more abundant (Parsons 1973) (Fig. 4). Carter (1973) showed a higher percentage of perennial herbs in Chile and a higher percentage of annuals in California. The significance of these patterns of vegetation and the associated climate can be explained by simulation models of photosynthesis and plant water relations.

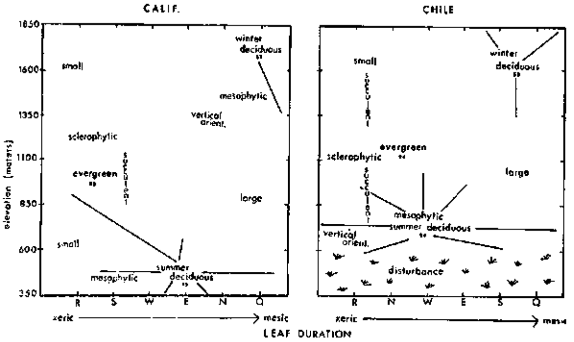

Figure 4. Distribution of characteristics of plant species along altitudinal and moisture gradients in California and Chile (from Parsons 1973).

SIMULATION RESULTS

Simulation of the seasonal course of canopy photosynthesis and water relations were run using physiological data for Heteromeles (Harrison 1971; Poole 1974), for which the most complete set of physiological data of the Californian and Chilean shrubs exist, and soil water potential data from California. The simulations used horizontal topographic positions and a canopy with a leaf area index of 0.5 in both countries. This leaf area index was estimated from the percent cover on ridgetops at both interior research sites and gave realistic surface soil temperatures and temperature profiles in the simulations. The actual leaf area index is somewhat higher but effectively reduced by the clustering of the leaves. The independent variables were the climates of California and Chile. The average daily courses of total and diffuse solar radiation, infrared radiation from the sky, wind, air temperature above the canopy, soil temperatures at 30 cm, vapor density above the canopy, and the average soil water potential in the profile for each month for each country were used as input data and the daily courses of vertical profiles of total, diffuse, reflected and absorbed solar radiation, downward and upward infrared radiation, wind, air and leaf temperatures, soil temperatures, vapor densities, leaf water potentials, leaf resistances to water loss, transpiration, water uptake from the soil, and photosynthesis were calculated. Output was compared against data on the microclimate, soil moisture, and plant water relations. The model proceeds in five minute time steps through the day (Miller 1972, 1973).

EVERGREENESS AND ANNUAL COURSE OF PHOTOSYNTHESIS

The results of the simulation showed that stand net photosynthesis is positive throughout the year at the inland sites, but is highest in spring and low in the summer, fall and winter (Fig. 5). Water use efficiency (mg organic matter produced per g water transpired) is high in the spring and fall, and low in winter in both countries. In the summer water use efficiency is low in California and high in Chile. Solar radiation absorbed by leaves is high in the summer and low in the winter. By the time fall and winter rains begin, absorbed solar radiation is low. The spring season has both available moisture and high solar radiation. Maximum and minimum air temperatures through the canopy show warmer daytime air temperatures and cooler nighttime temperatures in California than in Chile. Leaf temperatures departed more from air temperatures in California than in Chile, both during the day and the night. Soil surface temperatures were similar in both countries. The unusually wet spring in California in 1973 is noticeable in depressed temperatures in March. The calculated values for stand production are similar to those estimated by Specht (1969).

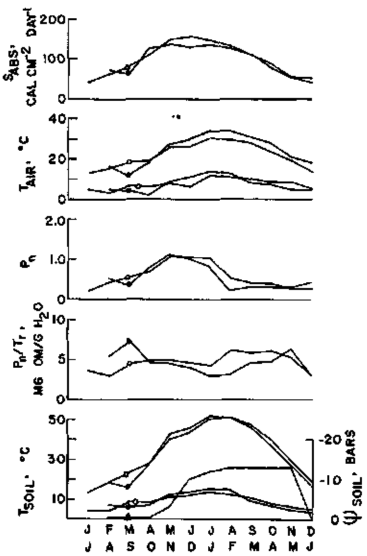

Figure 5. Simulated seasonal courses of absorbed solar radiation, maximum and minimum air temperatures, net photosynthesis, water use efficiency (mg organic matter produced/ g water transpired), maximum and minimum soil surface temperatures for California (●) and Chile (○) and soil water potentials for Chile, based on Heteromeles.

Evergreeness should confer an advantage in climates where photosynthesis is possible throughout the year. The relative advantage of the evergreen life form compared with the drought deciduous life form may be clarified with some simple bookkeeping. The density of new leaves of Heteromeles arbutifolia was 1.3 g d.w. dm^{-2} and of old leaves, 2.0 g d.w. dm^{-2} (Mooney, Parsons, and Kummerow 1973). The leaf densities of evergreen shrubs in Chile and California were similar (1.0-2.7 g d.w. dm^{-2}) and about twice that of drought deciduous shrubs (0.5-1.4 g d.w. dm^{-2}). The respiratory cost of producing this leaf biomass will be 30 to 50 percent of the leaf weight, depending on the biochemical composition of the leaves (Penning de Vries 1972). The construction costs of a dm^2 of an average evergreen leaf (2. g d.w. dm^{-2}) would then be about 2.7-3.0 g d.w. dm^{-2}. If the maintenance respiration cost is 1.5 percent of the dry weight per day (McCree and Troughton 1970), the cost of maintaining a dm^2 of leaf for 90-100 days will equal the cost of constructing a new dm^2 of leaf. The evergreen form should be more favored than the drought deciduous form in areas where photosynthesis is neglible because of soil drought or cold temperatures for a period of less than 90-100 days and less favored in areas of drought or cold temperatures lasting more than 90-100 days. The lengths of the soil drought at the coast and inland sites correspond with the greater incidence of deciduous shrubs at the coast than inland. At 2000 m, where the deciduous form appears again, cold temperatures may limit production for about 3 months.

The photosynthetic efficiency of different life forms has been summarized by Sestak, Catsky and Jarvis (1971), Mooney (1972), and Tieszen and Wieland (1973). The photosynthetic efficiency of evergreen shrubs is about half that of deciduous shrubs or annuals. For Californian and Chilean shrubs the maximum photosynthetic rate of evergreen shrubs was 10.2 mg CO_2 dm^{-1} hr^{-1} (range 4.5 to 16.) and of drought deciduous shrubs, 24.5 mg CO_2 dm^{-2} hr^{-1} (range 15-42) (Harrison, unpublished; A. Gigon, unpublished; Dunn 1970). Photosynthesis in the field will be reduced by lower solar radiation, temperatures above or below optimal, or when water stress forces stomatal closure during the day. If the photosynthetic return from a dm^2 of leaf is about 10 mg CO_2 dm^{-2} hr^{-1} for an evergreen and 25 mg CO_2 dm^{-2} hr^{-1} for a drought deciduous shrub and assuming 0.614 g d.w. per g CO_2, it would take about 480 hours (60-80 days at 6-8 hours per day) to regain the cost of construction of one dm^2 of leaf for an evergreen shrub and 192 hours (24-32 days) for a drought deciduous shrub. The evergreen shrub requires a productive period of about 2-3 months and a deciduous shrub a period of about one month to regain the cost of leaf growth. Photosynthesis beyond these periods can contribute to the cost of root maintenance, which might equal the cost of leaf maintenance, and to reproduction. If the photosynthetic period is less than these periods, both life forms are disadvantaged.

VERTICAL PLACEMENT OF PRODUCTIVE TISSUE

The seasonal course of absorbed solar radiation profiles indicates solar radiation limitation of photosynthesis at the bottom of the canopy throughout the year, but especially in winter (Fig. 6). Net daily production was positive at all levels in the canopy in all months, but at the bottom of the canopy production was limited by the low radiation. The levels of absorbed solar radiation found at the top of the canopy in winter are found at the bottom of the canopy in spring and summer. The California profiles show less seasonal variation than the Chilean profiles, because of the different levels of incoming solar radiation in the two countries. The profiles depend upon the incoming solar radiation and the interception of solar radiation by the canopy, which increases in the winter because of the lower solar altitudes.

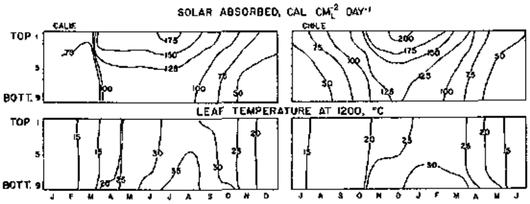

Figure 6. Simulated seasonal courses of the profiles of absorbed solar radiation and noon leaf temperatures through the canopy in California and Chile from 1973. March 1973 was unusually cold in California.

Profiles of leaf temperatures at noon show the hottest leaves within the canopy, because of higher air temperatures and lower wind speeds near the ground (Fig. 6). Leaf temperatures in California are higher than those in Chile, and are over 30°C at the bottom of the canopy in spring and fall and are over 30°C throughout the canopy in the summer. Californian leaf temperatures are about 35°C at the bottom of the canopy in summer. Chilean leaf temperatures are above 30°C only at the bottom of the canopy in summer. The profiles show the greatest differentiation from top to bottom in summer and least in winter.

Photosynthesis and growth depend on the temperatures and water status of the leaf. The relationship between photosynthesis and temperature usually shows a broad temperature range within which photosynthesis is near maximal, decreasing at temperatures lower or higher than an optimum temperature. In southern California the optimum temperature for photosynthesis of Heteromeles arbutifolia was about 25°C (Harrison 1971), but varies with species and acclimation history (Mooney and Harrison 1970).

The seasonal course of the vertical profiles of primary production and water use efficiency (Fig. 7) show the effects of limitation by solar radiation and temperatures. In this figure the profiles for each month have been standarized by dividing the photosynthesis rate or water use efficiency at each level by the mean photosynthesis rate (in mg CO_2 dm^{-2} leaf day^{-1}) or water use efficiency for the profile to eliminate month to month variation. In the winter, temperatures are suboptimal and solar radiation is low within the canopies, and maximum daily photosynthesis is at the top of the canopies. Water use efficiencies are high at the top and bottom of the canopies. In the spring, temperatures are nearly optimal in both countries, but cooler in Chile. Solar radiation levels are higher throughout the canopies and photosynthesis is similar through the canopy profiles. Water use efficiency is highest at the bottom. In the summer, temperatures are above optimal in California and slightly above optimal in Chile. Solar radiation levels are high throughout the canopy, but the temperature profiles are such that maximum photosynthesis and water use efficiencies are at the top of the canopies. In the fall, temperatures return to optimal and suboptimal but solar radiation is decreased. Maximum photosynthesis and water efficiencies are slightly higher at the top of the canopies.

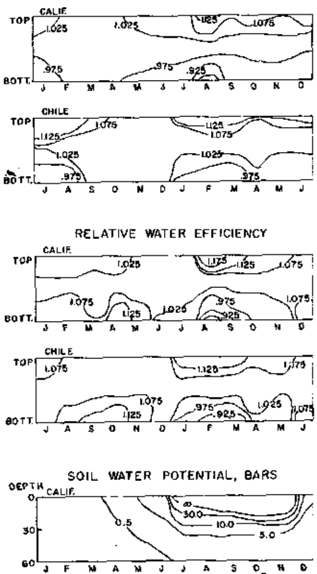

Figure 7. Simulated seasonal courses of relative production (photosynthesis in mg $CO_2\ dm_\ell^{-2}\ hr^{-1}$ at each level divided by the mean photosynthesis rate for the profile) and or relative water use efficiency (water use efficiency at each level divided by the mean water use efficiency for the profile) at different levels in the canopy for California and Chile, and of the profile of soil water potentials in California, using 1973 data.

The profile of soil water potential through the season for California shows water available throughout the soil profile in the winter and early spring. By late spring and through the summer, moisture is unavailable at the surface but is available deeper in the soil. When precipitation begins in the late fall and winter, solar radiation and temperatures are low.

The yearly course of the productive structure of the vegetation follows the pattern of having the productive structures located in the profiles where maximum photosynthesis and water use efficiency occur. In the spring, herbs tap the shallow soil moisture and are close to the ground while surface temperatures are optimum for photosynthesis, and die or become dormant in the summer when the surface moisture is gone and the surface temperatures are above optimum. In the spring and summer, shrubs tap the deeper soil moisture and are high off the hot ground where temperatures are cooler. In order to obtain deep soil moisture throughout the year the plants need deep roots, and to utilize this moisture efficiently the photosynthetic and transpiring tissue is placed off the ground surface in a shrub form, which increases photosynthesis and water use efficiency.

LEAF WIDTH AND INCLINATION

Leaf temperatures depend upon all the factors which effect the processes of energy exchange, such as solar and infrared radiation, wind, air temperature, and the vapor density of the air, and upon leaf properties such as orientation to the sun, width, mutual shading, absorptance, and resistance to water loss (Gates 1962, 1965, 1968). The convectional exchange of heat of leaf from air temperature is caused by a positive or negative radiation balance or by transpiration and the departure increases as leaf width increases. The photosynthesis rate may be increased or decreased by this additional temperature, over air temperatures, during the day depending upon the temperature of the leaf in relation to the optimum temperature for photosynthesis. Transpiration will tend to be increased by higher leaf temperatures. In the winter, when leaf temperatures are below the optimum temperature for photosynthesis, wider leaves will have higher leaf temperatures during the day and may have higher photosynthetic rates. Transpiration will tend to increase. In the simulations the total effect of increasing leaf width was to increase production slightly and to increase the water use efficiency. In the summer when leaf temperatures are above the optimum temperature for photosynthesis, wider leaves may have higher temperatures and lower photosynthesis rates. Transpiration will tend to increase. In the simulations the overall effect was to decrease production, moreso in California than in Chile, and decrease water use efficiency. Thus the simulations indicated that winter active plants should have broad leaves to increase production slightly and water use efficiency, and summer active plants, especially in California, should have narrow leaves (Fig. 8).

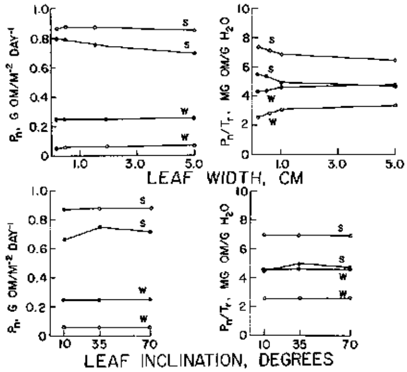

Figure 8.. Simulated effect of leaf width and leaf inclination on net canopy photosynthesis and water efficiency in summer and winter in California (●) and Chile (○).

California, compared with Chile, should have plants with narrower leaves and of a more consistent size, since production is more sensitive to leaf size in California. Measurements of leaf size support these predictions (Table 1).

Table 1. Relative percent cover of woody plants with the given leaf size in California and Chile (from Carter, unpublished; Parsons 1973).

Leaf size (mm^2)	Relative percent cover California	Chile
> 18,225	0.4	1.9
to 18,225	2.6	0.0
to 2,025	1.0	28.6
to 1,125	8.0	21.8
to 225	36.1	34.9
to 25	51.9	12.5
plants without leaves	0.0	1.9

In the simulations leaf inclination was related to production and water use efficiency only in the summer in California. Summer active plants in California should increase production and water use efficiency by moderately inclined leaves, such that the interception of radiation is minimized. Winter active plants in California and the Chilean plants could show a diversity of leaf inclination (Fig. 8). These trends are partially supported by available data on leaf inclination (Table 2), although the predominant plant on ridgetop in California, Adenostoma fasciculatum, was classed as having all leaf inclinations and the mutual shading caused by the clustering of leaves next to the stem may overide the advantage of leaf inclinations.

Table 2. Relative percent cover of woody plants with leaves predominantly horizontal, at 45°, and vertical. Plants without leaves of with leaves of all inclinations are excluded (from Carter, unpublished; Parsons 1973).

Leaf angle	Relative percent cover California	Chile
Vertical	24.0	28.6
45°	74.6	67.6
Horizontal	1.5	3.9

Thus, deep rooted summer active shrubs can increase photosynthesis by decreasing leaf width, a trend more important in California than in Chile. Winter active shrubs or herbs will increase photosynthesis by increasing leaf width, a trend more important in California than in Chile. Winter active shrubs or herbs will increase photosynthesis by increasing leaf width. The seasonal course of leaf resistances of Rhus, compared with Adenostoma (Poole 1974), indicate that Rhus is active in winter and early spring and Adenostoma is active through the year. Rhus has wide leaves for a chaparral plant; and Adenostoma, narrow. In addition, the growth form of Adenostoma maximizes convectional heat exchange, while Rhus appears not as effective in this process. The wider leaves of Rhus may condense more water from saturated air at night than the narrow leaves of Adenostoma, since the wider leaves will depart more below air temperatures at night. Before the November rain, water potentials and leaf resistances recovered from the summer drought earlier in Rhus than in Adenostoma, a possible response to this condensation.

CONCLUSIONS

Of the Mediterranean scrub areas of the

world, the areas of southern California and central Chile show broad similarities in climate and vegetation form and can be used to test ideas of the interactions between climate and life form. In both, precipitation occurs in the winter at cool temperatures and the summers are hot and dry. Vegetation is predominantly evergreen, schlerophyllous shrubs. Differences in climate and vegetation occur between the coast and inland of both countries. The period of soil drought is longer along the coast than inland and a greater frequency of deciduous shrubs occurs in both countries. On a finer scale, California has hotter and more variable temperatures than Chile, and a greater frequency of shrubs with narrower and more steeply inclined leaves. The evergreen form occurs where the carbon cost of maintaining leaves through periods of low photosynthesis is lower than the cost of producing new leaves. The deciduous form occurs where the carbon cost of maintaining leaves is higher the cost of producing new leaves. The shrub form, which is associated with the utilization of deep soil water in the summer, places the photosynthetic tissue above the hot soil surface increasing photosynthesis and water use efficiency. The herb form, associated with the utilization of shallow soil water in the spring, places leaves near the soil surface when surface temperatures are moderate, increasing photosynthesis and water use efficiency at this time. The narrow, steeply inclined leaves of hot summer active shrubs increase photosynthesis and water use efficiency. Leaf width and inclination are less important in plants active in the spring and in cool summers and are more variable in these plants. Thus, the evolution of vegetation from and function in the Mediterranean climate in California and Chile has resulted in a yearly course of productive structure which coincides with a pattern for maximum production and maximum water use efficiency.

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PARALLEL AND CONVERGENT EVOLUTION, AND BIRD DIVERSITY, IN MEDITERRANEAN HABITATS

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Summary & Introduction

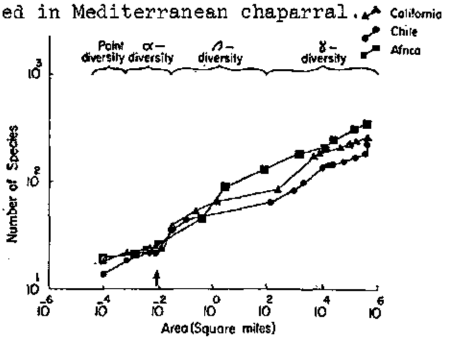
Through studies conducted with the IBP-Convergent Ecosystems project, I have compared bird diversities and community structure between a range of Mediterranean habitats in California and Chile, with particular emphasis on the scrub habitats of chaparral and matorral. The intercontinental comparisons have taken place at a number of different levels of resolution: at the species level, by attempting one-to-one species matching; at the community or sub-community (guild) level, by contrasting numbers of species and their niche sizes, shapes and positions in niche space; at the level of the habitat range or gradient, by comparing bird distributions over matched habitat gradients; at the continental level, to investigate the possibility that whole avifaunas are organized in similar ways between continents of similar climates and topographies. Diversity at the community level represents the species-packing characteristic of the particular habitat, or -diversity. -Diversity appears to be regulated by the universal process of competition, and -diversities are usually closely parallel on different continents in similar habitats. The rate at which species change with changing habitat over a habitat gradient is a second and distinct aspect of diversity, -diversity. -Diversities can be dramatically different between continents, and depend on the size of the fauna and the way in which it has been derived. A third type of diversity is -diversity, which measures the rate at which species are replaced between similar habitats in different geographic localities within continents, or the degree to which geographic replacement species have evolved. -Diversity seems strongly associated with -diversity, and appears to have a strong component of history and chance and to be strongly affected by the relative isolation of habitats from each other and of the fauna from potential sources of colonists. Comparisons similar to those between California and Chile have been assessed in Mediterranean South Africa and in Sardinia and Corsica, and these results serve to calibrate and amplify the initial two-continent comparison. Residual mismatches or "noise" can sometimes be resolved by a consideration of other taxonomic groups, such as ants and lizards, which can provide intertaxon competition for birds by use of some of the same food resources. Historical differences in plant composition can also account for some of this noise

Results

Comparison at the continental level

This comparison is most easily made by use of species-area curves. Figure 1 gives results for California, Chile, and South Africa. Although the total number of species is approximately the same, these species are accumulated with area in rather different ways among the continents. The curves correspond closely at the areal sample size that gives -diversity, but -diversity is far higher in Africa than in California, which in turn is higher than in Chile. These differences correspond to the relative isolation of the bird faunas in the Mediterranean areas of the countries, for South Africa has around 1000 species and the southwestern Cape region is not isolated by mountain barriers from the rest of the country, whereas California is partially isolated by the Sierra Nevada from a smaller continental avifauna of around 500 species, and Chile is very isolated by the Andes, and only some 230 bird species have easy access to the Mediterranean habitats.

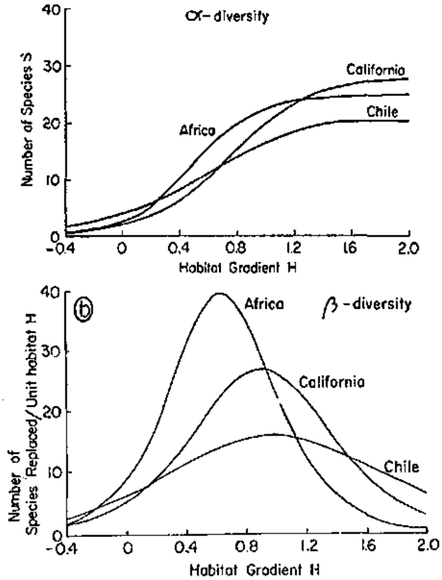
Figure 1. Species-area curves for Chile, California and South Africa. The censuses are centered in Mediterranean chaparral.



Comparison at the community level

I censused in detail bird communities on ± 2 ha sites in a series of Mediterranean habitat types, from, at one extreme, annual grasslands to evergreen woodland at the other extreme. These habitats can be ordered using principal components analysis along a single habitat axis H. As one moves from the grasslands extreme up the habitat gradient, new species are encountered as earlier species drop out. The rates of gain and loss of species are fitted with logistic (sigmoidal) curves: g(S) and l(S) respectively, which are both functions of habitat H. Then -diversity is defined as g(S) - l(S), and -diversity is defined as d/dH.(½(g(S) + l(S))). The -diversity and -diversity curves are plotted as functions of H in Figure 2. While the -diversity or species packing levels are not dissimilar among continents, the -diversity curves differ quite dramatically. Species replace each other extremely rapidly with changing habitat type in South Africa, but in contrast species have extremely broad habitat niches in Chile, where many species occur from short scrub to dense woodland!

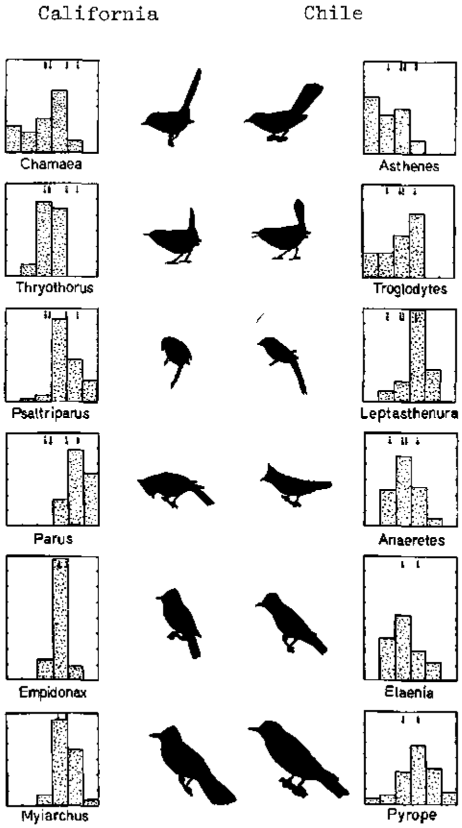
Figure 2. (above) -diversity, or species packing level, in 2 ha sites along a gradient of Mediterranean habitats H. Numbers of species increase smoothly with increasing habitat height and structure, at comparable rates among continents. (below) -diversity curves are very different between continents, with turover rates between habitats highest in South Africa and lowest in Chile.



At the guild level and below

In some communities one can identify species sets within which competition is severe and between these sets and the rest of the community competition is minimal. These guilds may show striking parallels between matched communities on different continents. Between California and Chile, for instance, there are four foliage insectivores at each site in chaparral, two sallying flycatchers at each place, one common hummingbird, two seedeaters, and one each of aerial feeders, pursuing hawks, and searching hawks. Each place also has two woodpeckers, one large and feeding low down the other small and feeding up off the ground. Thus the species in these two communities, one with 17 and one with 19 species, can be matched almost one-for-one. In addition, the feeding heights, feeding behaviors, and gross morphologies are similar between the two continents (Figure 3).

Figure 3. Six insectivores from Californian chaparral and their ecological counterparts from Chilean matorral. Three of the matches are of birds within the same family, 2,5,6, the others match species from very different families, 1,3,4. The bar graphs give proportions of foraging times spent at different heights above the ground (at the left) to 20' (atthe right). From Cody, 1974).



On the other hand, the species that feed at ground level cannot be matched at all with one-to-one precision. When one includes a third continent, South African macchia, equivalents of exactly the same six insectivores are found, including the four foliage species and the two sallying flycatchers. But the macchia has more fruit eating and seed-eating species, and the hummingbird equivalents number three rather than one. Again, the ground-feeding species fail to match accurately.

Only in the very simplest communities such grasslands and in the most discrete of guilds can one find clear one-to-one species correspondence. Table 1 compares two mid-height fields in Chile and Kansas, where the field structures were precisely matched, and the three passerine bird species of each field also matched each other with precision.

Table 1. Comparison of field structure and bird communities between two sites, one in Chile and the other in Kansas (from Cody, 1974b)

Vegetation structure	Kansas	Chile
Mean height	0.29	0.27
Vert.density	5.10	6.23
Horiz. density	8.68	9.26
Area of foliage profile	32.4	39.2
Bird community characteristics		
Number of species	3	3
Average between-species niche overlap in habitat	0.63	0.60
feeding heights	0.78	0.89
food/feeding behavior	0.18	0.21
Overall ecology	0.53	0.56
Bird species characteristics		
Eastern meadowlark and red-breasted meadowlark (*Sturnella magna* and *Pezites militaris*)		
Body size (mm)	236	264
Bill length (mm)	32.1	33.3
Ratio bill length/depth	0.36	0.40
Grasshopper sparrow and yellow grass finch (*Ammodramus savannarum* and *Sicalis luteola*)		
Body size	118	125
Bill length	6.5	7.1
Ratio bill length/depth	0.50	0.73
Horned lark and Chilean pipit (*Eremophila alpestris* and *Anthus correndera*)		
Body size	157	153
Bill length	11.2	13.0
Ratio bill length/depth	0.50	0.42

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PRODUCER - CONSUMER INTERACTIONS

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A study of the interactions among members of different trophic levels in a community is an essential part of any project attempting to understand the functioning of the entire system. Our group has concentrated its attention on the chemical defenses of plants and most of my comments will be directed to that part of the problem. All aspects of this work, including the development of theory and the design and execution of field work, has been truly a group effort that has pooled the skills of persons of very different training. In addition to myself the key persons are R.G. Cates, plant taxonomist and ecologist, D.F. Rhoades, organic chemist turned ecologist, and J.C. Schultz, insect ecologist.

General theory of selection for plant defenses against herbivores

In the world of adaptation, as in human affairs, one seldom gets something for nothing and defenses against herbivores are no exception. Costs to a plant of its defenses include its energy committment, losses in fitness due to the use of scarce materials having other uses that positively contribute to fitness, and losses in fitness resulting from the need to maintain structures that interfere with other important functions. Eventually we wish to express all of these costs in terms of fitness and the term investment is appropriate when we wish to refer to total affects on fitness. For a defensive system to evolve, the benefits resulting from an investment must be greater than all competing alternative investments of those resources to deal with other environmental contingencies. Therefore, the extent and kind of defenses plants have against herbivores will be a compromise between benefits arising from the defenses and benefits arising from alternative uses of the resources. We began our theories with a general attempt to deduce the nature and strength of selective pressures on plants of different kinds. From these deductions we derived a set of predictions relating to the types of defensive systems we would expect. These predictions have formed the basis for our field and laboratory work.

Our first deduction, and the one that has been investigated most intensively, relates the successional status of plants to their defensive systems. It is easiest to begin by contrasting annuals and late successional plants. Annuals survive unfavorable seasons as seeds, grow rapidly, reproduce and die in relatively short time spans. Therefore, a given individual plant is available for use by herbivores for only a short time. In addition, each individual begins its life in a new site, perhaps far from where its parent grew, as seeds may be dispersed long distances and local disturbances may favor growth in new areas. Therefore, each individual plant is an 'island' in space and time that must be discovered by potential herbivores during a short time span. Even if such a plant is undefended, it has a reasonalbe chance of escaping from its herbivores simply by not being found in time in its new location. In addition, one of the prices of investment in defenses is probably slower growth and maturation rates since energy and resources must be diverted from the production of new vegetative tissues to the defense of those already produced. Since annuals grow in disturbed areas where speed of growth may be important to attain maturity before competition becomes too severe, or in deserts where the wet period may be very short, investment in defenses may lower fitness substantially simply by slowing growth rates.

By contrast, late successional and climax species tend to be slow growing, to have long pre-reproductive periods and to therefore be highly predictable in space and time. Unprotected individuals will almost certainly by discovered by their herbivores long before they reach maturity and the herbivores will have the opportunity to pass through many generations before the plant is capable of reproducing. Therefore, we have surmised that the losses in fitness from being unprotected are on the average more serious for climax plants than for early successional species, whereas the costs of investment in defenses are likely to be more serious for annuals which have such a strong premium on rapid growth.

Our most important test of these predictions has been carried out using slugs as the test animals. Our test system consists of slugs housed individually in plywood boxes with moist dirt floors. Since slugs feed primarily at night, all tests are run at night and the results measured the following morning. Each slug is presented with six freshly cored discs of leaves, three of the plant to be tested and three of a control, arranged so that the nearest neighbor of each disc was of another species.

Positions of the discs were alternated to remove any left or right bias the slugs might have. The amount of the discs eaten during the night was measured geometrically. All slugs were starved the preceding night to raise their hunger levels.

From these data we calculated a Palatability Index (PI), which is the ratio of the amount of the test plant eaten to the amount of the control plant eaten. This index has a value ranging from zero, when the control is eaten but the test plant is not touched, to infinity, when the test plant is consumed but the control is not touched. Actually, in our experiments a much narrower range of values results because we have used exclusively two species of highly palatable plants as controls (Asarum hartwegii and Oplopanax horridum). Normally the three discs of these controls are mostly or entirely eaten by the slugs so that PI values much larger than one are unusual. Different control plants would, of course, give different PI values.

Fortunately, we have obtained remarkably low interindividual and interest variability in our palatability tests and are therefore able to test large numbers of species of plants with relative ease. The results to date (Cates and Orians, in press) provide striking confirmation of the prediction. Early successional annuals and biennials had much higher average palatabilities to both species of slugs (Arion ater and Ariolimax columbanius) than did early successional perennials, which in turn had higher palatabilities than late successional and climax plants. Average palatability values for the three groups were approximately 0.90, 0.55 and 0.20, respectively, with very little overlap among the groups. The plant species yielding highly variant values for their respective groups are being singled out for special study as they presumably reflect the importance of other selective pressures not included in the basic theory.

These results led us to test a corollary to the basic theory. If annuals have a lower committment to defense than perennials, they should be suitable food for a wider variety of herbivores because less specialized detoxification mechanisms will be needed to derive useful energy from their vegetative tissues. Perennials, however, will be difficult to use except by herbivores possessing the physiological capability to handle the more complicated physical and chemical defenses of the plants. If so, it follows that the herbivores on annuals are more generalized foragers, that is they eat a wider variety of species, than the herbivores feeding on perennials.

This corollary prediction is being tested in the Sonoran Desert environments of Arizona and northwest Argentina. This is an especially favorable test system since the flora consists of many rapidly growing species of annuals living together with many slowly growing shrubs. We have concentrated on Lepidoptera because they are more or less continuous feeders and are, therefore, easy to observe feeding in the field. Also, they adapt readily to the laboratory and will normally begin to feed within a few minutes of having been placed on a suitable food source. We have measured both the range of plant species utilized by the lepidopterans in the field and have tested many species in the laboratory to determine how many species they will eat when they have the opportunity and alternative foods are not present.

The results of this work are quite striking. There are specialized lepidopterans feeding on annuals but most of the species can be found feeding regularly in nature on up to ten species of annuals as well as on the less well defended tissues of some perennials. By contrast, none of the lepidopterans on perennials has been found on more than 2 or 3 species of plants except very rarely and we do not know how well they grow on these unusual hosts. These field host preferences are also reflected in the laboratory where the lepidopterans on annuals will eat all of the species we normally find them on in nature plus a few others, while the species that eat perennials normally refuse alternative foods even when nothing else is available to them.

Escape in space and time

The previously-mentioned studies are tests of corollaries of the prediction that annuals have a high probability of escaping in space and time. We have also attempted to measure escape in space and time directly. Our first quick test was made using Baltimora recta, a composite that invades pastures and cultivated fields in the Pacific Lowlands of Central America. In Costa Rica we compared the number of species of herbivores on the plants and the percent of the leaf surface area that had been eaten for (a) plants growing in isolation from conspecifics, (b) plants growing in medium-density populations along roads, and (c) plants growing at very high densities in overgrazed pastures. The latter had about four times as many species of herbivores on an equivalent number of individuals and about seven times the percent damage as the former, while the second group was intermediate in both features. These results were encouraging but represented only a single measurement at one point in time.

Therefore, more detailed studies were carried out during the summer (January-March) of 1974 in Argentina with several species of annuals and one invasive perennial. The most detailed study was made on Ibicella parodii (Martiniaceae), a species with large, readily countable leaves, common enough to yield large numbers but rare enough to provide many well isolated individuals. Over 150 plants were individually tagged and visited every 5-7 days during the growing season. At each visit counts were made of the number of damaged and undamaged leaves, flowers, fruits and the numbers of all herbivores. The distance to nearest conspecific neighbor was measured for each plant. These data provide an accurate picture of the seasonal pattern of attacks by herbivores and the total reproductive output of each plant.

Ibicella is attacked by a large sphingid, that is not known to utilize any other plant in the study area, plus several species of generalized lepidopterans and orthopterans. As might be expected, interplant distances were not correlated with extent of damage from the generalized herbivores but were related to damage by the specialist. The sphingid lays its eggs in clumps and the larvae are large enough to totally denude even large plants of Ibicella if more than a few are present per plant. The data from this study have not yet been analysed completely but interplant distance is correlated with the probability that a plant will be found by the specialist and the reproductive success strongly correlates with escape from the specialist. The large larvae completely consume even ripening fruits if they run out of leaves before they reach pupation age.

Interesting data were obtained for an invasive perennial, Grindelia pulchella (Compositae) and Calycera sp (Calyceraceae), an annual that grows prior to the rains in sandy soils. Both of these species are the only green food available in their habitats before the rainy season and in both species damage was the heaviest at this time and especially heavy on isolated individuals. For Grindelia, the extent of grazing damage declined when the flush of annual growth occurred following the rains even though the abundance of herbivorous insects in the environment was much higher. This work shows in detail the importance of the availability of alternative hosts for the nature and extent of grazing damage on a plant and this complication must be accounted for in all of our future experiments.

Tissue preferences of generalists and specialists

A plant is a complicated mixture of roots, stems, leaves, flowers and fruits, and the grazing pressures on these different tissues come from different herbivores for the most part. Also, these tissues perform different functions for the plant, are present for different lengths of time, and losses to them affect fitness of the plant in different ways. Therefore, the defenses of the different tissues are expected to be different and these differences should be reflected in the grazing patterns of the herbivores. In general, we expect defenses to be less in ephemeral tissues (flowers, young leaves) because of their ability to excape in time. Also, it may be more difficult to defend ephemeral tissues because of the time period of return from the investment and because many defenses are of a nature so as to interfere with the normal functioning of the tissues. Any toxin that is potentially autotoxic must be stored within the cells or tissues of plants in a manner to isolate it from the parts it might damage. Thus, their storage requires investment in subcellular structures that will be costly to build and may interfere in subsequent cellular divisions. For these reasons we have developed the following theory.

We expect the chemical defenses present in ephemeral plants and tissues to be effective primarily against generalized herbivores. Furthermore, these substances should be of a type that minimizes energy allocation and autotoxicity problems. Toxins of high potency at low concentrations, active against physiological systems peculiar to the herbivores are thus to be expected in ephemeral plants and tissues. Neurotoxic alkaloids, cardiac glycosides and saponins acting aginst muscles, and insect hormone analogues (Whittaker, 1970) are of this type. General metabolic poisons such as cyanide, isothiocyanotes, and 'non-protein' amino acids should be sequestered in combined form, usually as glycosides. There is considerable evidence from the literature that the concentrations of toxins is often higher in the younger leaves and among early successional plants (Kingsbury, 1964). Specialist herbivores should be able to detoxify such a system readily either by exclusion (Self, 1964) or by metabolism/excretion (Williams, 1959) and, thus, predictable plants (perennials, late successionals) and tissues (mature leaves, woody material) should utilize other defensive resources. The use of digestibility reducing substances among these plants and tissues appears to be widespread and may be a general strategy (Feeny, 1968, 1970). The tannins found in a high proportion of perennials and especially late successional plants, the resins of conifers, creosote bush (Larrea divaricata) and sagebrush (Artemisia tridentata) form heterogeneous complexes with plant proteins and herbivore digestive enzymes on maceration of the plant tissue (Rhoades, unpubl.). Powerful evidence has been provided by Cates who has found that herbivores feeding on desert perennials have a much lower nitrogen assimilation efficiency than those feeding on annuals. It is also significant that all three of the desert perennials investigated in detail by us (*Larrea*, *Artemisia*, *Prosopis*) contain a digestibility reducing system (Rhoades and Cates, unpubl.).

A significant feature of this theory is that it has implications for both the investment costs to the plant and the ease with which the defenses may be 'breached' by the herbivores. For example, acute toxins of high potency at low concentrations are both the cheapest to produce and easiest to detoxify. A simple enzyme system may permit the herbivore to detoxify the molecule and any herbivore with a long evolutionary history with these substances can be expected to be able to deal with them. On the other hand, if each plant species has its own acute toxins, it would be very difficult for a generalized herbivore to evolve the ability to handle many different toxins as each detoxification capacity adds approximately linearly to the total physiological budget of the herbivore. Therefore, we expect acute toxins to be effective primarily against generalized herbivores and to be concentrated in the ephemeral tissues.

A second level of defense that is more co costly but more effective against specialists are digestibility-reducing substances. Tannins are probably the most widespread of such defensive systems and they operate by forming heterogeneous complexes with the proteins of the plants, thereby rendering them unavailable to the herbivores. This requires, however, that they be sequestered within the plant cells away from all proteins but yet in a position where they will be released when an herbivore damages the cell. Such a defense is more costly to the plant but also more difficult to breach by the herbivore.

The final level of defense available to a plant is to produce its proteins in a difficult-to-digest form. It is well known that many fibrous proteins are notoriously difficult to digest using normal proteinases. Additional side linkages also reduce the digestibility of globular proteins. It is as yet difficult to surmise the total cost to the plant of having its proteins in such forms, but it would seem that such a defense would be the most difficult of all to breach because of the inevitable high energy cost of breaking down such proteins.

For these reasons we expect a correlation between the length of time a tissue is present, the kinds of functions it performs, and the type of antiherbivore defenses it has. As indicated in the main body of the proposal, there is suggestive evidence in the literature of such a correlation and we have begun some laboratory tests of the defensive patterns of plants. We have examined several species of conifers, a number of genera of climax species of rosaceaous and ericaceous shrubs in western Washington, and several genera of desert shrubs (*Artemisia*, *Larrea*, *Prosopis*), all of which have been found to contain a powerful digestibility-reducing system. This is reflected in low nitrogen assimilation efficiencies of lepidopterans feeding on their leaves, including the species specialized for those plants. We are currently testing many species of lepidopteran larvae in the laboratory to determine their ability to extract nitrogen from the leaves they eat. The larvae are brought into the laboratory, given a gut marker so that the passage of the test food can be known, fed the test plant, and the feces collected and analysed for nitrogen content. A leaf sample from the same plant is also taken and similarly analysed for nitrogen to determine the amount present per unit dry weight of tissue before passage through the gut of the herbivore.

The results to date show that when compared on the same tissue, specialists on that plant have a higher nitrogen extraction efficiency than generalists. However, since generalists usually are found on the poorly defended tissues, they actually have higher overall nitrogen extraction efficiencies than the specialists that are grazing on more heavily defended tissues. When offered choices, the insects prefer those tissues on which they have higher nitrogen extraction efficiencies and these are also the tissues we find them on in the field.

Our work to date has provided encouraging support for our preliminary hypotheses and has stimulated the development of new theories yet to be tested. The concepts are applicable to all ecosystems and have interesting implications for a number of applied problems especially in the field of agriculture.

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B4

Stable and unstable ecosystems with man as an integral component in different climatic zones

STABILITY IN ARID ECOSYSTEMS AND THE EFFECTS OF MAN ON IT

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In memory of Prof. N.H. Tadmor

Summary

The concept of ecosystem stability is multivalent and includes, among others, concepts of persistence and of resilience. Arid ecosystems in general show low persistence (due to the variable environment) but high resilience (due to the adaptations of populations to this environment). Arid ecosystems including human populations with different economies have for long periods fluctuated within well-bounded domains. Their resilience has been challenged only by transitions to a more intensive type of use and by contact with richer ecosystems.

What is ecosystem stability?

Ecosystem stability is supposed to be one of the "unifying concepts" in ecology. But this concept, and its relations with other attributes of the system (e.g. diversity), have caused much controversy, mainly due to confusion as to what is meant by "stability".

"Stability" is intuitively understood as the set of attributes of a system which minimize the magnitude, duration and irreversibility of the changes in its own state resulting from external changes or "disturbances". But this is far from being an operationally unique definition. There are many alternative definitions of stability (Lewontin, 1969), among which the investigator can choose one, or several, depending on his purpose. If "stability" of real ecosystems is to be measured, compared and correlated, further specifications are necessary:

a. what attributes define the "ecosystem state", changes in which measure stability? (biomass? productivity? species composition? trophic or physical structure?)

b. what time-scale of disturbances and responses is referred to?

c. stability against what kind of "distrubances"? (climatic, geomorphic, biological or man-induced? changes within the normal variability of the system's environment or beyond it? gradual or sudden changes?)

d. what stability properties are of interest? Qualitative stability properties include the existence of equilibrium points and limit cycles, their number and the distances between them, the behaviour of the system near them (convergent, divergent, oscillating), the sizes, shapes and limits of the domains (or "basins") of attraction around them. But often stability is meant also to include the speed of return to equilibrium and the number and amplitude of oscillations in the process.

The correlation between different measures of stability may be positive, but could just as well be negative, so that a given ecosystem is "stable" by one definition and "unstable" by another.

Maybe the many possible exact definitions can be consolidated into a few main concepts. The same symposium in which Lewontin presented the different meanings of mathematical stability, includes two totally different interpretations of ecological stability. Preston's (1969) "stability" is not in the ability of a population to minimize fluctuations in its numbers, but in its ability to bounce back after large fluctuations. Margalef (1969) considered also this meaning, but then chose to define "stability (persistence)" as the average turnover time . A step towards resolving the confusion may be Holling's (1973) distinction between two concepts: stability and resilience. "Stability" refers to the duration and magnitude of quantitative fluctuations around equilibrium. "Resilience" refers to the probabilities of qualitative changes: transitions from one domain of attraction to another, species extinctions and changes in the relationships within the system. Holling shows that systems may be "stable" but not resilient (lakes) or "unstable" but resilient (forest insects). He argues that a negative correlation between the two attributes is expected to result from the evolution of populations to adapt to the range of fluctuations experienced. Holling's "stability" is related to, though not identical with, Margalef's "stability (persistence)", while "resilience" is close to Preston's "stability".

Probably more than two such concepts have to be distinguished. But in the following, "resilience" is used in Holling's sense; "persistence" refers to both the magnitude of fluctuations (Holling's stability) and turnover rates (Margalef's stability-persistence); "stability" is retained as the general covering term implied in the title.

The questions that seemed to me to be implied in the title are: how stable are arid ecosystems, compared to other terrestrial ecosystems? which of their properties increase their relative stability and which reduce it? how do human populations affect it?

How stable are arid ecosystems?

Arid or desert ecosystems are understood here as terrestrial ecosystems in regions with less than 300-500 mm mean annual rainfall, which may be further subdivided into extreme arid, arid and semiarid regions. These systems are characterized by three features (Noy-Meir 1973): a) the main limiting factor for most biological processes, is the water input by rainfall; b) this input comes in infrequent and variable discrete pulses (rain events). c) the timing and magnitude of these pulses is to a large extent random (unpredictable).

What generalizations can be made about the "stability" of all ecosystems in this category?

In one sense, they seem to be the least "stable" of all terrestrial ecosystems. The fluctuations in population numbers, biomass, productivity, species diversity and composition of plant and animals, both within each year and between successive years, are characteristically largest and most irregular in arid ecosystems. This is most obvious in the most species-rich group of desert organisms, the ephemerals (drought-evaders), which appear in active form at all only for short favorable periods after rain and "disappear" (actually exist as seeds, eggs, etc.) for the long dry periods, sometimes for many years. For example, in a semiarid Australian site, there were in spring 1967: 3 ephemeral plant species, with a density of 1.2 plants/m^2 and 0.05% cover; in spring 1968: 28 species, 36 plants/m^2, 10% cover. Fluctuations of similar magnitude can be observed in the ephemeral fauna of deserts, in particular phytophagous and pollinating insects.

The second group of desert organisms, the drought-persistents, maintain at least some active biomass throughout dry periods. But many show considerable fluctuations in biomass, numbers and activity. The green biomass of many desert shrubs is reduced in the dry season by a factor of 4 to 20 (Orshan & Diskin 1968). Annual mortalities of 50-80% (and sometimes complete local extinction) are frequent in populations of some desert shrubs (Hall, Specht & Eardley 1964), and have been observed in populations of drought-persistent animals.

Are then desert communities and ecosystems inherently "unstable"? Most of them certainly are in the sense that they are phenomenologically very variable in time, over periods of months to a few years; that the turnover time of most biomass and populations is of the order of a few months; and that the dynamics of most components are so irregular, that it seems impossible even to define any equilibrium points or stable limit cycles in the usual sense, with reference to which fluctuations can be measured. In short, most arid populations and ecosystems show very low persistence.

However, in other senses, they seem to be remarkably "stable". Most of the extreme and irregular biological fluctuations can be observed to be in direct, rapid and proportional response to the extreme random fluctuations in the environment, in particular rainfall pulses. There is little evidence for autonomous oscillations, as would be induced by lagging responses. Rather, the impression is that biological fluctuations in deserts are easily reversible and repeatable, i.e. a similar sequence of climatic events at the same site in different years will result in population and biomass pulses of similar magnitude; good correlations between annual production and rainfall parameters can be established.

In a study site in arid Israel, 1972 was a rainy year (160 mm) with a diverse and dense annual vegetation; 1973 was a severe drought with virtually no seed production and large seed losses (Luria & Noy-Meir, unpublished); 1974 again was similar to 1972 in rainfall amount and distribution. Despite the intervening "catastrophe", 80% of the annual species that flowered in 1972 reappeared in 1974 in the same quadrats, attaining 70-90% of the 1972 total density and biomass.

Also populations of perennial desert plants and animals, decimated or locally wiped out by drought or overexploitation, often recover within a few years of better conditions.

Thus when viewed at a time-scale of decades, and in relation to the environmental variability, most biological components of arid ecosystems show remarkable "stability", or rather resilience (Holling 1973). This apparent paradox is not surprising, if we consider that they evolved in an environment where the normal pattern is more or less random alternations of short favorable periods and long stress periods. One might expect to find among desert populations, more than among temperate ones, preadapted resilience also toward some types of man-induced catastrophes (e.g. 99% destruction of seed or egg production in some years). Indeed, several desert species have become "pests" in agriculture (Edney 1966).

What are the stabilizing features?

1. Tolerance of extreme conditions. The first problem of a desert population is how to survive long periods of extreme drought (and heat). Ephemerals solved it simply by special dormant and resistant "reserve" forms (seeds, bulbs, diapausing eggs and larvae) which can survive for years. Drought-persistent plants and animals may reduce active biomass (shedding, aestivation, deferred reproduction),

but they had to evolve also special adaptations to reduce the susceptibility of what remains. The result is a variety of fascinating physiological and behavioural mechanisms which have been the subject of much research and review (Cloudsley-Thompson & Chadwick 1964, Schmidt-Nielsen 1964, Kassas 1966, Evenari, Shanan & Tadmor 1971).

2. Ability for rapid recovery. Once drought survival - at much reduced biomass - is assured, the next problem is how to make up in the short "good" periods for the losses of previous and future droughts. Most ephemeral desert plants and animals, and many persistents, are capable of very rapid pulses of growth and reproduction in favourable conditions: high growth rates, rapid succession of developmental stages and high fecundity (Edney 1966).

3. Adaptation of pulse-reserve transitions to uncertainty. Transitions between a dormant resistant "reserve" and a highly active "pulse" are thus characteristic of desert populations (Westoby 1972). The problem then is how to regulate timing and intensity of these transitions when incidence and duration of good periods is wholly or partly random. In a theoretical analysis Cohen (1966,1967) deduced that the optimal strategy for survival involved a cautiously opportunistic response (only partial commitment of reserves) in each pulse, and an ability to sense and respond to environmental signals correlated with length and reliability of the good period. To this may be added an ability to respond with minimal lag to such signals. Indeed, germination in desert plants (e.g.Gutterman et al.1972) and the onset of reproduction in desert animals of many groups (e.g. Keast 1959) involve specialized delay and trigger mechanisms to assure a response which is cautiously opportunistic and well synchronized and attuned to environmental signals.

4. Flexible and opportunistic feeding habits. Studies on the diet of desert animals of many groups have shown a wide dietary range and an ability to switch between foods as conditions change (e.g. Gauthier-Pilters 1965). Moreover, in deserts some carnivores (e.g. jackals) may occasionally turn to a mostly vegetal diet, while good herbivores (gazelles, hares) eat insects (Monod 1964).

5. Nomadic migrations. Mobile desert animals can compensate for fluctuations in food and water by utilizing spatial heterogeneity in these resources. Nomadic movements occur in most large desert animals and in desert birds (Keast 1959). An extreme case is the desert locust, "the locust without a home" (Bodenheimer 1958).

These adaptations of desert populations all increase their resilience and that of the ecosystem as a whole. But there are also some characteristic susceptibilities in arid systems, which reduce their stability.

What are the destabilizing features?

1. Sensitivity to damage to reserves. Any factor which drastically increases the mortality of the resistant reserve forms (e.g. a new efficient seed or egg predator) can bring a "pulse-reserve" type population close to extinction (Westoby 1972).

2. Sensitivity to lagging components. The prompt and synchronized response of desert-adapted populations of all trophic levels to climatic fluctuations is a major stabilizing mechanism. If a population is introduced which lags in its response (e.g. continues to reproduce into a drought), it may go into amplified oscillations; if it has important effects on other components, it may destabilize the whole system (rabbits and sheep in arid Australia?)

3. Low density, biomass and productivity. These properties do not necessarily reduce the resilience of arid populations and ecosystems, if a sufficiently large and heterogeneous area of desert is available. But they could make them susceptible in contact with systems with much higher density and productivity (e.g.irrigation areas).

4. Sensitivity to topsoil erosion. Due to low plant cover, erosion forces are high in arid and semiarid regions (Marshall 1972). In many of these regions, a thin top layer (5-10 cm) is critical for plant establishment and growth (germination sites, hard or saline subsoil, nutrient concentration - Charley & Cowling 1968). These two facts are elements of a positive feedback loop which endangers the stability of some arid ecosystems.

Would arid ecosystems be stable without man?

There are hardly any arid ecosystems not affected at all by man and domestic animals, but there are areas in which their effects have been slight. As indicated above, the impression is that in general such "natural" arid ecosystems have low persistence but high resilience; apparently the factors promoting resilience outweigh those which reduce it. Biological fluctuations are large but are usually well bounded within one domain and show consistent relationships with climatic perturbations but little autonomus oscillation. Species extinctions, or catastrophic erosion, may occur locally in severe droughts, but seem to be usually compensated for regionally and in the long term by migration and recolonization.

How does man affect their stability?

Though physiologically poorly preadapted to the desert environment, man has occupied it rather early and successfully, due to dietary flexibility, mobility and intelligence. Man has for long been an integral part of most arid ecosystems but the type and intensity of his effects vary greatly with the socioeconomic system. Four main types are considered, though various intermediates and combinations occur.

1. Hunting-gathering

At this stage (surviving in Australia and the Kalahari) man appears as a highly flexible and mobile top predator-omnivore, exploiting in diverse and ingenious ways the scarce food and water resources, with little attempt at managing or modifying them. Most arid zones have been occupied by such societies, and some anthropologists have found their existence to be fairly easy and secure (e.g. Lee 1968); but population densities remain very low (in part maybe socially constrained). Due to low density and flexible resource use, hunting-gathering man seemed to have only moderate effects on productivity and composition of arid ecosystems, certainly on their overall structure and stability.

2. Nomadic pastoralism

Through his livestock, man can utilize a much larger proportion of primary production than before, and hence maintain higher population densities. Management options include regulation of herd size and movements and development of watering points. Pastoralist economies which evolved in the arid zones of Asia and Africa are characteristically nomadic, with movements being either wholly opportunistic (central Sahara) or partly cyclic-seasonal (most other areas). The pastoral economies introduced into arid Australia (and partly America) became sedentary after a nomadic stage, but retain options of "motorized nomadism" in droughts.

Nomadism has been charged with "deterioration" of the desert ecosystem (or even its "creation"). Theoretically, this claim seems absurd. As discussed above, the nomadic habit of many desert animals is an excellent adaptation to the environment, which is likely to increase resilience. Nomadic grazing enables a more flexible use of regional resources than strictly sedentary grazing, and prevents extreme local grazing pressures. However, a destabilizing side-effect often is the competitive use of common grazing lands and the lack of incentive for any individual to use them conservatively or to limit herd size.

The transition from hunting-gathering to pastoralism, with much increased herbivore and human densities, must involve significant changes in the productivity and composition of the ecosystem. Evidence from Australia (Perry 1968) indicates that after violent initial oscillations, the system tended to fluctuate in a new range. The nomadic pastoralist ecosystems in Asia and Africa seem to have fluctuated for thousands of years within the same well-bounded stability domain (Monod & Toupet 1961). This is probably different from the pre-pastoral domain, but there is no evidence for progressive deterioration until recently. Stock populations generally fluctuated consequent on climatic fluctuations (though maybe with greater lag and amplitude than wild populations) and were prevented from "explosion" by incident droughts. Thus arid ecosystems with nomadic pastoralist economies have shown considerable long-term resilience.

A definite and accelerating trend of range deterioration and erosion has been observed in arid and semiarid zones in Asia and Africa in the last decades (Pearse 1970, LeHouerou 1974). It is associated with transition from a nomadic to a sedentary system, extension of cultivation, and increased contact with non-arid and urban systems (veterinary care, supplementary feeding). These developments have removed previous restrictions on human and stock populations, and allowed them to exceed in many cases the "carrying capacity" of the resources of the region, so that now they can be maintained only with inputs from other regions. The trend is stronger in the semiarid fringe than in more remote arid regions.

3. Sedentary pastoralism-farming

Such economies allow a more direct, efficient and complete utilization of primary production by man than nomadic pastoralism, and hence higher population densities. The integration of cultivation and livestock allows some stabilizing complementary and compensatory practices (Tadmor, Eyal & Benjamin 1974): grazing of stubble and, in drought years, of the whole crop; storing of grain; rotation; use of manure. Private ownership of grazing lands (or at least more permanent rights on them) can provide an incentive for conservative use and even improvement (though often this does not happen), and for the management of local water resources by runoff farming (Evenari, Shanan & Tadmor 1971).

But there are also destabilizing factors. The loss of stock mobility and its permanent concentration near settlements and waters, may increase grazing pressure there, particularly in drought, to a point where the vegetation-animal balance "crashes" (Morley 1964). A new balance may be attained but with much lower productivity and palatability (LeHouerou 1974). This is not prevented by supplementary feeding in drought since the handfed stock usually continue to graze. Thus large areas of productive range are turning into mere "Exercise grounds" (Pearse 1970). This is often accompanied by accelerated erosion of devegetated rangelands and of wrongly cultivated land.

Settled people usually require or expect a higher and more constant standard of living than desert nomads,i.e. they have higher and less flexible "maintenance costs" which are difficult to bear in droughts (insofar as the economy is based on the resources of the arid zone alone). This requirement for higher "persistence" reduces the economical (and psychological?) "resilience" of the society in an environment where droughts are normal rather than exceptional.

These factors lower the stability-resilience of sedentary grazing-farming ecosystems in arid and semiarid zones and increase the probability that a long drought will cause an irreversible "crash" or at least a severe crisis (more severe than in nomadic systems). In semiarid regions such systems have existed successfully for long periods despite the incidence of such crises. But attempts to extend them beyond a certain lower limit of rainfall (or of crop success probability) have often collapsed, causing abandonment or return to pastoralism (parts of South Australia). Improved management (erosion control, range conservation and improvement, proper integration) can certainly increase the chances for long-term success. But it would be dangerous to underestimate the strong ecological constraints, in particular the large and random fluctuations in productivity.

4. Irrigated and urban areas in arid zones

These are enclaves of essentially non-arid ecosystems ("artificial oases") which maintain high and constant population density and productivity on imported water and/or energy. Their stability is outside the scope of this paper,except insofar as they interact with the surrounding desert. Interactions observed include:a)exploitation of desert resources and populations by "oasis" populations (e.g.predation). b) exploitation of "oasis" resources and populations by desert populations (insect pests,raiding nomads). c) commensal use of water and food surpluses of the enclave ecosystem (which are considerable particularly in modern "oases":sewage and leakage water,food wastes) by desert populations (plants,wild and domestic animals).

Unless the enclave is very small, its richer and more productive ecosystem will affect the adjoining desert more than be affected by it. The effect may be stabilizing or destabilizing.

Stability,resilience and management

The thesis I have tried to support here is that arid ecosystems have low persistence but high resilience. The low persistence is dictated by the changeability of the environment;the high resilience has been attained by evolutionary adaptations of desert populations. Most of these adaptations do not enable populations to remain static despite climatic fluctuations,but rather to be flexible and fluctuate in harmony with them, while maintaining the ability to recover. The desert ecosystem,always being pushed around by the climate,thus bounces continuously back and forth within a large "stability bowl",but the walls of the bowl are steep and the system is unlikely to be bounced out of it. The introduction of man, and then of domestic animals,further widened this bowl and changed its shape, but in nomadic systems the probability of being pushed out of it remained low. The transition to a more sedentary and intensive agriculture,in an attempt to move the bowl to a domain of higher production and to reduce its diameter,often also lowers its walls.

If the available evidence is sufficient for accepting this thesis, what are the implications for the management of arid ecosystems? Holling (1973)distinguished between "stability" (persistence)-based management of natural resource systems, which aims at a constant yield, and resilience-based management,which accepts fluctuations in yield but aims at long-term containment of these fluctuations within some boundaries,by using the ecosystem's natural resilient structure. Holling suggests that for many systems,the second approach, which "would emphasize the need to keep options open, to view events in a regional context and to emphasize heterogeneity", might be preferable. In arid zones constancy of annual production is a notoriously difficult aim. Modern arid zone agronomy aims at reducing the variance of production, but sometimes this seems to be done at the expense of long-term resilience. Should we then apply Holling's idea to non-irrigated arid ecosystems and manage them only as "ephemeral" natural resource systems (rather than conventional agro-ecosystems) with high production in some years and virtually none in others? But isn't this incompatible with present-day agroeconomic and social requirements? Is ecological integration with non-arid regions or irrigated areas a possible, or desirable,solution? I can produce more questions but no more answers. But it seems that within the effort needed to design management strategies for arid ecosystems, there is still something to be learned by studying those strategies which have evolved within the arid zone. Despite their difficult problems of compatibility with today's world, these strategies seem to have been remarkably well-adjusted to the basic features of the arid environment and to have allowed man to maintain long-term useful production from its resources.

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MAN AND STABILITY OF SOME FOREST ECOSYSTEMS[1]

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Summary

Not only physical anthropology or physiology, but also archeology and cultural anthropology need to be synthesized into a view of ecosystems with man as an integral component.

Human adaptations of, and to, stone age and iron age tools suggest that the former required over five times as much energy and time as steel axes for equivalent work such as the clearing of forests for agriculture. Cultural adaptations such as the use of fire and the selection of appropriate lands for crops presumably were even more crucial for man's rather sudden advances into clearing woodlands in Neolithic and later times. Modern transportation and land-clearing technology make large-scale changes more sudden and risky then ever. Many impacts are completed before their full consequences can be recognized or counteracted.

Over large areas of the temperate and boreal zones (as in the tropics) forests maintain themselves by regeneration and ecological succession in patches. Feedback models can represent the resulting oscillations of biomass or energy (or carbon) storage in the unit module of forest in the landscape pattern. SERENDIPITY-1 of Goldstein and Harris also shows redistribution of biomass x (= $x_1 + x_2 + x_3$, the sum of small, medium and large trees) as compared with x_{max} = the maximum biomass which can be maintained over an extended time in a given part of the landscape pattern.

(a) In early prehistoric time man had little impact on the forest except for burning, but even this started changing the extent of forest by changing some of it to savanna or parkland. (b) By the Neolithic and especially Iron Age, temporary and permanent agriculture left the average x well below x_{max}. Patches recovering from shifting cultivation, averaging over the different stages of secondary succession, had much young growth; sometimes old stems; sometimes both (e.g. "coppice with standards"). Grazing and burning sometimes hastened degradation of stands (oak or birch woods to heath in Europe) which might have had slower deterioration under undisturbed conditions of slow postglacial soil profile development on sites of different productivity. (c) Since the industrial revolution, product-oriented forestry may leave some good and some poor sites to grow large trees, but large areas of pole stands, for pulpwood, are becoming more typical.

Forest influences cover many impacts on man besides our product and recreational needs. Appalachian Watershed studies (e.g., Oak Ridge, Coweeta) indicate prompt stand recovery from disturbance, and changes in water yield which may or may not last many years after clearcutting.

If the area of forest and (other) woodland and the live biomass were both reduced to 0.7 of the level for pre-agricultural postglacial time, $0.7 \times 0.7 \cong 0.5$ is the biomass (and carbon and organically bound energy) that would have remained after many historically sporadic episodes of deforestation and regeneration. Preliminary data suggest that the reduction has actually been, or soon will be, greater than half of the preexisting forest mass. In combination with forest opening by pests, plus hastened oxidation of humus by microorganisms, further release of dead organic matter to the atmosphere as CO_2 can be expected. Unless reforestation by man and natural processes is more effective than we now expect, this release may outweigh the enhancement of photosynthesis by increased levels of CO_2 in air. Thus, natural forces may reinforce the other causes of increased CO_2 just when burning of fossil fuels is accelerating most rapidly.

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Prediction of ecosystems response to human intervention

PREDICTING SHORT AND LONG TERM CHANGES IN THE FUNCTION AND STRUCTURE OF TEMPERATE FOREST ECOSYSTEMS

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Summary

Drawing upon US/IBP research, the authors present examples of recently developed capabilities in estimating photosynthesis, growth, forest composition, hydrologic properties, nutrient losses and turnover, including the effects of erosion. A major contribution of IBP has been in linking together critical variables to provide an assessment of a variety of forest practices upon ecosystems and landscapes.

Introduction

'The highest purpose of ecology is prediction,' so says the planetary ecologist in the science fiction novel 'Dune' (Herbert, 1965). And, indeed, development of predictive capabilities is one of the long term goals of the ecosystem analysis programs developed under US/IBP. Proper management requires an ability to predict consequences of various activities -- clearcutting, fertilization, road building, etc.,-- upon the functioning of impacted ecosystems and landscapes. What effects do human interventions have on productivity, rates of nutrient cycling, nutrient loss, water and air quality, community diversity and stability? Some of the great problems and controversies in management of forest lands have arisen specifically as a result of our lack of appreciation of how effects of a given intervention will ramify through an ecosystem causing unsuspected and undesirable changes in productivity and stability of forest lands and associated water bodies.

Although we are far from having an adequate predictive capability for many aspects of ecosystem function, we are making substantial strides in developing an ability to 'forecast' consequences of human intervention in temperate forest regions. In this paper we will outline some of the major aspects of ecosystem structure and function for which forecasting capabilities have been developed and suggest how these can be put to use in 'predicting' responses to human activities.

Primary Productivity

One of the prime concerns of land managers is knowing primary productivity, both now and in the future. Foresters very early on developed productivity 'models' in the form of yield tables and a variety of other devices. These, of course, focused strongly on yield of merchantable products and they are typically highly empirical. In more recent years a variety of stand growth models have been developed, but again, these have not focused on primary productivity or been based upon physiological processes and environmental conditions.

Under the IBP a quantum jump in our understanding of primary productivity and carbon cycling in general has been attained. Whether our forecasting capabilities have increased to a similar degree is still in question. But there are indications they have. The Eastern Deciduous Forest Biome (US/IBP) used their terrestrial energy model and atmosphere-soil-plant-water cycle model to examine the effect of climatic changes, such as might be induced by a supersonic transport fleet, upon productivity (Figure 1).

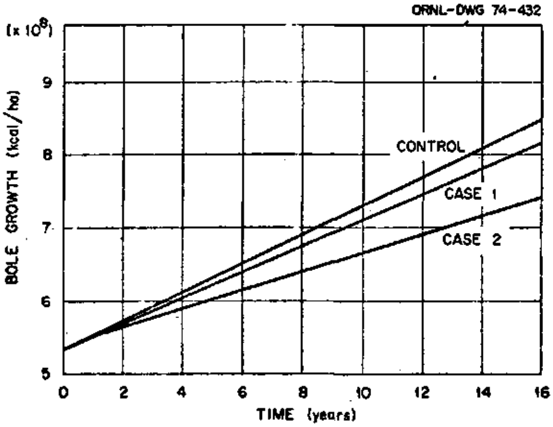

Figure 1. Bole growth of deciduous trees with present climate (control), 0.5°C reduction in temperature and 1% reduction in radiation, wind, and precipitation (case 1), and 2°C reduction in temperature, 2% in solar radiation, and 5% in wind and precipitation (case 2)(from Oak Ridge National Lab. 1974).

Simulations indicate substantial reductions in bole and root growth, severe effects on consumer populations, and a drastic shift in the seasonal pattern of decomposition. Similar exercises with other biome models in cooperation with San Diego State University and the Department of Transportation show interesting and realistic results associated with climatic change although there is no way of validating their accuracy.

One of the more exciting outgrowths of IBP productivity work has been the development of predictive productivity models based directly upon environmental factors. In the Coniferous Forest Biome (US/IBP), Emmingham (1974) has coupled carbon uptake to various environmental stresses. From measurements of radiation, temperature, and plant moisture stress the 'potential' carbon assimilation for a dm^2 of exposed Douglas-fir foliage is assessed as a function of average air temperature and daily radiation. Since observations of phenology are included, the potential in both the 'dormant' and growing season can be evaluated. Next, limitations from unfavorably low soil temperatures, frost, drought, evaporative demand, and nutrition are progressively introduced. From these restrictions, the 'predicted' carbon uptake curve (Figure 2) can be drawn.

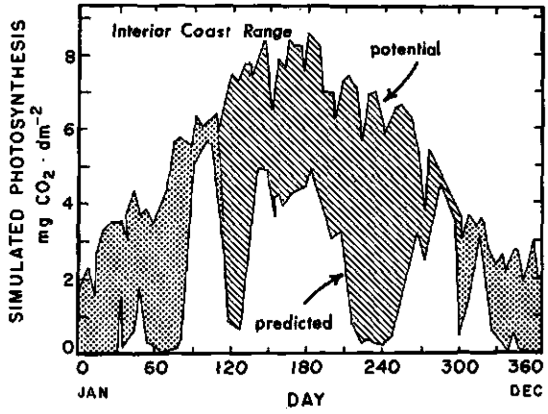

Figure 2. Photosynthetic assessment of an interior coast range environment in the Pacific Northwest. Potentially, more than half of the annual photosynthesis could occur in the dormant season but cold soils and frost are assumed to reduce this substantially. In the summer, drought limits carbon assimilation (after Emmingham, 1974).

This approach has three major practical applications. First, one can quickly assess the most critical constraints upon production to judge whether conventional forestry practices, such as fertilization or thinning to increase the available water supply to remaining trees will be desirable. Secondly, one can, by knowing the relative response of other major species, determine the best choice for a particular environment. Thirdly areas with similar environments can be identified, permitting management practices to be assessed on truly comparable sites.

Obviously, this approach does not permit actual yields to be calculated. To do this, the environment must be modified as a function of canopy structure. Also, the carbon uptake must be partitioned into roots, stems, foliage, buds, etc. This procedure has been followed by Sollins, et al., 1974, with some success. As an outgrowth, a renewed interest has developed in old-growth forest environments, for it is in such areas that net carbon uptake is balanced by respiration of living tissue. The more detailed stand growth model also permits one to assess the effect of defoliation or thinning.

Water and Nutrient Cycling

Poor forest management practices have often been sensed in associated water bodies long before they were apparent in reduced productivity of the terrestrial community. Man has also been interested in water quality and quantity because of its inherent utilitarian value. For this reason hydrologic models were among the first to be conceptualized at an ecosystem level. The earliest efforts at quantitative hydrologic models were by engineers and hydrologists who typically treated an entire watershed as the smallest unit of study. These models contained relatively little biology often solving the combined evapotranspiration term by subtraction.

The IBP-sponsored forest biome programs developed a general hydrologic model markedly superior in forecasting capability and is of greater intrinsic scientific interest. Improvements in realism and forecasting capability have been a consequence of looking in detail at internal physical and biological processes such as transpiration. The modular hydrologic model has a structure which incorporates canopy, snow, litter and soil storage and losses. Sets of equations incorporating both physical and biological relationships include those coupling soil water with available water, interception with foliage area, and stomatal conductance with transpiration.

The Coniferous Forest Biome (US/IBP) has recently added the ability to partition a watershed into compartments which reflect meaningful biologic and hydrologic subdivisions; i.e., divides a heterogenous watershed into relatively homogenous subunits. Stratifications of this type facilitate greater use of processes in the hydrologic simulator, assignment of partial contributions and point sources; for example, the combined contributions of six hydrologic units to seepage are illustrated in Figure 3 for a low elevation watershed in Oregon.

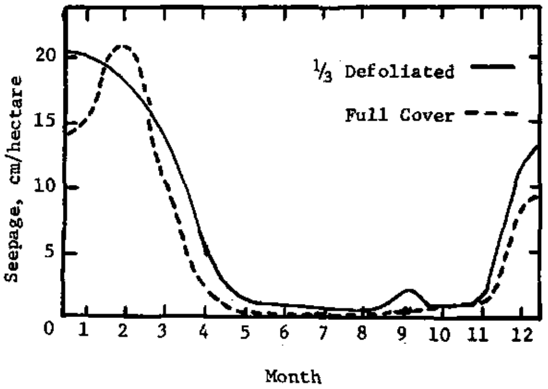

Figure 3. Average seepage to stream before and after defoliation of upper third of a 10.4 hectare watershed in Oregon (after Rogers, Coniferous Forest Biome unpublished).

Defoliating the upper third of the watershed leads to rapid snowmelt in January, higher streamflow in the summer and more rapid soil moisture recharge in the fall.

To date, IBP has contributed most by focusing research on the processes involved and by linking one process to another to assess ecosystem behavior. This has greatly increased knowledge of nutrient cycling models which are typically coupled to carbon and hydrologic models. What these models will do in terms of predicting nutrient losses following various land treatments largely remains to be seen. In the next two years they will be tested in both of the U.S. forest biomes to predict changes in nutrient cycling following major stresses (i.e. clearcutting). Predictions will be compared over a period of years with measured values from experimental watersheds.

Without question the nutrient cycling research has already had a profound effect on our views of the system and the importance of an understanding of decomposer organisms and the role they play as well as the belowground component in total. It has also brought our attention to the role of episodic erosional and deposition phenomena and the need for accurate estimates of weathering rates if we are to assess the long term nutrient balance of landscapes.

Successional Models

One peculiar feature of forest ecosystems is the long term perspective necessary in planning management strategies. While long term viewpoints (tens of hundreds of years) are essential in other kinds of ecosystems (agricultural and rangelands, for example) they are particularly important in managing forest stands whose life spans range from 30 to 100 or more years under managed conditions and extend to many hundreds of years for unmanaged areas. This perspective is necessary for scientists as well as managers for it relates to the ability to extrapolate results of short term studies over time.

Among the most progressive developments in this area of long term forecasting are the successional models. These are of highly variable form and at various levels of resolution but most aim at predicting changes in forest composition and structure. At Oak Ridge National Laboratory, a regional successional model has been developed which simulates changes in the extent of major forest types based upon (1) the present area of each type, (2) successional or replacement rates of one type or another, (3) types of perturbations, and (4) land use patterns (Figure 4) (Johnson, 1973).

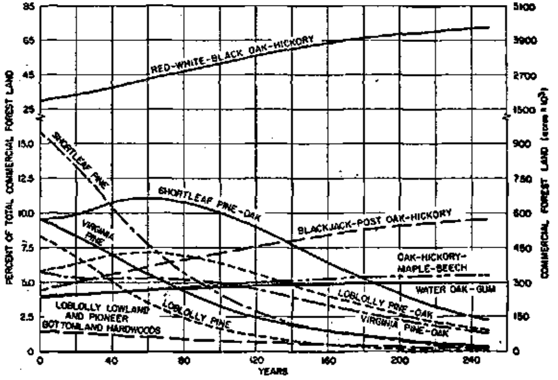

Figure 4. Simulation of the extent of forest types over 250 years in Piedmont region of the eastern United States in the absence of disturbances (from Oak Ridge National Laboratory 1974).

Thus, how much area a given forest type will occupy as a result of different land management alternatives can be estimated.

From the narrower viewpoint of the ecosystem scientists, the stand level successional models are perhaps more interesting. Several have been developed, including a general formulation focusing on early stages in succession and requiring a detailed ecological knowledge of participant species (McBride, 1969), a model based on a life table approach (Leak, 1970), and the environmentally based simulator of the type pioneered by Botkin, et al, 1973.

The Hubbard Brook forest simulation model (Botkin, et al, 1973) traces changes in forest stand composition, structure and biomass in a deciduous forest ecosystem (Figure 5) and appears to do it very well. However, its greater contributions are the concepts incorporated into the simulator. It combines a knowledge of the environmental conditions on the site or plot with the known environmental tolerances and optima for reproduction, growth, and mortality of potential species.

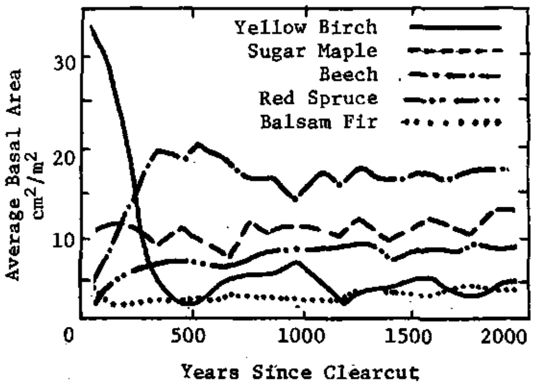

Figure 5. Simulation of average basal area for five species in the temperate forests at Hubbard Brook, New Hampshire for 2000 years in constant climate (after Botkin et al, 1973).

Growth is predicted from an optimum growth curve for each species which is reduced from the optimum in accordance with light, soil, and temperature conditions to which the individual tree is subject. Reproduction, represented in this case by introduction of saplings, is a stochastic process dependent again upon environmental conditions within the stand. Death is conditioned upon occurrence of minimal growth rates and maximal species age. There is too little time to consider the details of the model here, but the stands derived through simulation approximate very well real stands observed on comparable environments. Further the simulated long term successional patterns fit very well with those developed by ecologists using other techniques.

There are a number of problems not adequately addressed by the Hubbard Brook simulator such as the regeneration phase (seed to sapling stage), the way in which the environment is measured, and the changes in understory (e.g. shrub) components. Dr. K.L. Reed in the Coniferous Forest Biome (US/IBP) is attempting to improve all of these features in adapting the Hubbard Brook simulator to the temperate coniferous forests of western North America. The basic and key concepts are retained, matching knowledge of the environment of a site with ecological knowledge of individual species and using this integrated information to track changes in forest composition and biomass on a stem by stem basis.

Potential uses on successional simulators of this type are great in both management and research. Models of this type can directly incorporate the effects of animals as both consumers and controllers; e.g., reduction of leaf area by an herbivorous insect and destruction of individual trees by bark beetles. Indeed, it could be a particularly useful tool in placing forest pathogens -- insects and diseases -- in a long term forest ecosystem perspective and simulating effects of a whole array of pathogens and alternative pest control measures on a forest over an entire management cycle (rotation). Simulators of this type can be used to provide structural data for use in cycling models with shorter time perspectives and to provide better information on successional rates for regional successional models. Some interesting potentialities also exist for using models of this type to explore some basic theoretical questions about ecosystems such as relationship between diversity and productivity or stability.

Erosion Models

Erosional and other geomorphic processes are another area where a capability for forecasting long term changes is being developed. Developments in this area are not nearly as advanced as in successional modeling, but several conceptual models have already been developed. Processes such as mass soil movements, surface soil erosion, and stream channel erosion are extremely important in some forest ecosystems, but one or more are often ignored in classical short term nutrient cycling studies. Erosional and geomorphic processes take on added importance when we realize that the soil mantle in many, if not most, temperate forest regions is not entirely a consequence of in situ formation; it also reflects depositional and erosional processes often of a highly episodic nature.

The Coniferous Forest Biome's (US/IBP) conceptual erosional model incorporates the processes of mass wasting, surface erosion, and stream channel storage and transport. Driven primarily by hydrologic activity, it is being designed to answer questions concerning magnitude of nutrient losses due to erosion in its several forms and relative rates of erosion and soil formation.

Models of long term erosional, soil formation and related geomorphic processes will rarely attain the predictive capabilities of some of the successional models for several reasons, including the highly stochastic nature of many of the key erosional and depositional processes and difficulties in attaining accurate estimates of many variables such as weathering of parent materials. Nonetheless, they are important in providing better understanding of how the existing temperate forest evolved and surface some serious long term considerations for their management.

Conclusion

As a consequence of work initiated under the International Biological Program, we have markedly increased our ability to forecast the effects of various management practices as well as other stresses upon the composition, stability, and short and long term productivity of the forest landscape. At least as important as the increased predictive capabilities are the insights into processes and identification of additional research needs such as in the areas of belowground processes, decomposition and extrapolation of predictive capabilities in time and space.

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MANAGEMENT OF ECOSYSTEMS: INFORMATION SUPPLIED BY SIMULATION MODELS

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Summary

Although prediction of ecosystem response, in the strict sense of the term, is difficult because of the highly probabilistic events involved, it is, nevertheless, a feasible problem to estimate the probabilities of particular responses occurring. These probabilities usually cannot be determined from actual field data because of the large data sets which would be required, but can be estimated from the results of simulation models. Management models which use mean values and variances of ecosystem parameters can then be used to make better management decisions.

Introduction

In assessing the applicability of ecosystem studies to grassland resource decision-making, we are faced with the paradox that: a) there has not yet been a case where a decision involving grassland resources has been specifically based on ecosystem study results. This is not surprising, of course, since summary reports based on the research program efforts of 1967-74 have not yet been completed. The other side of the paradox is: b) that the methods for approaching the problems of grassland resource decision-making have been presented to international and various national audiences several times.

The procedures for treating the grassland resource decision-making primarily utilize optimization models. Professional journal articles include those by Whitworth (1973), D'Aquino (1974) and Bartlett, Evans, and Bement (1974). The procedures are also covered in book form (Jameson, D'Aquino and Bartlett, 1974).

On the other hand, ecologists typically do not arrange their information in the same format as do resource decision-makers. Scientists are more likely to use simulation models such as those utilized by Forrester (1968). Nevertheless, simulation models directed toward applied questions have been prepared (e.g., Smith and Williams, 1973).

It is generally the case, however, that resource managers have not used simulation models nor do the thoughts of many managers appear to be well represented by such models. The different conceptual structure of managers as compared to that of scientists has led to the frequent accusation by scientists that managers do not have specific questions that are researchable. Researchers, on the other hand, often appear to have a conceptual structure of problems which leads to simulation models, but generally have not utilized such models to improve the organization of research results about a particular question. Thus, managers have previously accused the researchers of taking too long to come up with relevant results and generally not dealing with relevant questions.

Most of these accusations are, of course, true, but the utilization of appropriate modeling procedures for managerial and scientific questions should greatly reduce this discrepancy.

Unfortunately, many scientists have thought that the detailed biological studies conducted by the biome programs would lead directly to management recommendations. We find, however, that no such studies, no matter how detailed they may be, lead to a "better" solution. Contrary to the belief of many ecologists, "good" and "bad" are not ecological properties. The research results and modeling efforts of scientists can, however, greatly facilitate the answering of if-then questions of managers.

It appears that there are three major attributes of biome type research which are relevant to grassland resource decisions:

(i) The biome research has led to entirely new approaches in ecological research. Previous ecological research has very often described conditions at a particular time and place. In the modeling vocabulary, these have been "state variable" measurements. The numerical value of such state variables depends on the unique combination of circumstances of that particular time and place, and very often is not generalizable to broader situations.

On the other hand, the biome programs have emphasized process studies which determine the rates or changes per unit of time. These rates or results of process studies can then be incorporated into models which are much less situation-specific than the state variable measurements, and consequently, can provide general indications of results for a wide variety of situations. We are now very nearly able, for example, to stimulate grassland systems for practically any climatic situation (Figure 1).

Thus, the advantage to the resource decision-maker concerning the biome results is that ecosystem and modeling approaches may lead to better research and thus, eventually, but nevertheless indirectly, to better management.

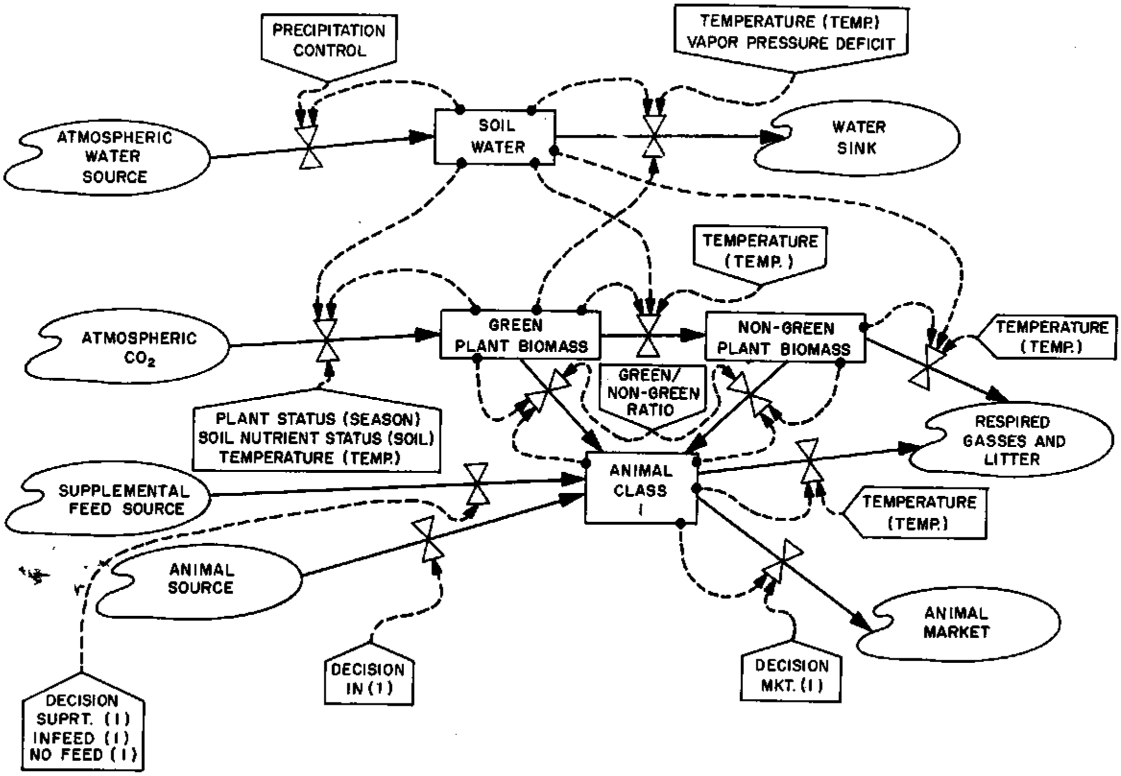

Figure 1. Diagram of a simulation model developed to produce information about state variables (boxes) based on biological and physical processes (arrows).

(ii) A second major contribution of the biome results is the clarification and emphasis of the filtering or stability aspects of ecosystems. Ecosystems in the grassland management context are driven by highly variable precipitation, temperature, and other climatic events. The first stage in reducing some of the variation is soil water. Subsequent filtering stages include live plants, dead plants, primary consumers (such as cattle), offspring of the primary consumers (calves) and, with economic systems, can include stabilizing components such as monetary reserves. From this very practical example, we can see that the ecological system acts as a filter mechanism which needs several stages (6-10) to result in a satisfactory stability for managerial purposes. Fewer stages than this yield unsatisfactory stability, i.e., instability. Additional stages may not be necessary for stability considerations but may add greatly to the difficulty of research.

(iii) A third major contribution of the biome approach is that it provides us methods of getting specific information which cannot be readily obtained experimentally. Biome models based on the synthesis of process studies information can be used to generate approximate data. Although these synthetic data will likely be less accurate than state variable measurements which would have been collected for the particular situation, they are also much cheaper and quicker to obtain, and thus have a higher probability of having a real impact on managerial decisions.

For example, managers usually need to know seasonal values of standing crop of herbage as influenced by varying management practices. The biome-type models provide a ready way of generating such values even though they would be somewhat difficult to obtain experimentally (Figure 2). These estimates from simulation models can be used in deterministic optimization in management models such as linear programming. The serialized model developed by Bartlett, Evans and Bement (1974) builds upon a linear programming model but allows for seasonal growth of vegetation and the buying and selling of livestock. This is accomplished by the discrete continuity equation (1):

$$sc_i + g_i - c_i = sc_{i+1} \tag{1}$$

where sc_i is the standing crop of forage at the start of period i, g_i is the forage growth during period i, and c_i is the forage grazed during period i. By placing the forage growth factor (g_i) on the right-hand side, equation (1) becomes (2).

$$-sc_i + sc_{i+1} + c_i = g_i \tag{2}$$

It is apparent that each of the terms of equations (1) and (2) can be derived from Figure 2.

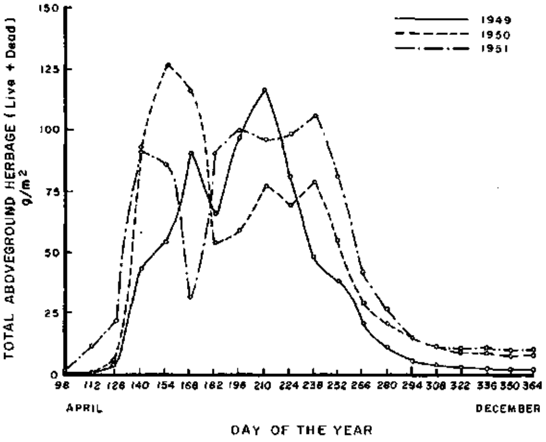

Figure 2. Three year average of total standing forage crop (live and dead) derived from the simulation model of Figure 1.

Equation (1) can also be adapted for the flow of livestock through the year. The livestock flow equation (3) becomes:

$$h_i + b_i - s_i = h_{i+1} \tag{3}$$

where h_i is the size of the herd at the start of period i, b_i is the number of animals bought at the start of period i, and s_i is the number of animals sold at the end of period i.

In other examples, some particular decision procedures require an estimate of the uncertainty about standing crop and forage. A model appropriately constructed can provide the necessary variance and co-variance approximations by running the model through several years. Even though we may assume, for simplicity, that we have perfect knowledge about the coefficients in such a model, probabilistic driving variables such as precipitation and temperature give highly variable results (Figure 3). Note that with the use of such models we are able to generate results for years and places other than those for which data was obtained for model development.

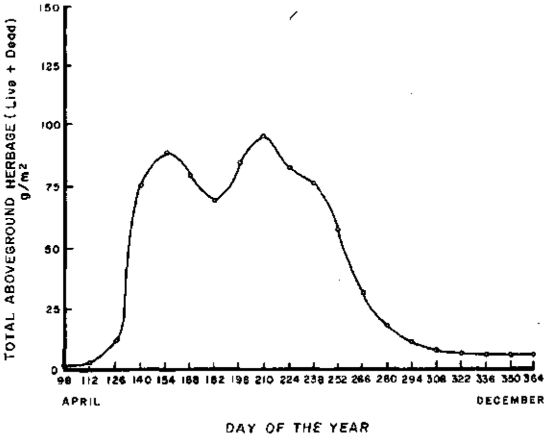

Figure 3. Individual year results of total standing forage crop (live and dead).

To be realistic, these climatic elements in grassland management cannot be assumed to be known with certainty. It is these elements that present problems of risk and uncertainty that are involved in making decisions about resource use. A mathematical approach which can handle some of the uncertain events and allocate resources in an optimal way is known as chance-constrained programming. This type of model makes possible the investigation of risk and uncertainty associated with resource management decision making. Because grassland managers must often stock their land before they are sure of the available forage, they are in essence assuming an ecological risk of over utilizing the forage resource or an economic risk of under utilization. Thus, the amount of available forage is an uncertain event with which managers must contend. The chance-constrained approach to decision making may be used when such uncertain events occur, provided that meaningful estimates of standing crop variances are available. Such estimates can be obtained from simulation models; obtaining the same estimates by direct measurements could be costly and time consuming. The methods of treating such probabilistic problems are too lengthy to be included in this paper; fuller treatments of the subject are given in Hunter (1974) and Jameson, D'Aquino, and Bartlett (1974).

Conclusion

We have previously had much difficulty getting enough information to make good grassland resource decisions. We are now on a threshold where biological data can be generated synthetically by the use of appropriate models. The models will also provide a clear identification of research priorities so that research can be more specifically directed to critical problem areas.

With the output of such models, coupled with better inventory methods which have become available through such accomplishments as remote sensing, the apparent lack of biological information will no longer be the limiting factor in resource decisions. A new set of limiting factors, therefore, will come into play. It appears that these will fall into two categories: (i) management models needed to better evaluate alternative plans and practices must be developed to better utilize the information made available by biome type research models, and (ii) social constraints will more clearly become the limiting factors in the resource decisions. The previous lack of biological information has obscured the necessity of appropriately including such social values in the decision paradigm.

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HUMAN IMPACT ON TRANSPORTATION AND DIVERSITY IN ECOSYSTEMS.HOW FAR IS EXTRAPOLATION VALID

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Interaction between man and the rest of the biosphere may be discussed conveniently in a number of separate items:

1. Exploitation.- To take something out of an ecosystem means a relative reduction of the ecosystems biomass, and, if productivity is not negatively affected, an automatic increase of turnover. Turnover is much increased by conscious management for a high yield. It can be said that selection is no more in the "interest of the ecosystem", but in the "interest of the exploiter", that is, man. Selection for prolificity is encouraged, and r-selection spreads across many layers of the ecosystem.

Exploitation has been made easier in areas subjected to a fluctuating climate, where simple persistence requires that ecosystems overshot some limit of primary production. It is a security system that leaves, more often than not, a surplus to go down a detritic and inefficient path, or else to be used by some outsider (man). Moreover, diaspores and ressilient stages apt to resist the inclement season could provide an acceptable food for man. The situation is characterized further by a periodic or persistent accumulation of nutrients in soil, and a high ratio production/biomass , with noticeable bursts of productivity. Weeds become exploitable and exploited crops; tendance to monoculture has been unconscious and, only later, purposeful.

Fluctuating ecosystems, in a given instant of time, have a lower diversity than ecosystems that remain more alike during the year over, and the result of exploitation is a further decrease in the diversity of communities.

In tropical zones, only the high lands and the areas subjected to periodical flooding (rice) could raise important crops.

Exploited animals should be at the end of rather short food chains. This is one of the reasons for the low exploitability of oceans. Only the sensible use of the behaviour of the same animals allows to make important catches; nevertheless, oceans provide only 1% of food of mankind. The richer areas in the sea are the upwelling regions subjected to constant or periodic enrichment, and to important fluctuations of populations. Ecologically they can be compared to the grasslands where agriculture was started.

2. Transportation.- There are three main stages in the use of nature by man. The key factor for moving from one to the next has been transportation, and the result has been increased crowding. This is not always negative, because it has been the source of our culture.

In a first -or paleolithic- stage, we have local exploitation, local feedback and a density that compares with the one attained by primate populations (o.3 to 1.4 individuals per square km).

Nomadism is a way to escape local feedback: exploit -and ruin- one area, go to the next, and so on. In agriculture supported human populations, density increases by two orders of magnitude.

The same result as moving back and forth people and animals can be obtained moving goods. Fields can be fertilized and watered and foodstuff supplied to large urban populations. On a world basis, and in present times, only 12 % of total energy degraded directly by man goes through the biological or endosomatic metabolism; the rest is cultural or exosomatic metabolism and a major part of it is used in the different forms of transportation. Transportation has also biogeographic implications: cultivated stocks, pests, germs, have been shifted by man. By the way, essential inequality of exosomatic metabolism, among humans and human groups, as compared with endosomatic metabolism, where variance is much less (death sets soon a limit), is the source of most political and social problems (Margalef, 1973a).

Pollution is related to transportation. Pollution is the result of one way and converging transportation. As a consequence, pollution acts as a buffer or a brake, slowing down natural cycles. Doubling the energy put in transportation could whip off the problems of pollution, closing and speeding up the cycles, but are we prepared for such an acceleration?

Transportation magnifies the impact of man as an exploiter. Transportation is less subjected to feedback regulation than nomadism is, and leads from local to global feedback. This could be modelled along the following lines: Consider a number of relatively independent small models, and in each of them a local human population in interaction with a local ecosystem.

Connections between the different blocks is feeble, each one has a homeostatic behaviour, and all are embedded in a biosphere, which state is not actually endangered by some extreme state in one of the blocks. Transportation means a stronger lateral coupling of the partial models, more in the part of the human level than in the rest. Man becomes apt to destabilize the system on a global area, and the systems cannot more be closed -or modelled- over a restricted area.

Development of natural ecosystems, along succession, leads to a development of a vertical system of transport, and, at the same time, to a regulation of the horizontal transport, that is kept to a minimum. Such reorganization of the path followed by the elements in the material cycle of the ecosystem seems quite general. The forest provides excellent examples, as well as the central areas of the oceans. It should be added, perhaps, that limitation of horizontal transport has not to be understood as an actual minimization of transported matter, but rather as a trend towards making symmetrical any transportation over an horizontal plane.

The impact of man over nature is a tremendous increase of horizontal transport, in all forms: erosion, pollution, concentration of produce in towns and along highways, etc.

3. Organic pollution.- Organic matter is concentrated, half used and dumped in small areas,carried on along converging paths. Pollution, thus, is a link between separate systems, and, in one of them, at least, creates a condition of stress. Stress is used here to describe a rather inefficient use of resources, that results in the separation of some nutrients out of the cycle, at least temporarily. This is a positive brake (see later), much more important that any feedback of esthetic or economical kind, the only present in the popular views about pollution. As well as upwelling and eutrophic systems, pollution is characterized by a high production/biomass ratio, and by communities of low diversity.

Diversity is low,either because "hard" conditions limit the number of species to a few resistant ones, or because fluctuations and irregular accelerations favour a small number of species, rather free of links with others and characterized by a high rate of multiplication. In recent times it is becoming popular to use as an index of pollution, any depression of diversity values below the initial or usual values.

4. Chemical pollution.- Introduction of molecules designed to interfere with vital activities of other species is a strategy for competition already in use by prehuman organisms, as low as red tide organisms may be. The input of unusual organic compounds and of elements in unusual concentrations have a variety of consequences, but at the ecosystem level, the results are often comparable. In general, pesticides lower the diversity of the communities, in part because species with a low rate of multiplication may be more affected than the true pests. In the distribution of pesticides and toxic elements through the parts of the body, and through the parts of the ecosystem, concentration becomes inversely related to turnover. It increases more in the higher trophic levels and, in consequence, mortality is expected to be increased in the same levels, adding another cause for a drop in diversity and for an increase of the ratio production/biomass. As a non negligible impact of man on evolution, the selection of resistent mutants should be added.

5. Thermal pollution.- Energy use by man implies a source and a sink, a more steep gradient and, more or less locally, an increase of temperature. No matter how the thing is presented, an increase of the temperature at which (biological) exchange happens, means a higher"production of entropy", a lower efficiency of transfer, an increased metabolism, and a lower ratio production/biomass. We find again the same result of human interference, and a lowering of diversity is to be expected too. The only foreseable exception in the last prediction could happen if heath output were organized in such a way as to stabilize natural ecosystems, giving off more heath in winter than in sommer, but this is not what usually happens in the instances of thermal pollution.

6. Radiactivity.- Ionizing radiation destroys a fraction of structure, but the structure left can continue activity and even increase it, profiting from "cleared" space. The predictable consequences of radiation, are a higher production/biomass ratio, and a lower diversity. Indeed it has been found that radiation lowers diversity in communities of plants and of soil animals, and such effect may be quite general. The increased concentration of chlorophyll observed in cultures of some species of algae, subjected to radiation, is consistent with the expected increase of turnover in radiated systems. Radiation affects interaction between species in the expected ways: in systems formed by a predator and a prey the predator is more depressed; in competion experiments, radiation favours the r-strategists (Auerbach, 1958; Blaylock, 1969).

All or most of the ways in which man interferes with the rest of nature, produce coincident or parallel effects. Diversity is reduced, horizontal transportation is increased, and the ratio production/biomass is increased also. If placed from the point of view of the non humanized ecosystem, accumulated and preserved organization can be considered as some measure of progress, it is claar, then, that forcing more energy through the system leads to a degree of simplification and inefficiency. The parallelism of change and its logical coherence represents a welcome simplification of the whole set of problems.

It can be said, in a very general way, that any system tends to internalize activity and develop homeostasis. When a system is exploited, it is forced open, and the changes that follow can be linked to its openess. But any open system becomes a part of a larger system, that itself can be relatively closed, or less open than the first one. In other words, and translating this in usual ecological terms, if there are general trends in succession, expressable through the maximization or minimization of definite variables, the same trends have to be recognized in the continuation of succession in the new system formed by the addition of man to the natural ecosystem. This would need often a reconsideration of the variables to be maximized or minimized, or of the selection of appropriate guide functions. Following such reasoning, inclusion of man must enlarge, and not damage, ecological theory. What I mean may become more clear through the following proposal: The function primary production/total biomass may be useful as a guide function in ecosystems in general, and specifically in non humanized systems. But in humanized systems, the guide function, to be predictive, has to include some human activities (we see later that they are not as exclusively human as it seems, and there may be advantages for general ecology in developing this point) and might take following form

$$\frac{\text{primary production} + \text{exosomatic metabolism}}{\text{biomass} + \text{artifacts relevant in survival}}$$

The mentioned artifacts expand influence over space and time, and are not different from strategies in evolution that combine events, through lengthening of individual life span, or through a more extensive use of an heterogeneous space.

In less abstract terms, human action can be viewed as a source of regression, as something that works again or runs contrary to succession, to the way towards a climax, a climax defined, of course, in the frame of non humanized systems (just as the minimum of the ratio primary production/total biomass). If exploitation plus interference in general, are in opposite terms with ecological succession, as usually understood, the consequence is to make any proposal for an absolute conservation an illusion. This needs a careful definition of conservation in every instance, always stating the allowed impact. Human activity, in general, can be considered as a "stress", that moves back the rest of the system - the "natural" system, that is- , opening it and coupling it with man as the exploiter, into a new system, in which eventually regularities in succession can be discovered.

The notion of stress might be useful, when ecosystems are considered as homeostatic systems. Stress is something that puts into action the mechanisms of homeostasis. Adequate models, along these lines, can be developed for almost any system. As an example I propose to consider the eutrophication of lakes. In aquatic ecosystems a number of homeostatic or stabilizing mechanisms can be identified. If a cybernetic description in terms of trends (or "goals") is not found abhorrent, it could be said that such mechanisms work to keep at a rather low level the primary production of plankton. For the purpose of presentation, parts of the mecanimss can be taken apart, but this procedure hardly does justice to the intimate coupling between manifestations that we tend to isolate. We can discuss several pieces of mechanism or brakes: 1) The selfscreening of plant pigments. The amount of active chlorophyll is limited to about 300 mg/sq m, and so is primary production limited. 2) The oxygen or photosynthesis valve. High production leads to oversaturation in the surface layers, leads to the diffusion of oxygen from water to air, and to interception of flow of oxygen from air to water. As a result, part of the synthesized organic matter is not oxydized, and this amount is not related with production in a linear way. The percentage of produced organic matter that finds its way to become incorporated into the sediment, increases as production increases. 3) High productivity increases pH, and a part of the phosphate is taken out, mainly in form of calcium compounds. Mineral phosphate keep accumulating in the sediments of eutrophic lakes as well as below the upwelling areas in the oceans. 4) Any excess of nitrogen compounds -specially after part of the phosphate has been precipitated- leads to a more active denitrification. Nitrogen is passed to the molecular or atmospheric reservoir of the element; its way back goes through nitrogen fixation by bacteria and blue green algae.

From extrapolation of the workings of these pieces of mechanisms, that are always non linear, it can be anticipated a slowing down of the cycles, and the minimization of the energy exchanged per unit of preserved organization. This is a trend materialized in ecological succession, but we can see here how stabilization and succession appear as results of the same mechanisms. If we put the system back, immediately we reactivate mechanisms that were still working with lesser activity, "creeping towards climax". In particular, any bypass, like the ones of carbon and phosphate through sediment, or nitrogen through atmosphere, acts as a brake or as a buffer. It works actually as an hydraulic buffer or damper. Of course, the concept may be useful in describing human action. Man sets temporarily stores of elements out of the natural systems; any lengthening of the pathways amounts to the same. This means that acceleration of natural cycles by man cannot be as high as man intends to.

The workings of the proposed mechanisms can be visualized at best, studying the development, in mutual interaction, of the vertical profiles in the distribution of light, nutrients and plankton, in water, as well as in the development of terrestrial vegetation. Trees grow in heigh, by success of illuminated branchs in competition, and in doing so expand in the vertical dimension the path followed by elements in their cycle. Always, the most probable final situation is of a low primary production. In fact it seems lower than actually is, due to the difficulties of measuring it appropriately in very mature ecosystems. Another important point is the development of a mechanism of vertical transport. It becomes necessary and limiting, and at the end, without a more active participation of organisms (migration, evapotranspiration, activities of man) it might tie down energy flow at very low levels, allowed by physical diffusion. In very "mature" systems the vertical transport system seems well organized and in such a way that the whole system can be spatially decomposed into a number of vertical prisms or columnar systems, placed side by side, and almost independent. This does not mean, of course, that there is no exchange between adjacent blocks but only that, if there is such exchange, it is symmetrical: approximatively equivalent amounts of matter and of energy and of organisms go both ways.

We could imagine a highly hypothetical "climax" condition, with a minimal energy exchange, and a rigorous vertical organization of the transport system, just as described, and ask what keeps any system *from coming down to such state. In fact the* biosphere is a mosaiclike structure, and everywhere there are spots of high productivity, associated usually with a depression in values of diversity and a not so advanced differentiation in layers. Now, any increase in net production is associated with a particular input of energy that can be qualified as auxiliary or ancillary, and that is not the electromagnetic energy of light. Such auxiliary energy comes in form of seasonal mixing in lakes, tides in the littoral zone, general marine circulation in the upwelling areas, drainage from croplands and towns in eutrophic lakes, transport of soil and fertilizers by water in lowland countries. I propose that a measure of stress might be the auxiliary energy involved. Response to stress is an increase in primary production (usually), and a more important increase of the fraction of the product that is taken out of cycle, at least temporarily -this is the reason for seeing in the process a stabilizing mechanist- . It is clear that auxiliary energy is strictly associated with some measure of horizontal transport, and moreover that the input of auxiliary energy needs a minimum horizontal size to be realized: obviously an eutrophic lake cannot be modelled by itself, but has to include the area from which nutrients come, and obviously an upwelling system requires the study of a large marine area to be understood. It can be suspected that there is a definite relation between the (forced) primary production and the auxiliary energy involved (Margalef, 1973b).

Man is a species characterized by its ability to tap and put into action exosomatic energy, and is able as well to drive such energy in ecosystems. Such activity is associated with exploitation, through a forced primary production. It is noteworthy that a plotting of yield of crops versus auxiliary energy, such as depicted in the book of Watt (1973), comes closely to my mentioned graph (Margalef, 1973b). The slope may be slightly different, but this is to be expected, because crops receive also energy in rain, water trasport, and not only through the work of man, beasts and tractors. The stress exerted by man and manifested in destabilization and regression of natural ecosystems may be equated with the effects of fluctuating climates, erosion and silting, upwelling, etc. I submit as an important subject the careful study of the necessary relations between input of auxiliary energy and the transport involved, manifested in the minimum horizontal dimension required to funnel or to make effective a given amount of work.

It seems intuitiv, at least to me, that

in a fluctuating system, or in a system formed by parts disjointed in space, but functionally connected, the diversity computed over samples that cover small blocks of space and time, has to be smaller than any diversity computed over the whole system, or of any comparable ecosystem less seasonal in its aspects or more uniform in space. If the upper limit of diversity (about 5 bits per individual in biotic diversity) is an asymptotic measure of the organization to be expected in a relatively closed system, any transient of such system should display a lower diversity. Exploitation and enhancement of horizontal transport has to result in a decrease of diversity in the exploited system.

Any attempt to prediction has two aspects:

1) The common consequences of exploitation, interference in general, enhancement of the input of auxiliary energy, and asymmetric acceleration of horizontal transport are: reduction of diversity, acceleration of turnover, and increase of the mutual dependence of systems far away in space -and in time, remember fossil fuels-. This is what happens and is expected to continue, at an accelerating pace. Ecosystems that never have gone through the selection of serious environmental stress, as tropical forests, coral reefs and oligotrophic lakes, will be the firsts to go. The amount of interference that a system can support is linked non linearly to its state. To produce a certain amount of change, it takes much less pollution in an oligotrophic lake than in an eutrophic one. Stressed ecosystems are more resilient to increased stress and can absorb more disturbance -short of final catastrophe?-.

2)Other aspects of prediction have to consider behaviour of man, more as a peculiar species of mammal than as a rational being with high qualifications. It can be anticipated that exosomatic metabolism will increase much more, and that natural ecosystems will continue to regress. Perhaps energy will take away the temporary brake provided by pollution. As exosomatic metabolism continues to be basically inaequal and injust, and in a certain way proportional to population density, conurbations will continue to grow, until perhaps to kill themselves. It seems difficult to anticipate success for more rational, reticulated, organization of space. Prediction based on sketched theory goes only to the point when cultural artifacts become useless and the whole culture becomes noise. Loss of grip, then, may become rapid, and signify"doomsday"for a species that feels overconfident. If anticipation is related to reflection, in the frame of a feedback mechanism, we are much in need of some reference value for maintaining a healthy feedback. I am inclined to believe that the implied values of reference have to be based more on moral considerations and restraint, than in the simple play of power.

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Critical evaluation of systems analysis and modelling in ecosystems research and management. Data collecting and processing for predictive purposes

THE HIERARCHICAL APPROACH TO MODEL BUILDING*

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Summary

Decomposition of ecosystems into sub-systems (for instance, by spatial or biological dividing lines) can greatly facilitate the modelling process. Another useful tool is the cross-classification of ecosystem components and processes, so that the same model of a particular process can be applied to numerous different ecosystem components.

Introduction

It is commonplace that all systems can be decomposed into sub-systems. If a system consists of a number of components, linked by various types of interaction, including flows of material and information, then any sub-set of these components may be separated as a sub-system, linked to the rest of the system by a sub-set of the interactions -- those, in fact, linking the components within the sub-set with those not in the sub-set. And in general a sub-system thus distinguished may be further decomposed into sub-sub-systems. A hierarchical or nested structure is thus implicit in the concept of a system. Ecosystems are no exception. Their complexity may be broken down in a variety of ways, giving a number of smaller entities, each simpler than the whole, but still capable of further subdivision.

To consider an ecosystem in terms of hierarchical structure has at least two advantages. In the first place, it facilitates thought processes. A system of any complexity is almost beyond the powers of direct thought; the human mind cannot grasp in a single effort the interrelations among a large number of components.

The second advantage of the hierarchical approach is practical. If one is concerned to study the behaviour of a system by modelling it, decomposition into simpler sub-systems greatly facilitates the task. Particularly if computer modelling is intended, the structure of programming languages lends itself excellently to the hierarchical approach, where each sub-system may be matched with a sub-routine, and sub-routines may, like sub-systems, be nested indefinitely.

To divide the task of modelling an ecosystem into sub-routines has many advantages. The likelihood of error increases at a rate more than proportional to the length of the programme, so that division of the programme into sections which may be written and tested separately usually reduces substantially the time, effort and cost involved. Also, subdivision of the task makes possible the allocation of sub-tasks to separate groups, thus spreading the work load, involving a greater range of personnel (perhaps with specialized knowledge), and enabling the modelling effort to proceed along several channels in parallel rather than as a serial operation with the resulting bottlenecks.

Principles for Recognition of Sub-systems

The ways in which an ecosystem may be broken down into sub-systems for modelling are legion, so we should give some consideration to the principles upon which this decomposition should be based.

In the first place, if a number of different individuals or groups of modellers are involved, an obvious factor will be the types of expertise available and required for different parts of the model. The optimum size of a group to take responsibility for a specific and limited modelling task is fairly small -- almost certainly under ten. This will be difficult if each sub-task encompasses a wide range of disciplines; consequently, a decomposition in terms of disciplines may well be appropriate, though it is important to provide opportunities for criticism of each sub-model from other disciplines.

Another criterion is concerned with validation. Models need to be validated by comparing a set of outputs from the model with those of real-life systems having the same inputs. And, if the model is constructed of sub-models, the latter should also similarly be validated. This implies that the set of inputs and outputs for each sub-model should be easily measured -- and, for preference, (in the case of inputs) controlled. Then the sub-models may be validated separately, and only the results of combining them need to be tested on the scale of the full model.

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Third: the various sub-systems should be selected so that they lend themselves to treatment at different levels of complexity. This will be particularly important if the development of each sub-model is the task of a separate group of modellers. So long as the inputs and outputs (a required set of outputs, and a maximum set of inputs) for each sub-model have been determined in advance, each sub-model can be developed in versions of varying complexity, differing only in their internal structure. The various sets of sub-models will then be mutually compatible. The process of modelling can proceed iteratively, but the iterations for the various sub-systems can be mutually independent.

Two other criteria suggest themselves intuitively. The first is internal homogeneity. The greater the similarity of behaviour of different entities within the sub-system, the more simply and accurately can that subsystem be modelled. A special type of homogeneity concerns the time scale of processes. It often happens that an ecosystem model needs to include processes at different time scales. The scale appropriate for bacterial activity is much shorter than that for vertebrate demography, for instance. If processes with very different time scales are included in the same sub-model, adequate computer treatment becomes very difficult; it may also be highly uneconomic.

Another criterion which appeals intuitively is that of limited interactions. Ideally, if the system can be divided into sub-systems which do not interact at all, the task of modelling at the whole system level is complete, and the whole operation can be performed at the sub-system level. Similarly, if the system can be so divided that the interactions (material flow, information transfer) between sub-systems are minimal, the major task will be in building the subsystem models -- which are, ex hypothesi, simpler to construct than those for the system as a whole.

Types of Subdivision

Let us consider, then, the ways in which an ecosystem might be divided for modelling purposes.

One obvious method is spatially -- both horizontally and vertically. One obvious place for possible division is at the surface of the soil. Many components of the system are either above or below the soil, but not both; and many processes, too, are limited to one or the other portion of the system. Horizontally, one also has the possibility of useful subdivision. Spatial patterning is a commonplace of ecosystem study. Substrate differences, topography, the organisms themselves, all serve to differentiate the system and its dynamics on the horizontal plane. Accordingly one may separate sub-systems horizontally which are much more homogeneous internally than the system as a whole.

Quite a different possibility is provided by the biological composition of the ecosystem. Conspecific populations of organisms show a high degree of homogeneity in their behaviour, so that the species constitutes a very natural sub-system in decomposing an ecosystem for modelling purposes. If one groups species, the loss of homogeneity may be fairly limited if they are grouped according to their interrelations with other species outside the group, so that they constitute a reasonably homogeneous set within the system as a whole. Clearly, subdivision in terms of biological categories (species or groups) lends itself very well to hierarchical treatment -- though the taxonomic hierarchy will usually not be the most appropriate.

Other ways of decomposing the system may in plants, for instance, be based on distinguishing organ types as separate sub-systems -- the foliage; the roots; the storage organs, and so forth. Stages of development may also constitute a useful basis for distinguishing sub-systems -- seeds may be separated from seedlings or mature plants, eggs from larvae or adult insects. For some purposes, these subdivisions could take the place of those based on biological species or group; for others, they might constitute different levels of a hierarchical structure.

So far, we have considered sub-systems in terms of components; but processes or groups of processes can also constitute sub-systems. Within the foliage of a species, one could for instance treat the processes concerned with photosynthesis, with translocation, and with leaf fall as separate sub-systems; or within an animal species feeding, mortality and reproduction could be regarded in the same way. And processes can be broken down hierarchically just as can components. Photosynthesis can be divided, for instance, into energy capture and conversion, carbon dioxide access, and carbohydrate synthesis; mammalian reproduction can be divided into ovulation, sexual encounter, fertilization, pregnancy and parturition.

Cross-Classification

It has become apparent from what has been said that a hierarchical approach alone may not be the most appropriate method of breaking down an ecosystem for modelling purposes. Classifications for different processes may interlock rather than subdivide, and the appropriate level of subdivision may depend on the particular process under consideration. In an ecosystem model, accordingly, one needs a structure more flexible than a strict hierarchy of sub-models -- the principles of cross-classification and ad hoc classifications need to supplement that of hierarchy.

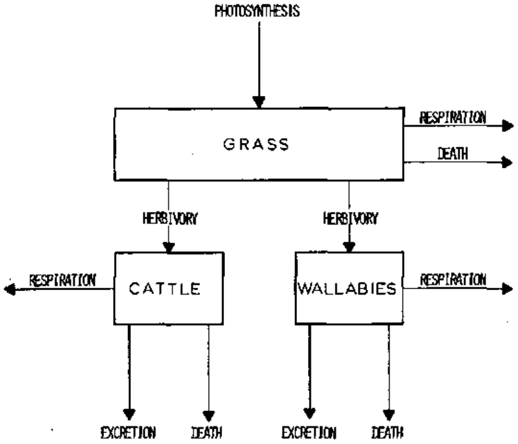
By this, I mean that the components and processes in an ecosystem may be classified in a number of independent but mutually compatible ways, and that the classification used may differ from process to process. Thus, one may classify plant tissue, for instance, according to organ type, species, age, and location vertically and horizontally. The process of photosynthesis, say, will be limited to certain organ types (those containing chlorophyll); but the rate will differ with all the cross-classifications of those organ types. The values of constants for the process may vary with organ type, species and age; the effect of location does not usually take the form of different values of the constants, but depends on local variation in the values of the factors which affect the process. If we consider, on the other hand, transfer of material from plants to large herbivores, location may be irrelevant, and only the three other classifications may be relevant.

Looking now at the large herbivores themselves, they may be divided (for instance) by species, sex and age. For the modelling of feeding habits, age may be of little importance and sex of none; but for demographic processes they are all-important. Thus, modelling should introduce the various cross-classifications only in processes to which they are relevant.

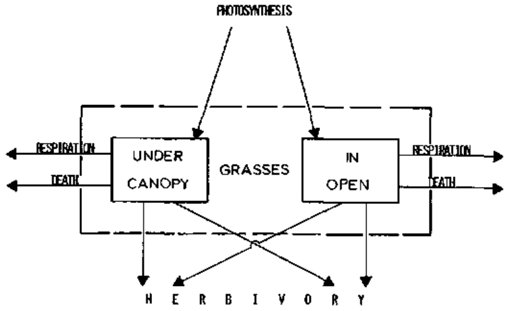
The general method of constructing ecosystem models which is adumbrated here -- with a hierarchical structure of sub-models, each of modular form, which can be replaced by other modules similar in respect of input/output structure, and with processes activated only in respect of those cross-classifications to which they are relevant -- lends itself to an iterative process of model construction and improvement. In each part of the model, alternative structures, and degrees of resolution in respect of the different cross-classifications, may be tested in their effects on the outputs obtained, and in their agreement with those of the real-life system modelled.

An Example

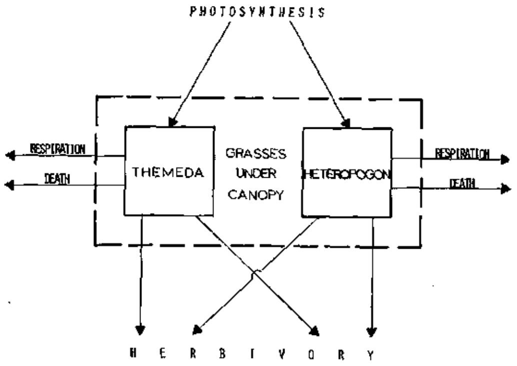
To fix our ideas, let us consider that we are to model an area of savannah woodland in Queensland, grazed by cattle and wallabies, and that our task is to predict the mean rate of gain in weight by the cattle, averaged over the whole year. Our first very simple model consists of three compartments only, with flows of energy among them:



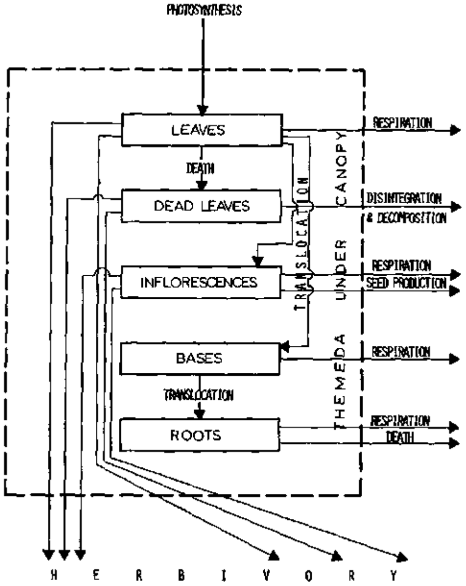
It is clear, however, that spatial heterogeneity is too important to ignore -- the grasses grow differently, and differ in proportions, under the scattered trees and in the interspaces; so the first decomposition distinguishes these two sub-systems within the "plant" sub-system of the simplest model:



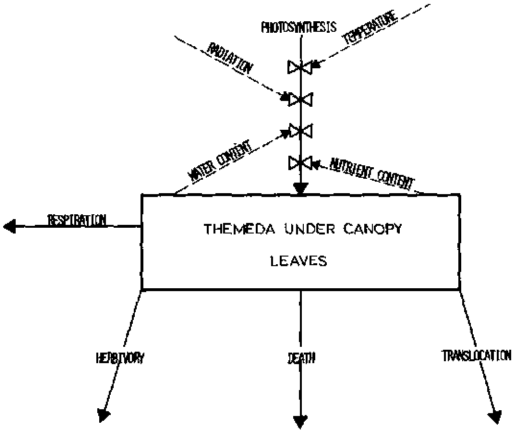
We now focus our attention on one of these plant sub-systems and consider in more detail what will be needed in order to model the foliage available for consumption by the herbivores, and thus determining the weight gain by the cattle. The grasses under the tree canopy gain energy by photosynthesis, lose it by respiration, by herbivore consumption, by leaf-fall and death. But there are two important species, Heteropogon contortus and Themeda australis, differing markedly in palatability to cattle, so this provides the next hierarchical decomposition of this subsystem:



Considering now the sub-system of Themeda australis under the tree canopy, we recognize several compartments -- the active leaves, the inflorescences, the bases, the dead leaves, the roots:



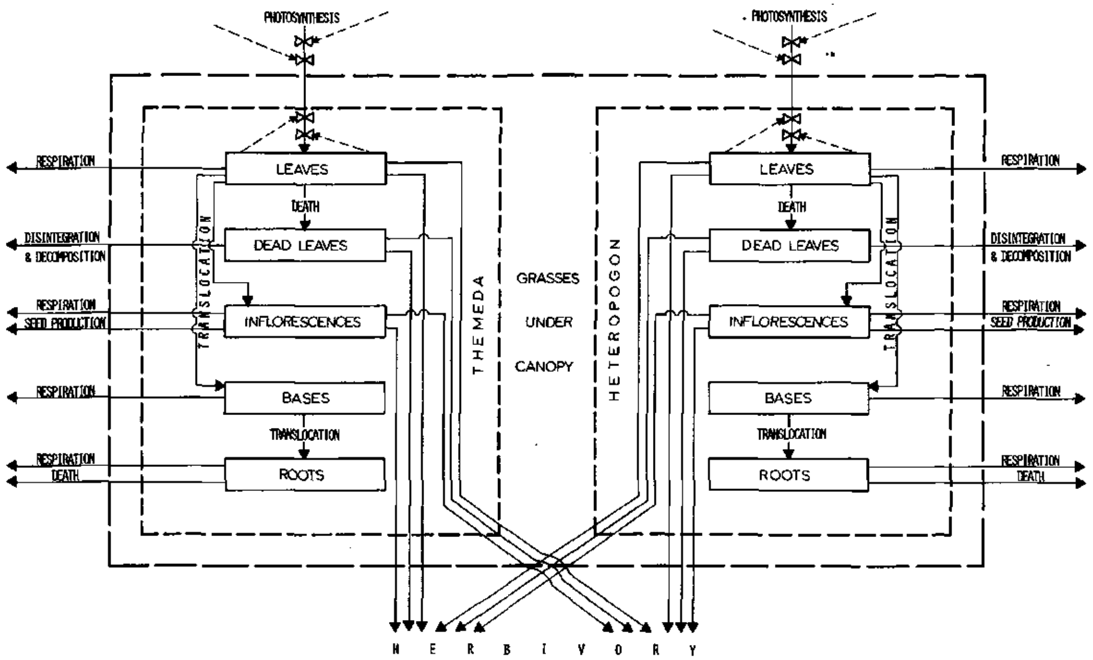
So we narrow the focus again to a still smaller sub-system -- the active leaves. Here again energy changes are a balance between photosynthesis, respiration, consumption and death, together now with translocation. And we focus our attention on photosynthesis, noting that the rate is dependent on certain external factors -- irradiation and temperature among them -- and some internal ones, including leaf water status, and the content of certain nutrients:



The irradiation and temperature are affected by the density of the overhead canopy, which must consequently now be included as a new state variable in the overall system. Internal water status and nutrient status are also new requirements for state variables within the Themeda-under-canopy sub-system, which will call for additional links with the other organ sub-sub-systems within this sub-system.

If we now turn to these other organ sub-sub-systems, we find that modelling of photosynthesis is required for the inflorescences too, that the factors affecting the rate of photosynthesis are the same, and that the function expressing this dependence is also the same, though the constants are different. This similarity between these groups of organs does not, however, extend to all processes. Respiration may be treated similarly; the same may be true of translocation, with a difference in sign; but "death" is different, this resulting in transfers in one case to dead leaves, in the other to seeds.

If we now broaden our focus again to include Heteropogon under the tree canopy, we find a division into organ sub-sub-systems exactly parallel with those of Themeda is called for:



Photosynthesis in both cases depends in the same way on the same factors, and the differences are solely in the values of the constants.

If we broaden our focus still more -- to include the areas between tree canopies -- we find that the structure within these major sub-systems are identical -- in their subdivision, their processes, their factor dependence, the functional form expressing the rates, and down to the very values of the constants in these expressions. Thus, though the grass sub-system has been decomposed into twenty sub-sub-systems, the modelling work is not multiplied by a factor of twenty. Thanks to the cross-classification, only five different types of sub-systems need to be considered, and the same sub-models can be applied, with appropriate inputs, to each sub-system within a type. Moreover, models of particular processes are even more generally applicable. By classifying the relevant constants of the system in parallel with the appropriate classifications of the state variables, modelling effort for this highly complex system may be greatly reduced. And, where particular processes apply only to certain classes within a classification (e.g., roots do not photosynthesize), these peculiarities may be incorporated in the model by a system of switches.

The process of photosynthesis in Themeda leaves, on which our attention was concentrated, could be handled in a variety of ways. A possible sub-set of influencing factors has been mentioned; but this list could clearly be expanded (with the expectation of more precise estimation) or reduced (if less precision is acceptable, or if availability of data dictates it). But also, with the particular list of four influencing variables mentioned, options are available. One could use an arbitrary polynomial to relate photosynthesis rate to these variables, or one could use a functional form which more accurately reflects the known biological features of the process. Or one could develop a sub-model which was more than a "black-box", and actually included, say, changes in stomatal aperture, or the process of acclimatization. All these would be legitimate alternatives for sub-models of the process of photosynthesis. And, if the data required are available, it may be worth building them all. The most complex sub-model -- that incorporating the most advanced biological knowledge -- is not necessarily the best for a particular purpose. And if the whole model has been constructed on the hierarchical principle, with interchangeable modules, this can easily be tested by exercising it with the rest of the model unchanged and the various treatments of photosynthesis replacing one another.

Since the whole model is directed towards prediction of an objective function -- in this case, the mean rate of gain in weight by the cattle -- comparison of its performance using alternative photosynthesis modules should be based on this prediction, and on its agreement with observed values. Where the domain of the model includes a variety of systems, or a system under a variety of conditions, the comparisons should in principle include several of these cases, and the performance of the model would be assessed over this whole range. Particularly if errors in the estimation of parameters are taken into account, it may be found that one of the less sophisticated sub-models is at present giving more reliable predictions; and tests of sensitivity of the objective function to these parameters may show that improved estimation would not be worth the effort.

Tests of alternative modules may also be performed elsewhere in the hierarchy. Instead of the sub-models at the leaf level, one may perhaps be considering sub-models at the plant species level. Here, too, the input of energy by photosynthesis could be treated in various ways, without considering the subdivision of the plant into organs. And these alternative modules at the higher hierarchical level could be tested in the same way as those for photosynthesis of leaves considered separately. Moreover, comparisons can be made between different hierarchical levels. The highly decomposed model with sub-models for separate organs may be compared with that in which decomposition does not proceed below the plant level.

The question may be asked: "If data for a model of higher resolution are available, of what interest is one of lower resolution?" One answer is that errors in parameter estimation may make the latter preferable for estimating the objective function. Another is the practical one of computer time. It may be that the cost of running a high-resolution or high-precision model would be prohibitive, and that some compromise with a model in principle less satisfactory must be accepted. But all these alternatives may readily be explored and pursued, if the model has been constructed on the hierarchical and modular principle.

Though this illustration has, at each hierarchical level, been limited to one subsystem, or one process, it can of course be extended throughout the system, so that (for instance) the cattle sub-system and the wallaby sub-system will have almost identical internal structure.

It seems likely that the principles outlined here of hierarchical organization, modular structure, and cross-classification will be widely applicable wherever ecosystem modelling progresses beyond the low-resolution stage.

EVALUATION OF MODELS

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Introduction

In the rapidly growing stream of publications on the use of computer modeling and simulation as research tools, one aspect is very often not treated to any great depth: the evaluation of the models.

Models originating from the field of technical sciences are based on detailed knowledge of the theory of the underlying processes, whose mathematical description is exact and such models hardly require experimental verification. Onze simulation of the moonshot showed that the operation was feasible, execution of the real experiment was not much more than a futile exercise and at best a proof of technical skill.

In the biological sciences however we are dealing with dynamic systems that are not man-made and in many areas understanding of the basic principles is so fragmentary that models are often not more than a subjective expression of our opinion about the operation of the system under consideration. Complex models, when properly formulated do represent a consistent argument based on these opinions; but that is still no guarantee of their validity. A model, like any theory, aims at summarizing and predicting. Thorough proof must be given that the existing data can be satisfactorily explained by the model, before any confidence can be placed on the predictive results. Verification of a model is therefore one of the most important parts of the simulation if this technique is to turn from art into a science. Results obtained from carefully designed experiments with computer models should be tested at all levels against results obtained from experiments with the real system.

In this paper some of the problems encountered in the evaluation phase of simulation are described and possible solutions for part of them are indicated.

Evaluation at different levels

a) Postulates

Whenever the modeling approach is used to investigate a problem, a number of decisions must be taken. The first and most basic problem is the choice of the postulates on which the model is to be based. This involves the decision on the boundaries of the system to be studied, determining which processes are included in the model and which are introduced as forcing functions. The choice is not always obvious. For example, if one is interested in the dry matter production of a maize crop, the macro-weather may be considered as an external variable which is not affected by the standing vegetation. When, however, the influence of a pollutant from a nearby chemical plant on the yield quality is the main interest, aerodynamic differences caused by the presence of vegetative surfaces may be of decisive influence on the effect of the macro-weather on the fate of the pollutant. The main criterion must be the purpose of the simulation, which should not be too ambitious to keep the model verifiable. The model should be designed in such a way that it yields the kind, the quantity and the quality of data necessary to draw conclusions relevant to its purpose. However, the postulates are chosen or entered the model implicitly by intuitive incorporation and/or omission of certain processes or interactions, at some point in the evaluation phase we must return to them and check how adequate they are and in which way they influence the results. Although this may seem obvious, the spectacular impact of the results of Meadows (1972) world model showed that the implied postulates were not explicitly recognized.

b) Processes incorporated in the model

Once the decision about the postulates and the boundaries is taken, a set of mathematical equations each one describing a relevant physical, physiological or ecological process or part of a process is combined to form the model. All mathematical relations must be subject to evaluation. In general the processes are studied under controlled conditions to establish the relation between external or internal state variables and the dependent rates. Often the technique to obtain maximum information from such experiments is the application of stepwise changes in state variables and recording the dynamics of the response. Such experiments serve as validation tests for independent submodels.

Such submodels may then be used in full in the final model when the dynamics of the processes are of interest or the results of the submodel are entered through analytical expressions or tabulated functions. This implies a hierarchical approach to modelling, which can help to make complexity manageable. An alternative to the use of dynamic submodels is the determination of a number of equilibrium situations, which are described by an analytical expression like the photosynthesis-light response curve of individual leaves in the crop growth model.

Yet another method to obtain compound relationships is the use of a "black box" approach, in which a specific programming technique is designed to "mimic" relations between inputs and outputs, when the causal relations are not known. An example of this all too widely used technique is given by Janssen (1974) in his model of germinating seeds of winter annuals.

All three methods described can be evaluated, either by statistical methods or by judging the accuracy of the relations from independent knowledge of the measuring methods. Often, however, no quantitative data are available at all and relations are introduced based on "intelligent guesses". This may not be disturbing when it concerns minor details of a model but when important relations are based upon this principle, model validation becomes a recreative pastime and the investigator should consider going back to experiments with the real system in order to establish the relevant relations. At best results obtained from such models may then serve as a guideline in designing proper experiments.

An additional problem arises from the parametrisation of the functional relationships. In plant production models often the quantitative reactions of plants grown under different conditions show large differences, though the processes are the same.

In general, studies at the process level yield most information in the evaluation phase of the model and most of the effort should be put in this aspect if we are to advance with simulation.

c) *Evaluation of output and model behaviour*

Testing of the whole model may still be done at two levels: gross output of the model, like yield in crop growth models, may be tested. Or we may test the internal behaviour of the subsystems, comprising the model. Testing the gross output is in general not very enlightening, especially with crop growth models. On the one hand the experimental data available are subject to sampling errors, which are seldom smaller than 10 %. This implies that the error in the measured growth rates is in the order of 20 %, so that, when statistical analysis is applied "reasonable agreement" is easily obtained. On the other hand, such models contain so many feed back relations that internal compensation may lead to levelling out of deviations caused by the introduction of erroneous relations.

When, however, only gross output data are amenable to testing, as is often the case in models used in ecology, proper evaluation should contain two phases (Wigan, 1972) calibration and validation. The calibration procedure is most honestly rephrased by the term curve-fitting. One set of data is used to adapt, within reasonable limits, weak or unknown parameters or relations, so as to reach the best overall agreement between simulated and observed results. Even the most simple ecological model, however, contains already such a large number of parameters that such a procedure often requires an unrealistic amount of experimental data.

In the final stage of validation still other sets of completely independent data must be used to show that the model yields proper results under different conditions. Many of the ecological models developed at present do not permit this full procedure because of lack of data. This implies that all or part of the same data are used in both the calibration and validation phase so that all that can be evaluated is to what extent the model regenerates its own inputs. Such techniques are widely accepted in econometric sciences and are completely based upon successive application of statistical methods to obtain goodness of fit. This may be called identification, rather than validation and it is questionable whether in such cases simulation has any advantage over multiple regression techniques. The most that can be concluded from such models is that historical events under a given set of conditions may be described by the generated set of equations but no insight into the dynamics of the processes is gained.

In general when results of the simulation and real system conflict with each other the individual processes should be reexamined and improved on the weakest points. This is done more directly, when the internal behaviour of the subsystems is used for validation. Although this may be a huge task in more complex models it is the only way to develop simulation models that are not only convincing in their summarizing behaviour, but have also predictive value and can be used to extrapolate knowledge from known situations to new areas or circumstances. A good example of this technique is the use of enclosure studies in which the processes of photosynthesis, respiration and transpiration are subject to direct validation (Van Keulen & Louwerse, 1974). Comparison of measured and simulated dynamic behaviour of these processes under different conditions, may lead to redesigning of the model, which in turn is a guide line for the design of new experiments (De Wit, 1970). Such an intimate relation between modeling and experimentation will generally not lead to the rapid production of a great number of models, but will certainly increase confidence in the results that are obtained.

Internal evaluation

So far we have been considering the validity of the model as a representation of reality. There are, however, in the validation phase of modeling some other pitfalls, that should receive proper attention. Before any comparison with the real world makes sense, the modeller must be sure of the internal consistency of his model.

There is firstly the problem of dimension inconsistency, but although this may create difficulties, the occurrence of such errors generally shows up in the early stages of model development. It would, however, be very helpful if the problem oriented computer languages contained a dimension check routine. A more serious problem is that of the correct computer implementation: programming errors and mistakes introduced during the writing and punching procedures. Especially in more complex models, which may consist of over 1000 statements, such errors are easily made and difficult to detect. The best solution is running the model in limit situations, where its behaviour is known. Such a test is not a full proof for the absence of these errors and thus far there is no technique to avoid them completely.

Sensitivity analysis

A technique often applied in the process of model evluation, specifically in situations where accurate input data are lacking is sensitivity analysis. It is most conveniently described as: a test on the relative influence of changes in input data and parameters on the relevant outputs of the model. A number of simulation runs is executed with a range of values for input data or parameters and the output values are compared. This is most helpful when it must be decided which subsystems should receive most attention. Relations with the strongest impact on the final results should be studied most thoroughly, while those exhibiting only little influence may be left alone for some time.

There is, however, a dangerous aspect in this technique: when the model contains conceptional errors in certain relations, which are important, their influence may not show up at all, and the research efforts will mistakenly be directed in the wrong direction. Sensitivity analysis should therefore be evaluated in the light of all assumptions that were made during development of the model. In many cases it is more significant to study the sensitivity of the model to different postulates, than to different parameter values.

Conclusions

As is clear from the foregoing, proper validation of simulation models is an extremely difficult and time-consuming procedure. It is, however, an essential procedure, as this phase of the modeling process must prove the validity of the opinions on which the model is based. It will also lead to the design of relevant experiments and thus to increasing understanding of the system in which we are interested.

But how useful are even thoroughly validated simulation models of ecosystems for predictive purposes? For proper prediction, the model should be properly initialised and the determination of these initial values is likely to disturb the system to such an extent, that different behaviour develops. Hence, if each ecosystem is unique we will never be able to find experimental data to test our model. This may lead to the conclusion that only systems that are not unique, that is systems that are controlled by negative feedback, are amenable to simulation. And this at a time, where ecologists claim or are asked for qualified opinions about explosive situations.

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MODELLING BY MAN-MACHINE CONVERSATION TECHNIQUE

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Summary

Conversational method using Graphic Display in model building of the ecological problems is described. Some results of the fundamental equations on ecological basic problems are shown as examples. They are (i) Plant growth model (ii) Population dynamics in prey-predator system. Efficacy of the interactive technique is concluded.

1. General scope of man-machine interaction technique

General concept of man-machine interaction system containing Graphic Display (GD) is illustrated in Fig.1. Graphic Display (GD) has Cathode Ray Tube (CRT). GD is on-lined to a host computer as one of peripheral equipments. Users can give informations to the machine (computer) through the screen of CRT by Light Pen. Both figure (pattern) and numeric are available as input data. Users can examine the displayed results and give data repeatedly.

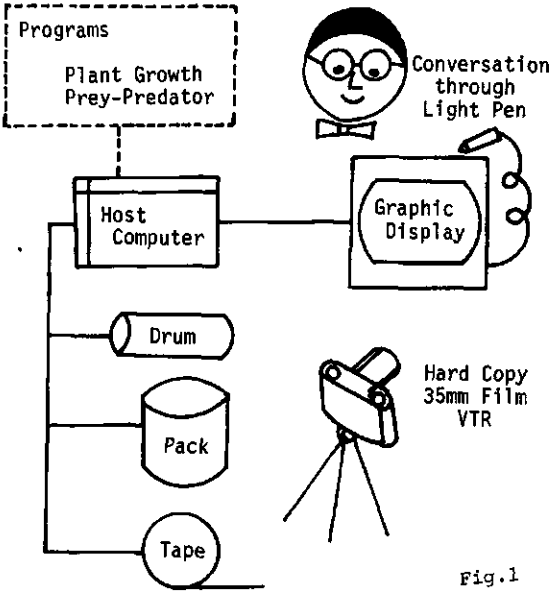

Fig.1

GD is suitable equipment for ecological problems, because data of pattern, e.g. shape of living body or geographical distribution of population, are main subjects in this field. When we use GD, we can select a picture of adequate case from a plenty of cases by the conversational technique.

Some results of fundamental equations of ecological models are exhibited bellow as a example. Most of the models have been already proposed by other reseacher but their plenty results were not shown graphically. All pictures except Fig.1 are obtained using the Second System at Nagoya University Compution Center. The system has FACOM 230-35 (approximately corresponds to IBM 360-40) of which capacity is 128KB. Size and grid points (Raster Unit) of the GD in the system are 30cm x 30cm and 1024 x 1024 respectively. To our convenience, though the system is not high class, users are allowed to operate the machine. Fundamental equations in ecology are in rather simple forms, therefore a special peripheral equipment like as GD and open-operational system is more preferable than large closed-operational system. The language to draw pictures on GD, which is called GSP (Graphic Subroutine Package), is in form of subroutine in FORTRAN. One ecologist will be able to use GD in several months, if he has general knowledge on computer system and FORTRAN.

2. Ecological models

(Programs are made by the member of our group)

(a) Plant growth model

Shinozaki(1961) proposed a model of plant growth, where vertical transport of biomass is considered besides photosynthesis. Basic equations are

$$\frac{\partial \Gamma}{\partial t} = (1-\alpha)s\Gamma - D\frac{\partial^2 I}{\partial z^2}$$ (photosynthetic part)

$$\frac{dI}{dz} = -K\gamma\Gamma I$$ (light intensity)

$$\frac{\partial C}{\partial t} = \beta\int \alpha s\Gamma dz - r_p C$$

(non-photosynthetic part)

$$s = \lambda(1-\frac{\Gamma}{\kappa I})$$

z: hieight D: transport coefficient
$\beta(z)$: allocation coefficien of photosynthates into trunks at z.

Figs.2 & 3 are picked up from many trials using GD. It is easy to recognize a reasonable pattern of canopy photosynthesis. Details of parameter values are described in Shimazu et al (1972).

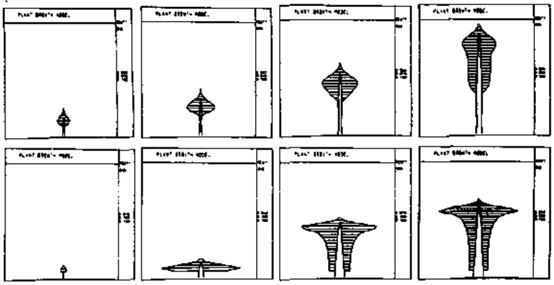

Fig.2,3

(b) Population dynamics of 2 species

Population dynamics in prey(x)-predator (y) system of 2 species is one of the most important problems. Recently the concept is employed even on social system problems. As Rosenzweig(1971) and May(1972) argued, main interest of this problems is whether its tranjectory forms a limit cycle or not. Basic equations by Shimazu et al (1972) are

$$dx/dt = Rx(1 - x/X) - xy/(1 + Hx)$$

(logistic and predation)

$$dy/dt = (1/R)y(1 - y/x).$$

(growth by predation)

Fig. 4 shows types of trajectory. Type depends on combination of values for R, X and H. Rosenzweig listed 6 growth equations. All of them are examined by the present author with GD. Some results are also shown in Fig.5. As May(1972) and Gilpin(1972) claimed, all cases results in either a stable equilibrium type or a limit cycle type.

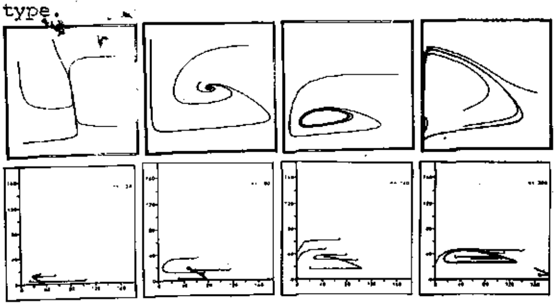

Fig.4,5

(c) Population dynamics of 3 species

Expansion of population dynamics problem up to 3 species is possible when we use GD. This problem is one of the most undesiable one for ecologist in spite of simpleness of the equations, since it is very difficult to image a three dimensional trajectory. Basic equation of a case of 1 predator and 2 preys, for a instance, are :

$$\frac{dx_1}{dt} = \lambda_1 x_1 (1 - \frac{x_1}{X_1}) - \frac{a_1 x_1 y}{1+a_1 h_1 x_1} \qquad \text{(prey)}$$

$$\frac{dx_2}{dt} = \lambda_2 x_2 (1 - \frac{x_2}{X_2}) - \frac{a_2 x_2 y}{1+a_2 h_2 x_2} \qquad \text{(prey)}$$

$$\frac{dy}{dt} = \lambda_3 y (1 - \frac{y}{K_1 x_1 + K_2 x_2}) \qquad \text{(predator)}$$

Three dimensional trajectroys are shown in Fig.5. They are drawn within a cubic in perspective of which two walls are displayed. When we look at the rotating picture on screen, three dimensional image becomes more clear than we see the sequence of printed pictures as shown in Figs.6.7.

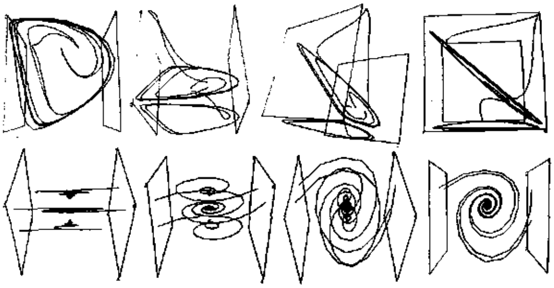

Fig.6,7

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FUTURE PROSPECTS OF SYSTEMS ANALYSIS IN ECOLOGY

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Introduction

This special symposium of the 1st International Congress of Ecology is intended to provide a critical evaluation of systems analysis and modelling in ecosystems research and management, and of data collecting and processing for predictive purposes in ecology. Born of the apparently unnatural liaison of ecology and mathematics - some would say the rape of ecology by mathematics - and reared in the heady atmosphere of the International Biological Programme, systems analysis is now seen by many ecologists as a precocious adolescent, pampered by over-indulgence, and accorded more value than it is worth by its association with sophisticated, and sometimes elegant, companions like computers, electronics, and graphics. It is sometimes claimed that systems analysis has, so far at least, produced nothing of lasting value and has dispersed much valuable effort into unprofitable avenues of research.

It would be relatively easy to support such a view by a biased sample of the results of systems analysis and modelling applied to ecology, for, regrettably, much that is either unprofitable or scientifically unacceptable has found its way into the mainstream of scientific communication, both published and unpublished. In part, the difficulty lies in the relative unfamiliarity of many ecologists with the philosophy and concepts of mathematics, so that, if they have turned to mathematical techniques at all, they have used them as tools, often for the wrong purpose and with little or no understanding of their constraints, much as an unskilled carpenter may use a hammer to drive home screws in his impatience with the more tedious use of a screwdriver. Some of the fault, however, lies with the mathematician who, eager to show his skill and the power of his methods, leaps into the arena to find applications for some branch of mathematics, all too often with a bland disregard of the complexity of ecological systems and of the many assumptions which underlie our frail understanding of the living world.

However, this is a biased view, and much that is sound ecologically, mathematically, and, more important, logically, has emerged from the application of systems analysis and modelling to ecology. Such work has most frequently come from small groups of scientists working with a well-defined and rather narrow focus, having made great efforts to link the modelling effort, from the start, with a carefully designed research strategy and with vigorous data validation. We may even argue, without undue casuistry, that the surge of enthusiastic effort in the field of systems analysis was necessary and useful, even where misapplied. The very small subset of models and modelling approaches that now seems valid has contributed directly to the advancement of ecology as a science, by identifying unanticipated factors and interactions that have subsequently proved to be important, by forcing modification of our experimental and survey procedures, and by illuminating critical weaknesses in our hypotheses and assumptions.

This paper is intended to review briefly the present state of systems analysis in ecology, and to suggest its future prospects. If it is felt that the review is over-optimistic, it may be relevant to ask if there are any other methodologies which, strategically or tactically, are capable of meeting the challenge to ecology posed by the need for the world to feed its population, meet its demand for energy, and control the impact of its technology on our environment.

What have we learnt?

The terms 'systems analysis' and 'model' are now used in so many different ways that they are in danger of losing specific meaning. However, in this paper I will assume the word 'model' to indicate a quantitative representation which, if complex, may require algebraic and arithmetic manipulation. Such models are essential elements of systems analysis, statistical analysis, and many forms of computer simulation. I assume 'systems analysis' to be the orderly and logical organisation of data and information into models, followed by the rigorous testing and exploration of the models necessary for their validation and improvement.

In ecology, as in other branches of science, models have been widely used as translations of verbal problems into mathematical form. The advantage of the mathematical representation lies in the abstract nature of mathematics, enabling the emotional overtones inherent in verbal descriptions to be substituted by neutral symbols, and forcing attention and emphasis on just those parameters and relationships which are essential to the hypothesis. In this form, much information can be assembled into a coherent whole, ideas can be clarified and thinking sharpened, new theories or hypotheses designed, and existing theories tested. From the comparison of the predicted responses of our model system with reality, we can draw attention to critical components of the system and identify those experiments which will enable us to eliminate contenders from among competing hypotheses.

Models and systems analysis have been increasingly employed by ecologists for the description of the population dynamics of plants and animals, for the exploration of spatial distribution of organisms, and for the representation of physical and chemical processes. Within the International Biological Programme, with its emphasis on the functioning of ecosystems and the flow of energy and nutrients through their major components, there has been a major incentive to exploit models of the complex interactions between organisms and their environment, and between several organisms. Success in the difficult stages of the formulation of the model has been dependent upon careful definition of the ecological problem, an understanding of the properties of the models proposed, and an adequate fit of the model to existing knowledge.

Above all, however, modelling is dependent on the availability of appropriate and reliable data. In the past, we have had to rely on such data as already existed, with a naive belief that all data can be made to serve our purposes and that, even where data are biased and unreliable, they can often lead us to the next stage of the systems analysis, to the formulation of the improved hypotheses. We now know we were wrong - indeed, we should have known we were wrong! Every form of data collection imposes its constraints on the subsequent use of the data. As I have argued elsewhere (Jeffers, 1974), the concept of the 'data bank' is rooted in the accounting theory of data collection, which assumes that the subsequent use of data is independent of the way in which data are collected. The statistical theory of data collection insists on the essential interdependence of data collection and data analysis, and, if we wish to use particular kinds of models, we must ensure that appropriate methods of data collection have been used. We have, too often, built our models on insubstantial foundations and the rejection of the models is a rejection of the foundations rather than of the model form itself.

If this were not enough, we have created a further problem. Models of complex systems are usually themselves complex, and we have not always appreciated the need to explore the models we have built, confusing this activity with the quite different activity of exploring data by the use of models. Perhaps one of the saddest sights of the last decade has been that of the plight of the new applied mathematicians in biological science, baffled by the complexity of the deterministic models of differential equations they have themselves created as analogues of biological processes. Having rejected the "untidiness" of statistical methods - or perhaps never known them - in favour of the mathematical exactness of functional relationships, they have often rejected the methods they now need to explore their models in the computer simulations. Even the most famous exponents of systems dynamics seem to have had difficulty in realizing that "... with separate experiments, we should obtain no light whatever on the possible interactions of the different ingredients, ..." (Fisher, 1935). We are now in the interesting situation of needing the statistical methods of design of experiments, developed to cope with the complexity of biological systems in the field, to explore the behaviour of models of biological systems.

A model developed from biological and mathematical theory, no matter how elegant in itself, is unlikely to be of value unless there is a practical way of assessing how well the theory fits the available data. "There is a sense of simplification, a mental ease which flows from any mathematically elegant summary of a wide copus of figures. Call it mental laziness or mental efficiency; the mind believes that it can grasp more and grasp that more more clearly." (Williams, 1951). But a model which is incapable of verification is an essay in metaphysics and not an expression of the scientific method. The methods of testing hypotheses against observed data are well-established and are being continually improved. In particular, we now have many of the necessary algorithms for the fitting of models by minimizing the discrepancy between models and data, and we have the necessary computer techniques for data handling, including the combination of data sets, selection of sub-sets, storage and retrieval. Yet the available techniques have hardly been used and are insufficiently widely known because of the lack of published texts.

The difficulties that have been encountered in the use of systems analysis in ecology are not, however, confined to the technical problems of ecology and mathematics. As Mar (1974) has pointed out, the process of modelling itself is seldom, if ever, recorded, being inadmissible as a subject for scientific journals, and the technology of modelling has not been captured. Each new project starts from square one and fails to learn from past experiences, because those past experiences have not been recorded. But the three major issues are always the same, and they are solved with variable success, namely:-

1. How to define and bound the model

2. How to orchestrate the team needed to address the construction and validation of the model

3. How to document and communicate the model and its results

Unless we can record our experience in the bounding of models, in project orchestration and documentation, and in the validation of models, the fragmentation and abuse of modelling will continue.

What are the prospects?

We now have a substantial body of experience with the application of systems analysis in ecology. While little of this experience has so far been recorded, and may, indeed, never be recorded within the conventions of the formal paper to a scientific journal, many of the exponents of systems analysis in ecology are still alive, and young enough to have a considerable influence on the developments of the next ten years. We have made our mistakes, and are in the happy position of knowing what they are. We have, therefore, no excuse for continuing to make the same mistakes.

In contrast, we are experiencing the unprecedented interest of administrators, managers, politicians and the general public in the changes taking place in our environment. This interest is too great for those concerned to be satisfied with polite evasions when we, as ecologists, are asked for information about the likely impacts of our search for more food, more energy, ever higher standards of life, and the right to dispose of our waste wherever and however we please. Ecology is no longer a gentlemanly pursuit for summer afternoons, and it can no longer be confined to the study of the rare and the beautiful, or to the confirmation of our prejudices about the appearance of the countryside.

In Britain, the acceptance of what has come to be called the 'Rothschild principle', that government has the right to expect the scientists it supports to devote at least a proportion of their time and effort to the solution of the problems of government, has been established and is already having a major impact on research policy. The environmental impact assessment procedures in the United States of America were established and are carried out under the National Environmental Policy Act of 1969, and the main thrust of the Act is to ensure that environmental concerns receive adequate attention at all levels of governmental planning, decision-making and action. Almost every country in the world is now expressing concern at the lack of essential knowledge of the ecology of our world. Whether or not ecology has achieved its maturity, it is already having to bear adult responsibilities.

Given the necessary expertise to implement a strategy of systems analysis in ecology and the demand for ecological knowledge in the solution of essentially practical problems for the survival of our planet, why should one predict an increased emphasis on systems ecology in research and management? First, because ecological systems are complex in terms of their relationships with their environment and in terms of their interactions with other systems, not excluding those created by man, it is unlikely that verbal descriptions and hypotheses can express the necessary complexity, and increased reliance on models is inevitable. Second, because we can no longer regard the publication of a scientific paper as the satisfactory end-product of ecological research, and governments, managers, politicians, and the taxpayer - the new patrons of science - will demand our results in a form in which they can make direct use of them, models related to the decision-making process itself will increasingly be expected as the outcome of our research: models which the decision-maker can use to test the outcome of his proposals. It would be naive to suppose that the decision-maker will surrender the making of decisions to the ecologist, no matter how great the latter's expertise may be.

Systems analysis, in this context of social responsibility, may therefore be expected to achieve a synthesis between data collection and modelling in which five successive phases can be recognised.

1. Setting of objectives and preliminary synthesis

   This first phase will require the definition of objectives, including the range of ecological systems concerned, the types of manipulation, modification, or disturbance to which the systems may be exposed, and the variables it is intended to measure and to predict. Much of the initial definition will require the review of existing and relevant information, and the objectives may have to be re-examined in the light of this information or its absence. An initial synthesis can then be attempted as a model capable of making predictions leading to valid tests of the hypothesis.

2. Experimentation

   The next phase will involve experimentation, both in the field and in the laboratory, during which the data necessary to test the output and functions of the predictive models will be collected. Experiments on the models themselves, after adjustment or revision to find a better fit to the new data, will provide for rapid transformation of information on the structure and operation of the models developed and will lead to new ideas on the management of the ecological systems. To do this effectively, greater communication between experimenters, modellers, and decision-makers will be essential.

3. Management

   The development of the improved and revised models should lead logically to the next phase, during which pilot-scale management studies will be implemented by the appropriate agencies.

4. Evaluation

   With increased confidence in the synthesis, achieved during experimentation and pilot-scale management studies, evaluation of the effects of changes of management proposed as a result of the increased knowledge about the structure, functioning and stability of ecological systems becomes possible, with particular emphasis on environmental quality and the quality of human life. During this phase of the research, new ideas should become available for the determination of policies for the management and use of natural resources and systems.

5. Final synthesis

   In one sense, there can never be a phase of final synthesis, as all models represent the starting point for new and improved models once it has been found that they are unsatisfactory in some respect. Models are essentially transient, the production of the scientific mind, but they are the true vehicles of knowledge, and we should talk of 'model-banks' rather than 'data-banks'. But, in the uneven state of ecological knowledge, there are many systems which we may be prepared to leave in a temporarily 'final' phase, while we concentrate our scarce research resources on relatively unworked and unknown systems.

All this is a far cry from our present fragmentary use of models and systems analysis in ecological research and management. It represents a radical change from our traditional and academic forms of research, in which the scope of our research is divided and limited by the segments into which it can be chopped to make the pieces suitable to be undertaken by the individuals and small groups from which our research organisations are assembled. A new orchestration of our efforts will be required if we are to meet the challenge of the demands made upon us and of the technology we now have in our hands.

Perhaps you, my readers, are pessimistic about the chances of this synthesis being achieved. I would join you in your pessimism if the phases I have described were not taken from the report of the expert panel on the role of systems analysis and modelling approaches in the programme on Man and the Biosphere (UNESCO MAB Report Series No. 2, 1972). The scientific approach of the MAB programme can be categorized as including major components on the analysis of ecological systems, reciprocal studies of man-environment impacts, integration of information over various spatial levels, and inclusion of modelling techniques to allow quantitative predictions. Within this approach, the programme is intended to:-

1. identify and assess changes
2. examine the structure, functioning, and dynamics of ecosystems
3. study the interrelations between ecosystems and social and economic processes
4. develop the necessary techniques for measuring change in the environment
5. increase global coherence of environmental research
6. promote simulation and modelling as tools for environmental management
7. promote environmental education.

MAB has adopted the philosophy of systems analysis as the basis of its thirteen major projects, not because modelling was regarded as a substitute for empirical studies, but because the basis of systems and modelling approaches in ecology is the concept of integration. This concept is central to ecology and provides the best hope for the future of finding an optimal allocation of financial and manpower resources, and for the development of tools for prediction and planning. We, too, may therefore hope to see our precocious adolescent come to full maturity, stimulated but sobered by the weight of the responsibility that systems analysis and modelling in ecology will have to bear.

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C2

Methods of experimentation with ecosystems, in the laboratory and in the field. Interpretation of laboratory results in terms of field conditions

SYSTEMS IDENTIFICATION: A THEORETICAL METHOD APPLIED TO TRACER KINETICS IN AQUATIC MICROCOSMS[1]

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Summary

A mathematical model of radionuclide kinetics in a laboratory microcosm was built and the transfer parameters estimated by multiple regression and system identification techniques. Insight into the functioning of the system was obtained from analysis of the model. Methods employed have allowed movements of radioisotopes not directly observable in the experimental systems to be distinguished. Results are generalized to whole ecosystems.

Introduction

An ecosystem can be described graphically with a flow diagram or mathematically with a dynamic model. This model can be a set of simultaneous differential equations,

$$\dot{\underset{\sim}{s}} = h(\underset{\sim}{x},\underset{\sim}{s},\underset{\sim}{u},t) \qquad (1)$$

where $\underset{\sim}{x}$ is a vector of n independent observable variables; $\underset{\sim}{s}$ a vector of m dependent model variables $(m \lesssim n)$, related to $\underset{\sim}{x}$ by a homomorphic $(m < n)$ or isomorphic $(m = n)$ relation; $\underset{\sim}{u}$ is a vector of parameters; and t is time. Model solution depends on specification of a set of initial conditions,

$$\underset{\sim}{s}(0) = \underset{\sim}{s}_0(\underset{\sim}{x},\underset{\sim}{u}), \qquad (2)$$

where $\underset{\sim}{s}_0$ is a vector of given functions.

Under certain experimental conditions the total ecosystem response can be derived from an understanding of internal processes and their contribution to observed behavior at the system level. Usually it is possible to measure some of the parameters ($\underset{\sim}{u}$). Sometimes these measurements are quite accurate, and sometimes only approximate. However it might happen that some parameters cannot be experimentally observed. In this case initial guesses of parameter values are used in model (1). Given $\underset{\sim}{u}$, the model can often be solved numerically with an analog or digital computer. Simulated and observed data are then compared. If the results are not satisfactory some parameters are changed randomly to search for a better fit (May, et al., 1972). This approach can be improved by a systematic procedure.

Berman (1963) proposed a method to quantify movement of a radioactive tracer among a few compartments. A few years later he expanded this method to handle larger systems (Berman and Weiss, 1971), but it required a large amount of computer storage and computer time. Leary and Skog (1970) developed a quasilinearization method which reduced the storage requirement, but which still needed a long computation time. Another drawback of these methods is that a highly good initial estimate of $\underset{\sim}{u}$ was required for convergence.

In this paper a method for rigorously computing an initial estimate of $\underset{\sim}{u}$, given $\underset{\sim}{x}$, is presented and the applicability of optimization techniques to ecosystem models is discussed. As an example of the potential of the technique for ecosystem modeling studies, the method is applied to studies of radioisotope movement in aquatic microcosms.

Mathematical preliminaries--parameter identification

Given $\underset{\sim}{x}$, the dynamics of the system can be approximated by a set of simultaneous, first order difference equations of the form

$$\Delta\underset{\sim}{x}/\Delta t = h'(t,\underset{\sim}{x},\underset{\sim}{u}). \qquad (3)$$

Over the interval $(t_i,\ t_{i+1})$, Δx can be computed as

$$\Delta\underset{\sim}{x}/\Delta t = (\underset{\sim}{x}(t_{i+1}) - \underset{\sim}{x}(t_i))/(t_{i+1})-t_i). \qquad (4)$$

Therefore, in Equation (3), the only unknown quantity is $\underset{\sim}{u}$. This can be computed by multiple regression by setting $\Delta\underset{\sim}{x}/\Delta t$ as a function of the independent variable $\underset{\sim}{x}$.

Models of the form

$$\dot{\underset{\sim}{s}}(t) = A\underset{\sim}{s}(t) + z(t) \qquad (5)$$

where A is a matrix of parameters and $\underset{\sim}{z}$ is a vector of inputs, have been used for several years to model ecosystems (Olson, 1963, was one of the first). A rationale for these linear, donor based equations is presented in Egloff, et al. (1975). The equations represent a special case of Eq. (1), A and $\underset{\sim}{z}$ being elements of $\underset{\sim}{u}$.

Using this model the system matrix A can be estimated by applying multiple regression techniques to each difference equation in the system. The $\underset{\sim}{z}$ values are usually known. The multiple regression problem to be solved for any compartment is then

$$\Delta\underset{\sim}{x}/\Delta t = \sum_{j=1}^{n} a_{ji}x_i. \qquad (6)$$

From theoretical considerations and from knowledge of the system being modeled we can predict that only a subset A^* of all possible

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transfers among components will have nonzero values. Thus, the task of identifying the system is considerably reduced.

Mathematical preliminaries--parameter optimization

Given a set of initial estimates of parameter values either from experimental measurements, guesses, or multiple regressions as discussed above, the parameter values, that best approximate the data, can be found. This can be done in a systematic way with a particular optimization technique. Actually, several algorithms are available for this purpose (Polak, 1971; Bard, 1974), and each one can be useful for a particular category of problems.

In general we wish to minimize the function

$$\phi(\underset{\sim}{s}) = \sum_{i=1}^{n} (s_i - x_i)^2. \tag{7}$$

The minimization problem can be solved if we can find $\underset{\sim}{s}^* \varepsilon\, S^\circ \subset R^n$, if it exists, such that

$$\phi(\underset{\sim}{s}^*) = \min_{\underset{\sim}{s}\varepsilon S} [\phi(\underset{\sim}{s})], \tag{8}$$

where

$$S = \{\underset{\sim}{s}\varepsilon S^\circ : k(\underset{\sim}{s}) = 0,\ g(\underset{\sim}{s}) \leq 0\}\ , \tag{9}$$

where

$$k: S^\circ \rightarrow R^p,\ g: S^\circ \rightarrow R^m \text{ and } \phi: S^\circ \rightarrow R. \tag{10}$$

The $k(\underset{\sim}{s})$ are equality constraints and the $g(\underset{\sim}{s})$ are inequality constraints, both of which depend on the particular problem.

If $\phi(\underset{\sim}{s})$, $g_i(\underset{\sim}{s})$ $(i = 1,\ldots,m)$, and $k_j(\underset{\sim}{s})$ $(j = 1,\ldots,p)$, are at least once differentaible with respect to s_1 $(1 = 1,\ldots,n)$, the following classical results apply:

The quantity $\underset{\sim}{s}^*\varepsilon S$ is a minimum of $\phi(\underset{\sim}{s})$ for $S = R^n$ iff

$$\nabla\phi(\underset{\sim}{s}^*) = 0, \tag{11}$$

where $\nabla\phi(\underset{\sim}{s}^*)$ is the vector gradient $\nabla\phi(\underset{\sim}{s})$ of the function $\phi(\underset{\sim}{s})$ evaluated at $\underset{\sim}{s} = \underset{\sim}{s}^*$, i.e.

$$\nabla\phi(\underset{\sim}{s}^*) = \left.\frac{\partial\phi(\underset{\sim}{s})}{\partial s_i}\right|_{s = s^*} \tag{12}$$

If $\phi(\underset{\sim}{s})$ is also strictly convex, every local minimum will be a global minimum and the necessary condition for $\phi(\underset{\sim}{s}^*) = \min \phi(\underset{\sim}{s})$, $S = R^n$, becomes sufficient.

When S has the particular structure

$$S^1 = \{\underset{\sim}{s}\varepsilon S^\circ : k(\underset{\sim}{s}) = 0\} \tag{13}$$

(i.e. there are only equality constraints), we can apply the following classical result:

Theorem (Lagrange)

If $\phi(\underset{\sim}{s})$ is continuously differentiable, and if

$$\nabla\phi(\underset{\sim}{s}) \neq 0,\ \forall \underset{\sim}{s}\ \varepsilon\ S^1, \tag{14}$$

the necessary condition for $\underset{\sim}{s}^* \varepsilon\ S^1$ to be a local minimum of $\phi(s)$ is that the vector $\underset{\sim}{u}^{**}\varepsilon R^q$ exists, such that the following equations are satisfied:

$$\nabla_{\underset{\sim}{s}} L(\underset{\sim}{s}^*,\underset{\sim}{u}^{**}) = 0, \tag{15}$$

where

$$L(\underset{\sim}{s}^*,\underset{\sim}{u}^{**}) = \phi(\underset{\sim}{s}) + \langle\underset{\sim}{u}^{**},k(\underset{\sim}{s})\rangle\ ,\ \underset{\sim}{u}^{**}\varepsilon R^q, \tag{16}$$

and

$$(\nabla_{\underset{\sim}{s}} L)_i = \frac{\partial L}{\partial s_i}\ . \tag{17}$$

The function $L(\underset{\sim}{s}^*,\underset{\sim}{u}^{**})$ is called a Lagrangian function, and $\underset{\sim}{u}^{**}$ is a Lagrange multiplier.

If, on the other hand, we deal with a particular structure

$$S^2 = \{\underset{\sim}{s}\varepsilon S^\circ : g(\underset{\sim}{s}) \leq 0\}, \tag{18}$$

or with the general structure (9), then we must employ relatively recent theories (John, 1948; Kuhn and Tucker, 1951). Computational methods for finding the global minimum when the solution surface is not convex, and when more than one minimum is present, are discussed in Fletcher (1969) and Polak (1971).

Application to experimental data

This method was used to quantify a model of radioisotope flux in aquatic microcosms, based on unpublished data of B. C. Patten. Radioactive elements were injected into six aquaria and followed for 114 days in 14 components (five species of rooted plants, two of floating plants, plankton, snails, newts, water, sand, detritus, and glass slides Samples were collected at 13 different times. Figure 1 shows the hypothesized food web. All the transfer parameters (arrows between components) could not be measured experimentally because of the complexity of iterations and feedbacks. Therefore, the parameter identification method described above was employed.

The flow diagram (Fig. 1) was described mathematically as

$$\dot{\underset{\sim}{s}}(t) = A\underset{\sim}{s}(t). \tag{19}$$

The radioactivity, expressed in pCi g^{-1} of each component $\underset{\sim}{s}$, was used to compute $\Delta\underset{\sim}{s}/\Delta t$ by Eq. (4). The system matrix A was computed by the multiple regression technique.

Once initial estimates of A were obtained, a simulation $\underset{\sim}{s}(t)$ was obtained using the formula

$$s_j = \sum_{i=1}^{n} c_{ij} e^{\lambda_i t}\ ,\quad j = 1,\ldots,n, \tag{20}$$

where the c_{ij}'s are the values of the ith eigenvector, and λ_i's are the eigenvalues or characteristic roots of matrix A. Eq. (20)

was minimized by the algorithm of Fletcher and Reeves (1964), which involves function minimization by conjugate gradients. In this case all the c's and λ's [Eq. (20)] were modified until a least squares convergence [Eq. (7)] was obtained, i.e. until $\phi(c,\lambda)$ reached a minimum [Eq. (11)]. The optimal values of matrix A were then computed by differentiation of Eq. (20).

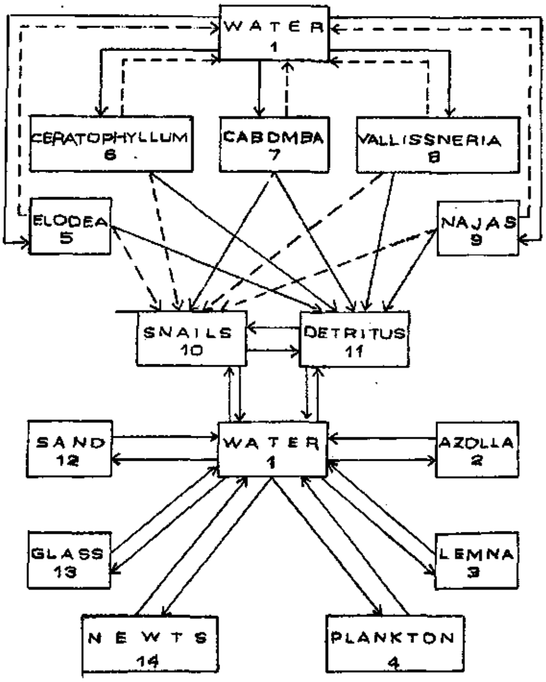

Figure 1. Flow diagram of model.

Equation (20) was employed for simulation and optimization for two main reasons. First, Eq. (20) is the analytical solution of (19) and thus the simulation is exact and there are no errors due to numerical integration approximations. Second, the simulation time is highly reduced.

Results

The method of obtaining initial estimates of the parameters from the experimental data was tested by simulating model (19) before applying the optimization algorithm, and comparing simulated and observed data. Figure 2 shows the behavior of ^{137}Cs in compartment 1 (water) and compartment 2(*Azolla* sp.). The simulated results are quite close to experimental values, and only after ten days the theoretical values become lower. This difference was due to too high a value of the turnover rate of these compartments, and was easily corrected by the optimization technique.

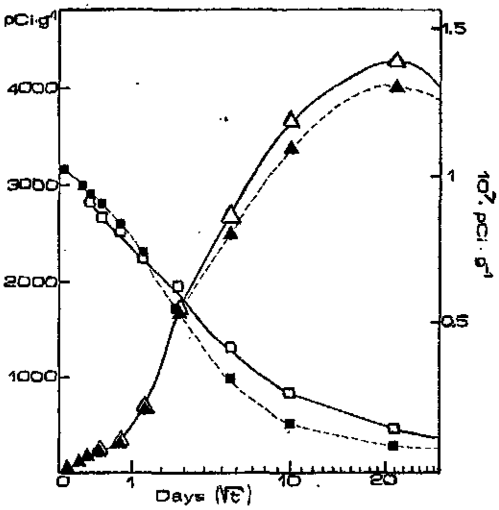

Figure 2. Water (□), *Azolla* (△). Simulated (●) versus observed (○) data.

However, this fit could have happened by a random combination of favorable events and should be verified. This can be done by comparing results from different replicates of the same experiments, i.e., using more microcosms. The data set used had three replicates of each experiment and thus similar results were expected. For example, the turnover rate of ^{137}Cs in water was 43.8, 46.6, and 50.9 $\mu Ci\ g^{-1}\ h^{-1}$, respectively, in the three aquaria. This implies that this procedure allows parameter values to be obtained that not only fit the data well but also, on the average, come fairly close to the true value of the parameter in nature and do not vary excessively from one set of experiments to another. Thus, if these several estimates are close, confidence in the estimated values is increased. This approach is more meaningful than averaging all experimental data for all compartments and then computing the value of the transfer parameters, because then there is no means of verifying or cross checking the results.

Discussion

From this analysis it can be concluded that the hypothetical model [Eq. (19), Fig. 1] accurately describes the experimental data. Some transfer parameters (dotted arrows in Fig. 1) could not be computed. The value of the parameter was zero, or it described a transfer in a direction that was not ecologically meaningful. Thus, it was assumed that such transfers did not take place in the aquaria, or that their value was negligible.

The multiple regression approach is useful because information from all compartments is utilized together and parameter values can be computed accurately. In this way various pathways are sorted out, even if no a priori information about the fluxes is available.

Whether small microcosms or natural ecosystems are modeled, the parameter identification problem must be faced. When a parameter cannot be measured, it must be decided if this parameter actually occurs in nature or if our guess is only arbitrary and we are adding some structure to the model that is not actually present. Thus, when we analyze results from natural ecosystems, and we wish to construct mathematical models, we must utilize some nonbiased techniques to decide whether to include specific transfers. The technique of identification employed here seems appropriate for this because the exclusion of some parameters, identified a priori, does not seem to affect the mathematical model. Eventually, the existence of these missing transfers can be examined when the model is verified against other experimental data.

The identification problem should be emphasized in the analysis of laboratory and field experiments. All results obtained from simulation runs that can be used for management purposes, the insight that is obtained from studying the transfer parameters, and the information revealed by systems analysis techniques ultimately depend upon the system matrix A. Thus, research into identification techniques and model estimation should be pursued by ecologists. Progress in this area in other disciplines is helpful, but the peculiar problems common to ecosystem modeling must find their way into identification algorithms which have true ecological utility.

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EXPERIMENTS TO ANALYSE THE BEHAVIOUR OF YOUNG SPRUCE FOREST AT DIFFERENT NUTRIENT LEVELS

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Summary

An experiment is described in which the nutrient regime of a forest ecosystem has been changed by repeated application of fertilisers during a seven-year-period. Nitrogen addition approximately trebled tree growth and dry matter production, apparently by increasing needle mass in the young, not yet fully closed, stand of Norway spruce. Tree growth was also increased by phosphorus application, although to a much smaller extent. Optimum type curves have been obtained for tree growth as a function of foliage nitrogen concentrations. It still remains to establish a reliable optimum range by continued experimentation. Since tree growth depends on both current conditions and the previous history of the tree, a relatively long experimental period is needed, in particular since supraoptimal conditions may rather consist in decreased resistance to adverse conditions than in directly negative growth effects. Adverse conditions may be climatic or due to herbivore damage; both types of injury were common during one winter (1969/70) and were much increased by fertilisation.

The treatments affected ground vegetation both qualitatively and quantitatively. By contrast, the effects on soil nitrogen turnover have been relatively small so far. Only the highest level of ammonium nitrate (in total 1 920 kg N per hectare) led to nitrate formation in the soil.

Introduction

The experiments described in this paper form part of a larger experimental series of so-called optimum nutrition experiments in young stands of both pine (*Pinus sylvestris*) and spruce (*Picea abies*). The purpose of these experiments is to discover both whether reliable nutrient levels for maximum growth can be established, and what the ecological effects are on the trees and on other ecosystem components, when these "optimum nutrient levels" are maintained for extended periods of time. Particular problems associated with the experiments concern the mechanisms by which the increased yields at higher nutrient level have been obtained, and the possible undesirable effects of maintaining a forest ecosystem at near-optimum levels of nutrition.

Experimental part

The experiment, described in more detail in a recent publication (Tamm et al., 1974 a), is situated 350 m above sea level in middle Sweden (40 km NE of Falun). The soil is a podzol formed on glacial till and the ground slopes towards W. The site had been covered by old spruce-dominated forest until 1957, when the forest was felled. The site was planted in 1958 after prescribed burning in the summer of 1957. The planted spruce grew very slowly and had attained an average height of 1.3 m in 1966. The needles had a yellowish colour and chemical analysis showed very low concentrations of nitrogen.

Several experiments have been laid out on this site, including comparisons between single applications of nitrogen fertilisers and repeated applications, effects of irrigation and liming, etc. (see Tamm et al., 1974 a). The experiment dealt with in this paper consists of a factorial experiment with four levels of nitrogen (N0, N1, N2, and N3) and three levels of phosphorus (P0, P1, and P2). Half the number of plots also received an application of potassium, magnesium and a mixture of micronutrients (Table 1). All treatments occur in duplicate and each of the 48 plots consist of a gross plot 30 m by 30 m

Table 1. Fertiliser regime in Experiment E26 A, Stråsan. N given as NH_4NO_3, P as superphosphate 28/30, K as "kalimagnesia" (also containing Mg and 2 per cent of a micronutrient mixture in 1967, 7 per cent in 1969).

Symbol	Amount given in element kg per hectare						
	1967	1968	1969	1970	1971	1972	1973
N1	60	60	60	40	40	40	40
N2	120	120	120	80	80	80	80
N3	180	180	180	120	120	120	120
P1	20	-	20	10	-	-	-
P2	40	-	40	20	-	-	-
K(Mg, Micro)	80 K 22 Mg	-	80 K 22 Mg		-	-	-

and a net (measuring) plot, as a rule 20 m by 20 m. Nitrogen has been applied every spring from 1967 onwards, the other nutrients at longer intervals (Table 1).

Fifteen trees within each plot were sampled every autumn for well-exposed current needles (second whorl), which were then analysed chemically (Table 2). The tree stand was measured periodically, first for height growth only, in 1972 for diameter too (Table 3). In the autumn of 1973 all above-ground biomass (except mosses and lichens, of very minor importance) was sampled. Field layer vegetation (including raspberry bushes) was sampled from 15 randomly distributed quadrats within each of 10 plots, representing the treatments N0P0, N1P1, N2P1, N3P1, and N2P0. Within the same plots (but outside the central measuring plot) sample trees representing all diameter classes were felled, 10 from each treatment except N0P0, where 20 trees were taken. These trees were weighed fresh and their biomass determined (by fractions: stemwood, stembark, branches, needles) on samples transported to the laboratory. New measurements of stem diameter and height were made, which made it possible to calculate stem growth values for the plots from the differences between these measurements

Table 2. Foliage nutrient concentrations in Experiment E26 A as a function of fertiliser regime.

N %	1966	1967	1968	1969	1970	1971	1972
N0	1.35	1.49	1.23	1.25	1.11	0.93	1.08
N1	1.34	1.97	1.84	2.01	1.73	1.28	1.46
N2	1.32	2.37	2.20	2.43	2.06	1.59	1.95
N3	1.32	2.66	2.57	2.69	2.24	1.73	2.11
P %							
P0	0.20	0.20	0.17	0.20	0.18	0.18	0.21
P1	0.21	0.28	0.24	0.30	0.32	0.26	0.25
P2	0.21	0.33	0.26	0.38	0.36	0.27	0.26
K %							
-K	0.76	0.63	0.54	0.79	0.80	0.83	0.85
+K	0.78	0.69	0.60	0.91	0.89	0.95	0.96
Mg %							
-Mg	0.10	0.11	0.09	0.10	0.09	0.08	0.10
+Mg	0.10	0.11	0.08	0.10	0.09	0.08	0.10

Table 3. Stand data in Experiment E26 A. (Biomass plots).

	Treatment									
	N0P0		N1P1		N2P1		N3P1		N2P0	
	13	46	10	36	12	30	26	50	2	52
No. of trees per plot	103	80	121	112	117	65	92	119	95	58
Average height in 1966, m	1.34	1.24	1.19	1.32	1.43	1.26	1.29	1.17	1.40	1.34
Average height in 1972, m	2.92	3.36	3.91	4.57	4.50	4.39	4.27	3.72	4.20	4.20
Stem volumes, m^3 per ha										
Total stand in 1973	7.8	8.4	19.8	30.8	38.9	22.5	31.6	32.9	29.3	19.5
Annual growth 1972-1973	2.2	2.0	6.5	9.1	12.3	7.4	11.0	11.9	9.3	6.0
Dry weight 1973 kg per hectare										
Stems	3500	3660	8320	11600	14930	8350	11880	13170	11180	7640
Branches	3080	3030	5290	7800	10310	5810	8260	9000	7140	4860
Needles	4060	4000	7490	10710	13960	7820	11140	12000	9670	6570
Sum Tree stand above ground	10640	10690	21110	30130	39200	21980	31280	34170	27980	19070

Table 4. Estimated aboveground dry weight production in 1973 on biomass plots of Experiment E26 A.

	Treatment									
	NOPO		N1P1		N2P1		N3P1		N2PO	
	13	46	10	36	12	30	26	50	2	52
Trees										
Stemwood	800	720	2230	2830	3960	2300	3430	3940	2940	1970
Stembark	190	160	490	590	760	460	700	810	600	400
Branches	640	610	1160	1850	2530	1440	2050	2180	2050	1370
Needles	870	830	1570	2510	3430	1960	2780	2950	2780	1860
Sum	2500	2320	5450	7780	10680	6160	8960	9880	8370	5600
Lesser vegetation										
Herbs & grasses (standing crop)	156	629	823	553	461	691	402	721	635	631
Dwarf shrubs (1/5 of standing crop)	161	28	7	146	0	3	0	0	1	7
Rubus idæus (current shoots+ leaves+berries)	0	3	2	6	25	526	769	54	408	308
Sum	320	660	830	700	490	1220	1170	780	1040	950
Sum above ground	2820	2980	6280	8480	11170	7380	10130	10660	9410	6550

and those one year earlier. It should be observed that stem growth values for such a short period are not very accurate as far as absolute amounts are concerned. However, they can be used for comparisons between plots. Annual needle production was considered to be equal to the amount of one-year-old needles, calculated from the amount of current needles, using the empirical relation $C = 0.815 \cdot (C + 1)$, where C stands for current needles and C + 1 for needles in their second year. Branch production was calculated using the relation branch production = 0.905 • (current needles), established for another site (Norberg, 1970). Herb and grass production was, for comparative purposes, considered equal to aboveground biomass in the middle of August, while raspberry (*Rubus idæus*) production was considered to consist of current shoot biomass + all leaves + berries. Dwarf shrub production (*Calluna* + *Vaccinium sp.*) was considered as 1/5 of aboveground biomass, very probably an overestimate, since the dominating species (*Calluna vulgaris*) is relatively long-lived.

The biomass data from the sampling just described are in Table 3 and the production data in Table 4. It is quite clear that the tree stand accounts for the dominating part of both biomass and production on all plots. This is the case even in plots with a small number of trees (No. 30, N2P1 and No. 52, N2PO), where tree biomass and production are considerably lower than in the duplicate plots with a larger number of trees. Qualitative changes in field layer vegetation are, however, associated with the treatments. The dwarf shrubs are apparently unfavourably affected by fertilisation, which on the other hand seems to be a prerequisite for increases in the raspberries. Herbs and grasses occur on both fertilised and unfertilised plots in fairly similar quantities, but considering the fact that the spruces on fertilised plots are much taller and denser, herbs and grasses on fertilised plots occur particularly in the areas between the crown projections, where they luxuriate. It can be expected that most of the present ground vegetation will be reduced when the canopy attains full closure, a stage which has already been reached in parts of the fertilised plots, but not on unfertilised ones.

A soil sampling was carried out in October 1973 and the amounts of mineral nitrogen (NH_4-N and NO_3-N) in mor samples (A_0 horizon) were determined both immediately and after incubation (Table 5). Very little mineral nitrogen was found on NO and N1 plots; the nitrate values observed there (values within parantheses in Table 5) are so low that they may be explained by the nitrate content of

Table 5. Nitrogen in fresh and 9-week-incubated samples of humus (A_o) from Stråsan. Samples collected, 1973-10-02. Percentage values within parentheses inaccurate on account of extremely low levels. (From B. Popović, in prep.).

	Treatment									
	N0P0		N1P1		N2P1		N3P1		N2P0	
	13	46	10	36	12	30	26	50	2	52
pH	4.0	4.3	4.2	4.1	4.0	4.5	4.1	4.2	4.1	4.0
N_{tot} per cent of loss on ignition	2.15	2.11	1.87	1.93	1.82	1.99	1.74	2.04	1.53	2.09
Mineral N per cent of N_{tot}										
At start	0.05	0.07	0.06	0.10	0.26	0.82	1.25	1.14	1.12	0.55
After 9 weeks	1.00	0.51	1.79	1.21	2.07	2.09	3.45	3.77	3.97	2.57
NO_3-N, per cent of mineral N										
At start	(42)	(60)	(51)	(36)	(18)	3	16	7	6	8
After 9 weeks	2	4	1	1	2	1	55	14	3	2

the rainwater. Samples from treatments N2P1, N3P1 and N2P0 contained moderate amounts of mineral nitrogen, the major part as ammonia nitrogen. Nine weeks' incubation increased mineral nitrogen in all samples, but nitrification was virtually absent in all samples except those from treatment N3P1, particularly plot No. 26 where more than half the mineral nitrogen was in the form of nitrate, in spite of the low pH.

In the spring of 1970 several types of injuries were observed on the spruce, which were recorded as examples of disturbances associated with high nutrient levels. As is shown in Table 6, there seems to be a relationship between damage classified as "winter drought" (brown needles, sometimes dead shoots) and nitrogen supply. Moose browsing, which hardly damaged the trees seriously (unlike browsing on pine), appeared to depend on both nitrogen and phosphorus levels, while rodent damage, in most cases affecting low side-branches and buds, increased with increasing nitrogen level, may be as a consequence of the better shelter in the luxuriating field vegetation. Common to all three types of damage was the fact that it did not affect trees without nitrogen to any notable extent. The frequency of damage has been much lower in subsequent winters, and it should also be mentioned that there are types of damage which appear to be unrelated to treatment, e.g. light attacks of *Sacciphantes (Chermes) abietis*.

Table 6. Damage on spruce recorded in the summer of 1970. Percentage trees with damage (note that one single tree may have more than one injury).

Treatment	"Winter drought"	Moose browsing	Rodent browsing
N0P0	1.6	0.0	1.8
N1P0	5.3	4.6	16.9
N2P0	2.8	5.4	34.0
N3P0	12.0	3.1	30.7
N0P1	0.0	0.0	5.3
N1P1	1.8	3.4	18.7
N2P1	3.6	11.4	26.8
N3P1	5.2	16.1	46.2
N0P2	1.2	0.0	2.9
N1P2	6.0	13.0	26.9
N2P2	5.7	15.2	27.1
N3P2	9.0	32.4	38.6

Discussion

The first results to be noted concern the relation between spruce stand growth and nitrogen fertiliser level. Optimum type curves for spruce growth plotted against foliage nitrogen were obtained for both the period 1970-1972 (Fig. 1). No clearly supraoptimal values were obtained, but the increasing frequency of injuries at higher nitrogen levels suggests that at least an ecological optimum may exist not too far from the levels studied. During the second period the optimum growth seemed already to be obtained at nitrogen levels which were suboptimal during the first period. This difference indicates one difficulty in experiments of this kind, viz. the frequently long course of the response to a certain treatment. The difference in foliage nitrogen levels between the two periods reflects principally the reduction in the annual application after 1969 (Table 1); tree growth depends both on tree size (attained by earlier treatment) and current treatment. At least one more revision period is apparently necessary to establish a more reliable optimum curve.

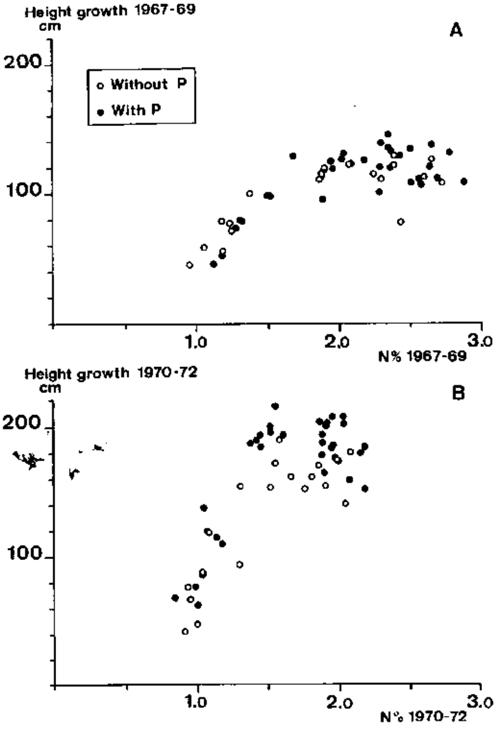

Fig. 1. The height growth of spruce as a function of the nitrogen concentration in exposed needles. Each point average for one plot.
A. Period 1967-1969 B. Period 1970-1972

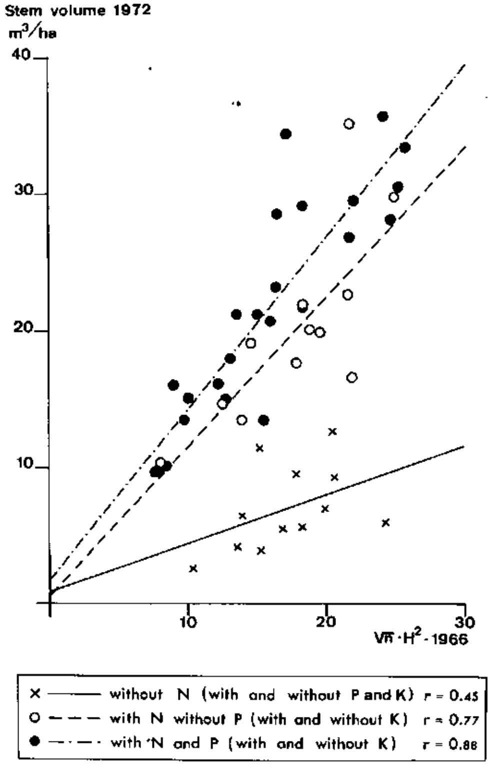

Fig. 2. The stem volume in 1972 as a function of stand condition at the start of the experiment, as expressed by the index $\sqrt{n}\cdot h^2$ (see text).

An approximately linear relationship appears to exist between stand volume and the expression $\sqrt{n}\cdot h^2$ (Bjørgung, 1968), where n stands for number of trees per plot and h for the average height at the start of the observation period (Fig. 2). Plots fertilised with nitrogen have a much higher volume than plots without nitrogen, but have similar initial conditions (as expressed by $\sqrt{n}\cdot h^2$), another way of illustrating the fertiliser response. The scatter around the regression line is higher for no-nitrogen plots than for nitrogen fertilised plots, as shown by the correlation coefficients. Such a difference in scatter would be expected, if the variation between measured and calculated volume were caused by differences in the soil supply of nitrogen available to the spruce. An artificial supply of nitrogen would then mask the soil differences wholly or partly. However, an alternative explanation would be that relative differences in growth would tend to decrease with age, particularly after the growth culmination following stand closure. This explanation seems less likely, since the data (Fig. 1 A and B; Tamm et al., 1974 a) indicate that the growth-rate has not yet decreased.

A further observation concerns the effect of phosphorus application. There is a statistically significant, positive interaction effect between N and P on height growth, which is apparent in Fig. 1 B (but not in

Fig. 1 A), viz. phosphorus application tends to increase growth of spruce already receiving nitrogen. The result is not unexpected, but it should be noted that foliage phosphorus is above the physiological deficiency levels established by Ingestad (1962), also in plots without P supply. There is as yet no evidence that the treatment K + P + Micro has increased tree growth.

The questions most relevant with respect to ecosystem research concern the mechanisms for increased net primary production on fertilised plots and also the fate of the large amounts of soluble fertilisers, nitrogen in particular, which have been added to the ecosystem. Final answers to both these questions would require more data than are available at present, but some conclusions can be drawn from the material presented here.

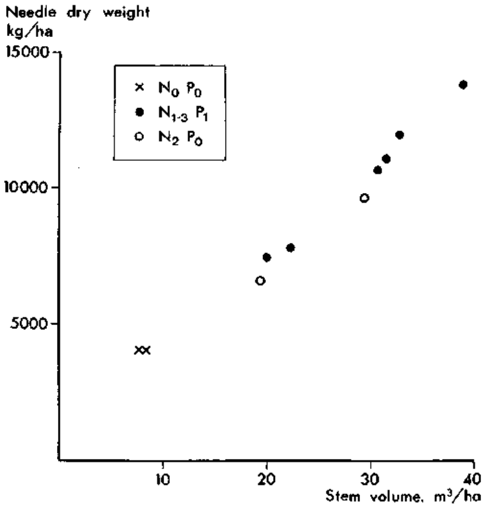

Fig. 3. Needle dry weight as a function of stem volume (biomass plots).

As concerns the question of the mechanism for increased production, Fig. 3 shows a very strict relationship between stem volume and needle weight. It may be added that a similar relationship also holds true for the individual trees, although the relations used for calculating individual tree biomass components have been allometric equations of the type: log (biomass component) = a + b · log (basal area). Fig. 4 then shows the equally good correlation between the net production of the tree stand and the amount of needles. The natural interpretation of these two diagrams seems to be that nitrogen application increases the amount of needles, which then results in an increased production. Similar results have been obtained in a previous experiment (Tamm, 1971 and in prep.). Physiological studies by Brix & Ebell (1969) and Brix (1971, 1972) indicate that the main mechanism underlying the growth response to nitrogen fertiliser in a forest stand was an increase in needle biomass rather than an increase in photosynthetic activity.

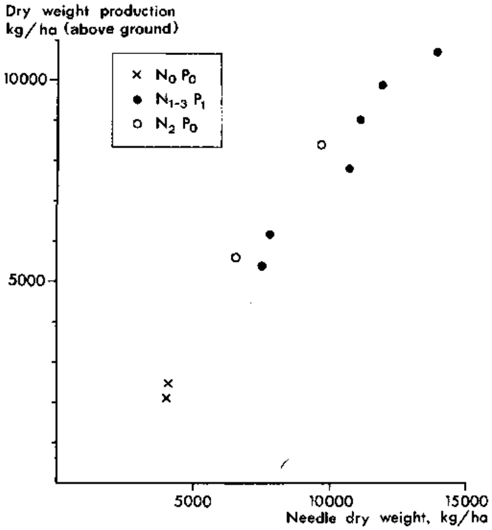

Fig. 4. Dry weight production above ground as a function of needle dry weight (biomass plots).

Studies of the fate of applied nutrients have so far concentrated on leaching of nutrients, nitrate in particular, to the ground water, and to some preliminary studies of soil nitrogen mobilisation. It was soon observed that the water of a spring situated below experiment E26 A contained nitrate in concentrations around one mg per litre, at least ten times more than a control spring in the neighbourhood. Quantitative estimates of leaching were, however, not possible here (cf. Tamm et al., 1974 b), because the infiltration area of the spring was not known. The results of soil incubation experiments (Table 5) seem to show that the repeated applications of ammonium nitrate have not yet led to nitrification in the soil, except at the highest nitrogen level. Therefore it is probable that the leached nitrate mainly originates directly from the fertiliser nitrate. A question of great interest, both scientifically and because of the practical consequences, is under what circumstances the soil in the coniferous forest ecosystem starts to transform ammonia nitrogen to easily leached nitrate (Tamm et al., 1974 b, Popović in prep.).

Concluding remarks

Experiments with entire forest ecosystems - even if the actual treatments are given to plots 30 m by 30 m as in the present case - require considerable efforts, both regarding manpower and costs. They also necessitate observations over extended periods of time, because growth in any one year is determined both by environmental influences in that year and by previous development of the tree stand. There is usually a lag period before the ecosystem can be considered as adjusted to a change in conditions.

Yet it is felt that such experimentation is very necessary as a complement to the types of experiments at present most common in forest research: either long-term trials of an applied type, studying e.g. the effects of various silvicultural treatments on stem growth, or short-term eco-physiological experiments, aiming at a better understanding of the mechanisms operating in the forest ecosystem. Forecasts can be made on ecosystem behaviour using simulation techniques, but it would be unwise to desist from the opportunity of validating the mathematical models by means of long-term experiments in the real world.

Optimum nutrition experiments in forest stands of the kind described here have so far only been laid out in Sweden (Tamm et al. 1974 a) and in Canada (Weetman & Algar, 1974), but also other types of long-term experiments with sufficiently good control of both treatments and ecosystem behaviour will be extremely valuable.

It is hoped that such experiments will provide new information regarding the productivity and stability of forest ecosystems, information valuable in itself but also useful for modern ecosystem research directed towards the construction of mathematical models simulating the behaviour of the entire ecosystem.

Acknowledgement

The present paper is an extremely condensed account of data obtained during seven years' experimentation. More detailed presentations are planned for various aspects of the work: Biomass sampling (by J. Redin & A. Albrektsson), soil nitrogen mineralisation (by B. Popović), growth responses (by A. Aronsson, H. Burgtorf, Å. Nilsson & C.O. Tamm). Financial support has been obtained from the Swedish Research Council for Agriculture and Forestry, from Stiftelsen Svensk Växtnäringsforskning, and from Cellulosaindustriens stiftelse för teknisk och skoglig forskning samt utbildning.

The optimum nutrition experiments have been part of the Swedish IBP programme and are now associate projects to the Swedish Coniferous Forest Project.

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C3

Ecological interpretation of remote sensing data

REMOTE SENSING INFORMATION SYSTEMS IN THE SERVICE OF ECOLOGY

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Summary

The broad application of aerospace remote sensing systems to identify, map, monitor, and characterize earth surface features is bringing new life to many studies in ecology. Multispectral cameras and scanners on aircraft and space platforms allow the ecologist to obtain data about man's environment hitherto unavailable. Information from these new aerospace remote sensing systems promises to assist in revealing the answers to many of the problems which have plagued ecologists for many years.

This paper describes briefly some of the remote sensing tools which are presently being used and some improved data acquisition instruments which are envisioned for forthcoming satellite observatories. A discussion is also presented on the advances which are being made in handling, processing, and analyzing the massive quantities of data which can be obtained by orbitting satellite scanner systems.

The success or utility of these new tools will ultimately be judged by the extent to which they benefit man through a better understanding of his environment.

Introduction

I bring to this symposium a background and interest in soil science, world food supply, and remote sensing technology. For the past eight years I have devoted much time to pondering, probing, studying, and searching for effective ways of applying aerospace remote sensing technology to the problems of vegetation mapping, crop yield predictions, soil surveying, preparing resource inventories, changing land use, assessing quantity and quality of water resources, and monitoring the environment.

For those persons who are interested in any of these aspects of ecology it seems appropriate to discuss briefly two situations which have a very important bearing on the need for better information systems for earth resources.

Remote sensing comes of age

I refer to the first situation as "remote sensing comes of age." Ecologists, agricultural scientists and foresters have been using aerial photography very effectively for years to accomplish a wide variety of tasks. Since the mid-1930's the Agricultural Stabilization and Conservation Service or its predecessor agencies in the United States Department of Agriculture have used aerial photography to map and measure specific cultivated crops under the various programs designed to limit production.

Since World War II essentially all county soil surveys prepared by the Soil Conservation Service in the United States have used aerial photographs as a base on which to prepare detailed soil maps. For many years the Forest Service has used aerial photography to inventory forest resources and to identify and map forest areas destroyed or damaged by fire, insects, and diseases.

The Bureau of Land Management, the Bureau of Reclamation, and the Forest Service have used aerial photography on a limited basis to monitor and, as a took, to manage forest and rangeland resources on the public lands in the Western United States. Aerial photography has been used in like manner in many countries of the world.

But remote sensing of earth resources did not come of age until the advent of the Gemini, Nimbus, Tiros, and finally the Earth Resources Technology Satellite and Skylab programs. And although we are only beginning to scratch the surface in harnessing the capabilities of these new remote sensing systems, we have ushered in a new era for observing, understanding, mapping, monitoring, developing, and managing earth resources. These new systems have gained public awareness, knowledge, and support of remote

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sensing as no other program ever has. In this sense then perhaps it is appropriate to say that remote sensing has come of age.

The changing world scene regarding food, timber, energy and mineral resources

The second situation strikes somewhat closer to personal experiences of many people. Millions of citizens of the more affluent nations experienced in 1973 for the first time in this generation a food shortage. That is, there have been times during the past several months when a trip to the supermarket met with frustration because the supply of certain foods was exhausted. Perhaps very few Americans or Japanese or Dutch went hungry because of this inconvenience. However the facts are that the large surpluses of feed grains, wheat, dairy products, cotton, and other agricultural produce which were politically frustrating if not morally embarrassing to the food surplus nations during the 1950's and 1960's no longer exist.

The rapidly accelerating affluence of North America, Western Europe, and Japan has brought increased demands for feed grains, meat, cotton, soybeans, timber, and recreational lands. This, combined with the increased purchasing power and demands from the People's Republic of China and the U.S.S.R. for large imports of feed grains, wheat and cotton have contributed to the diminution of the surpluses of agricultural products.

The past five years have brought severe drought and flooding which have resulted in critical shortages of agricultural products in many nations of Asia and Africa. No area in the world provides a better example of a deterioriating environment and mass starvation than the Sahelian zone of Africa. During the past growing season tens of thousands of cultivated hectares of millet and sorghum provided no harvest al all. Millions of animals and thousands of persons have starved.

The energy crisis has also had a direct bearing on agricultural production. Shortages of natural gas in some areas of the world have curtailed the production of nitrogen fertilizers which are essential to high yields of maize, sorghum, wheat and other grain crops.

For these and other reasons the food problem suddenly demands world attention as never before in modern times. The years ahead may provide the greatest challenge ever placed on the scientific community in the development and management of the land, vegetation, and water resources of the world. As a part of this challenge, what are the opportunities for the application to ecological problems of better information systems? How can the ecologist and agronomist use remote sensing as a tool in feeding a hungry world and maintaining a quality environment?

Data Acquisition

This discussion will be limited to data acquisition systems whose primary source of data is from remote sensing instruments. Remote sensing is here defined as the observation or measurement of an object or objects without contacting the subject under study. Today there are many remote sensing instruments, the camera being one of the most common. I have chosen to give major attention to the multispectral scanner (MSS) because it is the instrument on the first Earth Resources Technology Satellite (ERTS-1) which has been scanning the earth's surface and providing quality spectral data since the scanner was activated on 25 July 1972, two days after launch.

There are numerous reconnaissance aircraft equipped with multispectral scanners. Multispectral measurements can also be obtained from field scenes or test sites with spectroradiometers. Spectral information about the earth's surface obtained at distances ranging from one meter to one thousand kilometers should be of interest to many ecologists.

The launching of ERTS-1 ushered in a new era in remote sensing information systems. Man's capability to obtain data far surpasses his ability to analyze, store, retrieve and utilize data. In sun-synchronous polar orbit ERTS-1 covers the entire earth every 18 days, obtaining multispectral measurements of the earth's surface between 930 and 1030 hours local time. The MSS scans an area of 34,299 km^2 in less than half a minute. This area represents one frame of ERTS MSS data which consists of 7,553,520 data points for each of the four spectral bands of the scanner (Table 1). Each datum point represents the resolution of the MSS and covers an area of 0.45 hectares. With 7.5 million data points per band and four spectral bands, more

Table 1. Spectral bands of the ERTS-1 multispectral scanner.

Band	Spectral range	General description
4	0.5-0.6 μm	Visible green
5	0.6-0.7 μm	Visible red
6	0.7-0.8 μm	Infrared
7	0.8-1.1 μm	Infrared

than 30 million data points are being generated every 25 seconds.

Each datum point is a quantitative value representing the energy being reflected in a specific wavelength band from a specific address covering 0.45 hectares at the surface of the earth. Spectral data obtained by the ERTS-1 MSS are telemetered to and recorded on magnetic tape at receiving stations in the United States, Canada, and Brazil. From these data several products are produced, including single band black and white images, multiband color composite images, and computer compatible tapes.

Data Processing and Analysis

MSS data may be processed and analyzed by several methods. Presently the most commonly practiced approach is to produce images from the digital data and use photointerpretative techniques in the analysis procedures. In this approach the analyst is required to interact with the data through visual means. Many instruments are available which assist in the photointerpretative process.

A newer approach which has developed rapidly during the past decade involves the computer-implemented analysis of MSS data. In this approach the computer can examine the quantitative value for each datum point for each wavelength band, or it can use a sampling procedure to examine a fraction of the multispectral data from one or more spectral bands. Pattern recognition techniques are then used which provide the computer with programs to identify and classify each resolution element or datum point into a specific spectral category. This quantitative approach allows the computer to examine millions of data points very rapidly and make decisions for the classification of every point.

Two requirements must be met if this approach is to be useful. First, the classes or desired separations must be spectrally separable. Second, the results of the computer-implemented analysis must be related to the actual earth surface features under study.

Since the ERTS-1 multispectral scanner obtains data over the same scene each 18 days, it is possible to process the digital data from a scene such that the data for two or more dates are in registry. Then by computer-implemented analysis it is easy to identify quantitatively areas within the scene whose spectral condations have changed significantly during the time between ERTS passes. With this technique the ecologist can monitor and assess quantitatively the amount and kind of change which is occurring in an area of interest.

Implications for Ecology

One of the very interesting tasks to which this new technology is being applied is the preparation of a current land use inventory of the U.S. portion of the Great Lakes drainage basin. Multispectral data from ERTS-1 are being analyzed by computer-implemented pattern recognition techniques to provide a land use map for each of 191 counties covering an area of 33 million hectares. This task is being funded by the U.S. Environmental Protection Agency for the International Joint Commission (IJC) consisting of representatives from the U.S. and Canada.

In the Great Lakes Water Quality Agreement signed by the two governments on 15 April 1972, the IJC was requested to assess the present water quality and pollution problems of the Great Lakes and to take measures for maintaining or improving the water quality.

In order to make a rational assessment of the pollution problem, it is essential to identify the sources of pollution. A current land use inventory will help to define the sources of pollution related to land use.

The objectives of this study are

(1) to provide a color coded map of each of the level I land uses which include agriculture, forest, urban, and no major usage and (2) to provide in tabular form the percentage and area of each county in levels I and II land uses (Table 2).

These two objectives are being met over a period of nine months by computer-implemented analysis of digital data from the ERTS-1 multispectral scanner.

Another ecology-related task which is being performed by machine-processing of ERTS MSS data is the mapping and monitoring of earth surface features in the drought and famine stricken area at the interface between the desert and the savanna in the Sahel-Sudan belt of Africa. Rapid spectral analysis over an area of tens of thousands of square kilometers is providing heretofore unobtainable information about the resources of the area and about the movement of the desert.

In 1974 the United States Department of Agriculture removed restrictions limiting the production of feed and food grains. This removal of restrictions together with high prices has resulted in the new cultivation of millions of hectares of land which has been in permanent vegetation for many years. Much of this newly tilled land is highly susceptible to wind and/or water erosion. ERTS-1 provides an invaluable tool to map and monitor these regions of erosion hazard and to predict erosion losses and sedimentation damage.

Many other applications of remote sensing to ecology-related problems could be cited. Countless scientists around the world are using various remote sensing techniques to identify and map vegetative species, to observe the conditions of crops, forests, and wildlands, to assess the quantity and quality of water resources, and to characterize and monitor the environment.

Conclusions

The present earth resources information systems and those to come will provide increasingly valuable tools to the ecologist. In order to play an active and effective role in monitoring, developing, managing, and conserving earth resources, the ecologist must prepare to take advantage of this new technology.

Table 2. Classes in the land use inventory for the Great Lakes Watershed.

Level I	Level II
Urban	a. Residential - low, medium, high density
	b. Commercial/Industrial - low, medium, high density
	c. Transportation
	d. Extractive
Agriculture	a. Row crops
	b. Close grown crops
	c. Pastures/Meadows
	d. Orchards/Vineyards
Forest	
No Major Usage	a. Water
	b. Wetlands
	c. Barren lands

AERIAL PHOTOGRAPHY, REMOTE SENSING AND ECOLOGY

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Abstract

Aerial Photography (as other means of remote sensing) is a classic tool to take distance from the subject of study in order to oversee the total.

In each science, especially in ecological research, one can distinguish two major complementary approaches:

a. the so-called causal one (= description of models with the help of factor parameters).

b. the so-called "final" method (= description of the total, usually including classification).

Because the final approach demands a certain distance, remote sensing opens new possibilities there. It has given a stimulus to the "final" approaches that were not always appreciated because of lack of efficient tools ("subjectivity" in Vegetation science).

An important means of taking distance of features on the earth surface, before remote sensing techniques existed, was cartography. Hence those ecological studies using cartographic representations can benefit from using aerial photographs.

The difference between classic aerial photographs and the other means of remote sensing is that photographs provide a clear three dimensional image of the reality, at any scale wanted which reveals much of the total "character" of the ecosystems photographed. This can be compared with a photograph of a person, revealing, even for non-psychologists, much of the character of that person.

Photography, and especially other remote sensing means, can also be made more specific on certain parameters, disregarding the "total" character. This, in combination with modern automatic computer techniques, can be useful for various types of causal and even "final" research.

The classical photography (using Pan or Colour film materials) from aircrafts and satellites however provides, particularly for vegetation and landscape ecological studies, a highly valuable tool that, at this stage of the research, is fully operational and is in various cases preferable to more modern sophisticated remote sensing means, that often seem to appeal more to the imagination of certain ecologists and other scientists who have disregarded the complementary "final" method and who, so far, have never used stereoscopic photography. Examples of results and usage of a systematic interpretation method of aerial photos will be given during the presentation of this paper.

Introduction

One of the general trends of technology is to invent newer methods demanded by nobody, but giving work to many in checking their possible usefulness.

Also ecologists, who are inclined usually to study ecology, are sometimes baffled by the prophecies of agents of the technologists, talking about the possibilities of a new method of doing things of which the poor ecologist never had dreamed (unless in a nightmare), and often never will dream of because he may not be interested in it for his type of research; for which he has already sufficient techniques available.

Nevertheless some of these ecologists have to take the trouble to investigate the core of truth that is in the usually overdone propaganda for the newest developments made by, otherwise unemployed, physicists and their engineers. One field of those revolutionary technological developments is Remote Sensing:

It started 116 years ago when Nadar (G.P. Tounachon) made his first birds-eye pictures of the village of Petit Bicetre near Paris, which were taken from a balloon and it reaches its maximum nowadays via the radar images covering millions of square kilometres of the Amazon countries by jet-powered aircraft, into the sequential space-born satellite monitoring of the complete earth.

Taking distance

The essential aspect of Remote sensing of any type of scientific and practical application is: "taking distance" in order to see objects at least as a whole or preferably in context of the whole of which they are a part. This context appears first of all in its spatial aspects. The opposite type of observation is to be very close or even inside the object, which allows a lot of details to be seen but hampers seeing the coherence between the confusing details = "to see the forest instead of the trees".

Before air and spaceborn remote sensing was invited we already had a mean for taking distance: Cartography. Then that was the only trick to obtain a simular effect. The essence of cartography is to redraw the reality to scale so that it can be overseen. It is not only a way to convey knowledge as certain people may suppose. Everybody who has done real mapping work in the field knows the excitement and scientific satisfaction on discovering the apparent coherence between individual features after adding some more critical details. A growing field map of soils, or geology, or vegetation or landunits or landforms is like a flower that gradually unfolds and sometimes, even suddenly, in the end reaches a stage of full development and splendour. That is the moment one sees for the first time the "whole forest instead of the trees"! Without cartography we would still stroll around from tree to tree.

Remote sensing has greatly enhanced the possibilities of accuracy and efficiency of the classical cartography. It is mainly through this aspect of cartography, that remote sensing is of high value for ecological studies. That means that especially those aspects of ecology that in one way or another may benefit from cartography, (hence study of spatial forms at the earth surface) can benefit from remote sensing.

Causal and final methods

Science philosophers use to subdivide our scientific actions into two main groups, which are essentially complementary:

Causal studies: "The from factor to the whole study", which tries to understand the whole of the factors by a complete analysis of parameters of factors and via model studies, with the experiment as a final check.

Final studies: The "from the whole to factor studies", which consider the subjects as a subcomplex entity of which the factors and those detailed interactions may never be understood completely, but which nevertheless can be studied as a whole in its properties and behaviour and main factors. This type of study demands for classification systems, which describe the entities and by comparison also tries to detect coherence.

Although real scientific research has to make use of the methodology and starting points of both complementary approaches, it is interesting to see that scientists as human beings often have a clear personal preference for one of the two, and may even doubt the usefulness of the other.

For "discovering the mysteries of life" a certain degree of causal research will be necessary. However, nobody can hope that the model of life that could be tested repeatedly experimentally will be invented by the work of a few people, even in some highly qualified institutes in a few years time. But also in the field of ecosystem study, taking the existence of living material for granted, so far causal studies have not been able to build and test models for systems more complex than the simplest system found in nature.

More direct application of Ecology to the problems of living beings which occur in relatively too great a number (like men) or too small a number (like endangered species) cannot be solved by causal methods, because their problems will be solved by extinction or "irresistible" degeneration before the final test of the models can be done.

Even simple ecosystems are so intricate that a pure approach from parameters only, without some knowledge of the whole, is almost impossible. Ecosystem study is therefore a good example of research where, also for pure scientific aims, the final approach cannot be missed even if one is more inclined to do causal experimental work. Final studies require that the forest instead of the trees, be seen as quickly as possible and therefore demand for remote sensing. They are not only benefitted but also stimulated by remote sensing.

Stimulation of final method by Remote Sensing

Probably it is not by accident that, at this first international congress of Ecology, vegetation science (phytosociology), which is a typical final ecological science, is treated in connection with Remote sensing. Modern vegetation science, especially the applied form of it, has of all the ecological sciences the biggest advantage from remote sensing, particularly from the classical aerial photography.

After the relation between cartography and remote sensing has been noted there is no need to stress anymore how the making of vegetation maps is greatly benefitted by the use of aerial photos. The delineation and recognition of the legend units on a map however, is not the most essential advantage of aerial photography and remote sensing in general.

The literature on phytosociology or vegetation science is full of discussion about the objectivity of vegetation classification. Problems arise especially where floristical (or micro structure) criteria are used in the classification.

Always one way or another of statistical treatment is then required, either real mathematical-statistical or visual-semi-statistical by making tables by estimation.

Objective stratified sampling

A major problem is the selection of sampling sites. Theoretically this should be made at random. Practically however, this is impossible because it is much too time consuming for two reasons:

a. Plantcommunities occurring in a relatively large area will be overpresented compared with communities having a small acreage.

Often the communities in the relatively small areas are at least as important as the one with wider extension, so one has to adapt the number to the minimum required for the communities with low acreage. The result is a waste of time spent in the areas of large acreage communities. Moreover, only at the end of the survey sampling stage of the survey, will one discover that certain types are over and others are under-represented.

b. Another difficulty is that a vegetation community is more than a point and has a minimum area. This means that one should not do a sampling in a place where a steep gradient exists because the chance is very great that there will be more than one community in a certain area. This means an inhomogene sample with low (also statistical) value. In pure random sampling one cannot avoid having samples in such inhomogene places.

Therefore pure random sampling is only appropriate in pure scientific surveys on small areas, where nobody is waiting for the results, except the scientist, who is amusing himself and can afford to spend much time. However, for practical surveys of large areas the selection of the sample sites is made more subjectively by estimating the existence of communities in the field beforehand from the general physiognomy and terrain physiography. The total amount of the samples to be taken is then equally divided between these preliminary communities.

The literature is full of critics of these methods open to bias but often applied by the Braun-Banquet school scientists and others.

> There are indeed cases in which it is very clear that floristic diagnostic criteria were not a result of the statistical treatment but had been caused by the subjective selection method. It is especially "convenient" to be able to drop some records afterwards that did not fit into the preconceived ideas by deeming them "transitional" and taken by error.

Although some of these criticisms are a bit overdone, which is proved by the highly practical value of many of the resulting vegetation maps for the ecological management of large areas, and the critics themselves often are not able to produce maps of a useful scale in a payable time, the subjectivity in sampling remains a great problem.

The great advantage of Remote sensing is that it provides a mean for objective stratified sampling.

Value of various remote sensing means for vegetation study

The classical aerial photo from the existing remote sensing means is the best tool in the usual scales 1:10.000 to 1:25.000 to be used in vegetation survey, because it gives the most comprehensive three dimensional picture of the reality with a valuable resolution of differences in reflected radiation. The normal Panchromatic black and white film with yellow filter is the most universal one of all the filmfilter combinations, although in certain cases large scale colour photography can be very useful, but also rather expensive. Black and white infra-red, although for one or another reason often propagated, is only suitable in very special cases where one has less interest in the vegetation cover as a whole, but in some special (structural) aspects that are indicated by I.R. radiation. False colour, at present in fashion, combines advantages of panchr. film and bl. and w. I.R.

Although the statements made above can be read in any report of realistic surveys, there is a tendency for ecologists who have never used aerial photography to expect all kinds of magic from newer remote sensing techniques like Radar, Multispectral line scanning and Thermal images.

The main advantage of normal photography is that it provides an image with very high resolution on any normal scale required and, because of the possibility of stereoscopy, has an essential three dimensional character. The third dimension is even exaggerated compared with direct vision from the aeroplane, but its value depends strongly on the flying height. The lower the flight the more depth can be seen. So for medium and large scale photography it is an important aspect. In Satellite photography it still plays a role in recognition of large geomorphological structures, but less in the vegetation itself. Satellite photography has, however, one advantage in that the fourth time dimension can be recorded. Only with Satellite photography and other Satellite imagery is it practically feasible to do sequential recording over large areas with an interval that makes it possible to study seasonal changes.

Radar has for most vegetation surveys too small a scale, but can be useful in cloudy areas and rough exploratory surveys (RADAM Brasil!).

Thermal imagery cannot be compared with other imagery for vegetation survey. The temperature and radiation differences which it records are the result of an extremely complex combination of greatly varying factors in time. Therefore thermal imagery can only be used for a specialistic research.

Multispectral scanning compared with photography has the main disadvantage of having less resolution (for the time being) and no possibilities for stereoscopy. The advantage is that it gives more possibilities for combining parts of the spectrum and so manipulate with the spectral signature of the reflected radiation of the objects. This opens the possibility of callibrating the recording medium for special aspects or even parameters of the object. Recent research results suggest that in large homogeneous vegetation areas (croplands) this may have possibilities. For vegetation survey in semi-natural and natural vegetations this manipulation possibility might be very useful especially for satellite photography, but can hardly replace the missed stereoscopy. For further details and more positive remarks on the other remote sensing methods see the papers in this congress of Baumgardner and Hempenius.

Photo-interpretation primary base for Sampling, secondary for mapping (orientation-delineation)

One of the classical misunderstandings in the use of aerial photos is that photo-interpretation would eliminate field work. Fortunately this is not the case. Secondly it is a wide spread idea that photo-interpretation would be a specialization in itself. It should be stressed here that if systematically applied it is indeed a specialization, but on top of another one. A photo-interpretator sec does not exist. Photo-interpretation for one or another ecological aim should be done by an ecologist, who is specialist in that branch of ecology. Photo-interpretation for vegetation survey should be done by a professional vegetation surveyor. The same is true for using other remote sensing means for vegetation survey. The great advantage of an aerial photo is that it does not give all the details wanted. It gives us distance, it shows us the whole. Just as a picture of a person reveals something of his character, so an aerial photo reveals something of the total character of a piece of the earth. We see mainly vegetation and landform (relief).

Even on rather large (detailed) photos single plants are seldom recognizable directly.

Landscape units however, can be easily delineated and objectively classified. This means that the ecological photo-interpretator needs some landscape-ecological knowledge.

Photo-interpretation should be done systematically

The essential sequence in photo-interpretation is first to analyse the photo image as such; try to categorise all kinds of patterns, tones and textures (and hues, chromas values if colours are available), without immediately trying to recognize or identify photo features with reality. Second is to make a preliminary interpretation on the basis of these features + the general landscape ecological knowledge in order to delineate the preliminary photo-interpretation-units based on landscape units + all kinds of photo features that are judged to be relevant to the actual aim. The result is a preliminary photo-interpretation map. The main purpose of this map is to be the objective base for stratified sampling. It permits the subdivision of the area into main ecological units (based on general landscape ecological knowledge). These units however, are delineated on the photo without knowledge of the details as far as floristic and micro-structural aspects are concerned. So there is no possibility for a bias, because the items to be treated statistically are unknown at the moment of selecting the sample areas. This is in contrast to the case where the selection is done in the field. So the sampling stage follows a complete photo-interpretation stage which has culminated in a complete map of the area. Classification can be carried out after the sampling and then a re-interpretation is done of the photos, now with more knowledge of the field and better possibilities to recognize communities on not too small a scale or even single species via all kinds of indirect associative reasonings based on ecological knowledge. From the above described procedure it is clear that for such type of work a method using pre-prepared spectral signature combinations are less suitable. This would require prior knowledge of what has to be recorded. In the above (normal) case we do not know beforehand what exists before we do the sampling. The main use of the remote sensing means has been finished by then.

Stereoscopy can not be missed because we first of all need to determine the main macro-structural formation (forest, shrubland, heat, etc., etc.). On a stereo image of a good photograph of scales larger than 100,000 this can be easily done. Just as important is the possibility to recognize those important landform and relief types, that are used to coincide with floristic and micro-structural vegetation differences (that may not be seen themselves on the photo) like river terraces, different inclinations and aspects of slopes etc.

Using aerial photographs without

stereoscopic vision is wasting at least half of the information contained in it. The required landscape ecological interest and knowledge however, should be present, otherwise this information cannot be used.
A sufficient number of stratified sampling (random within the homogene strata of course) guarantees an objective result of the complex process of associative thinking, that is called interpretation, recognition, and identification.
Training people for photo-interpretation for ecology is therefore a combination of giving:

a. information in the field of remote sensing techniques and cartography including the qualitative and quantitative aspects of the obtained images, the limits of accuracy etc. and

b. teaching people landscape ecology as a holistic (final) means to understand the details starting from the whole. That same totality, which we wanted to be able to oversee at the moment when we went up in a balloon for the first time, and nowadays in jet aircrafts and satellites, to produce remote sensing images.

During the presentation of the paper, examples are given of results of photo-interpretation with ecological interest in a Savanne area in Africa and a brackish water estuarium in the Netherlands where various film filter combinations have been used.

INTERPRETATION OF TEMPORAL DATA FROM ERTS-1, DEMONSTRATING THE BROWN AND GREEN WAVE *

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Summary

Temporal data from ERTS-1, provided in digital tape form and supplied by NASA, was analyzed for 14 pre-selected mixed decidious forest sites in eastern and central United States. Locations varied from 30 to 46° N latitude and 68 to 100° W longitude. Data was analyzed by the Laboratory for Application of Remote Snesing, Purdue University, and demonstrated the capability of detecting leaf color changes, senescence, and regrowth in a cyclic pattern.

Introduction

This study, a part of the ERTS-1 program, was implemented as an experimental project to analyze scanner data of forest canopy sites in the Appalachian and mid-lands of the United States from Orono, Main to College Station, Texas. Scanner tape data in four wavelength bands [band 4) .5-.6 μm; band 5) .6-.7 μm; band 6) .7-.8 μm; band 7) .8-1.1 μm], were specified for areas 40 x 40 km around each site for the 14 locations for each 18 day pass. Usable cloud free data, from the tapes provided, was reformated and analyzed by the Laboratory for Applications of Remote Sensing (LARS) at Purdue University using the LARSYS system (4).

Data were analyzed to evaluate temporal changes which, if possible, would demonstrate canopy changes on site locations, describing the autumn brown and spring green wave of deciduous forest areas from 30 to 46° N latitude. Research by previous workers using aircraft overflights (1, 2, 3) have been successful in identifying differences in crops, timber, water, soil and land uses. These efforts have been confined to altitudes of 10 to 20 km. The ERTS-1 passes each 18 days were at 900 km scanning a path 144 km wide with an overlap of about 20% on successive days. From August 1972 to November 1973, a total of 26 passes were made. Twelve of the sites were also scanned the second day following the main pass making possible, with optimum conditions, 628 site evaluations. A total of 229 images were received for the 14 sites from NASA and 110 of these were satisfactory for detailed evaluation by LARS.

Results and discussion

This paper will be confined to comparisons between Lafayette, Indiana (40° N) and two other sites - Burlington, Vermont (46° N) and College Station, Texas (30° N). The latter locations represent extremes in latitude and are also sites providing the most usable data.

LARSYS Analysis of the Lafayette site (Table 1) illustrates changes in reflectance over time. For band 7 (.8-1.1 μm) relative spectral response values were at a maximum in early September 1972 when the site, a 22 hectare area, was in full leaf. As autumn progressed and leaf drop occurred these values decreased, then increased again with onset of spring regrowth. Gaps in data for Lafayette, caused by cloud cover on some dates, are supplemented with data from Burlington and College Station in Figure 1, and demonstrates the capacity of detecting the brown and green wave over broad latitudes. Differences in relative spectral response on successive dates of the same pass can be observed in Figure 1. For the Lafayette area this can be noted for September 30 and October 1, 1972, May 4 and 5, 1973, and July 15 and 16, 1973. These differences are thought to be due to varying amounts of water vapor and particulate matter in the atmosphere and, in some instances, to light diffusion from cumulus clouds near the site location. The effect of these parameters on day-to-day observations by ERTS-1 will be evaluated in a future publication.

By use of a band ratio parameter (band 7-5/band 7+5), differences in crop canopy over time are more apparent (Figure 2). This technique, utilizing the differences in reflectance between the visible (absorbed) and infrared (reflected) bands, provides a better indication of changes in canopy color and density. Band ratio parameter values in this study range from +.4 for the green wave to -.4 at senescence. At the Texas site less variation was observed than at the other sites due to lower canopy density and some species changes in Quercus. A low value (-.8) for one date in Texas in late May is not understood.

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Table 1. Temporal data for Lafayette, Indiana 9/30/72 - 11/18/73.

Location	Dates	Solar Elev. (0)	Relative Spectral Response Values (ERTS MSS Bands 4-7)								BRP **	Note ***	Weather Condition	Canopy Observation
			Normalized Mean*				Standard Deviation							
			4	5	6	7	4	5	6	7				
Indiana Lafayette	9/30/72	41.4	21.4	12.6	38.5	25.4	1.3	1.4	4.7	3.1	.336	F	clear	100% leaf-green
	10/1/72	41.1	20.9	12.5	33.3	20.5	0.8	0.9	2.0	1.6	.242	VG	cumulus East of sites	100% leaf-green
	10/19/72	35.4	26.4	25.7	28.5	15.6	1.6	2.4	2.7	1.6	-.245	G	clear	20% fall coloration
	11/24/72	25.4	28.4	21.6	23.4	12.7	1.2	1.3	2.4	1.8	-.259	G	clear	complete leaf drop
	1/16/73	22.8	30.8	23.7	23.9	11.5	0.9	1.2	1.7	1.2	-.347	E	ice or snow along river	dormancy
	2/4/73	27.1	28.3	22.1	22.8	11.4	1.2	1.2	2.2	1.3	-.318	E	haze near sites	dormancy
	5/4/73	57.0	23.8	17.1	38.7	22.5	1.3	2.1	3.0	2.1	.137	G	clear	80% leaf
	5/5/73	57.2	30.7	24.7	41.8	23.0	1.6	2.2	2.7	2.0	-.035	VG	haze near sites	80% leaf
	6/9/73	61.7	23.5	14.8	46.5	27.4	1.6	2.0	3.0	2.2	.297	F	clear	100% leaf-green
	7/15/73	59.6	19.3	11.8	42.3	27.6	1.6	1.8	2.0	2.0	.399	VG	scattered cumulus	100% leaf-green
	7/16/73	59.5	22.4	13.5	49.3	31.5	0.9	1.0	2.0	1.7	.400	G	clear	100% leaf-green
	8/21/73	52.8	19.0	11.3	40.7	26.9	1.5	1.4	1.9	1.2	.400	VG	clear	100% leaf-green
	9/7/73	48.3	20.3	12.4	40.2	25.4	1.7	1.9	2.1	1.7	.342	G	clear	5% leaf-brown
	10/14/73	36.0	20.7	12.8	33.3	20.4	0.9	1.3	2.5	1.9	.225	VG	clear	10% leaf-brown
	11/18/73	26.0	35.4	28.4	31.8	15.9	1.0	1.0	1.5	1.2	-.284	E	cumulus near sites	95% leaf drop

* Value corrected to 45° solar elevation angle

** Band ratio parameter - $\frac{7-5}{7+5}$

*** Quality of statistical output. E - Excellent; VG - Very Good; G - Good; F - Fair; P - Poor

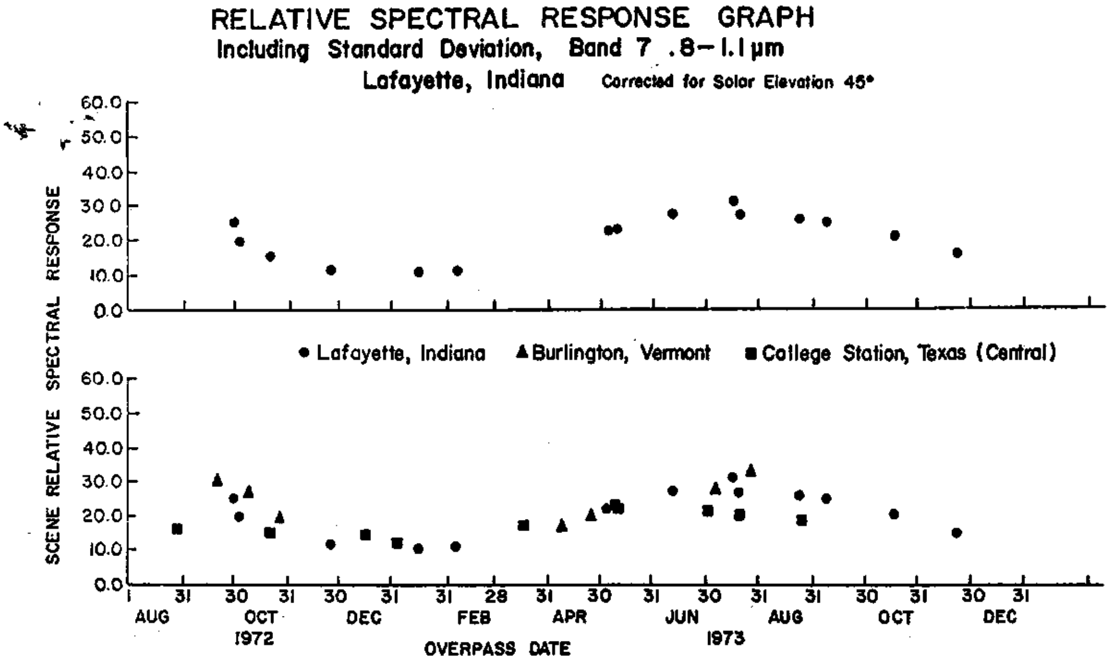

Figure 1. Relative spectral response at Lafayette, Indiana in comparison with Burlington, Vermont, and College Station, Texas.

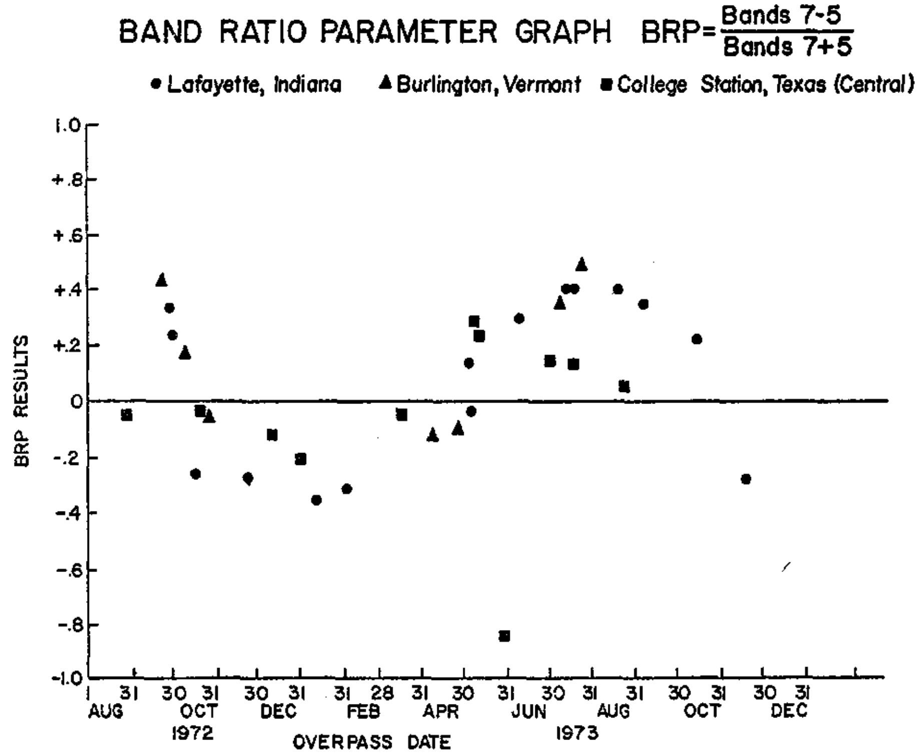

Figure 2. Band Ratio Parameters between August 1972 and November 1973 for Lafayette, Indiana, Burlington, Vermont, and College Station, Texas.

Conclusion

Temporal data from ERTS-1 received during a calendar year can demonstrate the brown and green wave progression. The cyclic pattern among sites at different latitudes, although varying slightly, do show the same general trends.

Cloud cover frequently prevents obtaining needed data in phenology studies where a continuous sequence of information is desirable, or where data over a broad latitude for a specific period is needed. Eighteen day passes are too infrequent for effective evaluations under these conditions. Also, the effect of atmospheric changes on day to day observations needs further evaluation.

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MULTI-LEVEL ECOLOGICAL APPROACH USING REMOTE SENSING TECHNIQUES

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1. The phyto-ecological approach

Most of the active ecological variables, including those which result from the historic and present action of man on the environment, come to be integrated in one way or another by the vegetation. It is thus proposed to bring all the efforts of remote identification to bear on the vegetation-targets, seeking however to bring out the most significant correlations between the various characters of these targets and their environment.

The synthetical nature of remote-sensing documents, and the global analysis of the biosphere that they permit, quite justify their utilization when studying the ecological status of a given area. The requirements and the constraints of the use of remote sensing techniques are then defined in terms of difficulties lying in :

- the heterogeneity of the vegetation cover
- the masking effect of some species
- the fact that the variables which may be studied at different levels of ecological perception are not of the same kind and have not the same activity according to the choosen level (Long, 1969). So, this is the combination "level of ecological perception and studied variable or theme" which determines the choice of an optimal remote-sensing data acquisition system (Long et al., 1971; Long, 1974).

2. Levels of ecological perception and optimal choice of remote sensing documents

a. Level of perception of ecological regions

The ecological regions, which result from the integration of the main variables of general climate, geomorphology and vegetation (broad land-use units), can be delimited on small scale documents as the ERTS images. For example, concerning the Languedoc-Roussillon (French Mediterranean area), the confrontation of the map of the ecological regions previously established (Le Floc'h et al., 1973), with the ERTS-MSS images has shown that satellite-type imagery is powerful for the delineation of significant ecological areas (Caballé, 1973, Caballé et al., 1974).

b. Level of perception of groups of ecological sectors

An approach at a scale of about 1/200 000 leads to the differenciation of elements of ecological regions, or of groups of ecological sectors; this is particularly easy with photographs obtained from stratospheric balloons (Rimbault in Long, 1974).

c. Level of perception of ecological sectors

The main variables perceptible at this level are :

- plant formations
- topographic positions
- types of superficial substrates

The perception of these variables and the identification of the dominant species are possible using remote sensing documents at a scale from 1/50 000 to 1/25 000; these documents are the basic elements of most ecological studies either toward research or management purposes.

d. Level of perception of ecological stations

The documents at a large scale (1/10 000 and more), particularly photographic ones, are well suited for detailed analysis of elementary environmental units. The study of microtopographic and edaphic variables, the identification of plant species and of their spatial structure, constitute the highest level of intervention of that kind of documents.

3. Contribution of photographic techniques in ecological study

The contribution of photographic data in the solution of an ecological problem will be decisive if the parameters of the photographic mission, the nature of emulsions, the time of the flight are choosen in accordance with the studied variable or theme. For example, the identification of different kind of vine-plants, from the observation of the foliage colours in autumn, require an optimisation of data acquisition techniques, which is valid for a given ecological region (Rimbault, 1973). The use of aerial photographs is sometimes limited for practical reasons (difficulties and cost of low altitude flights, high number of photographs ...), but the main constraints are lying in the characteristics of the film response (sensitivity domain, saturation effect, variability through the photographed field and from one mission to another), which make difficult the inference of a biological parameter (green biomass for example) from the only criterion of film density (Rimbault, 1974).

Consequently, although a direct processing of the structural information of a photograph is possible, especially with optical means (Boissard, 1973), the implementation of automatic recognition systems is more convenient using multispectral data.

4. Contribution of multispectral scanner sensing techniques

Multispectral scanners are a mean of obtaining a set of data consisting generally in several hundreds of thousands resolution elements, each element being associated with the values obtained after digitization of the analog signals which correspond to the different channels.

About the utilisation of these data, one must distinguish two kinds of objectives :

- short-term objective : utilisation of data as input into automatic classification systems and comparison of the results with those obtained from conventional methods.
- long-term objective : explanation of sensed reflectance differences in function of biophysical parameters of environmental units. In this purpose, the study of the interception of solar radiations by different types of vegetation (Méthy, 1974) and the implementation of reflectance models of vegetation canopies (Suits, 1972) are of a great importance.

We shall only develop here the problems related to the first objective : classification of data and interpretation of results.

a. Multispectral data classification

The "automatic" data classification consists in the elaboration of a particular taxonomic system :

- definition of a typology of criteria (the criteria are the different sensed levels of energy in the various channels)
- diagnosis of individuals (the individuals are the resolution elements)

The diagnosis procedure is generally not practicable in the original measurement space: a first step (feature extraction) is necessary and usually consists in a dimension reduction.

Concerning the classification techniques, we shall not compare here the intrinsic merits of supervised methods (Swain & Lindenlaub, 1972) versus non-supervised ones (Nagy et al., 1971; Lacaze et al., 1974), but we have to emphasize the problem of evaluating the efficiency of these different methods.

b. Efficiency criteria of classification methods

The optimisation of processing methods resolves to a choice between mathematical techniques according to a pragmatic and global criterion : the amount of good recognition of terrain classes, previously defined with another taxonomic system. The disparities between results often originate in the location of reference areas (training and/or test areas), rather than accuracy differences between mathematical algorithms.

In fact the hypothesis that intra-class variances of spectral responses are less than inter-class variances can be confirmed only when representative samples of object classes are provided. This requires the knowledge of the variation of the parameters which are influencing the spectral responses of individuals; it is thus convenient to implement a stratified sampling scheme for the location of reference areas (Curtis, 1974), which is quite comparable with the sampling strategy used in many plant ecology studies.

c. Conclusions

There are few results concerning automatic classification of native vegetation. If the broad types of vegetation communities are well discriminated (Driscoll & Francis, 1971), it is however necessary to carry out a great number of comparisons between automatic pattern recognition results and results of ecological studies and eco-physiological measurements, in order to understand the relationships between the "phenons" issued from remote analysis and the taxonomic units described by the ecologists.

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WHEAT STEM RUST WARNING USING SATELLITE IMAGERY*

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Abstract

In the light of present findings, giving a yes or no answer for the appearance of stem rust about 20-25 days earlier to their appearance in the field seems possible.

Wheat, one of our major cereal crops, many times results in complete failure due to stem rust of wheat (*Puccinia graminis* Pers. tritici Eriks. & Henn.), and hence development of a warning system is warranted. Hogg *et al*. (3) felt that a series of spore traps, trajectory studies, and even recognition of synoptic situations could give a good overview of spore transport. Early detection of primary inoculum by analysis of rainfall (6) could be useful in the development of forecasts.

The primary inoculum of stem rust, in India comes down with rain (4) Nagarajan (4) confirmed the Nilgiri hills in south India as the primary foci of stem rust. He also observed precipitation during November in Central India to be vital for the stem rust appearance. Backward trajectories drawn for the rain-borne inoculum for different heights, in most of the cases moved south and ended close to the Nilgiris. A study of series of trajectories drawn, showed that for an effective infection to occur, uredospores should be disseminated and deposited within 120 hours after take-off. It also showed that these uredospores are transported around 3,300 meters height (4). A study of satellite television cloud photographs (STCP) taken by weather satellite ESSA-9 brought out the close similarity between the path of the visible clouds and that of the trajectories drawn for the rainlborne inoculum for 700 mb level (4, 5).

The dissemination and deposition of wheat stem rust uredospores that are transported around 700 mb height were always associated with a particular type of upper air conditions and these were formulated as the "Indian stem rust rules" (4). Using these established guide lines attempts were made to give warnings on the appearance of stem rust.

The 700 mb height trajectory drawn for the rain-borne inoculum of Powerkeda (October 25, 1972) ended close to the Nilgiris and took 80 hours. The synoptic weather charts for 700 mb showed a tropical cyclone which interacted with the anticyclonic weather in a way satisfying the Indian stem rust rule. The STCP of October 24, 1972 showed a mature tropical cyclone over Somaliland, later resulting in cloudy weather over Powerkeda for 2 days. The STCP not only showed that the inoculum had moved from Nilgiris but also brought out the cloudy and rainy weather that prevailed over Powerkeda. A study of crop phenology and ground level climatology indicated that the infection would have occurred. So a survey was conducted on November 18, 1972. A 20% severe stem rust infection was reported from the same place on December 27, 1972. Similarly successful forecasts were made during December 9, 1972 for Jabalpur; January 1973 for Pusa in Bihar and during November 1973 for Maharastra state.

By a sanitation ratio of 100 (i.e., 99% of the initial inoculum destroyed) disease at maturity of the wheat falls from 50 to 1% severity (7). This means that for effective control the disease needs to be spotted at a very early stage. Hence, the usual warning models (1, 2) may not be of much use. The present attempt (4) makes forcasting of the disease possible long before it develops as an epidemic, and even before it becomes visible to the eye.

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Automatic Decision Classification Of Ecosystems And Their Pattern Recognition In Upwelling Regions

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Summary

Multispectral analysis of data obtained remotely from high altitudes over the ocean can be used to classify patterns which are caused by plankton and/or sediments. Presence of plankton patterns can be determined with interactive analysis of data collected by ERTS-1. Examples are given for the application of image annotation after using an automatic decision classification for different species of particulate material in the upwelling near Cape Timerif, Africa.

Introduction

Warnecke et al. (1971) showed the application of remotely sensed infrared data with the Nimbus II satellite in oceanography. Düing and Szekielda (1971), **Szekielda** (1972) demonstrated that oceanographic case studies can be done with data monitored from an orbiting platform. Infrared data recorded at high altitudes were commonly used for regions with high horizontal temperature gradients like the Gulf Stream (Rao et al., 1971 Strong and Derucke, 1973), the loop current in the Gulf of Mexico (Maul, 1973) or for large scale temperature fluctuations (Szekielda, et al., 1972). The standard deviation between single observation on ships and from satellite radiometers is still around 1.3C. (Szekielda, 1973).

Multi-channel approaches were used by Shenk and Salomonson (1972) to determine sea surface temperature from space.

The application of remotely sensed data from space in the visible part of the electromagnetic spectrum were limited to photographic material with a broad film response.

The multispectral scanner on ERTS-1 allowed for the first time the computer processing of selected narrow bands in the visible and in the solar reflected near infrared. Most of the oceanographic data were photo interpreted. Although a multi-channel system is available, no oceanographic approach was undertaken yet to use the information obtained in the four channels over water. The purpose of this paper is to demonstrate that a multispectral analysis of data recorded over the ocean gives an insight into the ecosystem of near coastal upwelling areas.

Results and Discussion

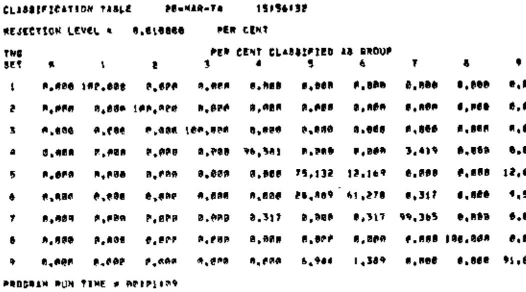
As part of the CINECA program, a NASA sponsored program, acquired data with the MSS on ERTS-1 along the NW coast of Africa. Data was analyzed only in regions where no river discharge appeared. Since the north west Coast of Africa shows strong upwelling throughout the whole year, natural plankton populations are also present throughout the whole year. From recordings in the infrared with the High Resolution Infrared Radiometer (HRIR) and the MSS on ERTS-1, we recognized a structured distribution in plankton and temperature.

Detailed analysis was done on patterns which were recognized in the ERTS-1 data, mainly in channel four. The geometric and spectral resolution of ERTS-MSS-data favored an interactive data analysis with a subsequent automatic decision classification. Pattern recognition and signature research was undertaken by using digitized radiance levels over the test site. Channels four and five were used to classify the recognition sites by image annotation record in color.

Spacial pixels which were qualitatively interpreted to be significantly different from each other, were used as training sets. Each of them is composed of a set of radiance measurements from each of the four bands in the MSS.

The eigenvectors and the standard deviation around their means were used for the decision processing mode. Hereby, the spectral recognition characteristics arising from any one of the oceanic pixels, as shown in Table I, were compared for each spatial resolution element.

Table 1. Classification of nine training sets.



```
CLASSIFICATION TABLE      20-MAR-74      15:56:32

REJECTION LEVEL =   0.010000      PER CENT

TNG                                 PER CENT CLASSIFIED AS GROUP
SET     0        1        2        3        4        5        6        7        8        9

 1    0,000  100,000    0,000    0,000    0,000    0,000    0,000    0,000    0,000    0,000
 2    0,000    0,000  100,000    0,000    0,000    0,000    0,000    0,000    0,000    0,000
 3    0,000    0,000    0,000  100,000    0,000    0,000    0,000    0,000    0,000    0,000
 4    0,000    0,000    0,000    0,000   96,581    0,000    0,000    3,419    0,000    0,000
 5    0,000    0,000    0,000    0,000    0,000   75,132   12,169    0,000    0,000   12,698
 6    0,000    0,000    0,000    0,000    0,000   28,469   61,278    0,317    0,000    9,924
 7    0,000    0,000    0,000    0,000    0,317    0,000    0,317   99,365    0,000    0,000
 8    0,000    0,000    0,000    0,000    0,000    0,000    0,000    0,000  100,000    0,000
 9    0,000    0,000    0,000    0,000    0,000    6,964    1,389    0,000    0,000   91,647

PROGRAM RUN TIME = 00:01:09
```

Final color annotation after the recognition judgement was displayed in the transparency mode.

From the data storage and production processing of ERTS data it was evident that with the help of five recognition sites, the areas which were covered by coastal water (1), plankton poor water (5 and 6) plankton rich water (7) high concentration of plankton (9) and open ocean water (8) could be identified (See Table 2).

Table 2. Area coverage of categories classified in Table I.

```
ERTS PROCESSOR      21-MAR-74      18:27:07

ERTS SCENE ID - 1340-11010
DATE OF SCENE - 29JUN73
CENTER OF SCENE - N20-17/W016-25
SUN COORDINATES - EL60 DEGREES
                  AZ078 DEGREES
SPACECRAFT HEADING -  189 DEGREES
TAPE NUMBER - 2
STARTING SCAN LINE =     1
ENDING SCAN LINE =   2340

   CATEGORY               PERCENT        ACRES        SQ. KM.
                          OF TOTAL

UNCLASSIFIED               27.07      573587.56      2321.22

CATEGORY 1                  4.46       94409.61       382.06

CATEGORY 2                  2.20       46511.15       188.22

CATEGORY 3                 11.50      243565.89       985.67

CATEGORY 4                  5.63      119269.36       482.67

CATEGORY 5                  8.74      185174.87       749.37

CATEGORY 6                 20.67      437932.09      1772.25

CATEGORY 7                  9.78      207187.34       838.46

CATEGORY8                   3.45       73130.47       295.95

CATEGORY 9                  6.52      138090.25       558.83
                           -----     ----------    ----------

    TOTALS                100.00     2118858.75      8574.70

PROGRAM RUN TIME = 00:35:25
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Major interaction between the signatures found in the water types are only recognized between two plankton poor water masses (5 and 6). In near coastal areas it is apparent that the different load in sediments also creates a different environment.

From the recognition judgement it was concluded that pure plankton populations are more abundant offshore and more closely correlated to the upwelling. This program

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REMOTE SENSING APPLIED TO THE GRASSLAND BIOME[1]

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Summary

From the study of panchromatic, color and infrared aerial photographs 13 separate vegetation types were distinguished on the Pawnee Site. Some were difficult to recognize visually on the ground because they were distinguished due to quantitative measures to a greater extent than they were to qualitative aspects.

The weighted average LAI of Bouteloua gracilis was found to be highest in the light use pasture and lowest in the heavy use pasture while that of Buchloe dactyloides was found to be the opposite. Grazing had a lowering effect on LAI as did seasonal advancement during which growing conditions, especially availability of moisture, became less favorable.

Upland sites offered more favorable conditions for growth of Bouteloua gracilis than did lowland sites. Consequently Leaf Area Index was greater for this species on the upland sites. The opposite was true for Buchloe dactyloides except that ridges also supported an abundant amount of this grass. Soil type was evidently the major deciding factor in vegetation type. The influences of soil and topography intermingled, however, to cause the large scale pattern of vegetation types found on the Pawnee Site. Spectral variation was readily visible for delineation of vegetation types with significant LAI differences. Inadequate processing control limited the derivation of LAI values from the photographic prints.

Introduction

This study was conducted on the International Biological Program (IBP) Grassland Biome location, the Pawnee Site in northeastern Colorado, USA. Significant phytosociological variation exists on the site resulting from the influences of soil, moisture, relief, and grazing treatment on the vegetation. The study was initiated to develop, for the spatial modeling effort of the Grassland Biome program, a detailed vegetation map with definitive type units no larger than 0.1 hectare (10 m x 10m). To this end, three forms of remote sensing stereoscopic imagery (panchromatic, color, and infrared photographs at a scale of approximately 1:5800) were utilized for first order delineations. All ground truth definition was based on leaf area indices derived from point contact data.

Review of Literature

Vegetation interpretation from remote sense imagery is a powerful tool when coordinated with ground truth data (Driscoll et al., 1974a). Aerial photography with panchromatic film has been widely utilized for rangeland inventory and classification. Remote sense imagery from color, infrared, near infrared, thermal infrared, multispectral and radar imagery provide an additional great variety of detailed information (Johnson and Atwood, 1970; Yost and Wenderoth, 1969).

Skilled interpreters can define very minute differences exhibited on various forms of imagery. Most recent developments with ERTS-1 imagery and computer tape output have shown that native plant communities of central Colorado USA, including montane grasslands, coniferous forests and deciduous forests were amenable to classification by visual interpretation and machine processing (Driscoll et al., 1974b). Spectral character was inadequate for accurate delineations of habitat or series level classification. Rouse et al. (1973) have shown that phenological progression could be monitored from ERTS-1 data of Great Plains grasslands from south Texas to North Dakota. Radiance values of some spectral bands were shown to be correlated with aboveground green biomass. ERTS-1 imagery interpretation and density contour mapping in the Laramie Basin, Wyoming, provided considerable definition of vegetative biomass and species composition estimation (Evans and Redfern, 1973). Much sophistication of interpretive concepts appeared necessary in all reports before detailed and accurate data would be available from ERTS-1 imagery as well as from Skylab photographs. In contrast to the distant character of the ERTS-1 imagery Tucker and Miller (1974) in Colorado have shown that ground based measures of composite canopy spectroreflectance can be utilized to determine biomass, chlorophyll, leaf water and underlying soil spectra.

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Knight (1973) described the dynamics and major factors affecting average daily herbage productivity on the Pawnee Site. He indicated that leaf area index, associated with other data and additional research, had some potential for predicting productivity and aboveground biomass.

Methods

To simplify sampling procedures, the study area of 405 ha was separated into 12 sampling units related to management and forage utilization criteria. Each sampling unit was delineated into vegetative "sub-types" by steroscopic inspection of the panchromatic, color, and infrared aerial photographs. Mirror and lens stereoscopes were employed in the interpretive work. Except for a few minor changes in sub-type delineations which were made during field sampling, final designations of type differences were established through use of this detailed investigation. The most important factors utilized in determining sub-types boundaries on the imagery were topographic location, texture, tone, and pattern. From these procedures a total of 66 sub-types were delineated on the entire study area.

Each sub-type delineated was defined in terms of Leaf Area Index (LAI). The point frame settings were distributed in each sub-type using restricted random and systematic selection procedures. Ten points were read at each setting before moving to a new location. The number of points required to adequately sample each sub-type varied from 400 to 600 depending on the denseness of the vegetation.

The weighted average LAI of Bouteloua gracilis, Buchloe dactyloides and the total of all species for each of the 12 sampling units and the percent of each sub-type within each sampling unit was determined. Each of these percentages were then multiplied by the respective LAI values for each sub-type and totaled for each sampling unit.

Preliminary analysis of the point data for each vegetation sub-type determined through photo inspection was conducted by computer. An H-Group program was used in this analysis (Govoni et al., 1970). From the species encountered during field sampling, the 19 which seemed to be most influential in the vegetation configuration of the area were selected for H-Group analysis. An F test was conducted on the groupings received from the H-Group program. This test was designed to determine how many of the groups were significantly dissimilar to warrant consideration of the groups as different types.

Results

The panchromatic black and white photography used in this study was lacking in some detail but this was compensated for by use of the color and infrared prints. Through differences in texture and tone, areas on the ground as small as one-half meter in diameter were noticeable on all three photo types. These forms of imagery provided an efficient method for delineation of boundaries between areas of significant spectral variation.

Bouteloua gracilis and Buchloe dactyloides were present over almost all of the study area. This presented a problem in determination of vegetation "type" definition on the Pawnee Site. Three "types" were easily recognized. These were Bouteloua gracilis dominant, Buchloe dactyloides dominant, and a mixture of the two species. Many of the sub-type areas which were delineated earlier by observable variation in the photo imagery were distinguishable as a result only of varying ground cover percentages of the two dominant grasses rather than on totally distinct differences in species composition. In a few areas ground inspection did not reveal the distinctions which had been noticeable during photo interpretation.

The 66 sub-types which were delineated were presented in the form of a vegetation map of the area. The H-Group analysis of LAI data was utilized in combination with the photo inspection work and a general knowledge of the area to combine these 66 sub-types into 13 significant vegetation types. Two of the 13 types were identified without the H-Group analysis. Because of soil and other microsite characteristics the two major grasses did not occur.

The remaining 11 types were derived from aerial photo inspection, extensive ground work, and the H-Group analysis. In conjunction with photo and field inspection, a significant F value was computed for 11 groups from the H-Group analysis, meaning that these 11 types were sufficiently dissimilar to warrant consideration as separate types. They were numbered in descending order solely on the basis of average LAI for Bouteloua gracilis, with type 1 having the highest value and type 11 the lowest. This order was initiated in an effort to reveal any existing relationships of Bouteloua gracilis LAI to that of Buchloe dactyloides and/or TOTAL LAI.

Soil type, topography, and past grazing use all were intricately involved in the determination of the vegetation type. Soil type probably had a more pronounced effect on vegetation than did any other single factor. This effect, however, was one of the most difficult to recognize due to the similarity in soil types of this region. Of the 11 soil types described for the area four were classified as some type of sandy loam and four of them as loams, leaving only three not described as a loam of some sort.

The effect which topography had on the vegetation was more apparent than that of soil type. Though there was really not much relief over the entire study area, what little there was had a definite effect on the quality and quantity of the vegetation. Those types which occurred on the level to gently sloping upland areas were definitely dominated by Bouteloua gracilis with only small patches of Buchloe dactyloides. All of these types had relief features similar to those described above. Each of these types also had similar associated species and variation in types was due almost entirely to density of vegetation.

When a type lay in a low drainage area, Buchloe dactyloides was the dominant species. There were some exceptions to this which have been pointed out. Here again the differences in types were intricately related in each of the lowland types.

Interpretation of livestock grazing influence in this study required evaluation of the long-term 30-year period of light, medium and heavy use continuously allocated to the same pasture units as well as the grazing impact of use which occurred throughout the sampling season. The current grazing impact was determined to be of minimal effect.

The weighted average LAI of Bouteloua gracilis was highest in the light use pasture and lowest in the heavy use pasture while that of Buchloe dactyloides was found to be the opposite. The total average LAI was nearly equal in all three of the grazing treatment pastures (light, moderate, and heavy use). Since each of the three grazing treatment pastures had been under the same intensity of grazing for more than thirty years it was expected that a stable condition existed in each of them. When the long term heavy grazing and consequent trampling of vegetation was taken into account it seemed reasonable to expect that plant vigor of Bouteloua gracilis would have been adversely affected, thus accounting for the lower weighted average LAI of this grass in the heavy use pasture. The LAI for Buchloe dactyloides was greater in the heavy use pasture than in either of the light or moderate use areas. This, together with a possible increase of LAI for some of the minor species apparently offset the decrease of Bouteloua gracilis since the weighted average LAI for all species was nearly equal in each of the three treatment pastures.

Sub-types delineated from steroscopic inspection of photographs were real and exhibited LAI differences which were utilized to classify and group into types with different amounts of Bouteloua. A limiting feature for predicting productivity and aboveground biomass arose upon comparison of sub-types which occurred in different photographic prints but which had been combined into a single type because of LAI data similarity. Inadequate processing control in the photography and print development resulted in spectral differences greater among sub-type units than was expected between types. Given adequate ground truth data and rigid control of remote sense information it seems likely that LAI could be defined from interpretation of remote sense data.

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HOW CAN ECOLOGY PREPARE ITSELF FOR REMOTE SENSING

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Summary

Three possible approaches of an ecologist towards remote sensing and aero-space surveyance are discussed by a physicist: Realistic estimation of the RS situation; Systematic evaluation of RS literature and experiments, especially regarding six resolution specifications; Imaginative forecasting of a RS scenario for the eighties.

Introduction

Ecological interpretation of remote sensing data - the theme of the special symposium - is the final action which brings the ecologist in direct touch with the modern and still unconventional, if not utopian, aerospace survey techniques. Remote Sensing (RS) - strictly speaking "the data acquisition at a distance" - is more remote from him, and the ecologist will hardly get involved in this primary action.

There are two other domains in which scientists and engineers are engaged in RS: design and development of remote sensing equipment and of processing techniques, routines and instruments, and determination of essential physical and chemical parameters re. the process of "interaction of radiation and matter". In the first activity, ecologists act occasionally as consultants; in the latter, ecologists should be in the team if vegetation is subject of study.

In the interpretation of the data, and especially in computerized analysis of the tapes, the ecologist has to play an essential role too. It is hoped that this symposium stimulates the professional occupation of these roles.

How can the ecologist prepare himself for remote sensing ? Three aspects of an ecologist's attitude towards RS and its application will be elaborated on in the next paragraphs:

- Be realistic and keep contact with the general situation in remote sensing R & D;
- Analyse what others have done and documented in terms of operational spec's;
- Design your own RS scenario and plans for the next 5 to 7 years and fit your activities into this futurology framework.

Estimation of a Remote Sensing situation

Remote sensing techniques have mainly been developed by or for the military, thus under classification conditions, within a limited period, with almost unlimited funding, and for non-civilian purposes. Even when the space research groups took over the implementation and application research, the development could hardly be called balanced (viz. competing experiments ERTS and EREP/SKYLAB). In addition education is lagging behind even more, due to the high priority of new and large experiments, which aim too often for a shortterm success.

Ecologists need not make all the mistakes made by others, as they have at their disposal many experimental results, new equipment, theories already tested and abundant literature.

A realistic attitude towards the RS circus might be based upon the analysis of the following three problem-areas and the subsequent synthesis.

a: Define the survey tasks which justify economically the application of costly RS techniques, including data handling and analysis, which usually are 10 times more expensive than acquisition (and may surmount it by a factor 100 in the R & D phase). In other words: Is it likely that somebody is willing to pay for the identification of vegetation type x versus any other type in the area, with a success score of $(90 + \varepsilon)$ % ? It certainly is practical to analyse the possible use of results by the decision makers if such survey data would be available today, and to estimate costs & profits. For example: "Should one attempt to identify strawberries, or would it not matter too much if this crop would often be classified as potatoes ?" The same applies to diseases, humidity stress, crop yield prediction, etc.

b: Analyse which characteristic properties of the object versus background might be used to exectue the job; which of these features are easily observable and measurable from a remote (moving) platform. Here it pays to know the objects, to have a feeling for the behavior of the leaves and the canopy under influence of climate and weather conditions, to know changes in colour and structure due to mineral deficiencies, to have an expectation of measurable quantities which vary with season, type of disease, soil salinity, etc.

Recent ESRO (now ESA) reports review many of these properties in an accessible manner (ESRO, 1972/73), and books with educational value gradually become available (Barrett & Curtis, 1974). The most concise advise is: "Study the interaction of radiation and matter"; a more pragmatic tip: "Observe your object world through the eyes of the RS sensor". For example, imagine how a low altitude side looking radar with polarisation would 'see' the testfields, how MSS from satellite altitude would sense your plant canopy, how temperature differences due to moisture stress in vegetation could be determined by an IR scanner.

c: Inventorise the RS techniques available in the region, list the sensors which will become available in the near future, and carefully check the conditions under which this equipment has to work in order to be economical.

Side looking radar has advantages for large area surveying, but give scales up to 1:100,000 or at best 1:50,000. A country like Brasil does not yet consider to use SLAR regularly.

Thermography with Infra Red Line Scanners on the contrary seems a large-scale, small area technique, but up to now there are hardly commercially interesting applications. When wind speed is over 4m/s at vegetation level, or when objects are frequently soaked with water due to rain, dew, or fog, this technique is not likely to give satisfactory results.

Multi Spectral Sensing is very interesting for ecological surveying, as it records vegetation in the same 'light' which plants need for the photosynthesis, and thus registers deviations in pigmentation, chlorophyl content of the leaves, water content, etc. However, MSS is at this moment not operational, although it is available for research flights in at least two European and two American countries. With the price of an n-band scanner being almost the n-fold of the price (30 k$) of a professional aerial camera, with an expected useful life of 3 to 5 years, (camera 15y), with the same or even less "flying days" in a season, and with processing and data analysis cost being one or two orders of magnitude higher than interpretation of aerial photographs, one should not expect a rapid introduction of MSS into the survey market.

Similar remarks can be made for other RS techniques. The situation is engraved by the relatively weak financial position of the small survey companies, which do not make much profit with classical aerial photography, and certainly lack the funds to purchase exoctic equipment for a few test flights.

The study of these three problem areas - Definiton of the survey task; Analysis of characteristic features of the objects; Inventory of available RS techniques - gives a first idea about possibilities for realistic experiments. The order in which these study areas are presented here is unusual. It may be the easy way to carry out an experiment with an accidentally available RS technique, but it is at best only useful for a Ph.D. thesis.

For ecologists, the realistic approach has still to be exploited. When starting 'task-and-object-centered', one will often find that an available RS system forces one to reformulate the task and the methods. This re-thinking the environmental problems under the pressure of possible 'outdoors physical measurement at a distance' may well be the biggest short term profit of remote sensing.

Evaluation of literature and experiments

Research workers write and read scientific papers, but it is said that the first activity is more intense than the latter. Indeed, the average scholar will admit that papers from (unknown) colleagues are seldomly studied in great detail; often one merely scans through the abstract and the conclusions. Similarly spending some time in filtering the bulk of the RS publications and reports which might be of significance to ecology, one might check the following points:

- Is the experiment successful from the scientific & technical point of view ?
- Is an economic application possible now or in the near future ?
- What are the conditions, specifications, procedures of the experiment ?
- Which type of information in the RS records has been used mainly ?

The first and second checkpoint are for the reader of the complete papers. The third and fourth rules will be applied to the papers of this session (for demonstration purpose only). First a short explanation will be given of the physical factors relevant to these rules.

Remote sensing of vegetation is almost exclusively using electro-magnetic radiation as the information carrier form object to platform. The measurable quantities in EM radiation are: direction; intensity; wavelength or frequency; time of arrival or propagation velocity; polarisation; degree of coherence; phase.

Any RS technique based on the physical measurement of EM waves determines one of these quantities as a function of one or more of the others. In aerial photography, intensity is recorded as a function of direction, in a certain wavelength interval (possibly, but this is usually not done, with a certain polarisation).

Side Looking Radar makes use of echo time measurements across the flight direction, instead of direction. Synthetic aperture radar applies phase comparison between two waves, and may determine intensity as a function of polarisation.

It is tempting to elaborate on this physical concept of RS, to try to fit the know EM techniques into a 7x7(x7) 2D or 3D matrix, but that falls outside the scope of this paper.

As to the specification of the data acquisition system, it is essential to define the smallest recorded increment of the said quantities. In its simplest form this is expressed as "resolution", and so there are, including "time" 8 resolution figures, of which usually only 4 are given:

- Spatial Resolution (from "direction" in x and y in the image);
- Spectral Resolution (the number of wavelength bands and the width per band);
- Temporal Resolution (the period after which another coverage is taken); and
- Intensities Resolution (the number of steps into which intensities are sampled).

Two more "resolutions" are occasionally seen:

- Polarisation Resolution (especially SLAR, defining the spread in polarisation angle);
- Temperature Resolution (in Thermography, where it replaces intensity resolution).

The conventional parameters scale, angular coverage, stereo overlap, distortion, time of the day, season, weather conditions, sun elevation, are not discussed here, but should not be forgotten when evaluating experiments. In addition, the cost per area, including processing, should be considered as an essential parameter (from fl. 1,-/ha to fl. 1,-/km^2).

Spatial Resolution "on the ground" is loosely related to scale, and as the scales range from 1:10^7 (Nagarajan) to 1:6000 (Fisser), the presented papers cover approximately a range of 1:10^4 in resolution. Aerial photography usually does not go below 0.3 m ground resolution, however large the scale is, due to "image" movement. Satellite imagery has at this moment a resolution of 0.1 to 10 km and may in future well go down to 10 m for limited areas and high contrast objects. Ecologists are interested in micro-scale details as well as in macro-scale phenomenae, as is shown by the papers. Whether their requests for high spatial resolution are always justified must be studied critically, because overasking here k-fold means a k^2 fold number of pictures (and picture elements = pixels), and thus a k^2 longer processing time and cost (approx.).

In Blair's paper one may find that on ERTS pictures the smallest identifiable area is 2 ha, thus 3 x 3 pixels with high contrast versus the surrounding, 8 ha (4 x 4 pixels) with medium contrast and 12 ha (5 x 5 pixels) to 18 ha (6 x 6 pixels) with low contrast. The condition is of course that these pixel areas have to be homogeneous in "colour"; an essential condition for MSS data processing. If these ERTS-results are applied to aerial photography, the smallest area to be mapped is at least 4 to 6 times the ground resolution, thus 2m x 2m for large scale picture (up to 1:6,000) and one millionth of the photo format area for medium and small scale photography, as normal photographs roughly contain 4000 pixels across the format. Similarly, thermographic and radar images can be analysed with regard to the smallest units visible.

Related to spatial resolution is "height resolution", which applies to Zonneveld's paper. With good quality professional aerial photography, flown with 60% forward overlap, the minimum height difference Δh visible under the stereoscope depends only on the flying altitude H: $\Delta h = 0.01\%\ H$. This simple relation holds even for ERTS imagery, provided that the format is equally large, and the overlap (usually here "side"-) is less than 30%, as the image quality is lower than of aerial photography, measured in the picture (Katsieris, 1974). Consequently, if ecologists are interested in seeing and measuring height differences of 0.1 m to 1 m in the pictures, the aircraft's altitude should be 1 to 10 km.

Spectral Resolution has two aspects: The number of bands in the visible and the near infra red (VIS & NIR) (for thermography in the middle and far infrared: MIR & FIR), and the width of the spectral bands (which can be expressed as a percentage of the central wavelength in each band: for instance with 5%: $\Delta\lambda = 0.05\ \lambda_{av}$). The first indication "number of bands" often gives sufficient information, as the windows in the spectrum are limited in size and the bandwidth per band is maximized to improve the signal to noise ratio. Multi spectral sensing is in - all authors apply spectral data with more than 2 bands, with Long being at the extreme with 10 bands. The big question for the coming 5 years is: "How many bands and which bands are necessary and sufficient for a certain survey task ?"

Discussing this essential problem, one should take into account two processing routines: Identification of objects (e.g. crop type) solely based upon multispectral information, versus Delineation and classification of objects by using all possible kinds of information in the records: size, shape, texture, height, location, etc., plus multi spectral data. It is obvious that the first approach needs more spectral bands than the latter; it is also fair to say that the first is indeed multispectral "work", whereas the second routine can at best be called "false colour image interpretation", in which the number of bands used is at most three.

Analysing the literature, one will find that little research can be classified in the first group, even visual interpretation of ERTS-1 pictures is mostly confined to 3 out of the 4 pictures. This is not saying that visual interpretation is of a lower class; on the contrary, the human photo interpretor is for a long time to come the most flexible and multi-feature image analyser. The use of different kinds of information often prevents gross mistakes and is more economical, especially when the objects possess characteristic shapes, texture, heights, etc.

Ecologists will usually be able to work with their own eyes and brain when analysing MSS pictures from (semi-) natural vegetation; the computer will probably only come into the picture when pictorial data is of no use for solving the problems. This is the case with agricultural crop identification, where other image characteristics than "colour" are not typical for the classification of the 4 to 20 crops in the region. The coming years will certainly show a concentrated effort to determine the minimum number of bands required for a particular task. The subjective expectations are: "Half a dozen, plus or minus a few, depending on the complexity of the problem".

The visual interpretator may do the job with a few bands less, if he can use additional clues in the picture (or if he has time for field checking).

Ecology can in this multi-spectral domain prepare itself for RS by filtering incoming papers and experimental results on this crucial question: "How many bands ?". However, in this formulation, the question is already outdated by recent developments. The following points are relevant in this context:

- Time scale for a good answer is 5 to 7 Y .;
- NASA gives the highest priority to MSS;
- Agricultural satellite MSS tends to 7 or 8 bands, other options will not be available.
- Cluster analysis with over 8 bands is impractical, even on large computers;
- ITC developed a multispectral projector for up to 8 images (Hempenius, 1974);
- Data compression of MSS records during preprocessing with Karhunen-Loeve linear transformation offers advantages in reducing number of pictures for interpretor (Mulder, 1974);
- Sufficient temporal resolution compensates low spectral resolution for dynamic objects.

Temporal resolution is an essential factor in RS for ecology, as vegetation changes considerably from week to week during the growing season. Moreover there is a general change from year to year (large in agricultural areas, small in natural vegetation except for natural or man-made disasters), and even during a 24 hours cycle vegetation will show variations, but these may hamper the interpretation of remote sensing records.

Remote sensing for ecology is surveying of dynamic objects, and hence the whole complex of RS activities should be carried out dynamically, at the correct moment, within an appropriate and usually short period. Repeated coverage is needed, although the repetition rate may vary from several years for forestry to a few days in disease detection for agriculture.

The importance of this temporal factor for ecology is demonstrated by all papers of this symposium. Hence the various applications reported in the papers should give an idea as to what temporal resolution is required for optimum vegetation RS. Depending on the timescale of the phenomenae investigated, the temporal resolution is 10 year for forestry mapping, 3 years for detecting changes in environmental quality and landscape, 1 year for landuse, some months for gross seasonal changes, one to two weeks for agricultural surveying, and down to a day for disease warning and forest fire control. The diagram of nonseasonal cycles in 8 tropical plants (Richards, 1973) shows that temporal coverage should be selective within a few weeks when surveying a tropical forest.

Since the launch of ERTS-1, many ecologists have for the first time come in touch with multi-temporal data, in this case with a temporal resolution of 18 days (and by virtue of the side-overlap of 1 day). Most of the users are aware that the main problem is the slow processing and analysis of the MSS data, and most will now realize that in an operational program the data handling has to be organized professionally and be as dynamically as nature itself.

A simple rule may serve to detect the bottlenecks: The ratios between the useful life-time of the map or interpreted data, the time needed for processing and analysis, and the time interval in which the RS acquisition should take place is 10:3:1. Thus Acquisition/Processing/'Life' = $1 : \pi : \pi^2$.

An essential advantage of properly timed temporal data is for identification of vegetation on behalf of different development during the season. Hardly anybody has experience with this aspect of RS of dynamic features. With aerial photography it simply could not be organised on a commercial scale to cover large agricultural areas every second week. It is here that satellites have to be applied; we may expect temporal resolution going down in the eighties to a few days.

Ecologists certainly face an interesting development, but it will be quite a job to understand nature well enough in terms of temporal and spectral variation, to be able to process the data. An adequate description method is to plot weekly the position of each crop type in a n-dimensional spectral intensity space. Connecting the points per crop gives specific "lifelines", which facilitate study.

Intensity resolution is not a significant property for the user, it seems, because the authors of the papers hardly point at it. The interpretor obviously does not directly come in touch with it. However, the computer scientist wants to know how many intensity steps he has to handle, what the noise is and how the various details are distributed over the steps (intensity histogram).

Also here the interpretor of ecological data may prepare himself by understanding the significance of this resolution.

The problem with multi-spectral, multi-temporal and multi-level data is the huge amount which has to be recorded, stored, processed, destructed. Therefore, development will go in the direction of minimizing the amount of data by a balanced choice of the four resolutions mentioned. The possibilities of MSS in satellites leads to a reduction of the spatial and intensity resolution. This loss is compensated by improved spectral and temporal resolution. The last is also necessary because of cloud cover, which allows in this part of the world to take only one in five pictures with less than 2 okta (25%) cloud cover. Research to support a balanced setting of the 4 resolutions has high priority. Ecologists may find it a rewarding study object.

Polarisation resolution is routinely applied in Side Looking Airborne Radar (SLAR). It is not specified in terms of how narrow the angular width is but, as in spectral resolution, how many "bands" and at which angles they are located. Active microwave systems with real or synthetic aperture can transmit and receive horizontal H and vertical V polarized radiation. Combination of these properties leads to four practical propositions: 2 "like" HH & VV and 2 "cross" HV & VH polarized SLAR's. Of the first pair, HH seems most useful for crop-vegetation, as it interacts best with the general structure of the plants. The "cross" pair are in fact equivalent, as the pictures will not differ if the polarisation state of transmitter and receiver are interchanged. The "cross" image contains information about the inclined structural details (strongest signals from 45° stems, leaves, branches). A recent paper (Ulaby & Moore, 1973) discusses the state of the art and shows for the first time spectral response curves of four crops through the freq. range 4.3 - 7.8 GHz. The typical difference with MSS is that SLAR measures "radar" reflectance mainly under incidence angles between 30° and 70° up to almost grazing incidence, hence "sees" even early in the season more vegetation than soil. The authors show measurements at 30° and 60°. Here again we see that understanding has improved in recent years, and that the future is to multi-spectral, triple-polarisation radar (in the eighties ?) for the ecologist mainly.

Temperature resolution is often indicated in IRLS experiments; values as small as 0.1°C are quoted. The tolerable error (absolute or relative) in T for a plant canopy lies closer to 1°C, and the uncertainty in emissivity of vegetation (under influence of structure, density, intercellular spacing, leaf surface morphology, angular position of the scanner, etc.) probably causes a bigger error. Planck's law, if differentiated, quantifies the emissivity effect: A change in ε of 1/10 varies the apparent T by 1% = 3°C in the MIR and 2% in the FIR. The real possibilities of IRLS lie in multi spectral thermography (MST), with a couple of bands in the MIR and FIR. The author's team explores this NASA initiated field and will in due time publish results in the ITC Journal. Ecologists are invited to define the necessary accuracy, the range over which plant temperatures vary, the changes and variability in emissivities of plants, also as function of wavelength and look angle, and economical applications.

An unexpected application may be in situ differentiation between the 3 and 4 carbon photosynthesis plants (Björkman & Berry, 1973), which have up to 10°C difference in optimum leaf temperature, and may show emissivity differences in the FIR.

Forecasting of a RS scenario for 1980+

Something has to be said about planning RS experiments in this decade. The reason is that not all the work what can be done to reveal RS secrets of nature should be done. Research is not a goal in itself (at least not for the tax payer); it should possibly be matched with the expectation of the technical and economic deve opments, in order to find an early application.

Those who have been in aerial surveying and remote sensing application research since the fifties are aware of the potential profits in remote sensing, but gradually are also realising that not all RS instruments possible will become available in the near future, not for research, nor for operational usage.

It seems to be more realistic to state that certain RS techniques will be mutually exclusive. If an operational MSS satellite survey program will be implemented in near future, then radar may not find sufficient application to economically justify it. Or, in another domain, if visual interpretation in a particular country is well organized and can cope with the survey tasks at hand, then it will not be likely that a somewhat faster but highbrown semi-automatic data processing will be introduced in a few years.

In both cases, it is not necessarily so that one stops research in the "loosing" areas; on the contrary, because no routine is gained, one should keep in touch through small research project. However, it is clear that if the situation develops for whatever reasons into an incompatability of potential RS techniques, one should draw his own conclusions with respect to the optimum direction in which most of the research has to go to be beneficial.

It is still too early to make a reliable prediction; the history of RS is too short and the development was too much beyond the civiliar boundaries to allow to draw lines which can be extrapolated. Moreover, futurology is difficult, although guidebooks can be found. In addition, most RS techniques have their pro's and con's, especially if studied in relation to the local situation. Climate, size of the country, state of the mapping activities, economic power, vegetation cover, sea versus land area, mountanous or flat, frequency of natural disasters, hydrological conditions, etc. they all may effect use or abandonment of a RS technique. These are all together sufficient reasons not to go into detail here; to forecast the scenario for region x, country y or continent z is a task for a (local) team, and once being done, it has to be updated every few years. We only would like here to stress that it pays to think once through the next few years and consider for instance the following statements.

Vegetation offers in principle five quantities which are significant for RS:

- Spatial distribution, shape, gross size, height (length, area, volume);
- Spectral reflectance in visible and NIR (molecular structure);
- Structural properties; micro-size; leaf-stand (resonance; polarisation);
- Temperature and emissivity in MIR and FIR (condition and cell structure);
- Temporal behavior during the growing season (development cycles);

Remote Sensing techniques for ecological surveying appear to concentrate on:
- Aerial photography with b & w, colour, and false-colour film;
- Multi Spectral Sensing from satellite orbit with 6 to 8 spectral bands;
- Side Looking Airborne Radar in some microwave bands and 2 or 3 polarisation modes;
- Multi Spectral Thermography, space borne or airborne, with 4 to 8 bands.

Economical and physical restrictions which may play an important role are:
- For frequent temporal coverage, use satellites, not aircrafts; calculations of orbits for an international agricultural satellite at ITC indicate the possibility of a few days temporal resolution.
- Photography is good for the spatial aspects, reasonable for spectral data (up to 1 μm), poor on structural information, impossible for temperature sensing; difficult to modify for other than the usual "colours".
- MSS is good for spectral aspects, poor for spatial data (at least from orbit), necessary for temperature sensing, inadequate for structural information, with proper preprocessing visual interpretation is feasible.
- MSS in combination with spacecrafts offers definite advantages for surveying of dynamic objects, as it is rapid in acquisition and in processing, offers synoptic views frequently, has little "noise" variation in the acquired data due to fixed scan-direction, exposure moment, and limited scan-angle;
- SLAR is promising for vegetation discrimination in the mid-eighties, as by then the yet still classified multi-freq., "multi"-polarisation will have developed into an operational system for civil applications.
- SLAR reacts typically on structural plant details, as resonance is maximum if the wavelength (8mm to 30 cm) matches the characteristic dimension of stems and leaves, and polarisation allows to determine directional features (vert., hor., in-between);
- SLAR is powerful in the sense that it can work day and night, independent of weather conditions (except heavy rain) and also because it can "cover" an area of 10^4 to 10^5 km^2 per 24 hours, thus is good for disaster surveying, reconnaissance at sea, etc., but difficult to find continuous application for;
- MST has still to be developed into an experimental tool, after which an evaluation has to show to what extent temperature data and difference in emissivity can be applied in ecological surveys even if atmospheric interference and weather conditions are compensated for either by selecting proper operational conditions, or by advanced pre-processing.

These and other expectations should be discussed e.g. within a governmental survey organisation, with eye on the available financial and human resources and on the survey tasks. When doing this, it will soon appear that only some of the mentioned RS techniques will be feasible in an average country. Which data acquisition and processing methods that will be, and in what year they will be available, depends upon the specific situation.

In conclusion, the author expects that ecologists will play an active role in filtering the past, forecasting the future, and specifying the present experiments, especially because remote sensing offers opportunities to survey dynamic features. For this reason ecology may well become the primary user of these unconventional tools.

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SOME RESULTS IN EARTH & OCEAN PHYSICS

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It has been two years since I presented an outline at the International Astronautical Congress on a new NASA program, "The Earth & Ocean Physics Application Program (EOPAP)", which this Agency intended to undertake over the next decade. As the name implies, this is an Application Program, that is to say, its major thrust is to make practical "use" of space science and technology for the betterment of man.

The purpose of this paper is to present some of the results we have already achieved under this now ongoing dynamic program. We have recently finished a rather comprehensive description of the earth gravity field of order and degree 16. This field is based upon 400,000 satellite observations of 27 spacecraft (using cameras, electronic ranging, Doppler, minitrack and precision laser tracking) and 20,000 ground gravity surveys. Based upon this field we further refined the geoid with two meter contour intervals and errors of 2 to 3 mgal. over most the land areas and 5 to 7 mgal. over the oceans. Recent altimeter data from our SKYLAB mission confirmed this geoid is a very satisfactory manner over wave lengths in the order of several hundred kilometers. New determination or rather details of the sea surface topography were further made showing such phenomena as trenches (Puerto Rican Trench), seamounts and sea slopes off the east coast of the U.S. This demonstrated the real capability of satellite altimetry for the study of the sea surface topography important for future applications in oceanography (currents, heat transport). We have obtained some preliminary results from our San Andreas Fault Experiment which I also mentioned two years ago. Our laser systems have recently been improved so that we now can measure distances to spacecraft (up to 5,000 km) to within an error of less than 10 cm. Further, the first Satellite-to-Satellite Tracking experiment (SST) between ATS-F, NIMBUS-E and GEOS-C is under way which will help us even more to improve our knowledge of the earth's gravity field and in the determination of precise spacecraft orbits, both of which are needed for spacecraft missions such as GEOS-C, SEASAT-A, NASA's first oceanographic satellites.

C4

Contributions of the study of parasitic systems to general ecology

CONTRIBUTIONS OF BIOLOGICAL CONTROL TO UNDERSTANDING ECOSYSTEM DYNAMICS

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Summary

Reviewed briefly herein are both early and recent contributions of biological control ecologists to the theory and understanding of natural control of populations and the role of phytophagous species as influents of species diversity and abundance of a specific species on natural vegetation. Introductions for biological control of plant and animal pests in many countries have served as vast experiments illustrating the roles of natural enemies and suggesting new ideas and supporting or refuting old ones. Insight and exemplification have been furnished of the importance of competition and examples of competitive displacement have been shown. Biological control ecologists have pioneered in modelling host-parasite and predator-prey relationships, and in developing techniques to assess the importance of various mortality factors, including stress factors (Burges & Hussey, 1971) acting on populations, both in the correlative, statistical sphere and by experimental manipulation. Other meaningful contributions include early work on the role of chemical messengers in the host distinguishing behavior of parasitic insects, the significance of various adaptations and of symbiotes and alternate hosts or foods for the control effectiveness of certain entomophagous species, and lastly, of the enormous significance of biotypes and the problems confronting colonizing species.

Introduction

Research on biological control has involved both theoretical and practical developments that have furnished basic insights into ecosystem dynamics. The practice itself consists of vast experiments which test the role of certain herbivores, carnivores or disease pathogens in the regulation of plant or animal pest populations, which are sometimes major components of semi-natural communities.

Such experiments have furnished estimates of the balance disturbing or restorative powers of natural enemy species, singly or in complexes. Also, estimates are furnished of parameters in, and the consequences of, competitive displacement and co-existence of exploiting species at various trophic levels. Most such work has been aimed at improving crops, ranges and forests, but some has concerned the control of aquatic vegetation and even, indirectly, human disease.

Some of those whose work we cite, while not biological control specialists as such, have devoted considerable efforts to the study of host-parasite or predator-prey relationships involving insect pests and their natural enemies, and such contributions may reasonably be taken to be in the area of biological control.

Biological control ecologists have been in the forefront in the theoretical, experimental, and methodological advances toward understanding agroecosystem dynamics, and we discuss contributions under the following seven headings.

1. The Balance of Nature--Processes, Complexity and Stability

It has been estimated that a bacterium able to divide every 20 minutes, would, if unchecked, form a layer 1 foot deep over the entire earth in a day and a half. Surplus reproductive potential is characteristic of every species. In nature, however, as every biologist knows, such surpluses are prevented, and, generally, at given seasons in undisturbed places the same species are likely to be present in the same relative numbers, year after year. This is what is meant by "balance of nature". Such a natural system seems to be self-governed--homeostatic.

Closely associated with this concept is the theory that for such homeostasis to exist the numbers of an organism must in some way be repressed by its own density increase. This was foreshadowed by Giovanni Botero in 1588 and by Thomas Malthus two centuries later, but the first attempt to classify and understand the different sorts of processes limiting population increase was made by L. O. Howard and W. F. Fiske (1911) who were working on the biological control of gypsy moth.

Working on the same project were two men, H. S. Smith and W. R. Thompson, whose contributions to these concepts and to biological control added greatly to understanding of ecosystem dynamics. Smith (1935) renamed Howard and Fiske's mortality-factor categories, using terms that have received worldwide acceptance: density-dependent factors that act with increasing intensity as population density increases; density-independent factors whose intensity does not increase or decrease with density; and inversely density-dependent factors whose intensity increases as the population declines. G. C. Varley, who did postdoctoral study with Smith, added the category delayed density-dependent factors, which act with a lag. Smith (1935) and Nicholson (1933), largely independently, developed similar theses on the natural control of animal numbers by, essentially, the action of density-dependent factors. Both relegated to a clearly secondary status the role of physical conditions and other factors not acting in a density-dependent manner. Nicholson's special contribution (Nicholson, 1933, 1957; Nicholson & Bailey, 1935) lay in stressing competition, which connotes density-dependence. Competition, in Nicholson's view, is the regulating mechanism, whether it operates directly on the population, or indirectly through its natural enemies.

Huffaker (1958) attempted to place in better perspective the roles of density-dependent and density-independent factors, claiming that the two types of factors (the former termed regulating and the latter conditioning) always act together to accomplish natural control. Pimental (1961a) drew attention to the genetic composition of the interacting populations, which is subject to selective pressure and interactive with normal density-dependent feedback. Hence, we have currently (Huffaker et al., 1971) a broad concept of natural control of populations which has been developed largely by biological control ecologists, and is consistent with the growing body of knowledge concerning the roles and importance of the various factors acting to determine population size and maintain balance. At the roots of this, the concept of density-dependence derives only from the axiomatic fact that as organisms increase in numbers they use up or defile the things they need, and attract or generate elements in the environment that are inimical to them.

Such population regulation is seen as operating on specific populations and does not itself imply homeostasis at the community level. Yet, single species population stability is certainly part of the fabric of community stability; indeed, often the degree of stability of a community is greatly affected by the stability of a single dominant component, as with a dominant tree species in a forest. The degree to which a potentially regulating insect attacking such a tree species is controlled by its natural enemies may be decisive. Biological control workers in many countries have noted beyond all others that the natural enemies of many such phytophagous species foster a plant species mixture and preserve a degree of community stability and plant protection (Wilson, 1943, 1964; Huffaker, 1957).

Biological control workers have sought to unravel the problem of whether greater stability in communities is necessarily dependent on greater diversity of species. Workers in Hawaii first questioned the desirability of introducing a complex of enemies, and contended that competitive action of a less effective species would reduce the efficiency of the more effective species, and that the total effect of the enemy complex would be less than that by the most effective species alone. Smith (1929) argued to the contrary, and the practice of introducing a complex of primary parasites has continued. Turnbull & Chant (1961) again challenged the practice, implying that competition with a "best" species will reduce the overall control potential. While some situations can be theoretically envisaged, particularly with non-host-specific enemies, in fact, no deliberate multiple introductions have been known to have such effects, while there is much evidence of the additive values from multiple introductions (Huffaker et al., 1971).

Such evidence implies that in a community greater diversity of enemies and greater stability go hand-in-hand, a contention elevated by some to the status of an ecological law. We have long contended (Wilson, 1943; Huffaker, 1957) that a host-specific phytophagous insect effective in biological control will, by controlling a dominant plant species, make room for other plant species. While Ridley (1930) had concluded that destruction of seeds by insects is a basic reason for the great plant diversity in the tropics, the significance of the insects' role in plant composition has been more convincingly demonstrated by the biological control of weeds. These results have suggested research in a whole new range of vistas concerning the numerical interdependencies between plants and their natural enemies. For the first time, a plant pathogen (Puccinia chondrillina) has recently been deliberately introduced into Australia for control of a weed (Wapshere, 1970). Huffaker (1971) demonstrated that increased species diversity followed the great reduction by the biological control of the weed St. Johnswort on California ranges. Janzen (1969) explored Ridley's hypothesis in Central America and found support for it in the attacks of insects on juvenile plants. One may assume that this greater species diversity, caused in part by biological control (Huffaker, 1974), also fosters a more stable community.

Although a greater complex of natural enemies often assures greater stability of control, this is not a rule or law: DeBach (1971) states, "One really effective enemy may be--and often is--enough to regulate a host species at low population levels even though its colonization may eliminate other natural enemies and actually reduce the diversity of natural enemies." Pimental (1961b), who studied the effects of species diversity and spatial dispersion on the natural balance of pests on collards, found that certain outbreaks occurred in plots of single plant species but not of mixed species.

Huffaker et al. (1963) showed that increase in the heterogeneity of the physical terrain in which a predatory mite and its prey interacted resulted in corresponding increase in the continuity and stability of the system. Thus, that greater species diversity means greater stability is supported by some results of biological control and placed in doubt by other results. (See also item 5.)

2. Host Parasite and Predator-Prey Interactions

Thompson (1923) developed equations to describe host-parasite interactions, but his major assumption that fecundity is all-important, assuming that entomophagous species unerringly find their hosts, and searching capacity commonly is a negligible factor, has found little acceptance. However, his work stimulated Vito Volterra and A. J. Nicholson separately to develop models that have been take-off points for more advanced models. Moreover, Thompson (1928), rather than Andrewartha & Birch (1954), was the chief opponent of Nicholson's (1933) and Smith's (1935) density-dependent concepts of natural control. Parenthetically, it is a misleading error to regard Lack's (1954) views as the chief refutation of Andrewartha & Birch's (1954) theory. Many zoologists (e.g. Orians, 1962; Boughey, 1968), ignoring Nicholson's prior and dominant role, erroneously conclude that Andrewartha & Birch's view is applicable to insects while Lack's, incorporating density-dependence, applies to the highly evolved vertebrates. Such analyses overlook the fact that Nicholson experimented mainly with insects and that his models were efforts to explain host insect/parasitic insect interactions. Such views take no account of the fact that most insect population ecologists deny that Andrewartha & Birch's theory is appropriate even for the insects (e.g. Solomon, 1957; Nicholson, 1958; Milne, 1962; DeBach, 1964; Clark, et al., 1967; Richards & Southwood, 1968; Huffaker, 1958; Huffaker et al., 1971; Varley et al., 1974.

Because Volterra's (1931) and Lotka's (1925) models did not incorporate delayed reproduction and development, Nicholson sought a more realistic model. A principal weakness in Nicholson's model is his assumption of a constant searching capacity (area of discovery). Hassell & Huffaker (1969a) showed that the area of discovery of the parasite Nemeritis canescens is not a constant but is reduced by mutual interference. This led to Hassell and Varley's (1969) development of a Nicholsonian-type model incorporating modification of the area of discovery by parasite density.

Work of Holling (1959 etc.) on predation has resulted in a more precise formulation of a predator-prey model. Ideally, step by step behavior is analyzed at the functional response level, and reproduction at the numerical response level (Holling & Ewing, 1970). The latter say of their simplest version: "The model is appallingly inelegant because it is realistic", and it remains to be seen whether the simple Hassell and Varley model is not more useful. More recently, Auslander et al. (in press) have developed a new model which shows that preference for a given age-class of the host can lead to development of discrete generations, where none exist in the absence of the parasite, and to a stable system, quite independent of a damping effect by mutual interference, as required by the Hassell and Varley model.

3. Ways of Evaluating Mortality Factors

Analysis of mortality is recognized as crucial in population dynamics. Biological control ecologists have led the development of concepts (above), and contributed valuable techniques. Thompson (1928) suggested a differentiation between mortality factors that are dispensable and those that are not. Bess (1945), in assessing biological control of gypsy moth, introduced the mortality-survival ratio whereby the indispensable mortality due to a factor is obtained if the final population is multiplied by this ratio.

Biological control workers have also emphasized that the importance of a mortality factor is not to be assessed simply by the mortality it causes in a given generation; also to be considered is which factor(s) is more responsive to density change and acts compensatorily, causing increased mortality in the absence of a previously acting factor. Workers seeking explanations of population dynamics wherein natural enemies were a significant factor have further developed evaluation techniques. Morris (1963, 1965) developed a key-factor analysis and methods for assessing contemporaneously acting factors, and Varley & Gradwell (1963) developed alternative methods which in some respects are better. Hassell & Huffaker (1969b) and Luck (1971) pointed to advantages and disadvantages of these methods, and Varley & Gradwell (1970) and Varley et al. (1974) present critical reviews. Huffaker & Kennett (1966) used three methods to assess roles of two parasites of the olive scale, including a new technique for clarifying the impact of each parasite despite the confusion arising from the interactions.

Biological control ecologists have long used experimental methods to evaluate the regulating role of natural enemies (as range ecologists have used exclosures to assess the influences of mammals on range plants). The method gives a direct measure of net effect which no statistical or correlative method can. Moreover, contrary to the general view, the difference in rate of host-increase when a given enemy is present, and when it is excluded, can be used to estimate the generation mortality attributable to the enemy, for use in life tables. DeBach & Huffaker (1971) describe results from the use of a number of such "check methods". Only recently have other ecologists appreciated that, despite some undesirable effects of manipulation on the natural state, such methods may give us insights not readily, if at all, otherwise obtainable.

4. Behavioral Pheromones

In the area of behavioral ecology, the classical work of Salt (1937 etc.) stimulated effort to gain insights into the efficiency of host utilization by parasitic Hymenoptera. The deposition of substances (pheromones) to "mark" parasitized hosts, and subsequently to avoid superparasitism, was clearly shown. It is now known that parasite species vary greatly in the degree to which they practice marking and avoidance of previously marked hosts. With some, the discriminatory avoidance is uncommon or breaks down under stress [e.g. Chelonus (Ullyett, 1949), Spalangia (Wylie, 1972)]; with others rigid discrimination occurs [e.g. Aphytis (Huffaker & Kennett, 1966) and Asolcus (Wilson, 1961)].

Studies on aggregation pheromones of bark beetles have shown that predators may respond to the pheromones as readily as the bark beetles (Wood, 1972). Efforts to use pheromones for control may therefore be complicated by adverse effects on enemies. It has recently been shown that substances (kairomones) produced by host insects may be attractive to certain natural enemies and stimulate more intensive host-searching (Jones et al., 1973). Understanding the role of sex pheromones in the mating behavior of various parasites and predators has progressed with developments concerning use of pheromones as monitoring tools for insect pests.

5. Competitive Displacement and Coexistence

Biological control ecologists have strikingly exemplified the fact of competition in nature--a mutually negative feedback effect resulting from the activities and utilization of resources by two or more co-inhabiting organisms. They have shown to be wrong a basic premise of Andrewartha & Birch (1954) that most animals do not compete significantly. The fact of biological control of a host or prey species by a rather host-specific species means necessarily that the members of such exploiting species compete intensively with one another. Intense competition for food, except for some territorial and socially and intrinsically limited species is a central feature in the lives of all predators (Huffaker, 1971). An equivalent situation exists with phytophagous species in respect to their host plants and, within limits imposed by their own enemies, they engage in intense competition for food, which reduces, sometimes greatly, the density of their host plants. The biological control of weeds (Wilson, 1964; Huffaker, 1957, 1974) clearly illustrates this.

DeBach & Sundby (1963), Huffaker & Kennett (1966, 1969) and a number of others have shown that such invertebrate enemies are not rare relative to their food resource, and that they not only engage in intense intraspecific competition but often in intense interspecific competition as well. The competition sometimes ends in the survival of only a single species, or, as instanced by Huffaker & Kennett (1966) in the survival of only two species. DeBach & Sundby (1963) give classic examples of the field displacement of species of Aphytis by other congeners, each such displacement resulting, significantly, in a higher level of control of the host. However, their explanation, based on laboratory experiments, of the process of this displacement has been criticized (Huffaker & Laing, 1972).

6. The Role of Alternate Hosts and Symbiotes

Success of entomophagous insects often depends on the hosts available; ability to exploit one, several, or many host species has evolved for each species in relation to intense competition from other predatory and parasitic species for the total hosts available. Some species are highly host specific or monophagous at one season, but require another major host at times when the main host(s) is not available. There are many examples of the need for alternative hosts in natural enemies that are efficient host population regulators of pest species (DeBach, 1964; Doutt et al. 1969).

Other work has shown the necessity of subsidiary foods if natural enemies are to be effective. Box (1925) noted the importance of nectar plants for adults of scoliid parasites of canegrubs, and others (see van den Bosch & Telford, 1964) have confirmed the importance of nectar and honeydew in various instances. Many workers in the USSR have successfuly used nectar-bearing plants as cover crops in orchards or intermixed them in other crops (Klassen, 1973). (See also Leius, 1967.)

The ecological balance involving primary and alternate prey in some crops can be so disrupted by pesticides that it may take several years for balance to be reinstated (e.g. Flaherty & Huffaker, 1970).

More subtly, Hagen & Tassan (1972) showed that certain tephritid flies cannot develop in the absence of specific bacterial symbiotes needed to convert their food substrate to assimilable form, and they suggested the need for introduction of the symbiote along with introduction of the natural enemy host of the symbiote.

7. Different Biotypes and Problems of Colonizing Species

The utilization of exotic natural enemies to control pests involves biological control scientists in problems of colonization, adaptation to new environments, and genetic diversity within species (DeBach, 1965; Wilson, 1965; Messenger et al., in press). Despite numerous biological control successes, many natural enemy introductions prove ineffective. The reasons for this, and their avoidance, require deeper knowledge (Wilson, 1960; Turnbull, 1967; van den Bosch, 1968).

Biological control research has accumulated vast knowledge of interspecific and intra-specific variation in the characteristics of natural enemies attacking various pests. The species of natural enemies and their relative abundance vary greatly throughout the range of particular pest species (e.g. Thompson & Parker, 1928; Wilson, 1943).

This diversity is a reflection of the high degree of ecological specialization of different enemy species, which often involves differences in adaptation to innumerable factors of significance for the capacity to regulate host abundance. Also, it is not uncommon to find that what at first appears to be a single species possessing uniform properties, actually comprises sibling species, subspecies or races having markedly different properties (e.g. Delucchi, 1967). Within these lower categories further significant genetic variation occurs. The complexity of such situations in respect of single host species is such that it would be difficult, for most unsolved biological control problems, to visualize reaching an end to the exploration of all potentially valuable avenues. The California red scale (DeBach & Sundby, 1963) is an illustration.

Intraspecific variability may involve any property of a species, such as reproductive capacity, time of emergence (Clausen, 1936), developmental rates, mortalities under different conditions, length of life-cycle, distribution, etc. (Flanders, 1931; Quednau, 1960), sex ratio and fecundity (Hafez & Doutt, 1954), hosts attacked (Simmonds, 1963) and differences in host-stage attacked (DeBach, 1958). In polymorphic species, such as *Chrysolina quadrigemina*, the morphs may differ in relative success in different habitats (Wilson, 1965). Elucidation of such diversity provides data for understanding the processes and results of the evolution of the complex of organisms associated with particular pest species, and an appreciation of the complexity of factors involved in the regulation of natural populations.

Genetic variability in parasites makes it possible by selection to obtain strains that differ in important properties, such as those listed above, and in host-finding capacity or DDT-tolerance (e.g. Wilkes, 1947; Pielou & Glasser, 1952). There is the possibility of creating in the laboratory natural enemies better adapted to control pest species that have so far resisted adequate biological control (DeBach, 1958; Simmonds, 1963; Wilson, 1965).

Biological control research provides good opportunities for field experiments relating to colonization (Wilson, 1965), and many problems of effective biological control (e.g. pre-introduction sampling, establishment, fitness, ability to regulate) require a genetical approach. These opportunities and problems are now attracting interest of geneticists concerned with problems of colonizing species (see Baker & Stebbins, 1965; Messenger et al., in press).

Conclusion

In conclusion, it is obvious that the pursuit of biological control has produced significant contributions to general ecology and population ecology in particular, in addition to the major worldwide practical benefits that have been gained in the control of insects, mites and weeds, in particular. It is clear that the contributions to a better understanding of both plant and animal ecology have not been negligible.

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STABILIZING MECHANISMS IN SOILMICROFLORA

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Summary

The present knowledge on mechanisms antagonistic to activity and survival of soil-borne plant pathogens e.g. parasitism, antibiosis, competition, fungistasis and lysis, is reviewed. Buffer functions in agricultural soils against epidemic development of pathogens comprise disease decline, existence of disease suppressive soils, and development of antiphytopathogenic potential induced or increased by organic amendments, crop rotation or tolerance of weeds. The need of integrated research on the underlying mechanisms is emphasized.

Introduction

Stability in the soil population has been characterized as the stability of a dynamic equilibrium in which individual units of the system are constantly changing, but compensating changes taking place in other components maintain the over-all functional balance (Burges, 1960). The plant pathologist is not primarily concerned with this kind of stability, but in maintenance and stimulation of mechanisms acting against the epidemic growth of plant pathogens.

Despite the constant disturbance of the microbial species composition in agricultural soils by frequent physical and chemical alterations, some soils possess the ability to maintain or develop a buffer function against plant diseases.

Recognition of differences in buffer potential of soils to plant diseases evoked by organic manuring, led to the concept of the antiphytopathogenic potential ("Antiphytopathogenes Potential des Bodens") introduced by Reinmuth in 1963.

The suppression of activities of pathogens and accumulation of their propagules in agricultural soils can be understood as the consequence of a complex of the biotic and abiotic conditions of the soil environment. Recognition of environmental factors acting against pathogens, with the aim of manipulating them by agricultural engineering, is the main impulse of those studying the ecology of plant pathogenic micro-organisms.

Mechanisms of control

Important contributions to our knowledge of mechanisms controlling the development of pathogens in soil came from Garrett and coworkers. Their studies led to the recognition of the properties of parasitic fungi which determine their success in competitive saprophytic growth in soil (Garrett, 1970). Important features are: rapidity of germination and growth; enzyme equipment; excretion of fungistatic and bacteriostatic metabolites; tolerance of fungistatic substances; amplitude of abiotic conditions of existence; resistance against exploitation; energy status. Any biotic or abiotic factor that inhibits the activities, or that approaches or exceeds the limits of tolerance of a pathogen, contributes to the antiphytopathogenic potential of the soil; some factors, however, may be of primary importance, called key factors. These key factors are different depending on the soil type, the pathogenic species concerned and on the type and phase of its saprophytic existence: e.g. dormancy, competitive saprophytic growth, saprophytic survival.

The abiotic environmental factors generally limit the population size and activity while biotic interactions adjust and shape the development of microbial communities. A lucid introduction to our present knowledge on microbial activity in relation to the abiotic properties of the soil - e.g. substrate composition, temperature, water potential and water content, pH, O_2 and CO_2 - has recently been presented by Griffin (1972).

With regard to biotic interactions, compatible relationships known as commensalism, mutualism and synergism, as well as incompatible relationships like competition, amensalism, predation and parasitism are known (Alexander, 1971; Stevic et al., 1971).

Especially during the last 10 years our knowledge in this respect has impressively increased (Baker and Snyder, 1965; Toussoun et al., 1970). Some recent information on mechanisms controlling soil-borne disease will be discussed here.

Parasitism and lysis

Numerous examples of predation and parasitism of soil-borne plant pathogens have been described (e.g. Boosalis and Mankau, 1965; Mishustin and Nikitina, 1973).

Most of them are based on in vitro experiments and offer little basis for evaluating their importance in the field.

The causes of mycolysis in soil, especially that affecting fungal spores and resting structures is still a matter of dispute. Lysis of mycelium and spores can be induced in vitro by incubation on membrane filters placed on soil or sterile sand leached slowly with running water; activity of lytic enzymes in mycelia of three fungi was correlated directly with susceptibility to lysis of the fungi tested. These observations support the view that mycolysis in soil is an autolytic process caused my microbially induced nutrient deficiency (Ko and Lockwood, 1970). Strains of bacteria and actinomycetes, however, have been shown to induce mycolysis in vitro by producing hydrolytic enzymes, such as β-1-3 glucanase and chitinase (Potgieter and Alexander (1966). Old and Wong (1972), and Clough and Patrick (1973) reported the discovery of bacteria which perforate the walls of fungal spores in soil, followed by lysis of the cell content. This is the most simple and convincing evidence of heterolysis of fungi in soil.

Cell wall degradation of resting structures of <u>Fusarium</u> <u>solani</u> in soil has recently been reported (Old and Schippers, 1973); further electronmicroscopical studies are required to elucidate the mechanism. More information is needed to evaluate the importance of heterolytic processes in soil.

Fungistasis, toxic metabolites

Fungistasis is an important mechanism limiting fungal activity and a common phenomenon in all soils; germination of fungal propagules and of mycelial growth is inhibited. Two controversial concepts, one based on competition, the other on amensalism, have been developed to explain the principle.

Lockwood and coworkers presented strong evidence that microbially induced nutrient deficiency is the primary cause (Ko and Lockwood, 1967). Differences in sensitivity of fungal species to soil fungistasis are supposed to be due to differences in their dependance on exogenous nutrients for germination (Steiner and Lockwood, 1970).

Recently, however, volatile microbial metabolites receive increased attention as possbile causes of fungistasis (Hora and Baker, 1970; Smith, 1973). Several volatile compounds like allyl alcohol, ethylene and ammonium have been suggested to be involved (Balis, 1973; Smith, 1973; Schippers and Palm, 1973). Smith's experiments demonstrate a strong positive correlation between level of fungistasis, ability of a soil to produce ethylene and its organic matter and total nitrogen content. Ethylene also appeared to inhibit the activity of bacteria, nematodes and actinomycetes, the latter being least sensitive. Therefore Smith considered it to have a marked influence on most soil processes including turnover of organic matter and mineralization of nitrogen.

Sulphur-containig volatiles, aldehydes and alcohols produced by microbial degradation of residues of Crucifers and alfalfa, respectively, were also found to exert pronounced inhibition or stimulatory effects on fungi and other micro-organisms (Linderman and Gilbert, 1968; Gilbert et al., 1969; Lewis and Papavizas, 1970). These observations indicate that volatile products originating from normal microbial metabolism may be important in controlling development of soil-borne micro-organisms. They may act as environmental growth regulators, not only of influence on the activity of pathogenic fungi, but also stabilizing the soil-microbial communities.

Despite much effort it has not been possible to prove a wide-spread production of non-volatile fungistatic or toxic substances in soil. There is evidence that specific antibiotics are found locally in pieces of natural substrate (Wright, 1956; Norstadt and McCalla, 1969) and in heavily amended soils that provide sites with relatively high nutrient status. Such toxic metabolites may for instance be of importance in the control of potato scab, when soybeans are used as green manure. (Weinhold and Bowman, 1968). A strain of <u>Bacillus</u> <u>subtilis</u> was found to be responsible for the production of the toxic metabolite. The production of the toxin per unit of growth appeared to be greater in water extracts of soybean than in those of barley. The antagonistic potential of a micro-organism thus may depend on the nature of the substrate on which the antagonist grows.

Decline, conducive and suppressive soils

An interesting phenomenon of natural control is the so-called "decline" in soil-borne plant diseases observed after several years of monocultures of certain crops.

A biotic principle, supposed to be identical with strains of Bacillus subtilis which produce toxic metabolites has been supposed to cause decline of potato scab caused by Streptomyces scabies (Weinhold and Bowman, 1968) and bare patch disease in wheat caused by Rhizoctonia solani, Pythium spp. and Fusarium spp. (Price et al., 1971, Broadbent et al., 1971). Only a few isolates of this common and heterogeneous species seem to be suitable for control. The induction of early fruiting in wheat after seed inoculation with these isolates, suggest, production in soil and absorption by roots of growth -regulating substances and draws attention to wider implications.

Another example of an adaptive and highly specific antagonism resulting in decline of disease severity of "take-all" in cereals caused by Gaeumannomyces graminis has been intensively studied by Gerlagh (1968). His experiments suggest some non-sporulating, antibiotic-resistant bacteria to be involved in the phenomenon. The influence of physical and chemical soil factors on the effectiveness of this antagonistic agent has been demonstrated by Smiley and Cook (1973): a decrease in pH of the rhizosphere soil induced by NH_4-fertilization increased the sensitivity of the pathogen to the antagonistic principle.

It has been noticed, that some soils possess a natural buffer capacity against epidemic development of a disease. Such soils have been called disease suppressive soils in contrast to disease conducive soils (e.g. Baker, 1972). According to this author, decline in disease severity is regarded as a consequence of disease-suppressiveness of a soil.

Reinmuth (1963), however, proposed the term "antiphytopathogenic potential", to characterize soils differing in an acquired buffer capacity against disease development. Extensive research on the ecological effect of organic manuring on a number of pathogens (Gaeumannomyces graminis, Plasmodiophora brassicae, Helminthosporium sativum) revealed that the antiphytopathogenic potential of a soil can be strongly increased by organic amendments (Bochow and Seidel, 1964). The antiphytopathogenic potential is also influenced by the crop and crop rotation and connected with soil microflora composition (Zogg, 1972). These experiences of Bochow and coworkers with organic manuring and of Zogg with crop rotation indicate that an antiphytopathogenic potential can be built up in a soil by proper agricultural practices. Little is known yet, about the underlying biotic or abiotic principle.

Convincing evidence, that a single abiotic environmental factor can determine the disease suppressive character of a soil has been given by Stotzky (Stotzky and Martin, 1963; Stotzky, 1972). The absence of the causal agents of Panama wilt of bananas (Fusarium oxysporum f. cubense) and histoplasmosis of man and animals (Histoplasma capsulatum) was proved to be closely related to the presence of a particular kind of clay, montmorillonite. It has been suggested that the presence of montmorillonite maintains the microhabitat favourable for the development of bacteria which, in turn, probably control proliferation of the pathogenic fungi (Stotzky, 1972).

It is of importance to clearly distinguish between these principles underlying the buffer function of soils. It is therefore suggested to restrict the use of "disease suppressiveness" of a soil to those cases where disease absence or slow rate of disease spread is based on an intrinsic abiotic character of that soil, such as e.g. the presence of certain clay minerals (Stotzky and Martin, 1963). The term "antiphytopathogenic potential" then could be restricted to acquired biological buffer functions of a soil against disease development, originating from crop rotation, organic amendments, tolerance of weeds, or induced by the pathogen itself.

Epiphytic rhizosphere microflora

Little information is available on the influence of rhizosphere organisms accompanying different plants on root pathogens.

A crop plant can be protected against pathogens by epiphytic rhizosphere micro-organisms from weeds in mixed cultures. In a long-lasting monculture experiment peas and flax after some years were attacked by Fusaria causing footrot and wilt, respectively; when grown together with weeds (Chenopodium album. Stellaria media, Capsella bursa pastoris), plants were not or only slightly attacked (Rintelen, 1973 a,b). Olive trees grown in California with sod or grass undercover developed less Verticillium wilt than if cultivated clean (Ashworth and Wilhelm, 1971). Increased competition for nutrients indispensable to form resting structures and to obtain infection may explain these phenomena. Increase in the production of specific toxic substances produced by competitors can not be excluded.

Conclusions

Some examples have been considered of mechanisms and principles that concern the biological control of soil-borne plant pathogens. Considerable progress has been made over the last 10 years in the distinguishing and understanding of phenomena in crop management which act against epidemic growth of certain pathogens (Mitchell, 1973; Wilhelm, 1973). Much is to be learned on the causal agents of decline and of the antiphytopathogenic potential as maintained or induced by crop, crop rotation, weeds and organic amendments and on favourable abiotic conditions for the development of microbial communities controlling pathogenic organisms.

Though some practical successes have been achieved (Papavizas, 1973), the outcome of cultural techniques aiming at natural control is often unpredictable. For further progress, integrated, cooperative research on the complex associations between soil micro-organisms, plants, pathogens and the abiotic environment by soil microbiologists, soil physicists, biochemists, plant pathologists, taxonomists and plant physiologists is urgently required. Papavizas (1973) therefore strongly recommends that administrative units in plant pathology all over the world that specialize in biological control should develop coordinated research in this challenging and promising field of ecology.

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POPULATION BIOLOGY OF PARASITES WITH SPECIAL REFERENCE TO THE EFFECT OF ECOSYSTEM CHANGES DUE TO HUMAN ACTIVITY

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Summary

The stability of parasite populations and the extent to which they are regulated in relation to those of their hosts is discussed. It is considered that intra-specific competition, host immune responses and parasite induced host mortality can function as negative feedback controls upon parasite population size, but that they do not do so in most natural situations, since parasite numbers are kept at a low level by heavy mortality incurred during transmission from one host to another. In the absence of feedback controls upon population numbers, parasite populations are unstable and so very susceptible to changes in their ecosystems resulting from human activities.

Introduction

Parasite populations, like those of free-living animals, are able to increase exponentially if their growth is unchecked, and their reproductive potential generally exceeds that of their hosts. At some stage in their life cycle all parasites are metabolically dependent upon another species, their host, and in order to avoid overinfection changes in parasite population density should ideally be related to changes in host population density. If no such relationship exists or the two populations are regulated completely independently of each other the relationship between them must inevitably be unstable.

The extent to which this ideal situation is in fact realised will form the topic of this paper. It is considered that true stability can only be achieved by the operation of negative feedback controls, and that in the absence of such controls parasite populations must be unstable and so susceptible to changes in their ecosystem. An attempt will therefore be made to assess the importance of such factors as intra-specific competition and host responses, which can operate as feedback controls, in the regulation of parasite populations as opposed to such factors as losses during transmission, which cannot. The extent to which parasite populations are regulated in relation to those of their hosts and the stability of the host-parasite system will also be considered.

Transmission of parasites

Reproductive potential

The reproductive potential of parasites is considerable, and extensive powers of egg production are often supplemented by asexual reproduction. It must, however, be considered in relation to generation time (Crofton, I966), as a female of *Haemonchus contortus* with a generation time of 3 days producing 5 eggs has a reproductive rate equivalent to one with a generation time of 2I days producing 2,000 eggs. Any change in generation time as a result of unfavourable climate or host response will thus have a pronounced effect upon the reproductive potential and so upon the rate of increase of the parasite population. This high reproductive potential is consistent with life histories in which there is a very heavy mortality and a very low probability of infection, and asexual reproduction ensures that if only a single individual survives to encounter a host the parasite numbers can still increase. Very few life tables are known for parasites, but Hairston's (I965) estimate for *Schistosoma mansoni* of a daily output of cercariae by snails of 3,500, a net reproductive rate in snails of II,252, the probability of succesful infection by a cercaria of $6.9 \times IO^{-7}$, a net reproductive rate in man of II,493 and the probability of succesful infection by a miracidium of $2.39 \times IO^{-2}$ emphasises both the high reproductive potential of the parasite and the enormous mortality experienced.

Probably the greatest mortality occurs when the parasite is being transmitted from one host to another. Some, especially protozoans, employ another animal to effect this transfer and so are never free living, whereas others pass at least one stage of their complex life cycle outside of a host. They may then be active and motile, or encysted. Many free living stages do not feed but rely on endogenous reserves, and active larvae in particular often have short life spans. Encysted forms may survive longer, but mortality at this stage in the life cycle is very heavy indeed due to failure to find a host within a limited life span. Free living stages are like free living animals in that they have preferred conditions, which differ from species to species, and are susceptible to climatic changes, especially moisture and temperature. Encysted forms being better protected, are more independent of climate. Nevertheless, small changes in climate may lead to enormous changes in survival rates of parasites by either affecting them directly, for example by altering the generation time or survival rate, or indirectly by influencing numbers of an intermediate host and so altering the probability of infection. When climatic conditions are favourable, as is often the case for sheep nematodes in spring and early summer, the parasite population may exhibit an exponential increase. However, natural cyclical climatic changes inevitably impose a limit upon the length of time when the rate of population increase is so high, and in winter this may decline to zero or lower. It is clear however that changes in climate or host numbers that reduce mortality during transmission can lead to considerable increases in parasite population size, and the dependence of parasites upon climatic conditions does enable them to take advantage of favourable situations.

Host location

The majority of parasites locate their hosts by chance rather than by specific taxes. Many larvae exhibit behavioural responses that bring them into the general vicinity of their hosts, but directional responses are uncommon apart from the reactions of some miracidia to snail exudates (Cable, I972). The probability of an infected intermediate host individual being ingested by the definitive host may be increased by the behaviour of the parasite (Holmes & Bethel, I972), but location of the hosts appears nevertheless to be a fairly inefficient process, associated with heavy parasite mortality. This may be increased further by incompatibility of host and parasite strains even after their contact, and by loss of parasites such as Onchocerca larvae through failure to escape from the intestine of their vector to the site from which they can re-enter a host. Even within a host population, many individuals will prove to be insusceptible to infection.

If parasites make contact with less suitable hosts, they may be able to survive but their growth rate is frequently slower and their fecundity reduced. Many parasites are in fact extremely specific and can occur in only one or two host species, or indeed in only one or two strains of a single host species. Duke (I972) has shown how, in a single rain forest, two discrete populations of Loa loa can exist, since the simian strain utilises canopy dwelling species of Chrysops as vectors, and these bite at night when the microfilariae are present in the peripheral blood. The human strain by contrast shows diurnal periodicity and employs diurnally biting Chrysops species which live in the lower regions of the forest. These ecological conditions ensure not only that the two strains do not interchange, but also that each encounters the correct host. This type of situation is probably fairly common, and the selection of the correct intermediate hosts or vectors and the conditions prevailing in any one locality probably ensure that most parasites do end up in the correct hosts. Where many other species feed on the animal selected as intermediate host the parasite is often not very specific and is able to survive in them.

It would seem probable, therefore, that the population levels of many parasites are kept at very low levels due to the high mortality and difficulties encountered during transmission. Even when contact with a host has been made, heterogeneity in the host population with regard to susceptibility to infection further reduces numbers, and prevents a situation of overinfection arising.

Relations with members of the same or other species

Nearly all parasites show a preference for a particular region on or within a host. Overcrowding within that region leads to competition for food or suitable space, manifested generally by reduced growth and lower fecundity. Infections of birds with 200 Eimeria necatrix results in oocysts with 50,000 spores each, where infections with 2000 result in only 2,500 per oocyst. This crowding effect is especially common in tapeworms. Evidence is accumulating, however, that although the mean number of eggs per parasite may decrease with crowding, the total number per host may remain the same or even increase and the generation time is unaffected. In such cases the effectiveness of competition as a negative feedback control upon the parasite population size must be called into question.

Inter-specific competition is uncommon. The restriction of species to preferred sites and the niche diversification shown especially by nematodes ensures that inter-specific competition seldom occurs (Schad, I966), although occasional examples have been found. Direct interference and predation of one species of larval digenean upon another within a snail host have been reported. Immune responses induced by one species may be effective against another, but the degree of cross-immunity produced is nearly always unpredictable and generally not reciprocal. It appears that inter-specific reactions seldom occur, and that when they do, they may have some effect upon the parasite numbers in a host individual but little upon the parasite population.

Effects of parasite on their hosts

Where a parasite is harmful to its host, it may regulate both its own numbers and those of its host species (Crofton,I97I : Pennycuick, I97I). Heavy infections of Schistocephalus solidus affect the reproduction of sticklebacks and eventually kill them. Thus, as an infection builds up, many fish die, or are eaten, or are prevented from breeding. This causes a gradual decline in the numbers of fish, and hence in the probability of infection and so in the size of the parasite population. As infection becomes lighter, the number of fish decreases and breeding is more successful, and numbers of fish start to increase again, enabling the infection to build up again. Both host and parasite numbers would thus oscillate, with the size of the oscillations being modified by factors such as food supply, climate and abundance of other host species. In such a situation the parasites are generally overdispersed, and a large number of parasites occur in a few host individuals. These are the ones that die as a result of the parasite's effects, and so the parasite population is reduced by many more individuals than is that of the host. Overdispersion ensures that few hosts are infected and keeps the infection to a moderate level. The intensity of the regulation of host and parasite populations will depend upon the degree of overdispersion and especially upon the size of the parasite population. Such a system is thus a stable one, with negative feedback controls operating upon both species populations.

If the heavily infected host individuals are eaten by a definitive host, then this may be advantageous to the parasite in that it has attained the next stage in its life cycle. It will however reduce the effectiveness of the population regulation, since there will be no loss of parasite to the population. The effectiveness of this as a method of regulation will also be reduced when only a part of the host population is susceptible to infection, as is often the case with vectors of protozoans.

If all parasites are capable of killing their hosts at some population level as Crofton (I97I) suggests then this method of regulation could in theory operate in all host-parasite systems. In practice, however, many parasites appear not to have any deleterious effects upon their hosts or not to reach lethal levels, and there must be some doubt as to how widespread this method of population regulation really is.

Host responses to parasites

Although most invertebrates appear to be capable of responding to parasites that do not normally infect them, their responses to their normal parasites, if manifested at all, seldom if ever appear to reduce the parasite population size. The same is true of many poikilothermous vertebrates. Fish are capable of antibody production, but only against two or three species of parasite such as Ichthyophthirius multifiliis does this confer any protection against re-infection. For the majority of fish, and for many invertebrates, the level of infection depends upon success of transmission and the degree of contact between host and parasite, and not upon host responses (Kennedy, I970).

By contrast, many homoiotherms respond vigorously to the presence of parasites by antibody production. Infections of Trypanosoma lewisi in rats are controlled and eliminated by host antibodies; by antibodies preventing parasite division, and by those killing the parasite. The majority of protozoans in birds and mammals elicit host responses, although their effectiveness varies. Helminths, especially nematodes, also provoke host immune responses, which are generally manifested by reduced fecundity, stunted growth, inhibited development, longer generation times and reduced numbers establishing on second and subsequent infections. These effects have been well documented in sheep nematodes such as Haemonchus contortus (Ratcliffe et al, I969) and the rat nematode Nippostrongylus brasiliensis, (Ogilvie and Jones, I97I). Most mammals also respond effectively against encysted cestode larvae.

Immune responses thus appear to be capable of acting as effective negative feedback controls upon parasite numbers. They are widespread amongst homoiotherms, and their intensity depends upon the degree of stimulation and hence the population size. It is becoming increasingly clear, however, that many parasites are able to avoid the immune responses they provoke. Trypanosomes and some species of Plasmodium do this by antigenic variation in response to host antibody production. Adult schistosomes avoid the response they provoke by incorporating host molecules upon their surface and so disguising themselves (Smithers,I968). Many nematodes only elicit a response when their numbers per host rise above a threshold level, the response may then be delayed until some individuals have reproduced, and some survive the response, albeit often in a state of inhibited development, and continue reproduction. Other parasites, such as Leishmania donovani, live in immunologically privileged sites where the antibodies are unable to reach them.

Host immunological responses have, in fact, been investigated most frequently in laboratory populations, and in hosts kept under 'unnatural' conditions such as farms.

There are few natural host-parasite systems in which they have been demonstrated. They may reduce the numbers of parasites in individual hosts, but appear to have little effect upon population levels. Host responses are often not provoked at all in natural host-parasite systems, and if provoked are avoided, and so it must be considered as doubtful whether they play any major part in regulating parasite populations.

Stability of host-parasite systems

In the foregoing discussion attention has been centred upon the parasite population at different stages in its life cycle, but it is essential to remember that at any one time the population contains individuals in one or more host species and outside of the host. Feedback controls operate upon the parasite when in one species of host, and may regulate the numbers of parasites per host individual or even the numbers of parasites in relation to the numbers of that particular host, but their effect upon the parasite population as a whole must be much less. Even when manifested, their importance must be compared with that of such factors as climate. It does appear that the success of transmission plays a major part in determining parasite densities in any locality, and that difficulties in transmission under natural, as opposed to experimental and farm, conditions keep populations below the level at which feedback responses operate. If it is accepted that feedback responses play little or no part in regulation, then it would appear that most parasite populations and host-parasite systems are unstable. Because of the close relationship between transmission success and climate it also follows that parasite population levels are heavily dependent upon local habitat conditions, both biotic and climatic. They must therefore be very susceptible to changes in their ecosystems, whether such changes be natural or as a result of human intervention.

Changes in the ecosystem may of course either increase or decrease the success of transmission, and so lead to epizootics or to extinction. Examples of both are to be found in all spheres of human activity, and especially in aquatic ecosystems. Formation of reservoirs leads to increased incidence of parasites using copepod intermediate hosts. Introduction of species may bring together susceptible hosts and virulent parasites. Eutrophication, with its associated faunistic changes, leads to characteristic changes in parasite fauna with an increase in bird dependent species. Irrigation schemes in tropical countries have often provided an increased area for aquatic snails, and so lead to a rise in schistosomiasis. Farming, by concentrating a genetically homogenous stock in a small area, greatly favours the spread of some parasites. On the other hand, drainage of swamps, by destroying sites for snails and mosqitos, may reduce both malaria and fascioliasis. In all cases the existing, but unstable, equilibrium has been upset by human intervention, and as with most unstable equilibria, the effects of disturbance are, in the current state of knowledge, unpredictable.

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MATHEMATICAL MODELS IN THE POPULATION ECOLOGY OF PARASITES

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(Extended Abstract)

The test of whether we understand a biological system is whether we can predict the changes it will undergo; if we wish to specify our predictions quantitatively and are able to measure the independent variables which may change the biological system, we are well on the way towards making a mathematical model. The type of model of a parasitic system to be made will depend on our requirements in terms of precision, realism and generality, as has been frequently discussed in the broader ecological context. The aims of parasite models and modellers fall into several groups:

1. Illuminating epidemiological understanding. The attempt to make a model will show up areas of quantitative ignorance and may encourage others, even if not the model-builder to go out and measure what he has had to guess at. When figures are put into the model, glaring discrepancies may arise and suggest qualitative omissions from epidemiological understanding. For example, Hairston's simple equilibrium model for <u>Schistosoma japonicum</u> pointed to a neglected alternative host from man, the rat. The intellectual effort of making a model forces us to tidy up woolly corners in our picture of what goes on.

2. Those most concerned to predict changes in parasite populations are usually paid to get rid of parasites and are therefore interested in obtaining the greatest possible reduction in parasites from the smallest amount of effort. Their models are to aid control strategy, and they ask three particular questions:-
(i) Will a control programme have an effect in an endemic area?
(ii) What is the likelihood of getting rid of the last few parasites from an area, and conversely, what is the chance of a few introduced parasites giving rise to an epidemic in a host population previously untroubled by the infection? They therefore have a principal interest in the stability of parasite populations at their upper and lower limits.
(iii) In the middle levels of parasite population what is the best combination of control tactics?

Models of parasites have been of two main types, as elsewhere in ecology: the complex realistic model, heavy on data, specific and precise. Lack of relevant data has limited the use and success of such models. Alternatively there are simpler, more general models, elegant but of little practical application. These have been pushed a good deal further by mathematicians than for other ecological models so that there are some complex mathematical edifices poised on the pointed bases of a few crude assumptions, especially for malaria and schistosomiasis. The field has been dominated by the sound but limited approach of a set of differential equations for changes in the numbers of infected, uninfected, and removed. More recently, with computer help, stochastic approaches and difference equations have tended to augment this classical analysis. But one can still draw attention to whole neglected.

A. <u>Spatial Structure</u>

A basic assumption of most models in population ecology and all in parasitic diseases is a homogeneous habitat: mosquitoes and men wander over a featureless plain at random. This is an oversimplification as most components of models are, and may not matter in malaria. When we consider clusters of people living around isolated water-holes containing small static groups of aquatic snails transmitting schistosomes, then the focality of transmission and the spatial structure of models of it may be the crucial aspect. Maynard Smith's models of patchy environments may point the way for parasitological work.

B. Aggregation of parasites

The distribution of parasites among hosts in nature is highly aggregated, yet most models assume random dispersion. The effects of aggregation on reproductive success of sexual parasites and on maintenance of transmission have been little explored, except in relation to mortality by Crofton. Where aggregation has been studied, mathematical distributions have been fitted to data and there are many ways in which they could have been generated. Some realism (hence more empirical data) is needed over the generating processes before this can be pursued further.

C. Pathogenicity

Models which incorporate pathology due to the parasite into their design are important in two ways. First, where mortality of hosts is appreciable it will affect transmission and Crofton has attempted a model in which this mortality is the main regulatory mechanism, though calculations by Gliddon and myself suggest that the cost to the hosts of such parasite regulation may be intolerably high. Second, host morbidity and mortality is the main reason for many parasitological studies and thefore a model that ignores this may be of limited utility.

D. Immunity

Survey of published models of parasitic infection shows a marked emphasis on transmission and neglect of acquired immunity within the hosts, particularly mammalian and avian hosts. At this point there exist potentially strong feedback loops. Models show one of two defects. Either they ignore the effect of acquired immunity as in Macdonald's models of malaria and schistosomiasis, or else they use very simple and unbiological ways of modelling immunity.

Such approaches tend to give an inaccurate picture of the stability of the endemic state. If the endemic level is used (as it often is) to calculate the parameters of the model (especially infection and recovery rates), these may be erroneous. Two solutions are available: either biological realism, even if the mathematics is messy, or a thorough theoretical exploration of the effects of a range of immunological assumptions to see how robust the model is in this respect. If acquired resistance occurs, delay factors in its gain and loss may be crucial to modelling effects of control measures and this has rarely been done.

E. Genetic change

Epidemiological models have assumed constancy of the host and parasite: genetic change has been ignored. Yet this is clearly untrue for one infection, myxomatosis, in which large changes in both virus and host occurred in ten years, and it would be rash to treat this as a unique case. Among potentially lethal parasites a form of group selection occurs, and that outside the contentions which normally surround group selection.

Models have also assumed genetic homogeneity of hosts and this too may be significantly untrue for such infections as leishmaniasis.

We may combine several of the aspects mentioned above. If we follow the concept of patchiness further, we find that the parasites show it in a very tidy fashion: the parasite patch is the individual host and parasite population biology is one extreme of island biogeography. Here is room for interaction between models in parasitology and outside. MacArthur and Wilson's models of islands are very relevant. They have produced the concepts of $\underline{r}$ and $\underline{K}$ selection. Although competition by other organisms is replaced by host reaction, these concepts can be applied to infections. Some parasitic microbes, such as the cholera vibrio and the smallpox virus, have adopted an $\underline{r}$ strategy of rapid multiplication and dissemination before the host's immune response acts; most protozoal infections follow rather a $\underline{K}$ strategy and persist by various means in the face of immune responses. The same is true of helminth infections which, because of their not multiplying indefinitely within the vertebrate host fit an immigration-death process and are formally analogous to breeding migrants, with often a strong territorial pattern preventing crowding.

Evolutionarily, one might envisage a change from $\underline{r}$ to $\underline{K}$ strategies, and this is observed in the evolution of myxomatosis in Australia.

For the future, epidemiological models will therefore need to add to their structure ways of coping with some of the following:

- Discrete nature of habitats (hosts)
- Spatial patterns of transmission
- Acquired resistance by hosts
- Host behaviour
- Genetic heterogeneity of hosts
- Increased realism in negative feedback mechanisms.

These aspects will be discussed, with reference to specific models in parasite epidemiology and considering the relation between models of infective systems and those of free-living animal populations. Sometimes parasitic systems can be interpreted using models from the rest of ecology, and sometimes hosts and parasites provide systems which can illuminate ecology as a whole.

THE ECOLOGY OF ONCHOCERCIASIS IN RELATIONSHIP TO THE ECOLOGY OF MAN

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Summary

The life cycles of Onchocerca volvulus and of its Simulium vector are outlined. There follows a consideration of the ecology of human onchocerciasis in the Sudan-savanna zone of West Africa, where the disease has far-reaching consequences as the cause of "river blindness."

Introduction

Human onchocerciasis embraces all disease caused by the filarial worm Onchocerca volvulus, which infects 20-30 million persons in the world today. To appreciate its ecology, one must understand the basic facts of the parasite's life-cycle as well as that of its insect vector, Simulium spp.

Life cycles of O. volvulus and Simulium

O. volvulus is a parasite virtually confined to man. Apart from the insignificant possibility of gorillas and chimpanzees acting as such, no reservoir host is known. The adult worms (males 5 cm and females 50 cm long) live encysted in fibrous nodules which may be single or conglomerate (up to 10 cm in their longest axis) and contain many worms forming an inextricably tangled mass. Some are palpable in the subcutaneous tissues over the bony prominences of the knees, trochanters, iliac crests, ribs, scapulae and head. Others, probably more numerous, are deep and impalpable attached to the capsules of the joints (especially the hip), in or between the muscles, or against the periosteum of the bones.

The adult worms live for up to 15 years, and the female throughout her life produces an abundant supply of first stage larvae, known as microfilariae (mfs) of dimensions 300 x 10 microns. The mfs find their way to the subepidermal layer of the skin, where they accumulate until either they die at the end of their life-span of some 6-30 months or, more advantageously but more rarely, they are ingested by a feeding female Simulium of an adequate vector species.

After ingestion by the intermediate host the mfs penetrate the gut wall and complete their development, without any multiplication, in the thoracic musculature. After some 6-12 days, depending on the ambient temperature, and having moulted twice, they become infective larvae (650 x 20 microns) which invade the haemocoele and pass up to the head and proboscis. When the now infective fly takes a further blood-meal from man the larvae escape from the proboscis and enter the definitive host through the puncture wound in the skin. They then migrate to the adult worm sites where, after a pre-patent interval of about 15 months, they mature and produce a new generation of mfs. As there is no multiplication of the young worms after inoculation into man, it is only from repeated infections acquired over a considerable period of time that the O.volvulus population in the body can build up to a high concentration.

The Simulium vector plays a vital part in the ecology of onchocerciasis. The flies are often locally very abundant and, although their flight range is commonly 5-20 or more km., they are always confined ultimately to association with fast flowing water-courses, which are essential to the survival and development of their eggs, larvae and pupae. It is only the adult females which bite, for the reason that they need a blood-meal to provide the nourishment necessary for the development of each batch of eggs laid. The interval between their blood-meals depends on the length of the gonotrophic cycle, and a fly which ingests mfs at its first blood-meal is not normally capable of passing on infective larvae until it takes its third blood-meal.

Although the chief African vector, S. damnosum, will feed on a multitude of mammals and birds, when man moves into its range he constitutes a particularly suitable source of blood-meals. He becomes the most abundantly available large diurnal animal, is readily detectable by the visual and olfactory senses, spends much of his time within easy reach of water, and has a large area of hairless skin from which blood is easily obtained. In addition, his hunting activities serve to eliminate most of the other animals near his habitations, so that the originally catholic S. damnosum often rapidly becomes highly anthropophilic. To a great extent the degree of anthropophily exhibited by a given S. damnosum population will govern its efficiency as a vector of O. volvulus.

Pathology of onchocerciasis

Most of the pathology associated with O. volvulus infection in man is caused by the mfs, which are thus ultimately responsible for the effects of the disease on his ecology. In the skin the products of their metabolism, and the tissue reactions associated with their death, may cause very severe itching. Associated lesions of fibrosis, with atrophy or thickening, may lead eventually to extreme dermal changes, enlargement of the regional lymph glands and a predisposition to herniae and elephantiasis. In heavily infected persons, and especially those with nodules on the head, the mfs from the skin invade the conjunctiva and then the cornea of the eye, where they may cause blindness from sclerosing keratitis. Recent work (Fuglsang & Anderson, 1974) suggests that a small, but pathologically important number may also pass from the skin *via* the lymphatics and enter the blood-stream. There they tend to accumulate in the kidney glomeruli (whence they pass to the urine), and probably also in the lung capillaries (whence they pass to the sputum), and in the choroid plexus (whence they pass to the cerebrospinal fluid, and thus may gain access to the brain, the optic nerves and the pituitary gland). They also pass by routes as yet uncertain (again possibly *via* the blood-stream) into the inner eye, wherein they can produce iridocyclitis, inflammation and/or atrophy of the choroid and retina, and post-neuritic optic atrophy, all of which are important causes of blindness in onchocerciasis (Anderson et al., 1974a).

Ecology of human onchocerciasis

Onchocerciasis is found throughout most of tropical Africa south of the Sahara, whereever watercourses suitable for the breeding of *S.damnosum* or *S. neavei* are found. It also occurs in several tropical Latin American countries, and there is a small focus in Yemen. The ecology of the disease and its effects on man vary from one geographical area to another. It is now thought that these differences result from the existence of several strains of *O. volvulus*, each associated with a different species of *Simulium*, or with a different sibling species of the *S. damnosum* complex (Dunbar & Vajime, 1971), forming distinct *Onchocerca-Simulium* complexes (Duke et al., 1966; Lewis & Duke,1966). There is little interchange of parasitic material between separate complexes, owing to the lack of transmissibility of the mfs by any but their own associated form of the vector.

As it would be impossible in a paper of this length to cover the ecology of human onchocerciasis in all areas, attention will here be confined to the disease in the Sudan-savanna zone of West Africa, wherein the highest prevalence of "river-blindness" is encountered, and where the effects of the disease on human ecology are most striking.

It is chiefly because of its adverse effects on the human eye that the parasite influences the ecology of man. Its failure to adapt perfectly to its host, and the consequent production of a severe human disease, is of no benefit to the parasite. It leads rather to the human hosts removing both themselves and the parasite from the environs of the vector, and later to a demand for control, which may eventually eliminate *O. volvulus* from large areas of its present range.

Although many theories have been put forward to account for the peculiar ocular virulence of onchocerciasis in the savanna zone, it is currently my opinion that it results chiefly from the characteristics of the strain or strains of parasite found there. Compared to strains from other topographical areas (as, for example, the West African Forest zone), those from the Sudan-savanna are exceptionally prolific of mfs, leading to very intense concentrations of these organisms in the skin and other tissues (Anderson et al., 1974b). These mfs also have an enhanced ability to invade the cornea and produce more severe lesions in that tissue, (Duke & Anderson 1972; Garner et al., 1973), in addition to the damage which they do in other parts of the eye.

The worst affected inhabitants of those savanna villages which are subjected to heavy transmission of *O. volvulus* may show concentrations of 100 - 500 mfs/mg of skin over the entire body, with as many as 500 mfs in each cornea, and 100 or more present in each anterior chamber at any one time.The total load of mfs in such a person may be estimated at around 50 - 200 million, and this population turns over *in toto*, as a result of death in the tissues and replacement births, at least once every 1 - 2 years.

Virtually 100 per cent of the persons living in savanna villages, where there is any degree of local transmission, are infected with *O. volvulus*. The intensity of their infections, which is a more important consideration than mere prevalence figures, varies with the amount of transmission, but in all communities it rises with age until adult life is reached, after which it levels out somewhat. Males are usually more heavily infected than females, which may be partly a result of a greater occupational exposure to the bites of *Simulium* or, since the sex difference in intensity is often more marked after the age of puberty, may be linked with hormonal differences (Duke et al., 1972).

Severe eye lesions and blindness are more common in males, but there are marked individual differences in the susceptibility of the eyes to the presence of the parasites. The reasons for this, which may be immunological, are not understood. For example, in the same village a child of 9 years may have been blinded by onchocercal lesions of the anterior segment, while other adults, whose corneas and anterior chambers are full of live mfs, apparently tolerate their parasites well and show only minimal eye lesions. In the worst affected but still just viable villages, whose economy is based on subsistence farming and a few cash crops, the overall picture is one of a blindness rate of 7 - 10% in those over 5 years of age (rising to about 20% if adult males alone are considered), and with some children who are totally blind before the age of 10 years. Above this level of blindness the community gradually ceases to be able to support itself. Families move away, new families do not move in and it is those which remain till the last who produce the startling temporary figures, such as six blind persons out of a population of nine, which are made much of by medical propagandists.

The rapidity with which children become infected, and the intensity of the infections which develop in any community, result from the degree of transmission of O. volvulus to which they are exposed. Theoretical figures for the transmission potential of the parasite may be obtained by estimating the total number of Simulium coming to bite a man exposed continously, during all the hours of daylight throughout a whole year, at a chosen point(s) in the village environment. By dissecting the flies caught by a fly-boy and observing the presence or absence of the fat body, the proportions of nulliparous (uninfected) and parous (potentially infected) females in the population can be ascertained. The parous flies are then further examined for infective O. volvulus larvae and the number of infective larvae available for transmission per man per year (i.e.the transmission potential) can thus be estimated. Although the figures obtained in this way are far above the actual level of transmission to which any person is ever actually exposed, they serve as a useful index for comparative purposes.

The biting behaviour of S. damnosum in the Sudan-savanna has a particular influence on the amount of transmission effected at different distances from the breeding sites. Nulliparous flies (young females in search of their first blood-meal) will readily fly considerable distances across country from their riverine breeding sites. Parous flies on the other hand, and especially those in search of their 3rd or subsequent blood-meal, which are the potentially infective section of the population, tend to stay confined closely to the water-side. They may however, move freely along the rivers and so bite close to the river bank at considerable distances from the actual breeding sites.

In one area, which I have studied, the biting density of S. damnosum 3 km inland from the nearest riverine breeding site was higher than that on the breeding site itself, but the parous rate in the flies caught there was only 30%, compared with 70% on the bank of the breeding river. This difference, coupled with the finding of a higher proportion of older and infective parous flies biting near the river, contributed to a transmission potential of about 16,000 infective larvae per man per year at the riverside, a figure which is almost certainly well above the level which could be survived by any community. It compares with transmission potentials of 2,300 near a village having 14.4% of blind persons in the over 20 age groups, and situated 3 km inland from the river; 1,100 at another village, lying 7 km from the river, having a blindness rate of 4.0% in the over 20's; and 300 at a third village, with no blind persons, lying some 25 km from the nearest permanent breeding site, but having a small rainy season site about 5 km away.

It is obviously important to know over what distance the sharpest drop in the biting rate of infective flies occurs. My experiments so far indicate that it is already marked at 1 km from the river bank, and it may well be that the majority of infective flies are reluctant to move more than a few hundred metres inland.

It follows that the distance from the nearest breeding site will largely govern the amount of transmission in the environs of a village, and that the amount of transmission may vary considerably from one part of the village habitat to another. Those whose outlying farms approach close to the river will be exposed to a greater risk of infection than those whose farms lie in the other direction away from the river. In this way marked differences in intensity of infection may arise among different families in the same village.

Likewise, persons whose occupations take them right to the river bank will be subjected to a much higher transmission intensity than those who work even 1 km from the river. Fishermen and ferry-men will thus be particularly exposed and indeed it is frequently found that very heavily infected persons, and those with severe eye lesions, will, if closely questioned, give a history of intimate association with the riverside at some period in their lives.

Many other factors influence the amount of transmission to which a village population is exposed. Even in a village lying several km inland from a main-river breeding site, small tributary streams near to the village, which are dry for most of the year, may start to flow during the rainy season and support breeding S. damnosum for perhaps 1 - 4 months. Infective parous flies will thus seasonally have a much easier access to the human population.

Again the location of a village near to a breeding river which has an attractive sandy beach, where the people go readily to bathe and wash, may lead to the population being exposed to a much heavier transmission than they otherwise would be. Or, should parties of fishermen spend the dry season encamped near good fishing pools (often just below Simulium breeding rapids) they may set up an extremely intense degree of local transmission among themselves.

It is a combination of such factors that may enable a village only 2 - 3 km from a permanent breeding site to survive with a blindness rate of nearly 10% in persons over 5 years old, whereas if it had been established at the riverside it would probably have long since been deserted. An example of the latter is quoted by Rolland (1972). An immigrant and previously lightly-infected community established a new village site on the bank of a river in a highly endemic area. Over a period of 5 years many had developed eye lesions and heavy infections, although none were yet blind. Four years later the village was reported as deserted. This incident suggests that previous estimates of 20-30 years being the period of time over which O. volvulus can build up to crippling levels in a new community exposed to maximal transmission (Duke, 1971), may have to be revised downwards.

The need for water and fertile soil in the arid West African savannas are two factors which tend to bring communities closer to Simulium breeding sites. Water requirements may lead to excessive exposure only if the breeding river itself has to be visited to satisfy drinking and washing requirements. The presence of a deep well, or even a seepage water-hole, near the village and away from the breeding sites, will obviate this risk to a great extent and should provide an added incentive to the construction of deep wells in all villages.

Although in general the more fertile land tends to lie in the dangerous zone near the breeding rivers, this is not always true. Wide fertile depressions with good soil but with no water suitable for Simulium breeding, often run for considerable distances at right-angles to the main river breeding-sites. Much depends on the local topography, and sometimes the rocky outcrops which provide the breeding stretches in the main river may be represented on the banks as infertile areas with poorer soil.

As we have seen, given adequate food and some cash crops such as cotton or groundnuts, communities are capable of surviving in equilibrium with O. volvulus, provided the blindness rate in those over 5 years of age does not rise above 10%. This is so despite the fact that they are condemned to suffer this great endemic disease as an extra burden on top of holoendemic malaria and the whole gamut of tropical epidemic diseases. Part of the explanation for this phenomenon is that many of the totally blind are not a complete loss to the labour force. They can still be led out to work in the farms, where they become adept at weeding the staple guinea corn and millet crops, and performing other simple tasks, by touch alone. They are also employed to scare monkeys from the farms, detecting their arrival by ear. Others, technically blind by western standards, with visual fields reduced to less than 5 degrees, can still perform an even wider variety of simple agricultural tasks. It has also been observed that the very highly infected and the onchocercal blind are often somewhat wasted and debilitated, and tend to have a higher mortality than those who can see to fend for themselves. Therefore they do not usually remain as a burden to the community into old age. They are particularly at risk from death by burning. Not only is there a perpetual danger from the home cooking fires but, in a country where all the bush is burnt annually during the dry season, bush fires frequently get out of control and stray sparks can turn a straw hut into a blazing inferno in a matter of seconds.

The socio-geographical and socio-economical aspects of onchocerciasis in savanna communities have been studied in northern Ghana by Hunter (1966), and in the Hawal valley in Nigeria by Bradley (1972). They have produced evidence of cyclical advances and retreats and other abnormal movements of the population for which "river blindness" is most probably the exciting cause. However, it should not be forgotten that in heavy onchocerciasis zones migrations of small groups of families, or even of whole villages, may take place for a variety of reasons unconnected with the disease. Some natural catastrophe or epidemic may give a place a bad name, and the remoteness of many onchocerciasis areas is a factor mitigating against settlement. Sometimes it may even be that the authorities order a village to move so as to settle the inhabitants in an accessible area from which tax can be more easily collected. I have once seen a village up-rooted from a remote corner of the bush where there was only light seasonal transmission, and obliged by the authorities to re-settle along a road running parallel to and 1 km away from a perennial breeding river.

Despite claims to the contrary, it is doubtful whether in Africa the biting nuisance of S. damnosum is per se a factor causing the people to desert fly-infested areas. In some places in the forest zone, where biting densities of up to 4,000 an hour are encountered, protective leggings made of banana leaves or other materials are sometimes worn; but there is nothing comparable to the assaults of Simulim in the north of Canada where, during the short arctic summer, their bites render life itself impossible without protective clothing. Without doubt an African riverside is a much more pleasant place without the attentions of S damnosum, but one still sees fishermen, diggers of river sand, ferrymen etc. working all day in places where the highest biting densities can be recorded by a trained fly-boy.

The importance of the itching associated with onchocerciasis is another factor which is sometimes exaggerated, at least as it applies to the natives of hyper-endemic savanna foci. The majority of persons who have been infected since early childhood do not complain of itching, nor do they show evidence of excessive scratch marks on their skins. The intensely itching skin lesions of onchocerciasis affect mainly those who enter the endemic areas for the first time as adults. This type of reaction is common among expatriates, as well as in African workers born outside the endemic areas. Fear of the "filarial itch", as well as a largely unfounded fear of blindness, may lead to great difficulty in recruiting the expert personnel necessary for development projects. They may refuse to work in onchocerciasis zones or to expose their families to the risks involved. This factor may well hinder the development in such areas, for there is as yet no chemprophylactic available against the parasite.

Control of onchocerciasis

The control of onchocerciasis which will in future be one of the main factors affecting the ecology of the parasite, would appear to be an essential prerequisite to the development of the full agricultural potential of the arid savanna zones of West Africa. In the areas of Upper Volta, where control has now been maintained for 5 - 10 years, there is good evidence that it permits the re-population of previously uninhabited or deserted areas, and thus leads to increased cultivation of food and cash crops. There is also an associated rise in the per capita income and over-all economic output of the population.

It is also necessary, when planning development projects, to consider their effect on the Simulium population and on the transmission of O. volvulus. Water conservation is often the vital factor in development, whether for agriculture, fisheries, or for hydro-electrical energy. The construction of dams to conserve the excess rainy-season run-off water may of itself be beneficial in that the lakes formed behind the dams will, by slowing the water flow, eliminate a number of upstream breeding sites. On the other hand, the dam spillways may provide an ideal new Simulium breeding site, and in this way have already led to the spread of S. damnosum into hitherto uninfested areas at the northern end of its range. Fortunately the spillways of dams can be designed in ways that facilitate the control of Simulium larvae in them.

Control of onchocerciasis, is at present based on the control of Simulium by application of larvicides to their equatic breeding sites. The larvae are killed at very low concentrations of insecticide (1 part of the active principle in 20 million to 1 part in 1 million maintained over 30 minutes, the dose decreasing as the flow-volume increases). Hitherto DDT has been used with great effect, but it is not readily broken down and thus accumulates in aquatic and other forms of life, especially in fish, which form an important item of protein in the savanna. This has led to its being replaced by the organophosphorus products, such as ABATE, despite their much greater cost. The use of light aircraft and helicopters in spraying remote parts of rivers has proved to be effective and economical.

In view of the long life of the adult O. volvulus, control of Simulium(as opposed to eradication, which is in most places an impossible goal) must be maintained for at least 15 - 20 years. Throughout this period transmission must be eliminated, or reduced to insignificant levels which have yet to be accurately quantified. Only then can the disease be expected to die out in the population. The applications of insecticide must be made at regular intervals, shorter than that needed for the development of the insect from egg to pupa (usually 7 - 10 days); and they must be continued for at least the maximum duration of the life of the adult flies (2 - 8 weeks). Furthermore, owing to the long flight range of the fly (40 km or more) - and the capacity of the larvae for casting off, floating long distances down-stream, and then reattaching - control must extend over wide areas and involve whole river systems. It must also be maintained with vigilant supervision for as long as the danger of reinfestation from outside continues; and the development of insecticide resistance must be obviated.

If Simulium can be temporarily eliminated from a considerable area, it may then be possible to confine control operations to a peripheral border zone so as to prevent re-infection from neighbouring infested areas. In Africa this means that many countries will have to co-operate in the control of onchocerciasis and Simulium over the large river systems which traverse their frontiers. Mutual co-operation through the auspices of international bodies becomes essential, and the first such scheme, organized by the World Health Organization, has just started. Operating with a very large budget, financed largely by the richer nations, and involving 7 West African countries, its primary aim is to control onchocerciasis on the huge Volta River system.

Supplementary chemotherapeutic measures, designed to reduce the reservoir of mfs available to the fly in the human population, are not at present a practical proposition. The severity of the reactions which occur in patients, when the parasites are killed by suramin or diethylcarbamazine, are too great for these drugs to be used on a mass scale. However, there is a definite role for careful treatment of those members of the population, small in proportion but large in total numbers, suffering from eye lesions that are likely, if left untreated, to progress to blindness.

It is along these lines that we may hope to achieve control of "river blindness", but only time, money and a great deal of hard work will tell whether the ecology of onchocerciasis can be altered to the permanent detriment of the parasite and to the significant benefit of man.

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Ecological consequences of deforestation for vegetation, soil and aquatic systems mainly in the tropics

EFFECTS OF FOREST CLEARING ON THE NORTHERN HARDWOOD FOREST ECOSYSTEM AND ITS BIOGEOCHEMISTRY

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Introduction

Forests and woodlands cover about 38% of the total continental area or 11% of the earth's surface (Whittaker & Likens, 1973). Since trees are long-lived and over time accumulate large amounts of their biomass as wood, they dominate the forest landscape and have provided man with firewood, timber and other wood products. However, man's demands often have been at variance with the structure of the forest ecosystem, and large areas have been cleared of forest vegetation. Such clearing is currently proceeding at an unprecedented rate in the tropics (e.g. Croat, 1972), the most productive ecosystem type of all (Whittaker & Likens, 1973).

Water in some form is usually a conspicuous feature of the forested landscape. Rain and snow not only supply the water which replenishes groundwater reserves, and fills stream channels, ponds, lakes, swamps and marshes, but also provide the moisture for forest growth in humid regions. Indeed the existence of these forests is dependent upon available water. Once water has fallen to the earth it may run off overland, infiltrate into the soil or evaporate (mostly by transpiration in humid forests), and thus complete the hydrologic cycle. Aquatic and terrestrial ecosystems within the same landscape functionally interact and are linked by water moving in the hydrologic cycle. Chemicals, particularly those without a prominent gaseous phase (e.g. phosphorus, calcium and potassium), are largely transported across ecosystem boundaries by moving water. This is especially true if the ecosystem's boundaries are taken as those of a watershed (Bormann & Likens, 1967).

Hubbard Brook Experimental Forest

Detailed studies, starting in 1963, have quantified the inputs and outputs of water and chemicals for several small, undisturbed forested watersheds of the Hubbard Brook Experimental Forest in the White Mountains of New Hampshire, U.S.A. (Fig. 1). The

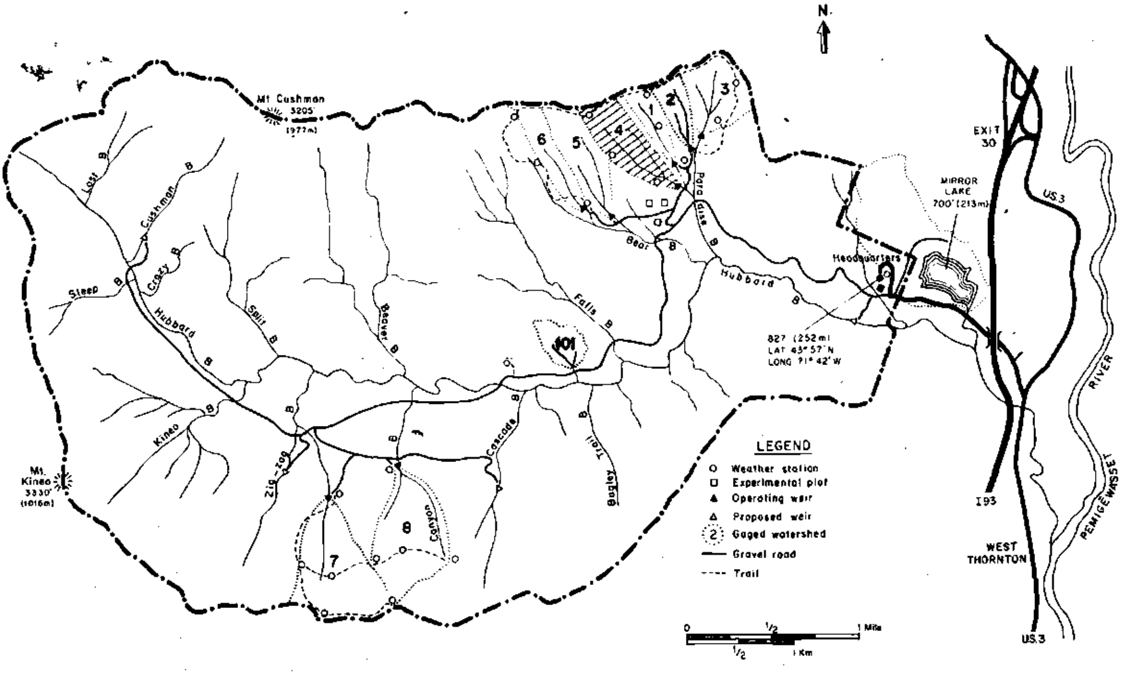

Fig. 1. Outline map of the Hubbard Brook Experimental Forest showing the gauged watersheds, experimental treatments, weather stations and streams tributary to Hubbard Brook.

Experimental Forest is dominated by a northern hardwood forest ecosystem, underlain by a highly metamorphosed sedimentary bedrock (gneiss). The climate is characterized by short, cool summers and long, cold winters. Annual precipitation averages about 125 cm of water, of which 30 to 40% falls as snow. Some 60% of this precipitation input is lost as runoff and the remaining 40% is lost as evapotranspiration (Likens et al., 1974). The monthly input is relatively constant throughout the year, whereas runoff varies markedly with season (Fig. 2).

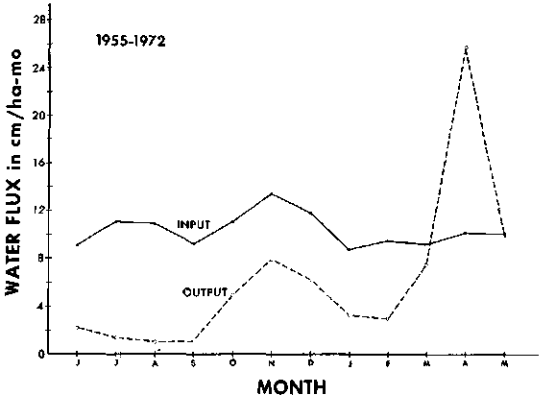

Fig. 2. Average monthly precipitation and runoff for the Hubbard Brook Experimental Forest during 1955-1972 (from Likens et al., 1974).

Undisturbed forest ecosystem

A significant finding from our studies was that the input of nutrients in rain and snow represents a major contribution to the chemical nutrient budget for these ecosystems (Table 1).

Table 1. Average annual inputs and outputs of dissolved substances in kg/ha for undisturbed watersheds at Hubbard Brook during 1963-1972 (modified from Likens et al., 1974).

Element	Input	Output	Loss	Gain
SiO_2-Si	*	16.4	-16.4	
Ca	2.3	12.5	-10.2	
Na	1.6	6.8	- 5.2	
SO_4-S	11.9	16.2	- 4.3	
Mg	0.6	2.9	- 2.3	
Al	*	1.9	- 1.9	
K	0.9	1.7	- 0.8	
NH_4-N	2.3	0.3		+2.0
Cl	6.3	4.6		+1.7
H	0.98	0.09		+0.89
NO_3-N	4.0	3.3		+0.7
P	0.11	0.01		+0.1

*not measured, but very small

In particular, more inorganic nitrate, ammonium and phosphorus are brought into these ecosystems in rain and snow each year than are lost in drainage waters. Sulfate and hydrogen ion, as chemical equivalents, dominate the precipitation at Hubbard Brook and the pH averages about 4.1. Concentrations of nitrate and hydrogen ion have increased in precipitation in recent years, presumably as the result of increased air pollution (Likens et al., 1972; Likens & Bormann, 1974).

Another major finding was that even though large amounts of nutrients may be input, stored or cycled, generally small amounts of nutrients are lost from these undisturbed ecosystems in drainage waters (Likens & Bormann, 1972; Hobbie & Likens, 1973). Stream discharge varies over several orders of magnitude during a year, but the chemical concentration of stream water remains relatively constant (Likens et al., 1967; Johnson et al., 1969). Year-to-year variations in stream-water chemistry also are small (Likens et al., 1974). Since the chemical concentrations are relatively constant in stream water, annual export of nutrients is directly related to stream runoff and is predictable.

The structure and function of the biota and soils of the ecosystem provide a major, stabilizing influence on the output of nutrients with drainage waters (e.g. Bormann et al., 1969, 1974). The biotic structure of these forested ecosystems alters both the potential energy and chemistry of water fluxing through the system. The kinetic energy of the falling raindrop is largely absorbed by the vegetation canopy and litter, and the potential for erosion is greatly reduced. Moreover, as precipitation comes in contact with the vegetation, its chemistry is altered significantly (Eaton et al., 1973). The biotic portion of the ecosystem tends to regulate not only the amounts and timing of runoff, but its chemical content, through ion exchange, biological utilization and evaporation. Loss of water vapor through evapotranspiration (mostly transpiration at Hubbard Brook) tends to conserve nutrient loss from the ecosystem, given that stream water contains some dissolved substances. Erosion also is reduced as potential runoff is lost as water vapor. Significant fractions of aluminum, carbon, iron, phosphorus, potassium and silicon may be exported in particulate matter. However, in general, losses of particulate matter normally contribute a small proportion (16%) of the total nutrient loss from undisturbed forested watersheds at Hubbard Brook, as nutrient loss occurs primarily as dissolved substances (Bormann et al., 1969, 1974). Overall, the intact forest ecosystem tends to have tight nutrient cycles, and is very conservative in its nutrient losses (Table 1).

Disturbed forest ecosystem

When the natural structure and function of the forest ecosystem is disrupted or manipulated, the system may lose its ability to retain vital nutrients and resist erosion. We have investigated a variety of forest manipulations in cooperation with the U.S. Forest Service and as part of the Hubbard Brook Ecosystem Study. These include complete deforestation with herbicide application to prevent regrowth (W2), commercial clear-cutting (W101) and commercial strip-cutting (W4) of forest vegetation on steep slopes (Fig. 1). We will attempt to summarize the biogeochemical results from these studies and compare them with those from the undisturbed ecosystems.

Deforested watershed W2

Watershed 2 was completely deforested in November and December 1965. All trees, saplings and shrubs were felled, but no timber was removed and no roads or skid trails were constructed within the watershed. Herbicides were applied during the summer to prevent regrowth of vegetation for 3 years after cutting.

The annual runoff averaged more than 30% (28.5 cm) greater after deforestation (Hornbeck et al., 1970). In addition, nutrient concentrations increased dramatically about 5 months after cutting for all major ions except NH_4^+ and $SO_4^=$ (Figs. 3 & 4; Likens et al., 1970). Concentrations of dissolved substances reached a peak during the second year (Figs. 3 & 4; Table 2). Measured nitrate concentrations in stream water rose to 82 mg/l in October 1967, and the pH was lowered by about one unit. Thus nutrient export from this

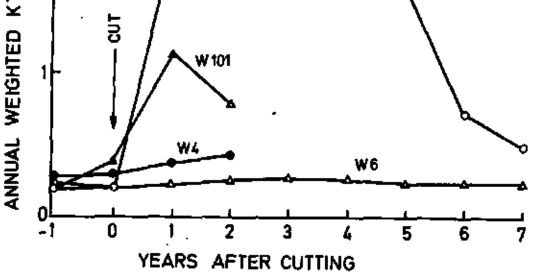

Fig. 3. Annual weighted concentration of potassium in stream water from W6 (undisturbed), W4 (strip-cut), W101 (clear-cut) and W2 (deforested). Watersheds were cut in different years.

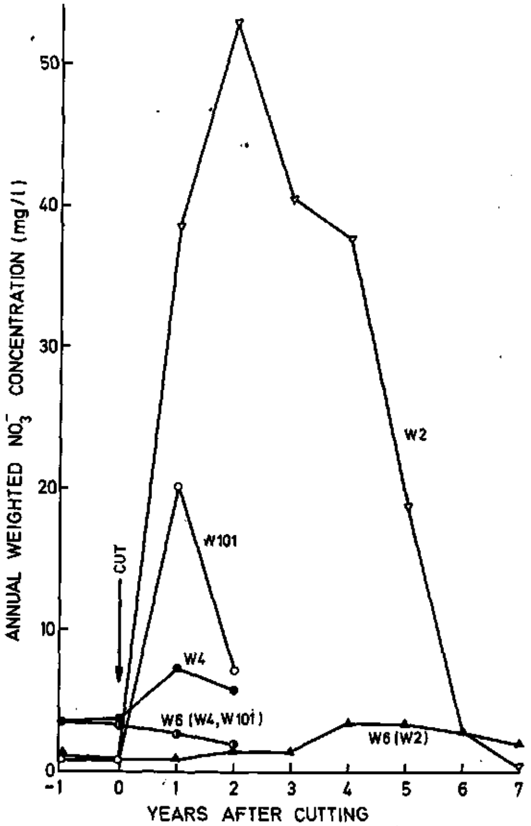

Fig. 4. Annual weighted concentration of nitrate in stream water from W6 (undisturbed), W4 (strip-cut), W101 (clear-cut) and W2 (deforested). Data for W6 from appropriate time periods are compared (as shown) with data for the cut watersheds.

Table 2. Weighted annual concentration in mg/l in streams of the Hubbard Brook Experimental Forest during second full water year after cutting.

Nutrient	Undisturbed	Strip-cut W4	Clear-cut W101	Deforested W2
Ca	1.66	2.44	2.17	7.55
Mg	0.39	0.44	0.50	1.51
K	0.23	0.42	0.77	2.96
Na	0.92	1.14	0.80	1.54
H	0.016	0.007	0.010	0.011
NH_4	0.01	0.02	0.02	0.05
NO_3	1.84	5.70	7.14	52.9
P	0.0012	-	-	0.0016
SO_4	6.2	5.7	4.4	3.7
Cl	0.55	0.63	0.61	0.75
SiO_2	4.45	6.16	4.99	5.66

disturbed ecosystem was greatly increased (Table 3). Nitrate-nitrogen losses were most extreme and exceeded 340 kg N/ha during the 3 years after cutting. Total P export in the second year was increased by tenfold (Hobbie & Likens, 1973). The average net export of all dissolved inorganic substances during the 3-year period was increased about tenfold relative to the long-term average for undisturbed ecosystems (Table 3).

Table 3. Net loss or gain (precipitation minus stream loss) of nutrients in kg/ha during second full water year (1 June-31 May) after cutting in the Hubbard Brook Experimental Forest.

Nutrient	*Undisturbed	Strip-cut W4	Clear-cut W101	Deforested W2
Ca	-10.2	-25.2	-21.2	-90.4
Mg	- 2.3	- 4.2	- 4.6	-17.9
K	- 0.8	- 4.0	- 7.4	-35.8
Na	- 5.2	-10.4	- 6.1	-17.3
H	+ 0.9	+ 1.0	+ 1.0	+ 0.5
NH_4-N	+ 2.0	+ 1.8	+ 1.9	+ 1.9
NO_3-N	+ 0.7	- 8.0	-10.4	-142
P	+ 0.1**	-	-	+ 0.08**
SO_4-S	- 4.3	- 6.1	- 0.3	0
Cl	+ 1.7	+ 4.4	+ 5.6	- 3.7
SiO_2-Si	-16	-31	-24	-32
Total	33.4	81.7	65.5	336.6

*9-yr average for all undisturbed watersheds (Likens et al., 1974)

**if particulate matter losses were included total P for undisturbed = +0.087; for W2 = -0.104

Accelerated decomposition of organic matter in the forest floor, coupled with increased nitrification, resulted in mobilization of nitrate, which quantitatively accounted for the net increase in total export of cations and anions from the deforested ecosystem (Likens et al., 1969). Whereas in the undisturbed ecosystem there is normally an annual net gain of inorganic nitrogen, a large net loss occurred in the deforested watershed. Losses in 3 years amounted to about 9% of the nitrogen in the top 30 cm of soil. With precipitation as the only input, it would take about 100 years to replace this loss. Particulate matter export was delayed for about 2 years after deforestation (Fig. 5); a maximum value of 38 m ton/km-yr was reached during the third year (Bormann et al., 1974). Thus following destruction of the vegetation the ecosystem quickly lost large amounts of dissolved nutrients, but maintained for about 2 years a residual resistance to erosion.

Watershed 2 was allowed to revegetate beginning in the summer of 1969. Nutrient and particulate matter losses then returned to near steady-state conditions in 4 years as the hydrologic cycle and erodibility were regulated by biotic factors (through primary succession).

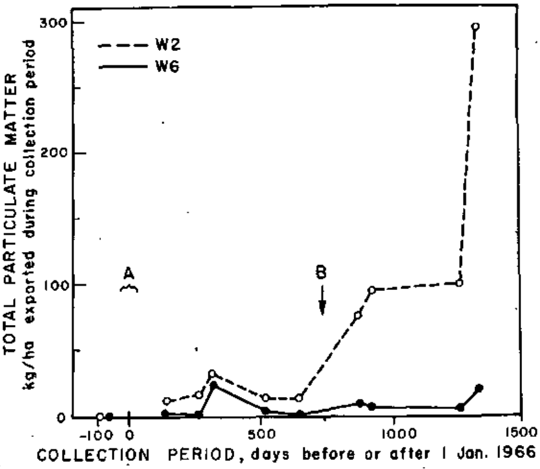

Fig. 5. Total particulate matter exported by runoff before and after 1 January 1966 for W6 (undisturbed) and W2 (deforested) (from Bormann et al., 1974).

Clear-cut watershed (W101)

The results from the experimental deforestation raised questions about nutrient loss and site productivity potential associated with commercial clear-cutting of the northern hardwood forest. Therefore, eight commercially clear-cut areas within the White Mountain National Forest were studied including Hubbard Brook W101, which was clear-cut in the autumn of 1970. Skid trails were constructed and merchantable timber was removed; no herbicides were used (Pierce et al., 1972). Generally the pattern of nutrient loss from these watersheds paralleled closely that of the experimentally deforested watershed (W2), although the response (i.e. nutrient concentration or loss) was not as large (Figs. 3 & 4; Tables 2 & 3). Increased nutrient export from these clear-cut watersheds ranged from a few percent to about 50% of the corresponding W2 value. Even though vegetation regrowth following clear-cutting was quite rapid, accelerated nutrient loss continued for at least 3 years. In one area increased nutrient loss was observed more than 12 years after logging (Pierce et al., 1972). Erosion was not measured in these areas, although it probably was greater than for W2, since roads and skid trails were constructed to facilitate timber removal.

The Gale River clear-cut had the largest export of dissolved nutrients of the commercially logged areas (Pierce et al., 1972). We estimated the nutrients removed in timber and added this to export of dissolved nutrients (Table 4). These data suggested that the total export of nitrogen and calcium from the Gale River watershed was equal to or greater than that from W2.

Table 4. Comparative losses of calcium and nitrogen in kg/ha during the first 2 years after experimental deforestation of W2 at the Hubbard Brook Experimental Forest and after commercial clear-cutting of the Gale River watershed (modified from Bormann & Likens, in prep.).

	Calcium		Nitrogen	
	Gale R.	W2	Gale R.	W2
Dissolved substance loss				
1st year	41	75	38	96
2nd year	48	90	57	140
Removed in timber	221	0	144	0
Total removed	310	165	239	236

Strip-cut watershed (W4)

In an attempt to provide a management alternative to clear-cutting, a study of strip-cutting was undertaken at Hubbard Brook. It was thought that this procedure might allow timber removal from an area, yet moderate the nutrient losses as compared with conventional clear-cutting of northern hardwoods. Watershed 4 was commercially strip-cut in the autumn of 1970. Timber was harvested from strips 25-m wide, alternating with uncut strips, 50-m wide. It is planned that 1/3 of the total watershed will be clear-cut every 2 years; the whole watershed being cut in a span of 4 years. The strips roughly paralleled the elevation contours. A narrow strip of trees was left uncut along major stream channels.

Small increases in stream flow were observed (Hornbeck et al., 1974); water yield during the first two growing seasons was increased by 54% and 23% over that which would have occurred if the watershed were not cut. This compares with increases of 414% and 380% in water yield from W2 during the first two growing seasons. Nutrient concentrations in the streams from W4 as well as annual export of N were appreciably lower than in the deforested or the clear-cut watersheds (Figs. 3 & 4; Tables 2 & 3; Hornbeck et al., 1974). Of special interest is the presumed biological effect of the uncut vegetation on reducing nitrate concentrations in stream water (Fig. 6).

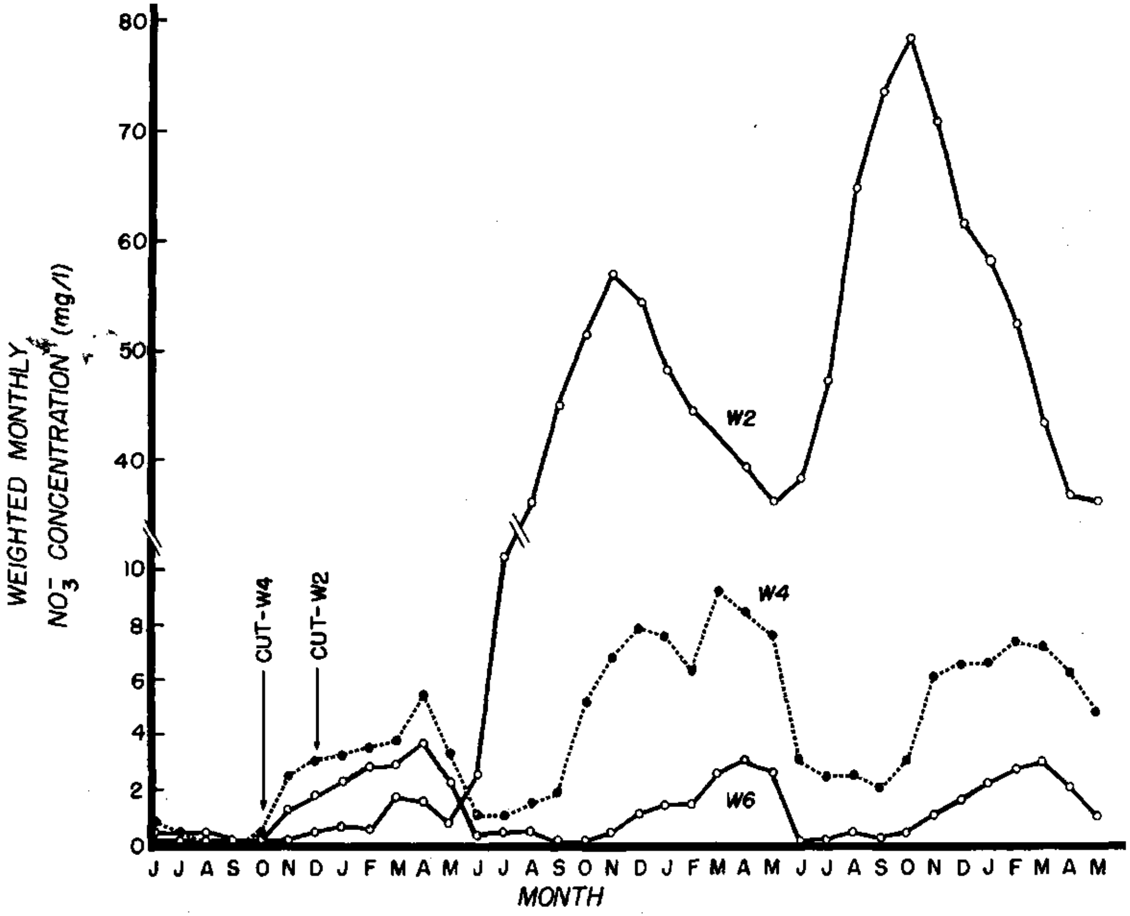

Fig. 6. Weighted monthly concentrations of nitrate for W6 (undisturbed), W4 (strip-cut) and W2 (deforested). The watersheds were cut in different years and curves for W6 and W4 (1970-1973) have been superimposed on the curve for W2 (1965-1968).

Johnson et al. (1969) have suggested that vegetation is effective in lowering the concentration of nitrate and potassium in stream water during the growing season. In W4 it appears that this mechanism effectively reduced export. Concentrations of nitrate increased significantly above the concentrations of the undisturbed watershed during the non-growing season (October through May) and then decreased to levels slightly above those of the undisturbed watershed during the growing season (June through October). This is in sharp contrast to the pattern observed in the deforested watershed (W2). However, the last strip will not be cut until the autumn of 1974, and final evaluation of this treatment must await that cutting.

Summary

The various interrelated hydrologic, biologic and geologic components of the northern hardwood forest ecosystem were significantly altered when the vegetation was cut or destroyed. The effects of such alteration reverberated throughout the system. Some of the responses were predictable, some were not. For example, nitrification was vastly accelerated. The normal structure and function of the ecosystem was repaired as vegetation regrew, but several years were required for dissolved substance losses to approach pretreatment levels. Losses of N and K after strip-cutting were well below losses that occurred from the deforestation experiment or normal clear-cuttings. Strip-cutting may represent a reasonable management alternative for timber harvest in northern hardwoods.

Acknowledgements

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STUDIES ON THE SECONDARY SUCCESSION OF TROPICAL LOWLANDS: THE LIFE CYCLE OF SECONDARY SPECIES[1]

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Introduction

We are living in an era that could be known as the "era of secondary vegetation". With a few exceptions there is no country on earth which has a larger land surface cover of primary (primeval) vegetation than of secondary vegetation. In addition, there is reason to believe that part of the so-called primary vegetation is in fact an old secondary one (Richards, 1963). We are spectators of one of the most important changes occurring in the history of life on earth. The native biota is being extinguished or is adapting to this condition at an impressive rate (Gómez-Pompa, 1971; Gómez-Pompa et al., 1973). In the tropical lowlands this trend is not the exception but the rule.

It is clear to us that man is the greatest cause of vegetational disturbance and, therefore, of succession; his activities represent the most important transient events occurring in nature.

Secondary species (species of secondary vegetation) today represent probably the most important biota of the tropical lowland areas because of their abundance, the remarkable versatility of their responses to disturbance, and their possible use for our generation and for those of the future.

There is not a clear cut difference between a secondary species and a primary one as their characteristics may differ from one species to another. This problem has been discussed previously (Farnworth & Golley, 1974) and in this paper we will deal with the typical "nomad" species which are easily recognized, at least in the lowland humid tropics (Van Steenis, 1958), after clearing a selva.

Several studies with different approaches and interests have been carried on in the tropics on the regeneration process. We can identify some trends in them such as, the ecosystem approach (Farnworth & Golley, 1974), the descriptive approach (Kenoyer, 1929; Budowski, 1961), the evolutionary approach (Gómez-Pompa, 1971), the population approach (Sarukhán, 1964; Rico & Gómez-Pompa, 1974), and the autecological approach (Gómez-Pompa & Vázquez-Yanes, 1974). It is difficult, however, to make clear cut distinctions between these approaches. Nevertheless, the most important fact is that there are two levels, one using the species as the basis for its studies and the other using the ecosystem. We believe that there will be no advancement in the understanding of succession without an understanding of the trends of behavior of the species in the recovery systems.

The problem

While studying the successional process in some tropical lowland areas of México, we have tried to discover what the adaptative characteristics are that permit secondary species to be successful in the disturbed environment in contrast with primary species. It is the purpose of this paper to analyze some of the characteristics that we found important and to present examples chosen mainly from our own work.

Important Characteristics of Secondary Species

Natural selection is the general process that models the phenotype by selecting those characters best suited for the changing environment that promotes succession. Selection can occur at all stages of the life cycle of a plant (Fig. 1) and for this reason our analysis will be presented following discussion of the life cycle.

Time of the life cycle

Secondary species have a short life cycle. This may be genetically controlled (as is the case with annuals and biennials) or evironmentally controlled. The group of species that are environmentally controlled are basically heliophytes that are eliminated by taller plants that shade them out. Of course, the stature of a plant is genetically controlled, but if no light competition occurs they may live for longer periods of time. The size and life form of many secondary species is variable and great plasticity is shown by many of them. Timing of life cycles is an important event in the successional working model (Fig. 2). Very little work has been done in this area and the only known data come from studies in the early successional stages (Sarukhán, 1964; Rico & Gómez-Pompa, 1974). The success of a species can be measured by knowing whether it has reached the flowering and seeding stage. The strategy of "nomads" is remarkably successful in this respect, as they exploit their fast growth and early flowering and in this way fill the time niche successfully.

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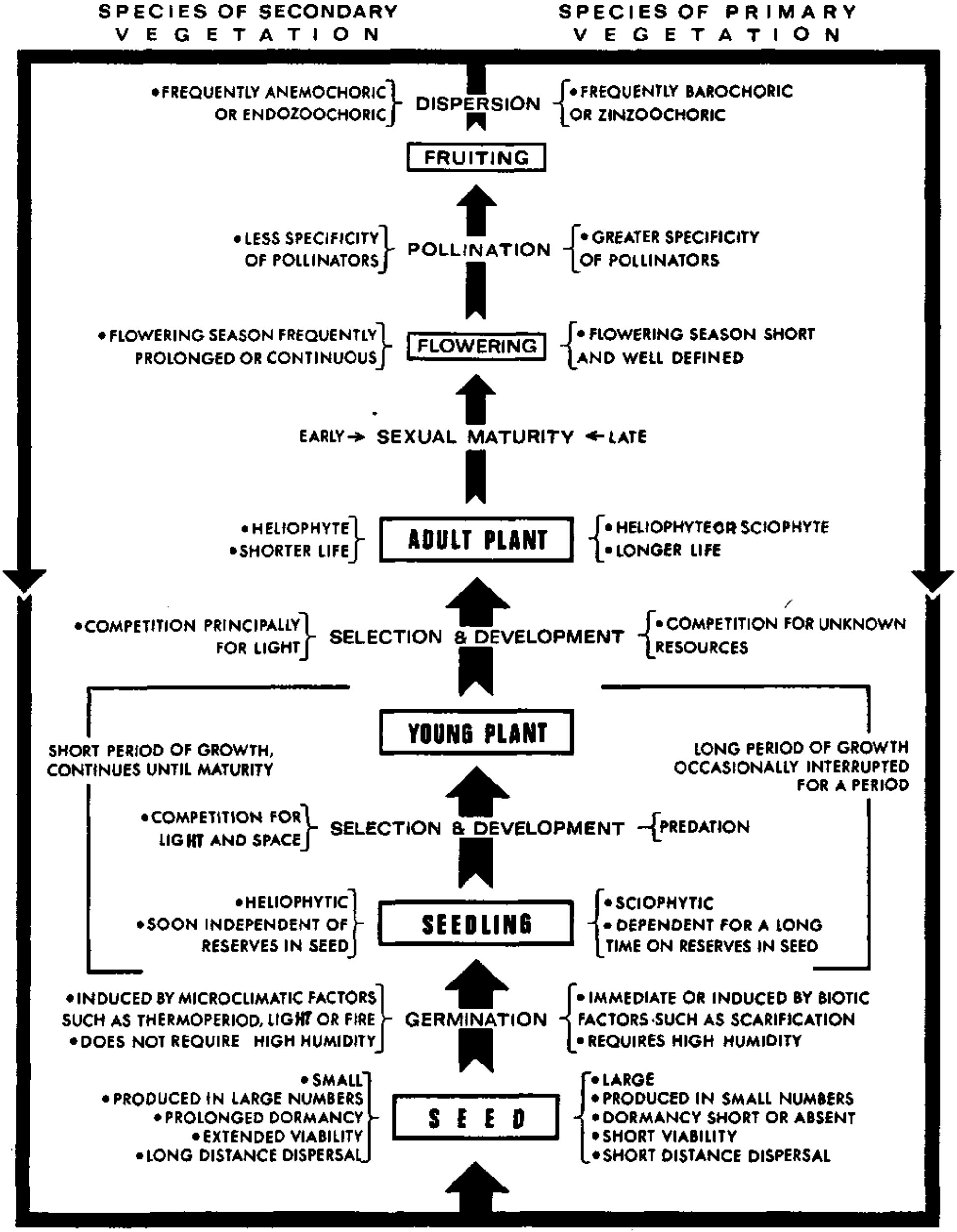

Figure 1. Life cycles of plants. Each step can be isolated and a series of research projects may be planned that will contribute to understanding the whole.

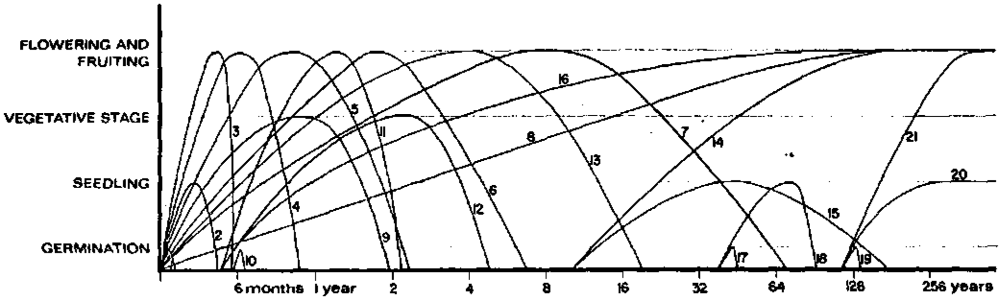

Figure 2. A model of life cycle patterns along a time gradient in the successional process. Each one represents a complete or an incomplete life cycle. 1) Species that germinate and die. 2) Species that germinate, produce a few leaves, and die. 3) Species that complete their life cycle in a few months. 4) Annual species. 5) Biennial species. 6) Species with a life cycle of only a few years (less than 10). 7) Species with a long life span, several decades, but eventually dying (species from old secondary forests). 8) Primary species with life spans of hundreds of years that have lived since the beginning of the succession. 9) Species that never reach the stage of sexual reproduction. 10) Species that germinate a few months after the succession begins and soon die. 11) Annual species that germinate after the succession begins. 12) Species that germinate after the succession begins but do not reach the stage of sexual reproduction. 13) Species with a short life cycle (less than 30 years). 14) Species with a long life cycle that germinate when the succession is well advanced. 15) Species that germinate when the succession is well advanced and remain in the seedling or "young" plant stage for a few years. 16) Species that germinate a few months after succession begins and then have a life cycle hundreds of years long (primary species). 17) Species that germinate and die in old successional stages. 18) Species that germinate and live at the seedling or young plant stage in old successional stages, and then die. 19) Species that germinate and die in the primary forest. 20) Species that germinate and grow to a seedling or "young" plant stage inside the primary forest and remain there waiting for suitable conditions for continuing growth. 21) Species that germinate and grow in the primary rain forest and may reach the reproductive stage after having long life cycles (primary species).

The role of time in plant and animal evolution have been considered in all classical evolutionary studies. Usually it is considered as a factor in evolution on a long term basis, not usually a factor by itself but in relation to environmental changes occurring through time. Even though we can not define time in concrete terms as an objective factor, it seems to us that in the successional process, time is indeed a factor that has acted as a selective mechanism in the evolution of species.

The length of time of the growing period for a secondary species to reach a reproductive stage may vary from a few weeks to months or years, depending on the species and also on changes in the environmental conditions. These changes can be caused by the type and frequency of perturbations, by the preceding species and by nonpredictable changes in the environment. For each set of changes there is a set of species that have a life cycle adapted to the time available. Time viewed in this way becomes a very important selective factor in the successional events.

Time as a selective factor has increased in importance through human activities in nature. In fact, many secondary species have adapted to the time cycles of human use of the land.

Seeds

A great part of the energy budget of secondary species is used for reproduction in comparison to the amount of material used for building the structure of the individual. Reproduction in secondary species is a fascinating phenomenon which is favored by the presence of many characteristics. Among those we wish to mention are, the large number of seeds per plant, the systems for wide seed dispersal, and also the systems for dormancy that permit seeds to persist in soils (Guevara & Gómez-Pompa, 1972) through long periods of time. These characteristics increase the probabilities of successful establishment when a disturbance of the original vegetation occurs (Salisbury, 1949). This is especially true in areas of frequent and continuous disturbance.

The production of seeds through the year tends to be continuous in many groups of secondary species. Examples occur in several species of Piperaceae, Melastomataceae, Malvaceae, and Compositae. One of these species is Piper auritum, a very abundant species in the early successional stages (2-10 years) in the American lowland humid tropics. In this species inflorescences and infructescences can be found simultaneously in almost any month of the year. A similar strategy can be found in species such as Trema micrantha, Urera caracasana, and Cecropia obtusifolia in which several fruiting seasons can be found in a year in different populations and for that reason we find that the production of seeds is also continuous and the only change is in the amount of seed produced through the year.

In some species which are wind dispersed such as several species of Heliocarpus, Ochroma, and many Compositae, the fruiting period is generally in the dry season. They produce a large seed crop and have efficient dispersal mechanisms; in these cases the accumulation of seeds in the soil occurs only in one season of the year.

Seeds of secondary species are mainly small, with low humidity content. Both characters favor long distance dispersal and also may have great value in providing better resistance to predation and attack by microorganisms.

The viability of seeds from secondary species in the soil may be long (Juliano, 1940) as has also been demonstrated in laboratory experiments with seeds from old herbarium specimens (Moreno-Casasola, 1973).

Seeds of secondary species accumulate and remain viable in the soil of primary rain forests (Keay, 1957; Guevara & Gómez-Pompa, 1972) where they form a notable seed bank that remains alive and dormant until the proper conditions appear and trigger germination. Dormancy in these seeds is imposed mainly by light conditions under the forest canopy. caused by the great number of species that have photoblastic seeds (Vásquez-Yanes, 1974b). Other species present tegumentary dormancy that can be broken by the effect of strong thermo-periods, high temperatures, or scarification as is the case with many Leguminosae, Ochroma, and Heliocarpus (Vázquez-Yanes, 1974a).

The microclimatic modifications that induce the germination of seeds of secondary species are produced as a result of the disturbance of the previous vegetation.

Seedlings and Young Plants

Once a seed has germinated, having been triggered by one of the several known mechanisms, the next step of selection occurs at the seedling and young plant stage. This stage is the most critical in determining the success of certain species and individuals over others. There are dramatic changes in numbers in the first months (Fig. 3) and the characteristics that enable the species to compete and succeed are not known. At these early stages light competition is the main environmental factor, shading may become the life or death factor for secondary heliophytes unless some meristematic dormancy occurs. At this time any factor affecting the

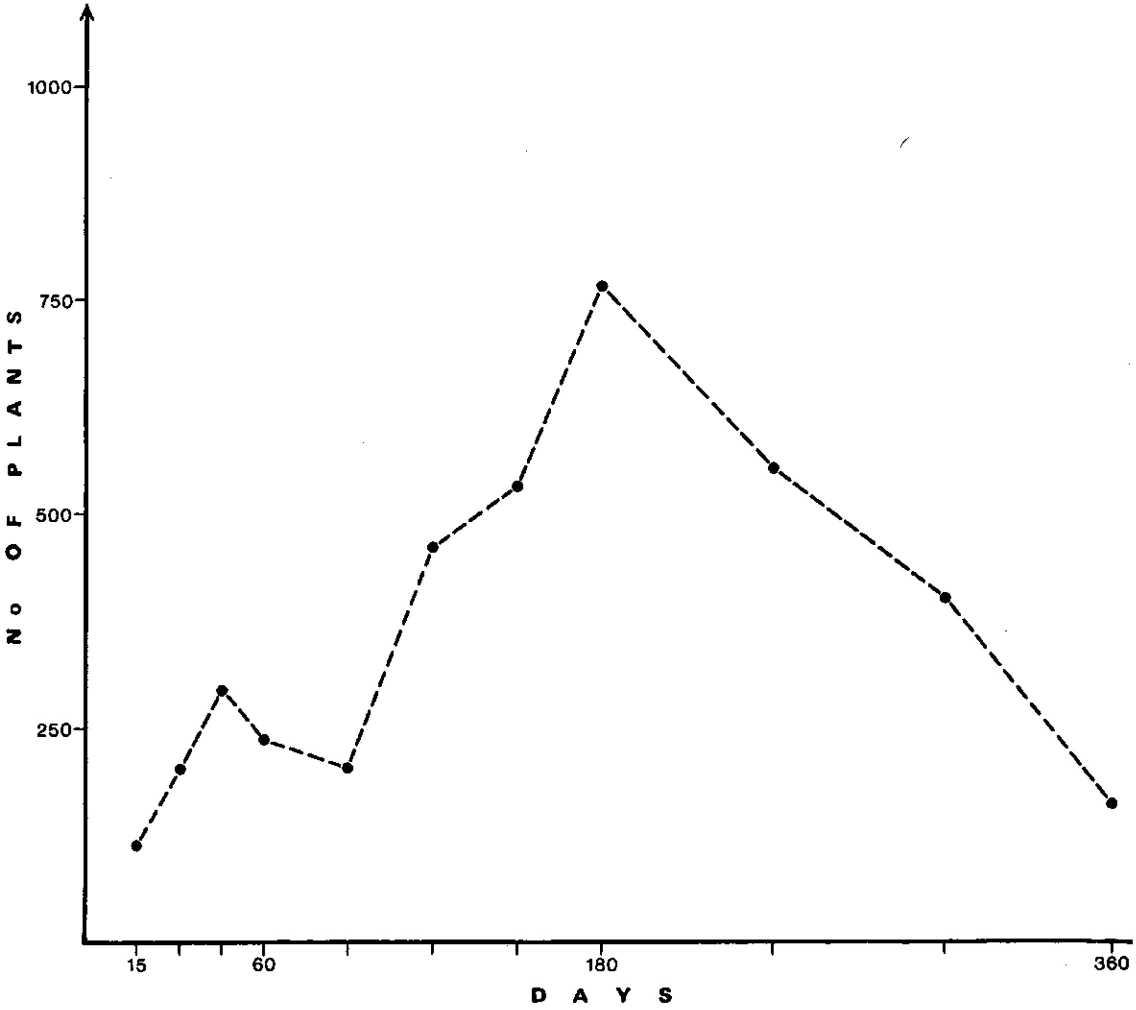

Figure 3. Population changes in the first year period of a cleared area in a lowland humid rain forest region of Veracruz, México.

growth of the plants may be of paramount importance; chemical competition seems to be a factor of much greater weight that had been suspected (Anaya & Rovalo, 1974).

As the survival of the species depends on success at this stage, several strategies are evident, such as the high number of individuals permitting greater probability of success for a few; fast growth that keeps them at the direct sunlight level. Another character of which we know nothing is the plants' defense against predators; competition for nutrients if it exists at all; and space competition mainly at the root level. Any advantage along these lines will increase the chance of success.

Seeds of small size and limited reserves such as the most common secondary species, originate small seedlings that become readily independent and in the presence of adequate light, start an active and continuous growth (Rico & Gómez-Pompa, 1974). This growth caused by an efficient photosynthesis in these secondary studies produces a fast growing body with a great amount of water, little woody material and with a great amount of cellulose. This growing strategy in full sunlight enables the species to have a large and efficient photosynthetic surface which, in biomass is greater in proportion to the rest of the plant body and is in contrast with what happens in old secondary and mature rain forests. This fact probably results in attaining the reproductive stage rather rapidly.

One important factor to which no one has paid much attention is the nutritional requirements of secondary species. These species have to germinate and grow in poor soils that usually have been abandoned after cultivations, and it is in these conditions where most of the species find their best environmental conditions. This means that most of these species should have very efficient systems for using the low nutrient content of the soil. They have to restore the nutrient pool through restoring the cycling capability of the recovering ecosystem. Great accomplishments should be expected in this area of investigation if a species approach is followed. It is worth mentioning that some experimental work done in Costa Rica (Hartcombe, 1972) applying fertilizers to a Cecropia obtusifolia plantation did not show a resultant increase of productivity when compared with the unfertilized plots. These results may help us to prove the hypothesis that secondary species have low nutrient requirements. According to Kellman (1969) some experiments in fertilization have shown that the requirements for certain cations and phosphorus are very low for secondary plants and an increase in them apparently does not affect the course of succession.

Plants of the primary rain forest may develop a complex system of endotrophic mycorrhiza that close the nutrient cycle. Secondary species in general lack mycorrhiza and have instead a very dense root system that enables them to capture nutrients from the soil. The root system of the secondary species being less specialized than that of primary species, can cope more effectively with the problems of establishment in naked and disturbed soils (Stark, 1969).

Many colonizing species in several well known families of the tropics such as Cyperaceae, Gramineae, Euphorbiaceae, and Amaranthaceae (Black et al., 1969) have a C_4 metabolism of carbon dioxide, which gives them advantages for colonization and competition at the early stages since it permits efficient photosynthesis at high temperatures, while the night fixation of CO_2 decreases water loss. More studies along this line may also further understanding of the success of colonizing species in the successional process of the humid lowland rain forest areas.

Another important feature of secondary species is the great capability of their resistance to herbivores. This can be accomplished by being unpalatable, as is probably the case for many C_4 plants (Caswell et al., 1973) to the most important herbivores; or by having a rapid recovery after a part of the plant is eaten by an herbivore. In fact, many secondary species are adapted to herbivores, including man, for their dispersal. They are remarkably adapted to withstand trampling and other drastic impacts.

One notable characteristic we have found in several secondary species is that in spite of being heliophytes, they can survive in low light conditions which change some of their structures and functions. In Piper we have observed that individuals in such conditions have limited reproductive capacity (low seed production). The physiological ecology of these selected populations of secondary species living inside the forest is of great importance. Are these populations genetically different from the outside populations, or do they have a plastic genotype ("many purpose genotype") that expresses itself differently in different environments?

The reproductive plant

Many of the characteristics mentioned for young plants can be applied to the reproductive individual. As we have said before, the great trend for secondary species is to reach the age of seed production as soon as possible, insuring the preservation of the species. This is important because the time available for reaching this stage may be limited as the succession advances. Some annuals or biennials may have only one occasion to leave seed progeny available for a new opportunity. For shrubs and small trees there may be only a few years to accomplish this before other taller species take their places. In this sequence we reach the taller size classes of secondary trees that may have many more years to produce their seeds, and finally we reach the stable stage with trees that can produce seeds for hundreds of years. In this sequence we may find different reproductive systems and dispersal strategies.

Almost no information is available concerning the compatibility systems of plants of secondary vegetation. Bawa (1973) reports from Costa Rica several species of secondary trees that are self incompatible, such as, Bauhinia ungulata, Cochlospermum vitifolium, Guazuma tomentosa, Luehea speciosa, Spondias mombin, and several others. It seems from his results that cross pollination is the most common trend in the group of species he studied. Our experience with a few species of Piper of Veracruz also indicates that this is the case.

It would be of extreme interest to study the breeding systems in the early colonizing species, especially those with short life cycles.

To a secondary flora there is a corresponding secondary fauna which interacts with it in several ways, mainly predation, pollination, and dispersion. These are intimately related, even though there is very little information about the relationship of the flora and fauna of secondary vegetation. For those secondary species that are pollinated by animals there is some evidence that very little specificity has been found. In Piper hispidum more than four species of bees have been identified as pollen carriers in one locality of Veracruz; a more drastic example is Ipomoea trichocarpa in which three species of bees and a hummingbird pollinate the species and a beetle and two species of butterflies were seen as possible pollinators also (Gónzalez-Medrano, Piñol & Toledo, personal communication). Both species of plants are common secondary species in the early successional stages of the lowland tropical regions of Veracruz.

Even though there are very few studies on this subject it seems quite obvious that the trend is rather general as these "nomad" species should find pollinators in many geographical localities and in various ecological conditions. The same trend also should be found in those species dispersed by animals. For Cecropia obtusifolia many different dispersors have been found, local or migratory, insectivorous and frugivorous birds; bats (which have been found to be important agents of dispersal), and probably other mammals, too. The seeds of Cecropia may germinate without passing through the digestive tract of the animal and for that reason dispersal also can be accomplished without the animals (Einsenmann, 1961; Olson & Blum, 1968, and Vázquez-Yanes, 1974).

Productivity

There is almost no information available on the difference in productivity through time for any tropical area. The few studies on productivity of tropical ecosystems have not considered time on the one hand and species differences on the other. The available data show that there is very rapid growth at the beginning of the succession (the first 5 to 10 years) and then a stabilization through time (Kellman, 1969; Jordan, 1971; Farnworth & Golley, 1974). It is clear, even though not proved, that a fast growing species should have a very efficient photosynthetic process which may be responsible for the high productivity of the early stages of succession, and this process should be evaluated at the species level.

Data from Puerto Rico indicate that the annual increase in biomass in a secondary vegetation two years of age is greater than in a mature forest (Jordan, 1971).

Final considerations

It is clear to us that much more research is needed at all levels and degrees of sophistication. It is of great importance to know more about species behavior in known localities through time, and in different environments in the lowland tropics of the world. The evolutionary approach seems to be the basic one for understanding the trends of evolution of these biota and will, at the same time, permit us to draw the guidelines for management of this vegetation type that covers a great portion of the surface of the earth.

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SUCCESSION STUDIES IN THE HUMID TROPICAL LOWLANDS OF SURINAM

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1. Summary

The succession within a number of permanent plots, established in virgin forest and derived vegetation, is studied by periodic recording. This paper deals with a plot in a mechanically deforested area. The results of the first seven years of observation are described. The course of the basal area is compared with that in two other plots in the same region which were established in forest clearings created by manual labour.

2. Introduction

2.1. General

Surinam, situated at the north coast of South America between 54 and 58° W. long. and 2 and 6° N. lat., has a permanently humid tropical climate with a mean annual rainfall between 2000 and 2500 mm. In the driest months, September and October, precipitation generally does not drop below 60 mm. Yearly variation in total rainfall and in rainfall distribution is considerable, however. The temperature is fairly constant throughout the year; at the capital Paramaribo, situated at sea level, it amounts to 27°C.

In a coastal belt of Quaternary and Late Tertiary deposits, ranging in width from 40 km in the east to 100 km in the west, drainage generally is impeded and various hydrophytic vegetation types predominate, as herbaceous swamp and swamp and marsh forest. On some coarse and excessively draining soils a xeromorph evergreen rain forest develops.

However by far the greater part of Surinam, including nearly the whole of the country's interior, is covered by mesomorph evergreen seasonal forest ("lowland rain forest" in the sense of Richards). This area harbours only a few tens of thousands of bushnegroes concentrated in villages at the banks of the rivers in the east; and some small Amerindian tribes living at the northern fringe of the inland forest and scattered near the country's southern border. Central, W. and S.W. Surinam are nearly uninhabited.

Up to a recent past human influence on vegetation was virtually limited to parts of the coastal belt and strips of land along the eastern rivers. Since 1953 parts of the northern zone of the inland forest have been made accessible by roads and selective forest exploitation proceeded at a rather large scale. Though in some areas agricultural fields became established afterwards, there was no real invasion of squatters in the regions opened-up by forest roads. Exploited areas were either regenerated artificially or left without further interference.

2.2. Ecological research

In the past Surinam has been the field for several ecological investigations. Schulz (1960) studied the environmental conditions, composition and dynamics of the rain forest in northern Surinam. The latter studies were continued by the local Forest Service and more recently by the Centre for Agricultural Research in Surinam (CELOS).

The investigations by CELOS are focussed on the dynamics of the rain forest and derived vegetation. Extensive field work was performed in the southern part of the coastal belt and the northern part of the inland forest, i.e. in regions with old land settlement and with recent forest disturbance respectively. Extensive information about these studies is given in a series of internal communications and in the Centre's quarterly reports (both in Dutch). Summaries in English appeared in the annual reports (Anon., 1968-1973).

3. Methodology

Succession may be studied either by direct or indirect methods. Direct studies mean the periodic recording of the vegetation in permanent plots for a certain length of time. Thus changes in botanical composition and structure are followed closely, giving a detailed picture of succession in the plots studied. If succession is studied indirectly the vegetation in a number of plots is analysed only once. On account of botanical composition, vitality and fertility of species, age class representation, structure, historical and other data, the mutual relationship between various vegetations is fixed and general lines of succession may be derived. The indirect approach has the advantage of leading to results more quickly; but the interpretation of the data is more difficult and may be subjective, details easily escape observation, and conclusions often are tentative.

The succession studies carried on by CELOS rely on both methods, though emphasis is on the direct method. Between 1967 and 1971 a total of 21 permanent plots, ranging from 0.1 - 1.0 ha, were laid down in deforested areas (3), on land abandoned after shifting cultivation (8), and in exploited forest (10). Earlier the necessary complementory studies in undisturbed forest had already been initiated by the Forest Service of Surinam, with which institution a close cooperation exists.

The periodic recording of the plots takes into account the following parameters of the vegetation: (I) stratification; (II) height, coverage and life forms of each stratum; and (III) girth and species of occurring trees. The plots generally are inventoried once a year.

For detailed studies special techniques were applied in several plots. As a rule sub-plots were used, e.g. for mapping of individual plants or plant-groups, labeling of all plants in the undergrowth or recording of the complete floristic composition with data on height, coverage, density, phenology and vitality of each species. In a few cases and for a limited time reinventories were repeated more frequently, up to bi-monthly.

Complementary information on the dynamics of vegetation is being collected from aerial photographs, micrometeorological measurements, experiments about the occurrence of viable seeds in the top soil of various vegetations, and from germination and longevity tests of some important secondary species after storage under laboratory and field conditions.

4. Results

4.1. Succession on deforested area

This paper mainly deals with the oldest succession plot established by CELOS. It is situated at Blakawatra, i.e. in the eastern part of the country at about 70 km from the coast. The location is near the edge of a dissected plateau of late Tertiary age at 50 m above sea level. The original vegetation was a mesomorph evergreen seasonal forest with a tendency towards the xeromorph forest, e.g. demonstrated in its floristical composition by the abundance of some Chrysobalanaceae (Licania incana Aubl., Parinari campestris Aubl., Couepia versicolor R. Ben.).

In August 1966, with the purpose of establishing pine plantations, the area was deforested by heavy equipment, which knocked down and uprooted both trees and undergrowth and caused a severe disturbance in the top soil. Following an unsuccessful attempt to burn, the debris resulting from clearing was piled in rows about 10 m wide, then the rows were burned in November of the same year, leaving a thick layer of ashes and the charred trunks and stumps.

The experimental area covers 80 x 120 m. Since 1967 it is surrounded by plantations of Caribbean Pine. The permanent plot occupies the central 50 x 90 m of the experimental area. It is divided into 45 subplots of 10 x 10 m. The plot comprises three sites, viz.:
(1) a well-drained sandy loam, relief nearly flat, debris removed (20 western subplots);
(2) a slightly sticky loam, relief faintly concave, debris removed (20 eastern subplots); and
(3) the same soil and relief as under (1), but ashes and piles of trunks and stumps cover the surface (burned row, 5 central subplots).

The succession on the three sites proceeded along different lines.

Site (1)

On site (1), where no intensive burning occurred, seedlings became established during the wet season following clearing. They were fairly evenly distributed over the area. At the first inventory in February 1967, i.e. three months after the attempt to burn and subsequent removal of the debris, 3 to 10 seedlings were counted per square meter, half of which belonged to monocotyledonous species (mainly Cyperaceae and Gramineae) and half to dicotyledonous ones. Moreover there were a few sprouts from roots that had stayed in the soil (0 - 1 / sq.m). The total vegetation cover was less than 0.1 %.

On this well-drained soil three more

stages could be distinguished during the first three years of observation:

A. (8 months after debris removal). Predominance of a few species having the ability to spread rapidly be it by vegetative propagation (Solanum subinerme Jacq.), by seed (several annual plants) or simply by the formation of long lateral branches (Scleria secans L.). Thus isolated single-species groups together with some shrubs (Solanum sp. div.) and tree seedlings constituted an uneven vegetation, up to 1.5 m high, covering 10 - 30 % of the surface.

B. (18 months after debris removal). A community consisting of: (I) a very open, up to 4 or 5 m high upper layer of Cecropia obtusa Tréc.; and (II) an impenetrable, 1.5 m high layer of Solanum spp. and Scleria secans interspersed with young secondary trees.

C. (3 years after debris removal). A clearly stratified wood comprising: (I) an open, 8 - 11 m high Cecropia-layer; sharply seperated from (II) a dense, 3 - 7 m high tree layer which mainly consisted of Palicourea guianensis Aubl., Maprounea guianensis Aubl., Goupia glabra Aubl., Isertia coccinea (Aubl.) Gmel., Laetia procera (Poepp. et Endl.) Eichl., Inga spp., Vismia spp. and partly moribund Scleria; and (III) a more or less open layer of overgrown Solanum spp. and Scleria including some small trees of the species mentioned above.

After the third year changes were less marked. In 5 years Cecropia reached its maximum height of 11 - 14 m and since recently this pioneer tree shows some signs of decline. The species of the second layer on the other hand kept growing vigorously and at the last inventory (March 1974) especially Palicourea and Isertia proved to be penetrating the upper layer. As a relic in this dense wood some thin veils of Scleria still persist, hanging down from tree branches 5 or 6 m high. But the Solanum shrubs could not keep pace with the developing trees and have died off completely in the dark interior of the wood. So the undergrowth got sparse, but it harbours an increasing number of species, including representatives of all strata of the original forest, e.g. Dicorynia guianensis Amsh., Paypayrola guianensis Aubl. and Ischnosiphon gracilis (Rudge) Koern.

A remarkable phenomenon was the establishment of Virola surinamensis (Rol.) Warb. from the fourth year onwards. Since then in most of the 10 x 10 m subplots bearing a Cecropia overstorey yearly there appeared about 3 to 10 seedlings of this species. Virola surinamensis, a Myristicacea, has seeds of the size and shape of nutmegs. It is a species typical for hydromorphic sites and the nearest potential seed trees are found scattered in the creek forest some hundreds of meters away. The young Cecropia trees, which initially remained unbranched, started developing horizontal branches in the third and fourth year. The open crowns of Cecropia, rising above the surrounding pine plantations, offer an easy resting-place for birds and it is presumed that the seeds were transported by birds, which are attracted by the palatable aril enwrapping the seed. Up till now the majority of the Virola seedlings could maintain itself in this atypical site.

Site (2)

The first colonization of site (2) was similar to the one described for site (1). However, heavy rainfall during May and June 1967 lead here to a temporary inundation, which caused the dicotyledenous seedlings, established a few months earlier, to die off. Only on a few higher spots the tree seedlings survived. After about two years a closed vegetation of Cyperaceae and Gramineae had developed with Rhynchospora cephalotes Vahl and Panicum pilosum Sw. as the main species. Thus a savanna-like vegetation originated.

During the next three years practically no new woody plants became established and the vegetation seemed to have reached a phase of relative stability. However, the trees on the small elevations grew up and their crowns begin to spread laterally over the low vegetation. Moreover two Vismia species, occurring in the border, now penetrate the grassland sprouting from horizontal roots. Fire hazard under the existing conditions is low and therefore it is to be expected that in the future a woody vegetation will gradually take hold of the site.

Site (3)

At site (3), where the debris was burned, a very heterogeneous vegetation sprang up. In the central part microorganisms among which algae were the first colonizers of the ash layer, soon forming a dark crust. Five to six months after burning annuals became established. Portulaca oleracea L. and Erechtites hieracifolia Rafin., the most common species, produced two or three generations within a few months. Then they had to give way to invading Cyperaceae, Gramineae and Solanaceae. Where stems and uprooted stumps are found and some soil has been accumulated, i.e. mainly along the edges of the row, the secondary tree species mentioned for site (1) got hold of the place and demonstrate a vigorous growth. As in the western sub-plots Cecropia obtusa gained dominance. Lianas are relatively abundant in the second storey and the undergrowth. A few herbaceous species are only found near or at the charred stems, as Phytolacca rivinoides H. et B. (restricted to the early stage), Pityrogramma sp. and Pteridium aquilinum Kuhn. It is remarkable that even now, more than 7 years after the burning, the more central part still bears a low vegetation mainly consisting of grasses (e.g. Panicum spp. and Paspalum spp.) and ruderal plants as Mikania micrantha H.B.K. and Wulffia baccata (L.) O. Kuntze.

4.2. Basal area

Since October 1969, girth at 1.30 m is measured of all stems with a girth 200 mm and over. Girth class distribution and basal areas have been calculated seperately for the individual species in the successive years. In 1969 - three years after clearing of the area and piling and burning of the debris - only Cecropia obtusa trees had passed the 200 mm limit. Densities amounted to 550 stems/ha for site (1) and 720 stems/ha for site (3). The next year these values increased to 725 and 920 stems/ha respectively, but hardly changed in the years that followed. The first individuals of the other species, listed in table 1, passed the 200 mm-girth limit in 1970; since then their number continues to increase. In 1974 already 56 % (site 1) and 38 % (site 3) of all stems 200 mm and over belonged to the latter group of species.

Data on basal area are given in table 1. Growth in basal area of Cecropia obtusa nearly stopped after 1971. In all years the values for this species at site (3) were about twice those at site (1). The corresponding values for the group of other species show insignificant differences only. The total basal areas 7.5 years after clearing (February 1974: 11.0 and 18.0 m^2/ha resp.) may be compared with the estimated basal area of the original forest at that place (24 - 28 m^2/ha).

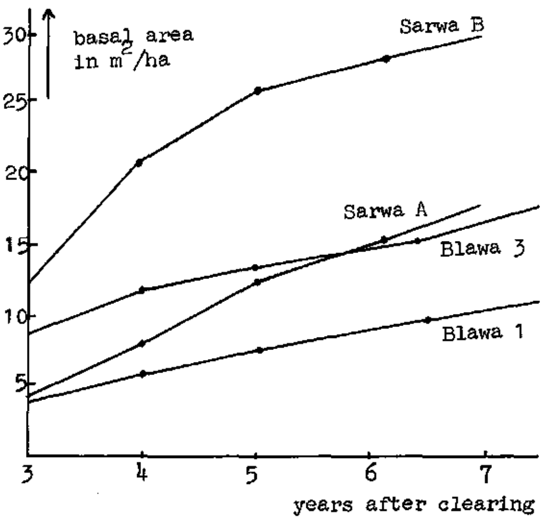
In graph 1 the course of the basal area is given for sites (1) and (3) of the plot at Blakawatra and for the other two plots which were established in deforestations. The latter, situated at Sarwadriesprong, are in the same region. The original vegetation was a mesomorph evergreen seasonal forest with a canopy at about 28 - 34 m and emergents up to 43 m. The measured basal area of the forest was 33 m^2/ha. The two clearings were created in 1967 by cutting the forest with the axe. They have a different size, viz. 0.64 ha (80 x 80 m) and 1.69 ha (130 x 130 m). The permanent plots, Sarwadriesprong A and B, cover the central part of each clearing and measure 50 x 50 and 100 x 100 m respectively. As in Blakawatra, trees of the genus Cecropia are taking a major part in the basal area during the early stages. However, at Sarwadriesprong C. sciadophylla Mart. became established next to C. obtusa. The former species

Table 1. Basal area in m^2/ha of secondary wood developed after forest clearing in 1966 and subsequent removal of debris(Blakawatra, site 1) resp. piling and burning of debris (site 3).

Species	Debris removed (site 1)					Debris burned (site 3)				
	1969	1970	1971	1973	1974	1969	1970	1971	1973	1974
Cecropia obtusa Tréc.	4.2	5.8	6.2	6.3	6.3	9.0	11.9	12.5	13.1	13.6
other spp.:										
Goupia glabra Aubl.		0.0	0.1	0.1	0.2					0.3
Inga spp.				0.1	0.3			0.2	0.5	1.1
Isertia coccinea(Aubl.)Gmel.		0.1	0.1	0.4	0.5			0.0	0.1	0.1
Maprounea guianensis Aubl.				0.0	0.2			0.0	0.1	0.3
Palicourea guianensis Aubl.		0.1	0.6	1.9	2.6		0.2	0.4	0.8	1.2
Parinari campestris Aubl.									0.3	0.5
Vismia spp.		0.1	0.2	0.5	0.6					0.2
others		0.0	0.1	0.3	0.5			0.3	0.6	0.9
total other spp.		0.4	1.1	3.5	4.7		0.2	0.9	2.4	4.5
total all spp.	4.2	6.2	7.3	9.8	11.0	9.0	12.1	13.4	15.5	18.0

generally attains a higher age and larger dimensions than the latter.

Graph 1. Basal area of stems 200 mm girth and over in succession plots at Blakawatra and Sarwadriesprong. Explanation see text.



Sarwa A = Sarwadriesprong plot A
Blawa I = Blakawatra site (1), etc.

Obviously the restoration of the basal area at Sarwadriesprong proceeds much more quickly in the large clearing (plot B) than in the relatively small one (plot A). It is not yet clear to what extent this fact has to be attributed to a difference in light conditions. As compared with the Sarwadriesprong plots the plot at Blakawatra, though fully exposed to incident light, is marked by a less vigorous growth of the secondary wood, even where the debris was accumulated and burned.

5. Conclusions

(1) In the mechanically cleared plot the pioneer vegetation originated from seeds already present in the soil (secondary tree species and presumably some perennial Cyperaceae and Gramineae), from seeds imported after the clearing of the forest (annual species mainly wind-dispersed) and – in minor part – from relic plant parts as roots (species of the original forest). Intensive burning caused the elimination of nearly all diaspores in the soil.

(2) In one part of the plot species with a rapid lateral spread played a dominant part in the early stages and lead to a vegetation chiefly composed of more or less isolated one-species groups. Later on species with a strong vertical growth such as trees took over dominance and a markedly stratified wood developed. In a next stage pioneer species that lacked the ability to develop sufficient height were eliminated.

(3) In another part of the plot a temporarily inundation during the first year brought about the dying off of dicotyledonous seedlings and in two years a closed vegetation of graminoid plants resulted. In subsequent years very few woody plants got established.

(4) Relatively small differences in the original environment, like a somewhat concave relief and possibly a slightly heavier soil in the latter part of the plot, are responsible for this remarkable divergency in succession.

(5) In the mechanically deforested plot, where the debris was either removed or piled and burned (Blakawatra), the basal area of the secondary wood after 7 years amounted to 40 - 70 % of the value for the original forest. In the plots, which were cleared by cutting and where the debris was left (Sarwadriesprong), the basal area of the wood attained in the same period 55 % (small clearing) to 90 % (large clearing) of the initial value. Soil compaction and disturbance of the soil profile, caused by the heavy equipment for forest clearing and debris removal, may be responsible for this difference in growth rate.

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INUNDATION OF A TROPICAL FOREST IN SURINAM (DUTCH GUIANA), SOUTH AMERICA

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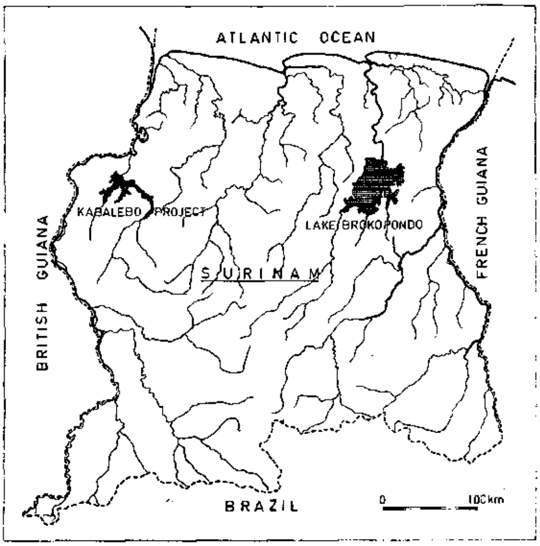
R.I.N.-Communication nr. 105

Summary

A description is given of the events which followed the inundation of 1,500 km^2 of tropical rain-forest in Surinam (South America), to form an inland lake in an undisturbed tropical environment. Eight years after this inundation of the forest, the water below the barrage in the valley still smells of sulphur hydrogen. The trees, which were not removed from the bottom of the man-made lake, remained upright under water, and the trunks of hard-wood species emerge from the surface. Stagnation of the river water soon led to a vigorous development of floating vegetation (water hyacinth), which covered 41,200 ha two years after the completion of the dam. This plant has now been radically exterminated by the spraying of 2-4-D from planes and boats. The succession of plankton communities is described. The lake is oligotrophicating as a result of the general character of the environment, lack of pollution by human activity, continuous discharge of water, and suppletion of oligotrophic river and creek water. The action of wind in the lake area has increased.

Introduction

It is well known that in earlier times The Netherlands had large areas of peat moors which were difficult to penetrate and even dangerous to cross. This natural landscape provided not only a place of refuge during the war with the Spanish intruders, but also peat for fuel. At that time there was no scarcity of energy, and old Dutch sayings refer to abundance in terms of peat. But history has shown that these reserves were not inexhaustable, and it would perhaps be wise to remember them in our present world, not least of all in relation to the immense tropical forest regions of Surinam. The people of Surinam have much the same attitude towards trees as the Dutch once had towards peat, but there is still time to ask wether this is wise.



Map of Surinam with Lake Brokopondo and Kabalebo project (in construction).

The inundated forest

Large parts of the interior of Surinam are covered by tropical rain-forest. Several rivers run from south to north and empty into the Atlantic Ocean. Along the rivers a small autochthonous population lives in villages, but most of the people of Surinam are concentrated in towns situated along the northern coast. The influence of man on nature is restricted to areas around the villages, where the native people plant their vegetables and hunt animals, birds and fishes.

The construction of dams across the rivers in these regions represents a much more radical interference with the forest ecosystem. It means that vast areas of tropical rain-forest will be inundated, which totally changes the ecosystem. An example of this process is offered by the formation of Lake Brokopondo, which started in 1964 and now covers an area of about 1,500 km^2. In the western part of the country the Kabalebo project has just been started. Both projects are intended to provide electricity for the exploitation of bauxite. Closer to the coast, the Stondansie project with barrages in the Nickerie river will serve agricultural purposes.

So far, only the effect of the damming of the Suriname River near Brokopondo have been followed. It took seven years for the lake to fill. Most of the forest remained standing under water. No attempt was made to clear the bottom of trees in advance, because they did not burn and other clearing measures were too expensive. The trunks of hard-wood species emerge from the water, but the soft-wood species broke off at the water line and decayed. It is to be expected that many of these trees will remain where they are perhaps for centuries, a hindrance to navigation and fishery and also hampering the management of the lake as a source of water of good quality.

As everywhere in the tropics, a vegetation of floating vegetation was expected to develop and cover the open surface of the water. Lake Brokopondo was no exception, and two years after the completion of the dam an area of 41,200 ha or 53% of the existing surface (at that time) was covered by mats of water hyacinth (Eichhornia crassipes) (van Donselaar 1968). The former riverbed showed only a sparce growth of water hyacinth, probably due to the rapid rising and falling of the water level in wet and dry periods. After stagnation, the plant spreads rapidly, forming islands with the dead trees as nucleus. The formation of these mats caused oxygen depletion of the underlying water, and the inundated forest seemed to have turned into a swamp. This was also indicated by analysis of the plankton communities in the water in the open spaces, which consisted mainly of species typical for shallow water. Among the roots of the water hyacinths populations of young fish, crustaceans, and insect larvae developed. (Leentvaar 1973).

The need for control of the water hyacinth was recognized by those responsible for the management of the lake. They initiated a programme of chemical control based on the spraying of 2-4-D by plane and boat, and by 1970 the plant was totally eradicated. As a result the reservoir now shows only dead tree-tops, a few islands, and open water. A strict watch is kept for signs of the redevelopment of the water hyacinth or the appearance of any other floating aquatic vegetation.

The consequences of suppression of the water hyacinth mats are considerable. The action of the wind on the water surface has increased, and after showers there are such high waves that navigation with small boats is dangerous. Above the surface of the water the lake shows only dead tree-tops with spiders' webs as the only sign of life. Birds are seldom seen. Under the surface however, there is a rich development of fish and plankton. Bottom flora and fauna are scarce. The action of the wind has improved the mixing of the water layers in open areas, but stagnation persists between the trees and this causes oxygen depletion locally already just under the water surface. The sinking down of dead water hyacinth plants is probably responsable for the slowing down of the initial improvement in the oxygen content observed in 1968. The fish are also affected by the disappearance of the water hyacinth, because the voracious pireng (Serrasalmus rhombeus), which was common before 1968, has decreased in number. This species apparently spawns in the roots of water hyacinths.

The transition on the banks of the lake to the living trees along the shore is sharp. There is no shore vegetation emerging from the water. It will probably take a very long time for rooting marsh plants to become established. Fluctuations in the water level will hinder the establishment of a shore-vegetation succession. In addition the nature of the subsoil, which is composed of a hard rock or laterite clay, is not favourable for rooting helophytes. The shallow and more or less sheltered parts of the vast lake area will in the time become favourable in this sense, after decaying organic matter from the surrounding forest has accumulated.

The conclusion to be drawn from these considerations is that large parts of this inundated forest - as a man-made lake - will be covered by floating swamp vegetation if control measures are not taken.

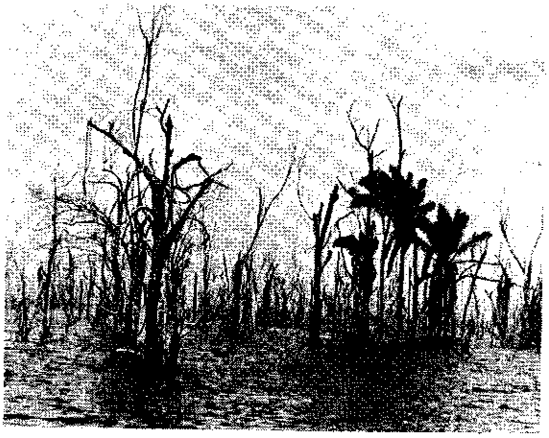
Environmental factors

The soil of the interior is poor in minerals, and therefore there is little leaching of minerals into the river from the forest. As a result, the water of the rivers has an oligotrophic character, resembling the rivers of the Amazon region described by Sioli (1968). Because the soil is poor in lime, the water has also an acid character. The average annual rainfall in Surinam amounts to 2,000 to 3,000 mm. During the wet season the river water is almost pure rain water with a very low mineral

Lake Brokopondo in 1964 some months after inundation. "Sea" of dead forest with some green islands.

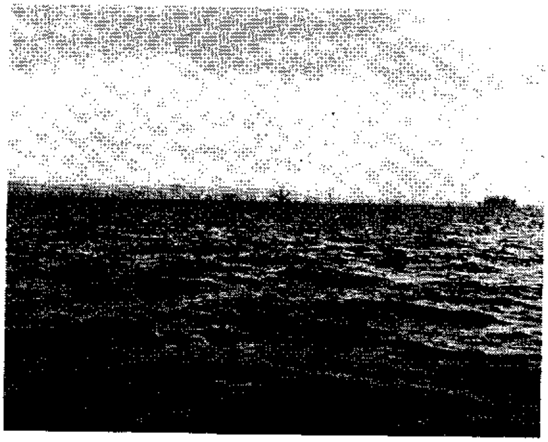
View of lake Brokopondo in 1973.
Photograph "Stichting Natuurbehoud Suriname"

Development of Eichhornia crassipes in 1968.

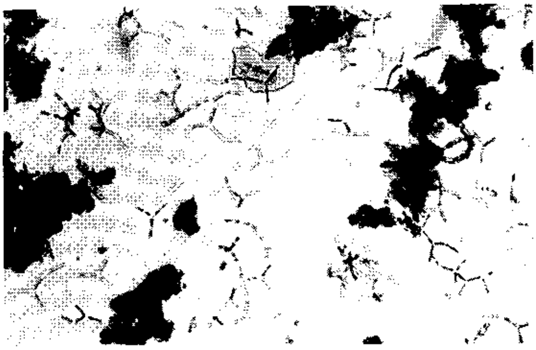


Part of the lake after chemical control of waterhyacinth.

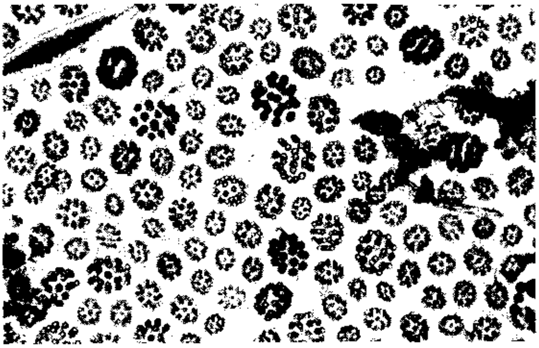
Lake Brokopondo. More absence of wind in 1968.



Lake Brokopondo. More wind and waves in 1972.

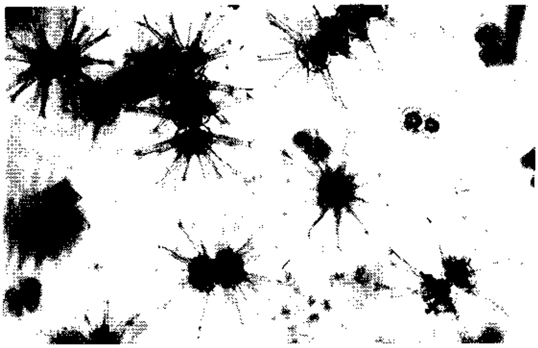


Plankton of the Suriname River.
The diatom Eunotia asterionelloides.

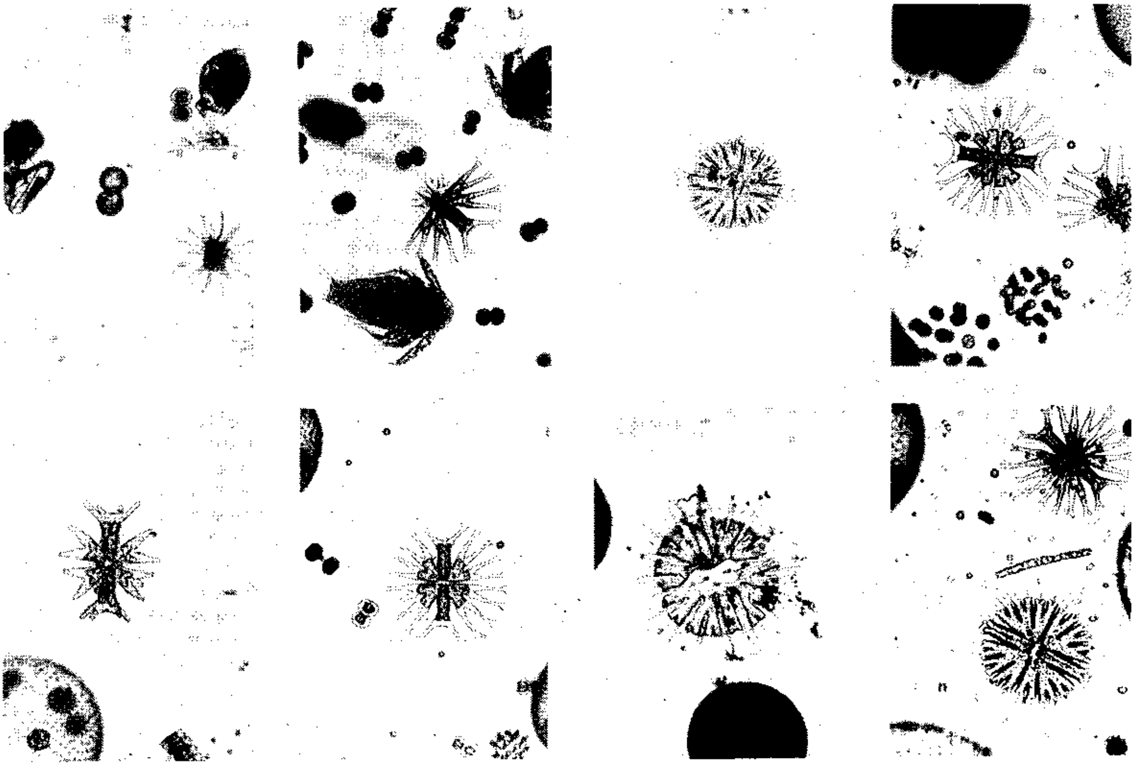


Bloom of Eudorina elegans some weeks after inundation of the forest.

Detail of left figure.
The desmid Staurastrum leptacanthum.



Bloom of Desmids in 1968.



Desmidiaceae from Lake Brokopondo, 1968.

content and few plankton organisms; in the dry season plankton, mainly diatoms and desmids, develops in stagnating stretches in the riverbed. Most of the tree species belong to the Leguminosae, and nutrients such as phosphate and nitrogen recycle in the forest. Little light penetrates the canopy of the forest, but when dying trees loose their leaves the ground is illuminated and a herbacious vegetation may develop. This started to occur as soon as the inundated trees were standing in a few decimeters of water. The reason for the death of these trees is not clear, because trees growing along the river banks are resistant to total inundation for several weeks. During the first phase of the filling of the lake area, the green banks of the river and creeks were in sharp contrast with the already brown dead trees of the submerged forest. The fact that trees of the inner forest die in such shallow water may contribute to the sharp transition between dead and living trees along the borders of the lake.

The increasing illumination of the water surfaces in the submerged forest area promoted the development of floating herbacious vegetation and phytoplankton. Stagnation of the current and increasing wind action also played an important part in the environmental changes in the inundated area. The water temperature rose from 29° to 31° C, with maxima from 35° C. The decomposition of organic matter must therefore be accelerated. On the other hand, after the inundation the acidity of the water increased which reduced bacterial activity. The pH dropped from 6.5 to 5.5. The decomposition activity was reflected in a sharp drop in the oxygen content of the water. In the normal river the oxygen content was almost at the saturation level (7-8 mg/litre), but after stagnation it dropped within a few weeks to zero from top to bottom when measured amongst trees. In open water the uppermost layers showed only a few milligrams of oxygen, with sharp diurnal fluctuations. The layers below 3-4 m contained H_2S and even after eight years the river just below the dam smelled of H_2S. Serious mortality of the fish was not observed; they probably escaped from the area or fled to shallow water. It is of interest to note here that severe fish mortality in the central Amazon region due to cold fronts has been reported (Brinkmann and Santos 1973). Rapid cooling of the air/water interface disturbs the thermal structure of flood-plain lakes by changing the thermal and chemical startification. The associated strong winds generate strong currents, which in time bring deep water containing H_2S to the surface. The mixing dynamics are such that the entire body of water is found to be isothermal within a period of about twelve hours. Similar rapid dynamic changes caused by wind after rain showers are also found in Brokopondo (see Leentvaar 1973).

The fact that H_2S is present in deep water under natural circumstances as well as in the flood-plain lakes means that H_2S will be a permanent constituent of the deeper water in the inundated Brokopondo forest. Because the oxygen content increased even at the bottom in later years it was expected that the formation of H_2S and the rotting of organic matter would stop, but the intensity of the biochemical processes at these high water temperatures gives rise to complicated effects. This was shown by the biochemical oxygen demand estimations (B.O.D.), which were carried out at various places and at different depths. In the river the B.O.D. was less than 1 in wet periods and 2-3 in dry periods; in the lake the value was 3-4, even in deep parts. Thus, the B.O.D. results gave no indication of the amount of available organic matter, which must be large during the first phase of inundation. Nevertheless, mineralization processes were going on, as was shown by the chemical analyses. A total absence of N, P, and S in the river before stagnation was followed by high values after stagnation. PO_4''' ranged from 0.70 to 1.5 mg/litre; NO_3' from 0-2.0 mg/litre. The low pH might explain why no denitrification took place in the anaerobic deeper water. $NH_4^{\cdot}$ could not be detected. Characteristically for this type of environment, in 1972 N compounds were absent in the water again, whereas PO_4''' was present in amounts of 20-40 γ/litre. The presence of Fe was probably responsible for the presence of dissolved PO_4''', NO_3' being soon depleted as a nutrient by phytoplankton in this N-poor environment. In the Amazon river only 1-3 γ/litre P is present in the water. Gessner (1960) showed experimentally that the sediments keep the P-concentration at this low level. The quantity of plankton can, however, be large and here the level of accumulated phosphate is much higher than in the water. The sediment acts as a P buffer. The presence of large amounts of iron in the Surinam rivers might play a role in this situation.

Succession of plankton organisms

In the acid oligotrophic river water, desmids and diatoms predominate. Zooplankton was very scarce. After stagnation of the water and inundation of the forest, successions of plankton communities could be followed. An example is given in the figure, taken from J. v.d. Heide and based on data collected at sampling station Kabel. The original river plankton disappeared, but certain elements developed in great numbers. The water acquired a green colour due to *Eudorina elegans* and other species of phytoplankton. Zooplankton such as *Cyclops*, *Diaphanosoma*, and rotifers also increased in numbers. This community also occurred in the river during disturbances associated with the beginning and end of a rain period, and offers an example of self-purification by a river under natural circumstances. The permanent disturbance caused by the valley interrupted the normal cycle, and the community was succeded by a saprobic plankton composed of many unicellular flagellates (*Trachelomonas*, *Strombomonas*) and numerous crustaceans and rotifers occurring only in the oxygenated region to a depth of 3 or 4 metres below the surface. Later, many green algae such as *Dictyosphaerium* and *Tribonema* with some desmids and also ostracods became dominant. The saprobic community gradually changed into a more eutrophic one. Oligotrophic elements remained present, indicating that the original oligotrophic dynamics of the environment were still in play. After three years, a more definitely oligotrophic lake plankton with many species from shallow stagnant water became established. The plankton is now characterized by *Volvox*, many desmids, and crustaceans. It is interesting that no explosion of blue algae took place, although P, N, and organic compounds were abundant in the water. This phenomen can be observed in enriched acid oligotrophic waters of the same type in regions with a moderate climate. In some quiet places between trees a thick film of iron bacteria covered the surface temporarily, and other spots showed mats of filamentous green algae. Duckweed was also present during a short period, another indication that large amounts of organic and inorganic matter were present in the water. When the tops of the trees gradually disappeared under the water and wind action increased, the iron bacteria, filamentous algae, and duckweed disappeared.

Generally speaking, it may be said that the community of river plankton is replaced by a saprobic community which in turn is followed by an acid oligotrophic plankton composed mainly of desmids and crustaceans. The latter community seems to be the character type of the lake plankton. However, the large numbers of the individual desmid species may indicate that the environment is not yet stabilized. The final character of the aquatic environment will evidently be oligotrophic with desmids dominant - a rare case of oligotrophication of a man-made lake. This diagnosis is based on facts pertaining to the character of the total terrestrial and aquatic ecosystem. The Brokopondo region is situated in midst of an immense tropical rain-forest with an oligotrophic character. The affluent waters, together with the added rain water, carry very low amounts of nutrients. There is no pollution of the water by human activity. Therefore, all of the factors involved tend to induce regeneration of a stable oligotrophic ecosystem.

Conclusion

During the third International Congress on Man-made Lakes held in 1971 in the U.S.A., an administrator stated that all of the world-wide potential energy gained from damming rivers will be exploited in the future. Plans are being made for damming of the Amazon system. The Brokopondo case can teach us a great deal about the implications of inundating tropical forest. This process involves a risk of a major change in climate after a rain-forest is replaced by an inland "sea". It is fortunate, that the World Bank, which finances dam projects, has stipulated that ecological research must be included in such planning. This is being in the recently started Kabalebo project in Surinam.

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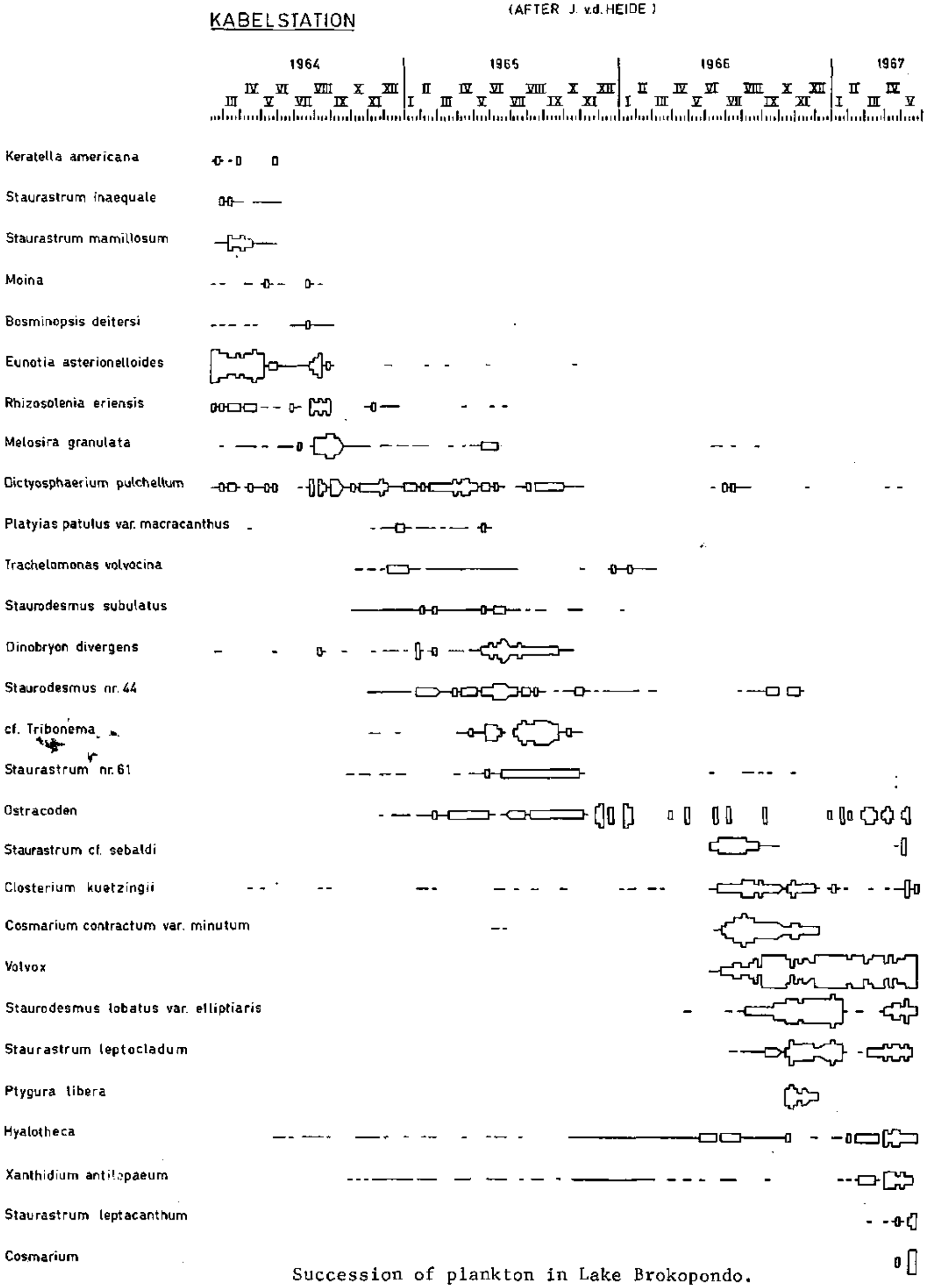

Succession of plankton in Lake Brokopondo. Abundancy for the dominant species is indicated.

INFORMATIONS ABOUT THE CONSEQUENCES OF ACCELERATED DEFORESTATION IN BRAZIL

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Summary

The present paper contains some historical data concerning the problem of deforestation in Brazil, a process that started before the arrival of the europeans but was greatly accelerated afterwards. Some present-day data will be given.

The consequences of accelerated deforestation will then be discussed, especially in areas of denser population, in the South and all along the coast.

How can this problem be solved? Indications of reversal of situations when human interference is suppressed will be given, grounded on the Author's experience concerning the "cerrado"-vegetation (savanna). Evidence of progressive degradation will also be presented.

The urgent need for a revision of many ecological concepts evolved in countries with completely different climatic and edaphic conditions will be explained. In doing so, the Author will take into account data gathered from different types of vegetation in Brazil, especially "cerrados" and "caatingas" (deciduous-Northeast), as well as forests of different types (evergreen "caatingas" of Alto Rio Negro, in the Amazon; the Atlantic tropical and subtropical rainforests; the *Araucaria* - forest of Southern Brazil).

Finally, consideration will be given to the problem in the Amazonian region, with a brief discussion of what seems to the author to represent a real danger and what seems to be unsound speculation, with especial consideration of the so much debated "Transamazônic" road.

Devastation before the discovery

Documents written soon after the discovery of Brazil by the Portuguese (1500) show that at that time the country was already being devastated by the Indians in their search for food, which consisted mainly of fish and meat, as well as of roots, grains and fruits, that they either gathered from natural sources or from their own crops.

The Indians, of course, also covered their primitive huts with palm-tree leaves or dried grass-stalks; besides, palm-leaflets were interwoven to form the walls, while different species of plants (most frequently palms) were used to make the house structure.

Their hunting and fishing instruments were made of plant materials. Different tribes used different plant species to prepare them. *Tecoma impetiginosa* and *Dalbergia nigra*, among other species, were used to make the bow, and fibers from *Astrocarium campestre*, several species of the genus *Bactris* (Palmae) and *Bromelia karatas* were used to prepare the string. The arrows were made from such plants as different species of *Bambusa*, and were ornamented with diversely colored feathers of birds, firmly tied down with fibers of several types.

Besides, the Indians made hammoks of several fibers, prepared an alcoholic beverage, called "cauim", from fermented manioc roots (*Manihot utillissima*) or corn grains that were chewed by old women and spit back into a big earthenware bowl, and frequently painted their bodies with paints extracted from *Bixa orellana* and *Genipa americana*.

First reports on Brazilian Nature

The first reports on our country were written by Nóbrega, Anchieta, Hans Staden, Léry, Thevet and Gandavo, among others. They mention, among the plants cultivated by the Indians, cotton, tobacco, manioc, sweet-potato, corn, beans and peanuts.

Nóbrega came to Brazil with Tomé de Souza (1549), when the Portuguese King appointed him as the first Captain-General of the country. He makes reference to the use of tobacco by the natives, stating that it was very good for the health. In 1553 Anchieta came to Brazil with Duarte da Costa, the second Captain-General. He mentions, in his correspondence with Europeans, that the Indians used extracts from several plants to poison fish. Thus, they killed more fish than they could eat.

Hans Staden, who came to Brazil in 1550, was made prisoner of the Indians (tupinambás) but cleverly managed to survive, went back to his country, and published a book on his adventures, containing details of his tragedy. His work offers a great deal of information on the nature of this country and on the habits of the people who lived here in the early stages of the history of Brazil.

A little later (1576) Gandavo wrote another book giving information on the different crops that were grown at the time. He makes references to the manioc, the banana, and other plants.

There is also an excellent book by Jean de Léry, whose trip to Brazil, like Thevet's, was connected with the foundation of Antarctic France by Villegaignon. His book was first published in 1578, and, among many interesting bits of information, he gives a description of our forest trees. The pau-brasil (*Caesalpinia echinata*) is given a special consideration. Some trees of that species were so thick that three men were required to embrace their trunks at breast height. He describes the way these plants were cut down by the Indians, who prepared the trunks and carried them on naked shoulders (sometimes for 10-15 kilometers) through difficult paths, up to the French and Portuguese ships anchored at some point near the coast.

In 1587 Gabriel Soares de Souza wrote another important book in which precious information is given concerning our agriculture, the herbs and trees that were used for medicinal purposes, the trees which furnished wood for house-building and furniture making, the trees that furnished fibers, and so on. He also gives additional information about our animals and minerals.

With Nassau, who for a few years lived in Northeastern Brazil, then under Dutch rule, came a few scientists, among them Piso and Marcgrave. The latter wrote a book called "Historia Naturalis Brasiliae" that was published in 1648 by João de Laet. It was translated into Portuguese by a priest, D.José Procópio de Magalhães, and edited by the "Museu Paulista" in 1942. Marcgrave made excursions through the States of Maranhão, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe and Bahia.

His contribution to the Flora of Brazil was more important than that of Piso who was a physician mainly interested in the therapeutic properties of our plants. His observations were also published in 1648, and translated in 1948 by Alexandre Correia.

Some Brazilians, then, began to study the Brazilian vegetation, but their efforts, though enormous, often went unrecognized by the Europeans. Saint-Hilaire writes in his book:

"Foreigners visiting Brazil seem to believe that they owe nothing to the Brazilians and that the Brazilians owe everything to them; I have seen some of them, specially Germans, treat the Brazilian people with a disdain that nothing could justify"

At the begining of the 19th Century there occurred an intense movement of scientists, who singly or in groups, visited our country. Langsdorff, Sellow, The Prince von Wied-Newvied and Saint-Hilaire stand among them.

They all contributed, to a greater or lesser degree, to the knowledge of the Nature of our country at that time.

Saint-Hilaire is to my belief the one who made the greatest contribution during that period. He arrived in Brazil in 1816 and remained here until 1822. He travelled through the States of Espírito Santo, Rio de Janeiro, Minas Gerais, Goiás, São Paulo, Santa Catarina and Rio Grande do Sul. In his trips he collected precious botanical and zoological samples and observations in the fields of Human Geography, History and Etnography. As far as botanical material is concerned, Saint-Hilaire collected 30,000 samples of 7,000 species, more than 4,500 being unknown until that time.

In one of his books he describes the enormous devastation of our forests that was carried on by the Europeans, a continuation of the process started by the Indians. He refers to the practice of burning the fields every year, as a way of getting fresh grass for the cattle. He says that our forges at Ipanema, near Sorocaba (State of S.Paulo) instead of burning coal used big logs of peroba (*Aspidosperma polyneuron*), a most useful timber.

The devastation increased since then at an ever accelerated speed, as we can conclude by comparing the situation, described in the historical documents, to that we can observe today.

Saint-Hilaire indicates that in Casa Branca (State of S.Paulo) the Brazilian Government settled several families from the Açores. These people, scared by the size of the trees they had to fell down before preparing the soil for sowing, run away, crossed all the State (then Province) of Minas Gerais and went to Bahia, which was, at that time, the seat of the Crown, to implore the King to remove them from that place.

Casa Branca is today a desolate place, with a poor "cerrado vegetation" (a savanna-like type of vegetation) and a few spots of poor forest - especially along the rivers (gallery forests).

Andrade-Lima (1966) calls our attention to the fact that the Atlantic forests in Northeastern Brazil are not well known because, in the past, they were not studied, and, in the present, they practically no longer exist.

He also says that man reduced the area previously occupied by "true caatinga", a type of deciduous thorny forest that drops almost all the leaves during the dry season. In this caatinga (the word caatinga is of Indian origin and means "white forest") the tree is the dominant component, with a continuous canopy. Other types of "caatinga" (bushy caatinga and bush scrub), in which trees do not form a continuous canopy and as a rule are not the dominant element, along with other types of vegetation, such the "cerrado" occupied areas previously covered by tree-caatingas, which were destroyed by man.

If this happened in the Northeast, we know that in Southern Brazil the same thing happened in the past and is happening at an ever increasing speed nowadays, with other types of forest.

The situation at present

In Central-Eastern Brazil the forest devastation has been tremendous. Even today the iron industry in the State of Minas Gerais every year destroys forests in an area of more than 1,000 km^2. Very little remains of one of the most magnificient Brazilian forests of that area: the forest of the Rio Doce Valley.

In the very South, the *Araucaria angustifolia* has been felled for many years and in some places it has completely disappeared.

When one travels in Southern Brazil during the dry season, one is astonished to see the number and the extension of forest fires.

Somebody described this fact with some humor stating that when the dry season comes the Brazilians feel a hitch in their hands which does not stop until they start a fire. In fact, fires are started for different reasons: to prepare the land for cultivation, after felling down the forest; to clean a certain area already cultivated but invaded by weeds; to kill animal and plant pests; to burn old and dry grass in pastures thus forcing the sprouting of new green grass for cattle, and for several other reasons.

Accidental and criminal fires also deserve mention. In the first group we should for instance include those fires caused by cigarettes that are thrown away without the desirable care, though with no criminal intention. Besides, in some parts of Brazil there still run old trains moved by the energy of burning wood or coal. Burning ember carried by the wind can easily start a fire.

Criminal fires are those that are deliberately set to cause damage to somebody. Though uncommon, they exist.

No matter its reason, the fact remains that fire is an important ecological factor that was present in Brazil before the discovery, increasing in frequency and intensity afterwards. There is not, necessarily, a correlation between the size of the population of a certain area and the extension and intensity of the fires that are set.

Recently (1973) Richards published an interesting paper on "The tropical rain forest", in the "Scientific American". He includes a picture, taken from an artificial satellite, which shows a big fire made by Indians, in the Amazon. In that picture we can see how wide was the area affected by such a fire, set by a small group of Indians, close to their huts, for the cultivation of manioc.

People recently travelling by the Belém-Brasília road have told me their unpleasant experience: during the night long stretches of the road were illuminated by fires on both sides; the heat was awful and they had to go through at a great speed, for fear that the gas tank of their car might explode.

These two examples show that big fires may occur in almost unpopulated areas. But, generally speaking, the felling of trees and the burning of cultivated areas increase in the region of denser population, because of the greater need of food and of many other utilities that derive from the land. Modern man needs more houses, more furniture, more fibers to weave tissues for their clothes, and, among other things, more cellulose paste to make much more paper than in the past. The computer has considerably increased our need of paper. In view of all that demand, Governments, following the advice of agronomists, with the support of economists, dictate laws that as a rule are not approved of by ecologists.

This is a case in which there is a clear conflict of ideas between people with different backgrounds. Agronomists, for instance, look for a greater production in a shorter time, whereas ecologists prefer a smaller production on a continuous basis; economists on the other hand, tend to agree with the agronomists, because a greater production means more financial benefits.

Thus, in Brazil, the felling down of *Araucaria angustifolia* which was replaced by *Pinus ellioti*, was widely approved of by agronomists and economists, because more cellulose paste could be obtained from the imported species than from the *Araucaria*. But the ecologists lamented that fact. It was not a question of being against a species or in favor another simply because it was native. The position of the ecologists was dictated by the fact that they knew that an ecosystem was being completely destroyed, giving place to an "artificial" ecosystem whose behaviour, in the area it was implanted, was entirely unknown.

In many parts of Brazil, for years, there were endless debates around the question whether *Eucalyptus* should be planted or not. Many arguments, for and against it, were brought forward. I shall not go through all of them, but I shall say that *Eucalyptus* protected from destruction many a stretch of natural forest. Of rapid growth, it can furnish a great deal of burning wood in a short time, thus preventing the felling down of natural forests. And they were preferred because they were very uniform, whereas the natural mixed forest gave a very irregular burning wood, as far as hardness, thickness of the log, amount of potencial energy are concerned.

Those who were against *Eucalyptus* generally pointed out the fact that it is a great water consumer. In fact, it is. But many native Brazilian species of plants were shown to consume even more water than *Eucalyptus*. An example was given by Villaça and Ferri (1954), who made calculations from data obtained by Rawitscher and Ferri (1943). These authors studied *Cedrela fissilis*, which has an enormous water consumption. Sugar cane was proved to consume a great amount of water as well

(Meguro and Ferri, 1956; Meguro, 1963).

Thus, nowadays, this kind of discussion is rather meaningless, since man needs wood, paste, sugar, alcohol, etc. and all this has to be paid for one way or another. In the example we have given the payment is represented by the water consumed. The quicker the plants grow more materials they will produce and more water they will spend.

Today the emphasis is put on the modification of the whole ecosystem. Attention is not given to a single component of that system, but to the modifications man may introduce in it, sometimes in an irreversible way.

What happens to the vegetation as a whole? And to the animals living in it? What happens to the soil or, possibly, to the climate of the region, as consequence of the modifications introduced by man?

In only a few cases we can have answers to these questions. But to demonstrate the correctness of the answers, experiments should be undertaken. Since these experiments were not made under rigorous scientific control, we often have to rely only on past experience and on common sense.

If we take the case of the Amazonian region, for instance, we come to the conclusion that the forests that grow there have attained maturity, and consequently there is an equilibrium between the amount of oxygen liberated during photosynthesis and the amount consumed by respiration. And, also, that there is a compensation of the organic matter decayed by the organic matter that is produced. There is no loss; there is no gain.

We know, however, that the soil in large parts of the Amazonian region is almost pure sand, covered by a layer of decaying organic materials (litter formed mainly by leaves, but also by stems, flowers, fruits and other dead materials, such as the carcasses of birds, mammals and other animals). We know that the forest covers this kind of soil, giving it an excellent protection. It has been estimated that between 90-95% of the sun light, that falls over a certain area covered by that forest, are absorbed by the different layers of the canopy, and that only 5-10% reach the soil surface.

Thus, once suppressed the forest, much more sun radiation will reach the soil surface. Its temperature will rise considerably. The result will be a tremendous increase in the speed of oxidation of the organic matter. This increase will be even greater if we consider that aeration is also increased by the removal of the forest.

The effects of rain-water should also be taken into account. The annual rainfall may reach 4,000mm in some parts of the Amazonian region. With the forest present, the impact of the rains on the soil is greatly decreased: they fall with their whole weight on the canopy, and only reach the soil after running along the trunks or dripping from the leaves.

If, however the forest is removed, the soil will feel the whole impact of rain, sometimes in the form of heavy downpours. Thus the soil particles are easily disaggregated and carried away. In other words, the amount of material that will be removed from the soil surface, by running or infiltrating water, will be considerably scaled up.

We shall then have a soil which will very quickly become poor. Thus, in defending the idea that the exploitation of the Amazonian region is very dangerous, we should not use arguments that do not have a good scientific support, such as the statement that those forests are the "world's lungs", or that they supply the world's oxygen. We should make use of the true facts, and point out that we must be extremely careful in dealing with such an ecosystem, because it is very fragile. If we introduce modifications in it, we know *when* and *where* we are starting them, but we do not know *when*, *where*, and at *what cost* they will be stopped. We will be possibly starting the desertification of very extense regions.

The Transamazonic Road

All this leads us to a highly controversial question, in Brazil and elsewhere: the building of the Transamazonic Road. Is it a dangerous process? Should this road be built or not?

Of course, this is a problem that concerns every Brazilian citizen, not only a few ecologists, economists or politicians.

It is my belief that the construction of that road is, in itself, a good rather than a bad thing. But great care should accompany its construction, to avoid the bad consequences that the opening of such a road might bring: the large scale use of defoliating agents should be avoided, because it may affect other areas; the use of big bulldozers to unroot big trees, a process of violent aggression to Nature, should also be avoided.

Besides once built the entire road, care should be taken so that it might be turned only to good and not to bad purposes. A good purpose is the integration of that enormous area with the rest of Brazil. A bad purpose would be the exploitation of the forest without the indispensable precautions. If the Transamazonic Road serves to retaliate the whole Amazonian forest without due care into small pieces of land, by secondary and tertiary roads starting from the main artery, it will then represent a really great danger. But the fault will lie not in the Transamazonic Road itself, but in the men who did not make good use of it.

I believe that a good "simile" for this is the liberation of atomic energy. When man discovered how to liberate it, he got hold of something which could be used either for destruction or for the welfare of Mankind. If man, instead of using it for pacific purposes, decides to turn it into a destructive weapon, he is the one to be blamed, and not the discovery of atomic energy. The same reasoning could be applied to many human discoveries and inventions.

As a conclusion, then, one might say that the Transamazonic Road is a good thing, but care must be taken so that it is not used for bad purposes.

Another related point, that deserves mention, is the idea that the exploitation of the Amazonian as well as other forests is unavoidable for the development of Brazil. This may well be true, but it is equally true that enormous care should be taken in this process to avoid results which most certainly will be undesirable and, what is more, irreversible, at least during the short span of our lives.

Transformations in the "cerrados"

In some cases transformations are predictable; in other cases not. Great areas of the Brazilian territory are covered by "cerrados". Some of these are primary, in the sense that they always existed. Some are secondary, in the sense that they occupied places that were previously covered by other types of vegetation, for instance a forest, that was continuously felled down and burned by man. The result was a complete modification of the soil surface, so that such an area could not be occupied by a forest again, but only by cerrado vegetation.

If man carries on his aggression to this cerrado, cutting down its trees and burning it every year as the practice has been, this kind of vegetation will also become poorer and poorer. From "cerradão" (dry type of forest with several species belonging to the "cerrado-vegetation"), or from a "cerrado" we shall go to a "campo cerrado" and to a "campo sujo", which are impoverished degrees of the same vegetation.

If, however, this poor "cerrado" is protected against devastation, then, little by little, shrubs and trees will become higher, thicker, more robust and more numerous; there will be more shade, less ventilation, more humidity on the soil surface; there will be a small change of the microclimate, and a small change in the soil conditions; some plants will not stand the competition of others; the biomass will increase, improving the quality of the soil by adding more organic materials that will decay.

Thus a continuous process of microclimatic and edaphic changes will be followed by changes in the composition first of the flora and then of the fauna.

We are quite familiar with this process because we protected a "cerrado" in Emas (near Piraçununga, State of São Paulo) and could follow for 30 years the modifications that occurred. During that period there was an accidental fire, but without any great damage. On the contrary: shortly after everything started growing again and with an unprecedented vigour. The heavy addition of ashes was probably responsible for this. We came thus to the conclusion that a fire every few years is beneficial rather than harmful to this kind of vegetation. What is harmful is the practice of burning it every year. Especially harmful is the cutting-down of trees and woody-tall-shrubs, because in this case, even if the root system and other underground organs remain alive, the growth above ground has to begin again at the soil surface. If the burning is not preceded by the cutting-down of the vegetation, trees and woody-tall-shrubs with thick bark remain alive, and can sprout at their tops. In this case, the new growth can continue at a distance from the soil surface.

I believe that this is the only example of an experiment which has had some control in Brazil, and the only case in which we can establish some relationship between human interference in a Brazilian ecosystem and the modifications that can be introduced in one or in another direction.

If a forest may eventually develop in this protected area, starting from clearings that we often find there, we are unable to predict.

Main conclusions

1 - Deforestation in Brazil started with the Indians and increased with the Europeans, soon after the discovery. Today it has reached enormous proportions.
2 - Fire of different types is an important factor.
3 - The Transamazonic Road can be considered a good thing in itself, but it may be bad if man does not use it properly.
4 - Other types of vegetation, such as the "cerrados", can evolve towards a more or towards a less exhuberant type depending upon the treatment they receive.

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THE SOIL EROSION PROBLEM IN JAVA

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Summary

The data of the sediment load of several rivers in Java show that soil erosion has reached serious levels. Furthermore it appears that the rate of soil erosion is increasing with time.

The underlying cause of soil erosion is akin to overgrazing. Therefore soil erosion control should be attempted by (i) reducing the population pressure on the land and (ii) increasing the carrying capacity of the environment.

To increase the carrying capacity of the environment energy subsidies are required. Care should be taken, however, that the energy subsidies do not compete with local manual energy and that there occurs an equitable flow of energy through the ecosystem. Otherwise the energy subsidy would not increase the carrying capacity, but rather would decrease it, resulting in a deterioration of the soil erosion problem. It is important that a significant portion of the energy subsidy should be invested in education to enhance the technical capabilities and the managerial and marketing skills of the rural people.

Sediment load of some rivers in Java

Soil erosion has received much attention in Indonesia. The State Committee for Environmental Affairs has identified soil erosion as one of the major environmental problems. However, exact figures of the extent of the eroded areas are difficult to obtain. This is partly due to the lack of standardization of the terminology used in the assessment of soil erosion by the various government agencies.

One of the good indications of the extent of erosion is the sediment load of rivers. From May 1973 to April 1974 the monthly measurements of the sediment load of the Citarum-river at Warungjeruk in West Java, where it flows into the Jatiluhur reservoir, gave an average figure of 0.523 mg/l. Since the estimated annual flow of the Citarum at the site was about 5×10^9 m^3, the total sediment load during that period was about 3.1 million ton. The sediment load of the Solo-river in Central Java was reported to be 8.6 million ton during the five months of the rainy season of 1971 - 1972. This was estimated to be equivalent to an erosion of a layer of top soil of 17 cm thick from an area 3,910 ha (Hadipurnomo, 1974). During a recent visit to East Java, the writer was told that the Konto-river deposited 130,000 m^3 silt in the Selorejo-reservoir during the period December 1971 to June 1972. The annual deposit of the Brantas river in East Java during the period 1951 - 197o averaged 2.4 million m^3 per year (Suryono, 1974). Part of this, however, was due to two eruptions of Mount Kelud.

A more distressing picture of the erosion problem is that it appears to increase in magnitude with time. The yearly erosion of the Cilutung basin in West Java was 0.9 mm in 1911/1912 and 1.9 mm in 1934/1935 (Van Bemmelen, 1949). Recent estimates gave a figure of a yearly erosion of 5 mm (Netherlands Engineering Consultants and Snowy Mountains Engineering Corporation, 1973).

Figure 1 gives another example of the deteriorating conditions of erosion in the Citarum basin. Although other quantitative examples of yearly measurements in recent years are not available to the writer, the Citarum may not be an exceptional case of such fast increase of erosion.

Surface run-off of water is a primary cause of soil erosion. Therefore it can be expected that serious soil erosion is associated with large fluctuations of water flow. Hadipurnomo (1974) cited the occurance of flash floods in the Solo-river after rainfall. The flashy nature of the river flow was also reported for the Cilutung, whose catchment area suffered from heavy erosion (Netherlands Engineering Consultants and Snowy Mountains Engineering Corporation).

The data of the Citarum, as presented in figure 1, seem to indicate changes of the seasonal flow characteristics of the river.

Discussion

From the data cited above it can be concluded that soil erosion has become a serious problem in many places in Java. The erosion problem is not only a menace to agriculture, but also to various development projects, particularly to dams, water-reservoirs, hydroelectric generators and irrigation. In earlier times these projects were planned as purely engineering ones, detached from their relationships with the environment. Fortu-

Fig.1. SEDIMENT LOAD OF CITARUM - RIVER

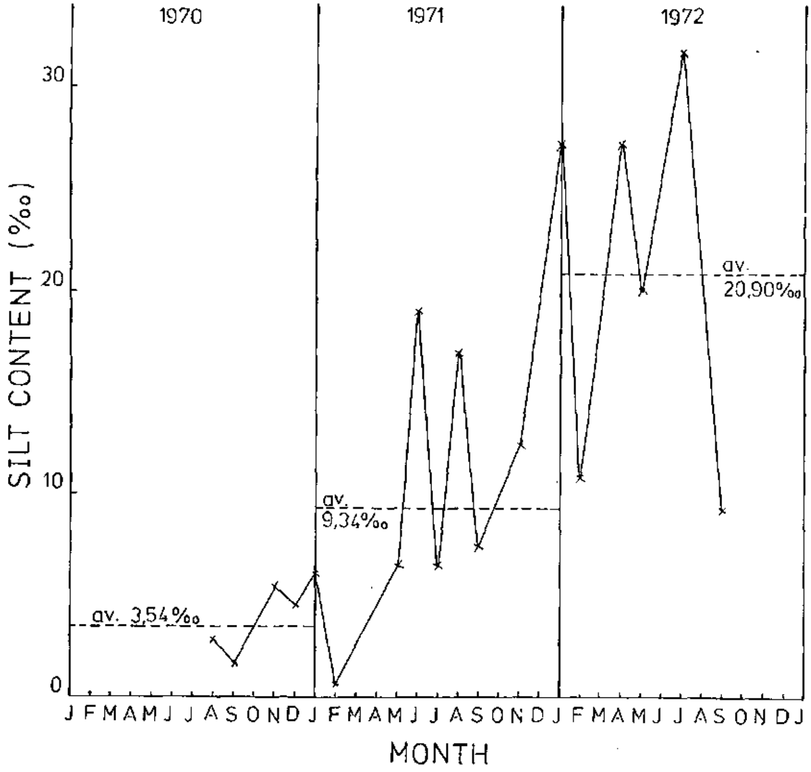
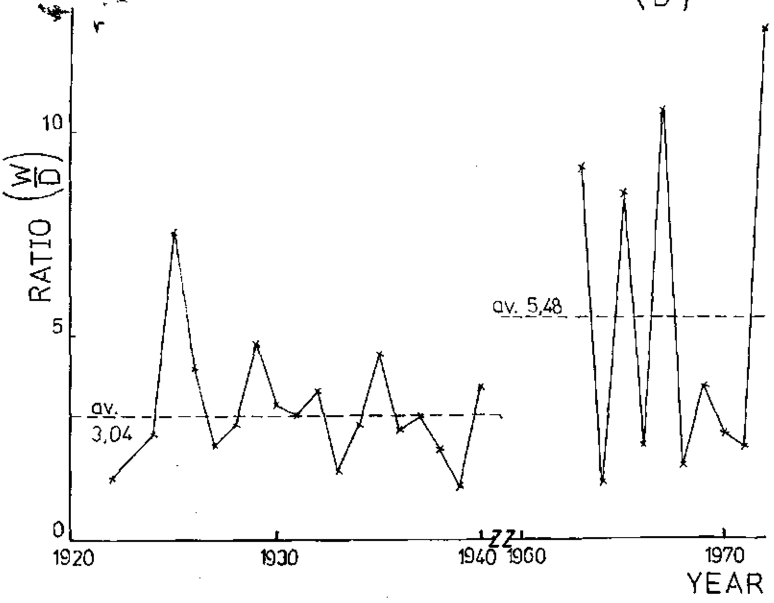


Fig 2. RATIO OF WATER FLOW OF CITARUM-RIVER IN THE WET AND DRY SEASON $\left(\frac{W}{D}\right)$



nately the awareness is growing for the need of an interdisciplinary approach in development, particularly in river basin development (Institute of Ecology, 1974). The Cimanuk development project is an example in which soil conservation has become part of its feasibility study, although other aspects of ecology have not been concluded (Directorate General of Water Resources Development, 1973).

In Java the problem of soil erosion is remarkably similar to the one caused by overgrazing. The overall population density of Java and Madura is estimated to be 576/km^2. The density of the Brantas basin was reported to be 850/km^2 (Suryono, 1974) and in the Upper Solo-river basin the average was 700/km^2, with a minimum of 250/km^2 and a maximum of 1,500/km^2 (Hadipurnomo, 1974).

Socio-economic studies in 13 villages in the Upper Solo-river basin revealed that 10.1% of the people did not own land and the average farm size was 1.68 ha with an average annual income of Rp 13,200/family (about US$ 33/family), while the mean family size was 5.5 (Hadipurnomo, 1974). The income of farmers in the Citarum-river basin was estimated to be equivalent to 367 gram rice/person/day (Soediarto, et al., 1966). Since part of this product was sold, the consumption was expected to be lower. These income figures indicate that the population density had reach the limits of the carrying capacity of the rural environment. The continued rapid growth of the population forced the people to move up the hill and mountain slopes to cut forests for the cultivation of upland crops, which resulted in erosion of the steep slopes, or to migrate into the cities.

Accepting "overgrazing" as the underlying cause of the erosion problem, it become clear that a two-prong approach in erosion control should be attempted, i.e. (i) reducing the population pressure on the land and (ii) increasing the carrying capacity of the environment.

The family planning program, which is now being vigorously pursued in Indonesia, would not reduce the population pressure on the land, since population growth would not cease. However, if successful, it would effectively reduce the rate of increase of the population pressure. The transmigration program, i.e. moving of people from overcrowded Java to the other islands, had achieved very little success sofar. Between 1935 and 1969 the maximum number of people transmigrated in one year was only 60,000 (Iskandar, 1973). Although transmigration could become an important factor in the development of the other islands, it would remain insignificant as a factor to reduce the population density in Java, since even to maintain the population density at the present level about 1 million people per year would have to be transmigrated. This would be beyond the capability of the government in terms of bidget, logostic support and other infra-structural requirements for such mass movement. Mc Comb (personal communication), however, proposed a transmigration scheme to reduce the population densities of selected areas in the Upper Solo-river basin, which theoritically would be feasible.

Efforts to increase the carrying capacity of the environment as related to erosion control had received little attention. And yet it was obvious that under the present land-use system the population density had reached the limits of the carrying capacity of the environment and was at a subsistence level. Therefore any effort in erosion control, which would decrease the carrying capacity of the environment, would inevitably meeti with failure. The currently practiced greening and reforestation programs were in fact decreasing the carrying capacity, since the trees would shade the crop plants and part of the available land was taken out of cultivation. The affected people knew this and - understandably - they often deliberately killed the replanted trees.

It appears that the problem of soil erosion control is not only a technical problem of how to rehabilitate the eroded soil, but even more difficult is how to keep the population from bringing the forested areas into cultivation again and to prevent them from encroaching farther into the forests. If left undistributed, the vegetation in the eroded areas will be able to regenerate to form a belukar and finally a forest, although reforestation may speed up this process.

Certain development projects, which took large areas of land out of production from the rural people, although economically justified from the regional and national point of view, ironically reduced the carrying capacity of the environment for the local people and hence magnified the erosion problem, since the allegedly creation of new jobs did not benefit the local people, who were unskilled and were not suitable for the jobs. This was observed, for instance, with the development of the industrial estate in Banten, West Java, and it was warned that it would endanger the water supply of the industrial estate (Soemarwoto, 1937b).

To increase the yields of an ecosystem substantially, it would not suffice to rely solely on the solar energy fixed in the primary production. Energy subsidies should be supplied to the ecosystem (H.T. Odum, 1971). In the agricultural sector it was estimated that to increase food production two-fold, a ten-fold increase of energy subsidy in the form of respectively fertilizers, pesticides and mechanical power was required (E.P. Odum, 1971). This would indicate the order of magnitude of investment needed, if one would expect a chance of success in erosion control. Since Indonesia has an abundance of fossil fuels, it was suggested to use more fossil fuels as direct energy subsidies, rather than to export them and re-import finished goods (Soemarwoto, 1973a).

In river basins a relatively untapped source of energy is the potential energy of water. When harnessed, however, the produced electricity was usually exported to the industrial centers. Very little, if any, was used to rehabilitate the structure and functioning of the river-basin ecosystem. Used for rural industrialization rural electrification would increase the carrying capacity of the rural environment by improving the quality of the agricultural products and providing new income from new products and jobs. This would divert part of the population from the agricultural sector and would decrease the population pressure on the land.

More important rural electrification would boost education and this in turn would enhance the technical capabilities of the people to increase the carrying capacity of the environment. The enhancement of capabilities should include skills for management and marketing.

Care should however be taken that any form of energy subsidy should not compete with local manual energy and that it should be distributed equitably, as discussed in another paper presented in this Congress (Soemarwoto, 1974).

From short term considerations, provision of massive energy subsidies to rural areas may not be economical. However, considering that the destruction of the water regime and the erosion of the top soil are very serious offences to the life support system of the country, which, if unchecked for an extended period, will cause irreversible damage, such policy may well determine the long term survival of the country. Furthermore in Java and Madura about 85% of the people live in the rural areas.

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ECOLOGICAL EFFECTS OF THE REGRESSIVE SUCCESSION MUHULU-MIOMBO-SAVANNAH IN UPPER-SHABA (ZAIRE)[1]

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Summary

The authors review dry evergreen forest, woodland and savannah regarding their ecological differences. They successively analyze macro- and mesoclimate, role of fire, pedology, qualitative and quantitative aspects of plant and animal communities, litterfall and litter breakdown. Finally the ecological consequences of deforestation on river systems are discussed.

Introduction

Climax vegetation in Upper-Shaba (formerly Upper-Katanga) is mainly dry evergreen forest (muhulu). Centuries of human activity, e.g. fire and hatchet has induced woodland (miombo), a pyroclimax which is now the more frequent vegetation type (around 87 % of the area). However near towns, villages and roads, woodlands disappear and are replaced by open woodland and related savannah. This regressive succession provides a strong support for studying ecological effects of deforestation in Upper-Shaba. The data deal with the Luiswishi experimental site (L:11° 29' E, l:27° 36' S, alt. 1208 m), a typical situation for the surroundings of Lubumbashi (Malaisse, 1973).

Macro and mesoclimate

The macroclimate of Lubumbashi is characterized by one dry season with a mean of 185 days between May and September; one rainy season with a mean of 118 days between November to March and two transition months, October and April. Mean total rainfall is 1270 mm. The average yearly temperature is about 20.3°C, lowest at the beginning of the dry season (July) and falling occasionnaly to the freezing point (-1.5°C). September and October are the warmest months. The relative humidity of the air follows the rainfall pattern, with a minimum in October (53 %) and a maximum in February (90 %). The mean total solar radiation is 16.8×10^9 Kcal/ha/yr of which about 61 % of direct solar radiation. The minimum average of total daily radiation occurs in the rainy season (398 cal/cm^2/day in January) and the maximum during the warm dry season (593 cal/cm^2/day in September). Mean daily hours of insolation are lowest in December and maximal in September. The yearly mean is 2803.7 hours with an annual daily mean of 7.67 hours (Freson, 1971).

Concerning the mesoclimate, the sequence muhulu-miombo-savannah demonstrates the effect of the density of canopy on temperature, total solar radiation, atmospheric humidity, throughfall precipitations and soil water content (Table 1).

Table 1. Mesoclimate data of the three ecosystems (Freson, 1973 and unp. data).

	Muhulu	Miombo	Savannah
T(°C)	19.2	20.6	22.1
ΔT(°C)	10.4	16.5	20.8
Hr(%)	81.7	71.8	64.0
P(%)	57.7	78.8	100.0
W(%)	27.6	16.7	18.7
G(%)	2.3	26.8	100.0

T = annual mean temperature, ΔT = average daily amplitude, Hr = annual mean relative humidity, P = throughfall precipitation, W = annual mean soil water content at 10 cm, G = total solar radiation at 1.30 m level.

Therefore, the annual mean temperature increase from muhulu to miombo and savannah and the air relative moisture decrease are correlated in these three biotopes. In spite of the respective throughfall of precipitations, the soil water content points out the existence of a better water storage in muhulu than in miombo and savannah. The potential evapotranspiration

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(Penman's formula) in miombo varies between 100 and 200 mm with a total of 1600 mm annually. The yearly value of real evapotranspiration is 1050 mm of which 200 mm evaporate directly and 850-900 mm is used in transpiration (after Alexandre in Malaisse & al., 1972).

Fire as ecological factor

All over African dry tropics, bush fires are known in savannah and woodlands and they are a very important factor. In Upper-Shaba, early fires, which take place from the beginning of the dry season to the end of June, have to be distinguished from late fires (from July to the beginning of the rainy season) on the basis of their ecological effect. Indeed the latter occur during the austral spring's vegetation bourgeonning and has a strong depressive effect. On the other hand early fires provide generally a lower impact, as they take place at the end of the vegetation period. Space and time variability of fire induces a large heterogeneity of miombo which is in fact in constant evolution.

Edaphotope

The three biotopes lie on zonal soils of Kaponda series (type A_2, Sys and Schmitz, 1959). There are ferralitic, red-yellowish, deep and well drained soils. In relation to the forest canopy's density and fire incidence, thickness of the superficial organic soil layers however significant decreases in miombo (2-3 cm) and in savannah (0-1 cm) with regard to muhulu (5-10 cm).

Soils belonging to the Kaponda series are acid. But average pH values (Table 2) appreciably increase in the soils of woodland and derived savannah. These variations result, at least for the superficial layers, on the one hand from the well known effect of fire (ashes) on the miombo and savannah soils (Sys, 1957), on the other hand from the abundant humic complexes produced through the high biological activity in the dry evergreen forest soil.

Finally, the soil mineral composition is characterized by the dominance of argillaceous elements. However, in comparison with the muhulu soil where the rate of fine material (0-2µ) may reach 60%, against 35 to 50% in the other soils, the miombo and savannah soils contain more rough elements (20 to 2380µ: silt and sand), that is to say with rates corresponding to 40 to 50 %, against only 20 to 30 % in muhulu soil.

Table 2. Average pH values of the muhulu, miombo and savannah soils (Goffinet, 1973 b).

	Muhulu	Miombo	Savannah
A_1	4,2	5,3	5,9
-10 to -20 cm	4,5	4,6	5,6

Structure and biomass

Diversity among plant species offers a large range of variation according to vegetation types and sites. The great expanse of woodlands has permitted the differentiation of numerous varied taxa and this evolutive process is still occuring today. Muhulu, which is still impoverished in area and plant species, has a total phanerogamic flora of about 105 species with

Table 3. Plant species diversity on the study sites (Malaisse & al., 1972 and unp. data).

Families	Muhulu		Miombo		Savannah	
	sp. f	ind. %	sp. f	ind. %	sp. f	ind. %
Tree and Shrub layers						
Apocynac.	2	2.8	1	21.9	1	14.7
Caesalpin.	2	45.7	4	15.2	-	
Combretac.	1	0	1	6.2	1	29.4
Dipterocarp.	-		3	12.9	-	
Euphorbiac.	-		5	12.4	1	2.9
Fabaceae	1	0	4	10.5	2	2.9
Rosaceae	1	22.9	1	2.4	-	
Rubiaceae	5	0	4	3.3	-	
Others(23)	18	28.7	20	15.2	5	50.1
Total	30		43		10	
Herb layer						
Acanthaceae	-		4		4	
Asteraceae	-		11		4	
Commelinac.	-		5		4	
Cyperaceae	-		4		2	
Fabaceae	-		14		4	
Iridaceae	-		4		2	
Lamiaceae	-		5		5	
Poaceae	4		14		9	
Rubiaceae	1		12		5	
Others(29)	6		39		29	
Total	11		112		68	

sp.= species, f= absolute frequency, ind.= individuals > 10 cm girth.

a site-mean of only 37 species per ha, while these values become 480 and 138 for miombo. On the other hand, savannah, which is progressively increasing in area, takes up a medium position with respectively 330 and 66.

From a structural point of view, muhulu is a dry evergreen forest with some abundance of creepers, mosses and liverworts epiphytism; while miombo is a "raingreen forest" (Lieth, 1974) with few vines, mainly orchids and lichens epiphytism. In the latter one, the shrub strata is sparsely distributed, each shrub taking a coppice outline due to fire effects. Savannah provides a stronger seasonality than miombo and muhulu. The former presents no flowers in June, while some flowers can always be found in the miombo, representing at least 7 % of the total flora (Malaisse, 1974). Some plants in the miombo are evergreen which becomes general in muhulu.

Table 4. D.B.H. classification, tree and shrub stem density (%), vegetation height (m) and sectional area at 1.3 m height ($m^2.ha^{-1}$) (Malaisse, 1973 and unp. data).

	Muhulu	Miombo	Savannah
0- 4 cm	85.1	40.1	14.7
5- 9 cm	9.4	30.0	26.5
10- 19 cm	2.0	19.5	38.2
20- 29 cm	1.1	6.1	17.6
30- 39 cm	1.1	2.0	2.9
40- 49 cm	0.7	1.6	0.0
50-109 cm	0.7	0.7	0.0
No ind./ha	8,580	890-530	34-67
Veg.height	18-22	14-18	1.1-5
Sec. area	39.6	21.7	0.5

For the studied sequence, vegetation height, tree and shrub stem density and sectional area at 1.3 m height decrease rapidly.

Total biomass is still being studied and rough estimations give respectively 320, 150 and 10 $t.ha^{-1}$.

Litterfall

Most trees and shrubs of the miombo are deciduous (92 %) while muhulu is mainly evergreen. The litterfall is continuous throughout the year with maxima in August-September and minima in January-February. The main values of litterfall correspond with the end of the dry season and are generally correlated to the gusts of wind which arise just before the first rains. About 54.3 % for miombo and 66.5 % for muhulu of total litterfall are deposited in the dry season. The total annual litter is 3.5 times lower in miombo than muhulu.

Table 5. Litterfall data (g/m^2) in miombo (1972-1973) and muhulu (1968-1973) (D.S. = Dry season, R.S.= Rainy season).

	Miombo		Muhulu	
	D.S.	R.S.	D.S.	R.S.
Leaves	87.1	49.1	363.9	99.8
Fruits	38.9	21.0	97.0	39.0
Wood	19.7	52.4	156.2	170.8
Total	268.2		926.7	

The greatest part of litter consists of leaves (50.7% in miombo and 50.0% in muhulu). Tree and shrub leaffall presents a significant seasonality. Values are low from December to February, after which they increase progressively until September before an abrupt decrease. Fruits (referred to fruits, flowers, bud scales and seeds) represent 14.6% in muhulu and 22.3% in miombo. But this last percentage is due to shedding of some heavy fruits of forest tree species in September-October 1972. Ordinarily, fruits show relatively insignificant fluctuations during the year. Wood (referred to branches, twigs and barks) contributes about 26.8% of total litter in miombo and 35.2% in muhulu. Yearly twigfall is 803 kg/ha in miombo and presents seasonal fluctuations with two maxima respectively due in January-February to the high moisture of the rotted wood and in September-October to the gusts of wind.

Epigeous fauna

With the exception of Molluscs (Table 6) aspects of epigeous fauna have only been studied in miombo and savannah. The presence of Molluscs indicates an unusual variation with a minimum size for miombo.
Comparison of the active invertebrate macrofauna populations inhabiting the herb layer and litter has been followed up on a twelve month period in miombo and savannah according to the method of a collecting square on a 25 m^2 area basis (Gillon & Gillon, 1965, 1967). Table 7 summarizes the results obtained on a four time monthly collection.

Table 6. Seasonal mean density of Molluscs in different ecosystems (ind./100 sq.m) (Van Goethem & Malaisse, unp. data).

Season	Muhulu	Miombo	Savannah
dry	10	0.0	0.4
rain	762	2.3	24.6

Beside the specific difference, which will not be discussud here, average number points out a better representation of Araneida, Grylloidea, Blattodea and Heteroptera in miombo than in savannah. Another important difference between both vegetations consists in the fact that savannah burns totally each year, while in woodland, destruction is partial. For the reference period fire runs on July 5th through a half of miombo. The groups most susceptible to destruction in these fires appear to be Heteroptera, Mantodea, Blattodea and at a lower level Araneida, Coleoptera and Caterpillars. These results present large similarity to those obtained by Gillon & Pernes (1968) in an Ivory Coast savannah. With a lesser herbaceous strata miombo however is characterized by a higher mean population density than savannah (10.5 versus 6.9 ind./m^2) like a higher mean biomass, on a fresh weight basis (0.95 versus 0.42 g/m^2). This seems related to the more depressive effect of fire in savannah.

Table 7. Comparison of the monthly average number (N) and biomass (B, in 10^{-1}g of fresh weight) per 100 sq.m of the main animal groups in the herb-layer strata for dry and rainy season in miombo and savannah during 1973-1974.

	Miombo				Miombo						Savannah					
	No fire				Fire (5.VII.73)						Fire (5.VII.73)					
	D.S.		R.S.		dbf		daf		R.S.		dbf		daf		R.S.	
	N	B	N	B	N	B	N	B	N	B	N	B	N	B	N	B
Araneida	236	28	308	108	147	35	39	10	257	84	140	12	29	2	176	56
Acridoidea	227	582	118	253	296	884	26	43	124	240	62	107	27	54	342	365
Tettigonioidea	33	32	29	41	41	37	0	0	29	32	8	4	0	0	80	78
Grylloidea	55	36	164	166	65	41	19	18	190	240	26	2	2	+	66	88
Blattodea	96	24	203	79	137	32	89	14	123	63	91	8	20	2	109	38
Mantodea	25	39	57	50	28	36	5	3	29	31	9	11	4	4	37	36
Heteroptera	131	51	208	135	201	67	10	6	86	56	45	10	8	1	60	25
Homoptera	82	12	58	17	92	20	16	1	71	22	234	11	16	1	69	10
Coleoptera(ad.)	22	12	87	90	32	18	2	+	74	79	11	4	3	2	283	58
Caterpillars	5	6	50	75	20	11	1	1	34	60	20	15	2	3	52	84

D.S. = dry season, R.S. = rain season, dbf = dry season before fire, daf = dry season after fire.

Pedofauna

As shown in Table 8, the successive stages of deterioration from dry evergreen forest to savannah gradually bring about significant modifications of the zooedaphic spectrum's pattern. Thus, the sequence muhulu-miombo-savannah is generally characterized by a decrease of average abundance and/or biomass of most animal groups (as for example Rhizopoda testacea, Acarina, Collembola and many insect orders) with however the exception of Oligochaeta and especially intercalic termites (=termites inhabiting the soil between the small and large termite mounds as defined by Goffinet & Freson, 1973) which largely increase in importance in the half-open and open ecosystems.

But the peculiar status of each soil biocenose in this natural succession is particularly demonstrated by the typical distribution of the ecological termite groups. Indeed, deforestation induces a progressive substitution of the large active epigeous colonies of mushroom-growing lignivorous termites (Macrotermes falciger) by humivorous termites (Cubitermes) which construct small size colonies as well as an increase of importance of the humivorous hypogeous termites (Anoplotermes, Crenetermes, Ophiotermes, ...). From this point of view, the large mounds scattered on savannah areas are left in most cases by their original builders and replaced by other species.

Litter breakdown

The annual rate of litter decomposition may be obtained by the ratio litterfall to litter accumulation expressed in % (Nye, 1961). According to the previous data, it appears that the annual rate of tree litter decomposition, in absence of fire, is 1.3 higher in dry evergreen forest (140) than in woodland (111).

Table 8. Comparative abundance and biomass of the main taxonomic animal groups inhabiting the soil of the three ecosystems (Goffinet, 1973 a-b).

Animals groups	Muhulu		Miombo		Savannah	
	N	B	N	B	N	B
Rhizopoda testacea	4.54×10^6		1.44×10^6		1.65×10^6	
Oligochaeta	4.7	0.24		2.96	13.1	1.75
Acarina/Collembola	396,000	1.83	96,000	0.50	75,600	0.43
Macroarthropods (excluding termites)	1745.6	6.8	580.1	7.4	92.9	3.4
Termites						
- Hypogeous (intercalic)						
Lignivorous	102.4	0.08	469.9	0.59	1082.6	0.25
Humivorous		0.17		2.47		5.26
- Epigeous						
Lignivorous (1) (Macrotermes)		(19.0)		(9.5)		(0)
Humivorous (Cubitermes)	0	0	8.6(2)	4.91	22.6(2)	17.33

(N) average number of individuals per sq.m, (B) biomass expressed in kg of dry weight per ha. For the humivorous termites, these values do not include the gut content, (1) Approximate values established on the basis that one colony of Macrotermes falciger contains about 2 millions of individuals, (2) in millions of individuals per ha.

First monthly experimental data obtained on the basis of weight loss of dry mixed litter placed on the two soil types confirm this ratio, since about 50 % of dry organic matter is destroyed during the 5 wet season months in *miombo* (Malaisse et al., 1974) when a similar loss in the muhulu occurs in only 2-3 months.

Apart from fire, the processes of litter disappearance may be regrouped in three main categories : pedoflora and pedofauna in general and lignivorous termites.

Pedoflora and pedofauna present a relative spacial homogeneity but a well defined seasonal periodicity. Generally, the biological activity of soil organisms is attenuated during the dry season but this reduction is more important as the system is degraded. Thus the ratio of average abundance of soil intercalic macrofauna extracted successively during rainy and dry season, decreases respectively from about 4/1 in savannah to 3/1 in woodland and to 1,5/1 in dry evergreen forest (Goffinet, 1973 b).

Among the lignivorous termites, the mushroom-growing group (especially Macrotermes falciger, Odontotermes, Pseudacanthotermes spiniger, Microtermes) are the most determinant in litter breakdown. Foraging of superficial organic matter by these termites occurs often in covered access routes or areas which assure their protection. Soil samples extracted at this time particulary reflect the high termite activity : for example, abundance and biomass (fresh weight) of Odontotermes can reach respectively more than 15,000 individuals per sq.m and 100 g per sq.m (i.e. more than 1 t/ha !). Foraging activity of mushroom-growing termites is above all observed in miombo and muhulu, from November to June, with a maximal intensity during the months of seasonal transition.

Water Mineral content output

The Upper-Shaba includes three main hydrographic basins : the Lualaba basin with a drainage area of 63,090 sq.km at Bukama, the Lufira with an area of 53,100 sq.km before its confluence with the Lualaba River and finally the Luapula with a total area of 218,460 sq.km at Pweto. This last one has a great part of its basin in Zambia.

Table 9. Mean discharge (m^3/sec) and specific flow-rate (l/sec/km^2) of the main hydrographic basins in Upper-Shaba (Freson, 1974).

Basin	Discharge	Mean specific flow-rate
Lualaba	314	4.97
Luapula	565	2.60
Lufira	196	3.69

The water cycle in the miombo ecosystem shows that a small quantity (23.3%) of the annual rainfall returns to the streams and rivers. This is equivalent to a yearly water layer of 160 mm. The flow-rates of rivers is important and presents seasonal fluctuations with the maxima in February-March and minima in October-November.

Table 10. Mean concentration of the major ions (mg/l) and the quantity output annually (t/yr) from the three main hydrographic basins (Freson, 1974).

Ions	Lualaba		Lufira		Luapula	
	mg/l	10^3t/yr	mg/l	10^3t/yr	mg/l	10^3t/yr
Ca	28.9	286.2	45.5	281.2	7.4	131.8
Mg	12.3	121.8	24.8	153.3	4.4	78.4
Na	5.4	53.5	21.2	131.0	4.6	81.9
K	1.5	14.8	2.4	14.8	1.8	32.1
HCO3+ CO3	68.3	676.5	92.6	841.0	23.6	418.4
Cl	4.2	41.6	17.3	106.9	3.4	60.6
SO4	1.6	15.8	21.5	132.9	1.8	32.9
SiO2	22.6	223.8	8.5	52.7	10.5	187.1

The water mineralisation depends primarily on the alteration of rocks and soils just as the bioreduction of organic matter accumulation on litter (9.3 t/ha/yr in muhulu and 2.6 t/ha/yr in miombo) and from the yearly burning of the herb layer. Thus early fires provide in miombo 275.6 kg/ha/yr of ash and 25.1 kg/ha/yr of mineralisation or 629 × 10^3 t/yr for the Upper-Shaba (Freson, 1973).

The precipitation/evaporation factor presents a seasonality with high dilution in the rainy season and strong concentrations at the end of the dry season. The respective ratio of the water mineral content between the dry and wet season is about 1.27 for the Lualaba, 1.65 for the Luapula and 1.71 for the Lufira.

Generally the water in Upper-Shaba is hexaionic belonging to the carbonate calcio magnésian type, i.e. with Ca (± 48%) and Mg (± 25%) preponderance for cations and HCO3+CO3 (± 83%) for anions.

The yearly mineral content output for Upper-Shaba is 4,171 × 10^3 t/yr or 124.0 kg/ha/yr.

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Symposium on seagrass ecosystems

DYNAMICS OF SEAGRASS ECOSYSTEMS

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Summary

The dynamics of an ecosystem are an expression of stability -- the tendency for the system to maintain or renew itself in a state recognizable with its history. Too often in ecology the concept of dynamics has been equated with rates of the principal component processes of the system -- principally production, consumption, and decomposition. But dynamics can also be applied to a larger view in which the ecosystem becomes the unit of study. In this view the dynamics of the component processes are only a part of the story, a part that must be integrated with structure and maturity. At this point time scales become important boundary conditions. Dynamics in the usual sense deals with the short term -- hourly, daily, yearly -- time scales of process rates. But these are imposed on a larger time pattern -- a type of life span or generation time of the system -- in which dynamics are essentially expressed in terms of community succession within the ecosystem. Of course all of this is embedded in a much longer time unit -- evolution -- that results in replacement of the ecosystem as we know it. So where do we study the ecosystem? What boundaries are chosen? Traditionally it is dynamics in terms of rate processes with some allusions towards succession and maturity. Only Margalef (1968) has attempted to make this coupling for life in the sea. For too long now the only theory applied to marine ecosystems has been an extension of Lindeman's (1942) trophic dynamics. Although this principle is vital to understanding an ecosystem it has been dogmatically applied. Understanding of ecosystem dynamics involves a much broader perspective, one rarely applied to biological systems in the sea.

In our view seagrass ecosystems present one of the few examples where dynamics of the overall system can be examined. The crucial experiment has been done largely without our knowing it. The experiment in seagrasses is known as the "wasting disease" of eelgrass (Zostera marina) that caused widespread destruction of the eelgrass meadows of the North Atlantic in the early 1930's (Rasmussen, in press). We now know that this catastrophic elimination of the eelgrass was a natural phenomenon, a result of extremely high water temperatures in those years (McRoy, 1966; Rasmussen, 1973).

Following the disappearance of eelgrass populations sediment conditions changed and populations of benthic algae appeared (Rasmussen, in press). In ten years sparse patches of eelgrass appeared; 20 years later dense stands were noticeable, but not until the early 1960's were really dense widespread eelgrass meadows again apparent, with a continued increase since then. This pattern of reestablishment was described for the shallow sea surrounding Denmark, but it can be generally applied to eelgrass in the North Atlantic. Now, what is the significance of this event in terms of ecosystem dynamics? The fact is that given a suitable habitat the seagrass meadow and its implied community is a climax ecosystem that if eliminated will eventually replace itself with a continuity that is recognizable with its evolutionary history. Dynamics in this sense refers to the stability of the overall system in resisting exogenous perturbations and to replace itself in the event of catastrophe. We believe only Margalef has seen this, but because he works with pelagic ecosystems the time and space boundaries are almost too vague to comprehend. Imposed on this concept is the one of ecosystem maturity, which must be viewed more in terms of evolutionary time and probably proceeds by step intervals. In other words, what is next after a seagrass ecosystem? It will not be a mangrove community, which Margalef (1968) views as successionally replacing seagrasses in the tropics. This is only an edge effect of two overlapping ecosystems. Neither mangroves nor seagrasses will ever replace each other. The same is true for salt marshes and seagrasses but apparently it is not true for benthic macrophytic algae and seagrasses. In fact, in a larger view coral reefs are really a part of seagrass ecosystems. One need only consider the impoverished reefs of Hawaii where seagrasses are sparse to see that full reef development occurs primarily in association with dense seagrass meadows. So a seagrass ecosystem can be viewed as a climax stage at this point in evolution and as ecologists we should be concerned with those dynamics of the ecosystem that maintain its stability in the face of environmental perturbations short of the catastrophic level. We think a good deal more can be learned from the study of seagrasses on the ecosystem level, and perhaps with this as an early step, marine ecology can finally proceed beyond the limits of trophic dynamics.

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ymposium on aspects of human ecology

HUMAN BIOLOGY AND THE ECOSYSTEM CONCEPT

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Summary

Biome studies based on an ecological approach have concentrated hitherto either on "natural" or "primeval" systems in which human interference is regarded as non-existent or minimal, or on disturbed or modified systems which imply certain specific human actions on the environment. Although the importance of the human involvement is not in doubt there has been little systematic treatment on a strict ecological basis. The various pathways, including feed-back and other control pathways, between the human group and other sub-systems, both biotic and abiotic, have not been accorded, even theoretically, anything like a comprehensive analysis. Here the modelling approach would be highly appropriate since it would be based on an extension of the fairly sophisticated analysis already in use with the non-human components of the total ecosystem.

When an ecosystem is looked at primarily from the standpoint of the human group (outwards as it were) focussing on the interface between the human group and the rest of the biotic and abiotic complex, it seems legitimate as well as convenient to describe this activity as 'human ecology'.

Human ecology involves an ecosystem analysis which comprises all the pathways already described in the case of 'natural systems' but also goes beyond these. There are of course the same three major elements - the dynamic process at the interface, the throughput through the 'human' compartment, and the relation of these movements to population 'state' characters. There are, however, a number of important differences.

In simple terms one may generalise that the interface between the human components and the rest of the system comprises four major pathways: (1) the flow of energy, nutrients and water, (2) the movement of pollutants and other toxic materials, (3) the transfer of disease-producing agents, (4) a communication and perceptual relationship involving conscious response to a variety of environmental stimuli including light, sound, spatial configurations, movement, etc. These four interface pathways are of course not entirely separate.

Human ecology is certainly not confined to the analysis of these pathways of interface activity, crucial (and neglected) as that remains. In addition, like any sub-system or component, the essential structural and functional properties of the human population itself have to be accurately charaterised. This demands a specification of the flow of energy, nutrients, water, pollutants, toxic and disease agents <u>through</u> (and within) the population. This represents one segment of the total cycle (including interface phases) of the processes at work in the functioning of the total ecosystem.

This leads to a second level of analysis, within the population. The human ecologist has also to relate the basic 'throughout' processes to 'state' characters of the population. These have for long been of interest to many kinds of human biologist but who have seldom viewed them in the context of a comprehensive ecological analysis. We may list these 'state' characters as:

(i) population size (or biomass), population composition, and demographic constitution;

(ii) nutritional status of the population;

(iii) developmental and physical (anthropometric) status;

(iv) physiological fitness and functional efficiency;

(v) medical and hygiene status;

(vi) psycho-social status (a wide ranging category to include such attributes as suicide rates, criminality, etc.).

An additional category is:

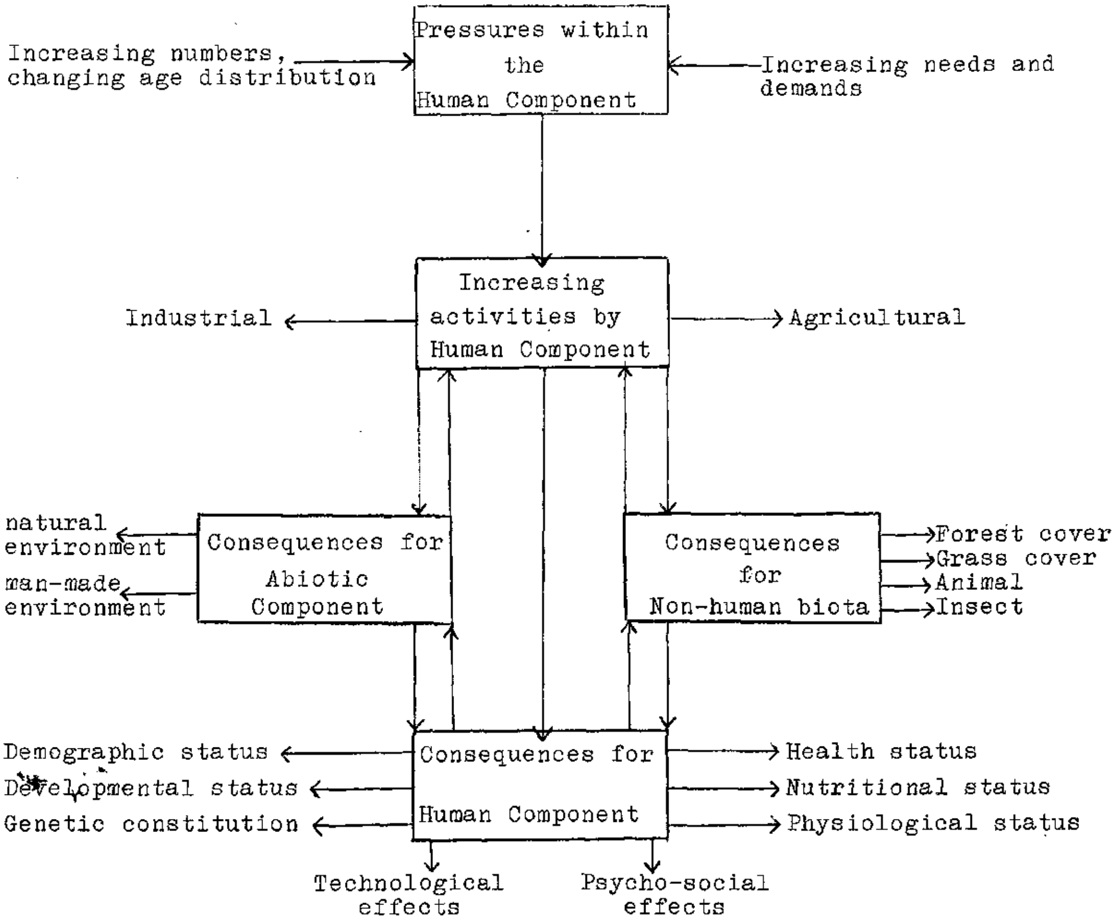
(vii) genetic constitution.

There is one particular consideration of which careful account must be taken in making a study of the human element in any system. It is essential to adopt both an auto-ecological and syn-ecological point of view, that is, the reaction of both the individual and of the community must be assessed in the ecological context, though the focus of interest will be determined by the kind of question which is being asked. Budgetry balance sheets of energy or water utilization, the need for raw-materials and the resultant waste are obviously relevant to the standard of living of the community as a whole. An overall evaluation of 'fitness' (medical, nutritional or physiological) can be given for the population (provided sampling is adequate), as indices of morbidity, mortality, density or longevity. Nevertheless, in practice, it is the individual response which must be ascertained and indeed the range of variation in a population needs to be taken into full account in setting standards, in longitudinal monitoring or in making inter-or intrapopulation group comparisons.

A model for human ecological analysis

As in all ecological situations, it is necessary to be able to view the condition of the human compartment both in a steady state or in a changing system. The latter characterizes the human condition to a far greater extent than the former. The model shown in fig. 1 will be discussed.

Fig. 1 shows a simple scheme to illustrate the system described



HUMAN ECOLOGICAL STUDIES OF CIRCUMPOLAR POPULATIONS

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Biological and behavioral processes responsible for the adaptation, population maintenance and recent population increases were examined in 3.000 Eskimos living in four villages in arctic Alaska and compared with other circumpolar human populations.

The Alaskan population can be categorized with high levels of statistical confidence as to body size, shape and somatotype, describe its genetic consitution, amount of chemical constituents in blood and urine, effects of circadean and circannual light cycles on biological rhythms, describe aerobic and anerobic abilities to do work, make definitive statements as to past and present physical and psychological health and social history, and make some predictions for the future.

This population was known to the Western World as early as 1842 and broke its long term genetic isolation by the early 1850's. Today, some one hundred and twenty years later, one village is approximately 37% hybridized and one other is 25% hybridized by contact with non-Eskimo whalers. Fifty three percent of nutritional energy is calculated to come from external sources.

Hybridization and nutritional contact (especially the importation of refined carbohydrate) has led to a secular trend acelerating body growth and time of maturation.

The population was biologically successful because of a high birth rate, a high death rate (especially of infants) and a differential survival of the children. Western medicine and public health programs introduce death control, then birth control after twenty years had elapsed.

There are strong indications of biological adaptations to arctic life in the operation of the biochemical machinery of individual Eskimos. Amylase, sucrase and lactase levels are low. The population has a greater capacity for intestinal absorption of cholesterol than what are considered normal amounts.

The population has adapted behaviorally by, for example, inhibiting any interpersonal aggression in adults by childhood training whereby enabling a peaceful human existance in the small confines of an arctic household.

Future work will be directed toward the effects of modernity and cultural change on the health and biology of these people. Nutritional change, responsible for accelerated physical growth, has ruined the dentition. Now dentures for the edentulous will not fit properly because of a large protruded mandible which is a characteristic of the population. The exploding population, with half of its members under 17, can soon be unsupportable under natural conditions on the arctic coast. Young women are now marrying out of the population leaving an excess of young unmarried men. This fact alone should have serious consequences for the future of their small populations. Both biological and behavioral characteristics which were adaptive in the past are becoming less useful with time and some are maladaptive at the present.

This program has produced 47 reports, twenty-five of which are published, and has produced data used in 3 Ph.D. dissertations and 2 masters' theses. Graduate students, post doctoral students and foreign scientists as well as our own have had the experience of studying a common human population as members of a multidisciplinary team and have benefited from the exchange of ideas and change in points of view that were necessary to accomplish this task.

E3

Symposium on optimization in ecological systems

NUMBERS OF SPECIES AND OPTIMIZATION IN BIOLOGY

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Introduction

Questions regarding numbers of species such as those of Hutchinson (1959) and MacArthur (1955) are fascinating. Attempts to relate the stability of a system to species numbers attract great attention and have resulted in numerous studies. May (1973) has summarized and extended this discussion.

In another quarter of the ecological community system characteristics are analyzed in terms of optimization criteria. Ecosystem organization (Morowitz 1968, Cody 1974), plant morphology (Parkhurst and Loucks 1972), animal behavior (Rosenzweig 1974) etc. are all interpreted as the product of an optimization process.

These two sets of studies converged in researches conducted by Dr. John A. Wiens and the author on the bioenergetics and population dynamics of avian populations in a grassland ecosystem. The initial objective of the study was to determine the effect of the avian population on ecosystem dynamics. Simple estimates (Wiens 1973) indicated that these consumers were removing very little of the available food material. More sophisticated estimates (Wiens and Innis 1973,1974) gave little indication that the impact on specific food items at critical times was significant to the dynamics of the food item. It seemed natural to ask why there were not more birds and bird species in this apparently rich environment. Such questions led to the literature on the numbers of species and that on optimization in biology.

I have drawn the following conclusions from these studies and will expand on them below. First, questions regarding the numbers of species do not lend themselves to objective analyses because of the subjective nature of the definition of "species". While the word is well enough defined to be useful in descriptive biology, it is not well enough defined to deal with questions of numbers of species that existed at some time in the past nor the change in numbers of species with time. One can seriously answer Hutchinson's "why are there so many species?" with "because one of them, homo sapiens, has chosen to identify that many."

Second, optimization in the mathematical sense of best possible subject to certain constraints is an exception, if indeed it ever occurs, rather than a rule in biology. Most of the studies using optimization principles to explain biological phenomena begin with the assumption that optimization occurs and seek to discover the objective function which yields the observed characteristics. While such analyses allow one to represent observed dynamics with optimization principles, they do not demonstrate that the basic premise, optimization occurs, is valid. Indeed there are a number of important results that indicate that organisms do not and, perhaps, can not afford to optimize anything in a random environment. They must, instead, maintain flexible positions.

Numbers of species

G. E. Hutchinson's (1959) classical paper "Homage to Santa Rosalia or Why Are There So Many Kinds of Animals" asks not only why there are so many species but why there are no more. More specifically, he asks for "a theory at least predicting an order of magnitude for the number of species of 10^6 rather than 10^8 or 10^4." My attempts to answer this question invariably founder on the notion of species. How is a species defined? When are closely related organisms classified as separate species and when are they not? What is the development time of a "new species"?

There appears to be some consensus that Hutchinson's estimate of 10^6 species now living is correct. Simpson (1952) gives this value. In his note he touches on the question of durations of species. He guesses (his words) that the mean durations of species is from 500,000 to 5,000,000 years but does not describe the way in which he decides that a species begins or ceases to exist. F. E. Smith (personal communication) has called my attention to such problems as the renaming of species (resulting in an apparent extinction?), the continual change of species through evolution resulting in new species without any clear disappearance of its predecessor and the rate at which modern techniques and intensive efforts are discovering new species. Hyman (1955) acknowledges the value of the discussion of numbers of species but concludes that "a comparison of the number of extinct and living species of animals seems rather useless."

Clearly any attempt to answer Hutchinson's question must address the potential for speciation of the biosphere in the past and must, then, compare the number of living and extinct species. Any attempt to develop a theory which prescribes the order of magnitude for the number of species must deal with an objective definition of species. As stated the question is not well posed; it will have to be rephrased in well defined terms before an "answer" is possible.

This conclusion leads to doubt about the significance of the dialog on relationships involving species diversity. There are subtle but real differences among various author's use of the language. This fact is recognized and acknowledged relative to such ideas as stability and diversity but less so regarding the loose definition of species(witness the discussion in Hyman (1955) of different people's estimates of the numbers of species of some organism). It is not surprising that the results reported are non-conclusive. I have urged elsewhere (Innis 1974) that biology and ecology move rapidly toward the development of an unambiguous language.

Optimization in biology

In some respects the problem of optimization in biology is like that mentioned above, ie. words are not used carefully enough. Maximum, minimum, optimum and optimization are all well defined terms. They are used in rather distinct contexts, however, without appreciation for that context. As one example, we can speak of the maximum of a collection or the maximum possible (Cody 1974 mentions this distinction). The maximum age of a given species of animals illustrates this distinction. It is a relatively easy matter to determine which of those recorded ages is the maximum It is a different (and generally unsolved) problem to estimate accurately the maximum possible age of individuals of that species. Indeed the concept may not even be useful in light of current research.

As another example, the distinction between local and global maxima, minima, etc. is important. A local extremum is an extremum for some locale or population. A global extremum is the extremum over all space or all populations. The maximum age for people in Western Europe is a local maximum; the maximum age for people of the world is a global maximum.

Consider the travels of a bug (point) that can sense the slope of the terrain in its present location and always chooses to move uphill. Such a bug will, with high probability, move to a nearby peak, mound or pebble. At that point, any movement would be in a down hill direction and hence it is "trapped"on a local maximum. Many larger peaks may be nearby but each is inaccessible to the bug. The peak on which he arrives depends completely on his starting position and the terrain.

The peak of Mt. Everest and the depths of The Challenger Deep are thought to be global maxima and minima respectively for the elevations (reference to sea level) of solid portions of the earth's surface. The bug, starting at a random point on the earth's surface would have very little chance of arriving at the peak of Everest--even if it started on the lower slopes of that mountain. Many foothills, mounds, boulders, rocks and pebbles would lure the bug to local maxima that would be lower than the global maximum.

I submit that natural selection operates in a way analogous to a variation on the bug above wandering about on some complex surface. The new bug is assumed to have limited sight and step size so that steps too large are impossible (improbable is better). The starting point for the bug's travels is the organisms existing at the beginning of life. Returning to the analogy of the earth's surface, we can see that a bug with only a few meters or kilometers as the limit to his sight and step size would have a low probability of reaching the summit of Everest.

D'Arcy Thompson's principle of optimal design, apparently a source of the optimization concept in biology, states "natural selection leads to organisms having a combination of form and function optimal for growth and reproduction in the environments in which they live" (Parkhurst and Loucks 1972). What does he mean by optimal? If optimal is used in the sense of the best that have existed, we can hardly reject the hypothesis but it is then a tautology and analytically useless. If optimal is used in the sense of globally the best possible (as my interpretation of this work and later efforts indicates is the case) then I would reject the principle on the basis of the preceeding paragraph.

Rashevsky (1965) also rejected optimal design as a criterion for biological structural analyses for reasons similar to the ones mentioned here. He substituted "adequate design". Generally speaking the idea is that the design must be adequate to the performance of prescribed functions under specified varying environmental conditions. Adequate design would not be expected to yield unique solutions to problems of system structure for prescribed functions. Rashevsky indicates that the principle has predicted previously unobserved phenomena that have later been experimentally verified.

Slobodkin (1960) describes the development of ecological theory in terms suggestive of adequate design. Empirical technique allows the rejection of certain hypotheses (the bounding of structure and behavior of biological systems). Within these bounds, system dynamics may proceed without reference to goals or objectives.

Holling's (1973) discussion of resilience and stability of ecological systems draws conclusions like those of Rashevsky and Slobodkin but from a quite different starting point. He argues that natural systems may have multiple domains of attraction. System persistence may depend more on an ability to move from one such domain to another than on the nature of the dynamics in a given domain. An adequate design for an ecosystem might be any one of several sequences of domains of attraction through which the system could move.

Parkhurst and Loucks (1972) in their classic application of the principle of optimal design recognize three possible reasons for failure to achieve optimality; inadequate time in a given environment, the environment not constant for a long enough time and important variables omitted. By working from this principle they derive an objective function whose solution describes observed leaf shape in a forest canopy. The real test of the construct will derive from treating the predictions of this theory as hypotheses for testing in situations distinct from those for the hypotheses developed.

Amongst the proponents of optimization in biology there is some disagreement as to the level at which it applies. Rashevsky and his colleagues in early studies worked at the cellular level; Parkhurst and Loucks at the organ level; MacArthur and Rosenzweig at the species level and Morowitz and Cody at the system level. The first three of these can be thought of as local optimizations and the last as a global optimization. Unfortunately, the conclusions can be counter to one another, i.e. local optima may be mutually exclusive or preclude global optima. Furthermore, optimization at the subsystem level is difficult to reconcile with succession (Margalef 1968).

A nonlinear physical system result

Norbert Wiener (1964) proved that nonlinear systems with certain properties (a Hamiltonian dynamical system) have the characteristic that the generalized harmonic analysis of the state of the system reveals a peaked or line spectrum. He used this analysis to explain the destruction of the Tacoma Narrows Bridge and certain aircraft. In the discussion of this paper he mentions biological applications such as biological clocks.

The work has not (to my knowledge) been extended to more general situations of biological interest and indeed one can show that Wiener's result does not apply to certain systems with rather biological appearing characteristics (this will be expanded upon in a later publication). In spite of this last mentioned result one can imagine that there will be biologically interesting systems for which the spectrum has this peaked or line characteristic. For these systems, the random environment in which they operate can be expected to occasionally excite oscillations at the frequency of the lines in the spectrum. The result would be a large amplitude oscillation or series of oscillations. (Could these oscillations be the ones that Holling (1973) alludes to in his discussion of resiliency?) If the system is crowding the limits in which it can operate (maximizing an objective function subject to some constraints), then such oscillations will be detrimental or even fatal as in the physical examples used by Wiener. Survival for such biological systems would demand the maintenance of a buffer zone between themselves and their environmental limits (constraints) which is suboptimal performance in terms of the given criterion.

Such a theory as Wiener's has interesting implications regarding the question of succession or evolution in "constant" environments. The sense of constant must be clarified. Surely the intent is not "unchanging". More likely an environment is "constant" if the statistical distribution from which it is drawn is unchanging. Such an environment has a probability of exciting oscillations at the frequencies associated with the spectral lines for the system. If species are occasionally eliminated as a result of such effects, then an ever changing species list would obtain as the state of affairs in a "constant" environment.

Conclusion

Solution to theoretical questions on numbers of species and related diversity issues must await an objective definition of species. This situation does not mediate against the use of species concepts in laboratory and field research. It may bode ill for many when an objective definition is adopted which is less than perfectly consistent with the current operational definitions.

Optimization as a general principle in biological systems is difficult to rationalize. The determination of an objective function such that observed phenomena optimize that function subject to constraints is not a vacuous enterprise. It stimulates deeper thinking about experimental observations and their implications relative to other ecological principles. It may "explain" phenomena and suggest experiments. The empirical nature of biological science must not be lost, however, and in the end any construct must submit to empirical testing.

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MODELING AND MANAGEMENT OF ECOSYSTEMS VIA OPTIMAL CONTROL THEORY

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Abstract

A complete ecosystem analysis may be possible from an optimal control theoretic point of view. Such an analysis has three parts, (1) Determination of model structure, (2) Determination of coefficients for a giv given model, and (3) Determination of optimal management programs for the model obtained by (1) and (2). The methods of optimal control theory are suitable for examining each part separately. The essential ingredient for each part involves an optimization concept.

Only the second and third part are examined in detail here. For concreteness, a specific model structure for a prey-predator system is used. It is then shown that certain coefficients of this model are predicted directly given that the predator feeds in such a way as to maximize his caloric intake. By adding mans external controls to the model, the system can then be managed in a fashion to minimize some cost criteria.

To illustrate this latter point, the methods of optimal control theory are used to determine a management program for controlling water quality in a natural lake at a minimum cost. Mans control is represented by the application of an algacide on the Phytoplankton-Zooplankton (prey-predator) system in the lake. The introduction of temperature dependance as a driving force in a simple dynamical model appears to be adequate for the determination of the optimal control program.

Model Structure via Optimal Control Theory

There have been numerous attempts to model certain ecological systems using the process of "modeling by reasonable hypothesis" in which case a model is built by mathematically stating certain reasonable relations between variables of interest. Such a modeling procedure can take a variety of forms. For the same ecological system two to a thousand state variables may be considered. The model may be deterministic or stochastic. In light of the wide spectrum of the ways to arrive at an ecological model, it is not surprising that there may be disagreement as to what even constitutes a model let alone the mathematical for the model should take.

More formal approaches to building models as compared to "reasonable hypotheses" have also been investigated. Leitmann (1971) has expanded on Volterra's (1939) notion of "quantity of life" to obtain a population model for a single species using a minimum principle. (The well known analog to this idea in mechanics involved the process of obtaining the equations of motion for a dynamical system by minimizing a Lagrangian function. Indeed, in Leitmann's analysis, terms appear that are analogous to "kinetic energy" and "potential energy" for the biological system.) Leitmann refers to this process as *Modeling by Criteria.*

This idea has apparently occurred to others. For example, Yamashiro and Bekey (1971) discuss the search for a viable performance index which describes the heart-lung action. Katz (1974) is able to explain the feeding behavior of Qualea based on the criteria that the species minimize feeding time.

Specifically the modeling by criteria concept is to seek criteria which together with suitable constraints, are minimized by the actual operation of an ecological system. Knowledge of such criteria would not only give a concise description of the system but may give valuable insight into the working of the system. For example, MacArthur (1973) has demonstrated that with the Lotka-Volterra population equation for species competing in one resource dimension, competiveness minimizes the integrated difference between resource production and resource utilization.

We will pursue this point no further here except to note that while the use of modeling by criteria may be quite useful for the determination of the structure of a model it is not essential for what follows.

Coefficients via Optimization Methods

Over the past ten years a number of simple optimization procedures have been employed by ecologists for predicting optimal diets (Schoener, 1971; Pulliam, 1974; Charnov, 1974). However, little has been said about the use of the same procedures in the modeling of the dynamics of community change. The set of prey captured by foraging predators is obviously important in the nature of predator-prey relationships and in determining the degree of competition among predators.

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The procedures of optimization theory give a possible tool for predicting the diets of predators and we show that the prediction of such optimal diets may determine the nature of the density-dependent and functional responses made by predators to prey abundance. Thus, we use optimization procedures to determine certain foraging coefficients in a model of the dynamics of a biotic community with several species at each of two trophic levels.

We now confine our attention, in what follows, to prey-predator systems only.

A predator encounters N_i prey items of type i per unit search time. Upon each encounter, the predator may pursue and eat the item (with probability p_i) or may ignore the item and continue to search (with probability $1 - p_i$). If the predator pursues a prey item he is always successful in capturing and eating it and this will require t_i units of time and yield C_i calories of reward. Let $\overline{X}$ be a vector representing the realized capture rate per unit search time; thus X_i, a member of $\overline{X}$, equals $p_i N_i$. Since the predator encounters $\sum_i X_i$ prey which will be eaten per unit search time, the search time per encounter is $1/\sum_i X_i$ and the total time per prey encountered and eaten is $1/\sum_i X_i + \frac{\Sigma X_i t_i}{\Sigma X_i}$. Similarly, the expected gain from a prey is $\frac{\sum_i C_i X_i}{\sum_i X_i}$. Combining these, we have:

$$F(\overline{X}) = \frac{\Sigma C_i X_i}{1 + \Sigma t_i X_i} \qquad (1)$$

as the expected caloric yield per unit time.

The basic diet optimization problem is to maximize $F(\overline{X})$ subject to some set of constraints. In general, the constraints are of the form

$$\overline{0} \leq \overline{X} \leq \overline{N} \quad \text{and} \qquad (2)$$

$$\sum_i \rho_{ij} X_i \geq M_j, \quad j = 1,\ldots,m. \qquad (3)$$

The first n constraints simply refer to the fact that a prey cannot be taken at a rate lower than zero nor higher than the rate of encounter between predator and prey. The final m constraints allow for the fact that a balanced diet must contain a minimum (M_j) of some necessary nutrient j of which there are ρ_{ij} units per prey of type i.

The solution to this maximization problem is characterized by the Kuhn-Tucker conditions using the method of Lagrange multipliers (Intrilligator, 1971). Although these conditions characterize the solution, they do not directly give the maximum value $\overline{X}^*$ of $\overline{X}$. A number of computer algorithms exist to find $\overline{X}^*$. Many of these algorithms start at an arbitrary point and move along the preference direction towards the value of $\overline{X}$ which maximizes $F(\overline{X})$. The preference direction is the direction of fastest increase in $F(\overline{X})$ and is given by the vector of first order partial derivatives of $F(\overline{X})$.

A solution to the maximization problem is illustrated for the two prey type situation in Figure 1. The constraints are shown as the encounter rates of the predator with the 2 prey types. $F(\overline{X})$ equals $(C_1X_1 + C_2X_2)/(1 + t_1X_1 + t_2X_2)$ and the preference direction is given by

$$\frac{\partial F(\overline{X})}{\partial \overline{X}'} = \left(\frac{C_1 + C_1t_2X_2 - C_2t_1X_2}{(1 + t_1X_1 + t_2X_2)^2} \; , \; \frac{C_2 + C_2t_1X_1 - C_1t_2X_1}{(1 + t_1X_1 + t_2X_2)^2} \right) \qquad (4)$$

Now assume that prey type one yields more calories per unit pursuit time than does prey type two, that is $C_1/t_1 > C_2/t_2$. The condition that $\partial F(\overline{X})/\partial X_1$ be positive is that $C_1t_2 - C_2t_1 > -C/X_2$ and this is always true. This result is shown geometrically in Figure 1 by the fact that no matter what point is taken initially, the X_1 vector component always points to the right so long as $X_1 < N_1$. At $X_1 = N_1$, the X_2 vector component may be positive or negative. This is because $\frac{\partial F(\overline{X})}{\partial X_2}$ is positive if $N_1 < \frac{C_2}{C_1t_2 - C_2t_1}$ and negative if $N_1 > \frac{C_2}{C_1t_2 - C_2t_1}$. The dependence of the sign of $\frac{\partial F(\overline{X})}{\partial X_2}$ on N_1, is shown geometrically in Figure 1 as the direction of the X_2 vector component.

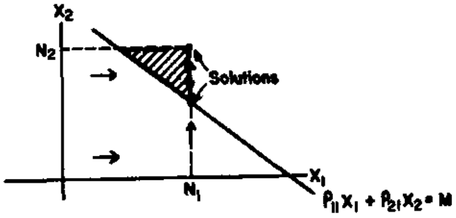

FIGURE I. TWO PREY TYPES

The nutrient constraints restrict the minimum value of X_2 and $\frac{\partial F(\overline{X})}{\partial X_2}$ is always positive along (N_1, X_2) until X_2 is in the feasible set (the hatched area). Within the feasible set the sign of $F(\bar{X})/ X_2$ depends on N_1 in the same way as in an unconstrained diet problem.

The predators choice of prey obviously is important in determining the dynamics of any predator-prey system. Consider the familiar form of the differential equations describing a simple prey-predator system:

$$\begin{aligned} \dot{N} &= rN - aNP - bN^2 \\ \dot{P} &= kNP - dP. \end{aligned} \qquad (5)$$

Now aN is the rate of prey removal per predator and kN is the rate per predator of conversion of prey into predators. If we allow for pursuit time as previously discussed (5) becomes

$$\begin{aligned} N &= rN - \frac{aNP}{1 + Nt} - bN^2 \\ P &= \frac{eNP}{1 + Nt} - dP, \end{aligned} \qquad (6)$$

where e is the efficiency of conversion of prey into predators. If there is more than one prey species and still just one predator species the system allows for the preferences of the predator to switch depending on the abundance of the preferred prey by simply adding the appropriate terms.

Management via Optimal Control Theory

The motivation for model building is for predictive capabilities. We wish to emphasize that to date, control of a system is usually inferred by means of this predictive capability. (See for example, Slobodkin (1962)). Our means for obtaining a control program (via a model) are different. The methods of optimal control theory will be used to obtain control programs. The value of such an approach has been recognized by other investigators, for example Patten (1971) states "The whole area of optimization theory is certainly pertinent to renewable resource management and could be used for... management schemes." To date there is a limited literature on the use of optimal control techniques for the determination management of biological systems (See for example Vincent, 1972; Goh et al., 1974; Botsford and Narch, 1973; Mitchiner et al., 1974). A major difficulty is in establishing the existence of reasonably accurate deterministic models of reasonable complexity. However, it has been shown that control theory in conjunction with idealized models yields both, unexpected and unique ways for controlling a system.

Goh et al. (1974) has shown that even for ill defined systems certain optimization criteria may lead to satisfactory sub optimal control programs.

We wish to point out here that the need for relatively simple models appears to not be overly restrictive for a number of prey-predator systems. Generally models are built with an eye to only the internal structure of a biological system. The internal structure is understood if we think of the actual dynamics of a system to reflect the response to both internal and external circumstance. The external circumstances are those that the environment imposes on the system. The internal circumstances are those related to the biological action of the species themselves, i.e., the system dynamics remaining after external causes have been removed.

By simply adding dominant external effects to these models, their predictive capabilities may be vastly improved. For example, see Lee, 1972.

Once an appropriate model of community dynamics is established, such a model may be used for management of an ecosystem subject to human controls. We illustrate such management possibilities by applying dynamic optimization procedures to a model of a complex aquatic community. The methods used are very general and could be applied to any ecosystem once the appropriate model is found and rational decisions are made concerning cost-benefit functions. Consider the following common situation. A lake is located in an arid area near a population center. Because of its location, not only is it a vital resource for both drinking water and recreation, but it is subject to heavy growth of phytoplankton due to ample sun light and ample nutrients from mans activities.

The phytoplankton is grazed naturally by zooplankton and to an extent keep the phytoplankton in check. However, from mans viewpoint, the phytoplankton level from time to time becomes undesirably large. If the water is to be used for domestic purposes, we have two alternatives, to treat it by means of a water purification plant on the way to the customer, or treat the lake as a whole. In the first case we take the water as the lake provides it to us and in the second we attempt to maintain the phytoplankton at a proper economic level before it goes to the purification plant.

The management question that we wish to investigate here then, is what level of controls (if any) should we impose on the lake as a whole in order to minimize the cost of water delivered to the consumer.

We will lump all species of phytoplankton together and represent their biomass by P. All species of zooplankton are lumped and their biomass is represented by Z. We thus have only two species and we represent the system by equations (6) (Note we have replaced N by P and P by Z).

$$\dot{P} = P[r - \frac{aZ}{1 + Pt} - bP] \qquad (7)$$
$$\dot{Z} = Z[\frac{eP}{1 + Pt} - d]$$

We must now examine the coefficients further in terms of this specific example. In general the intrinsic growth rate r is a function of sunlight, temperature, and nutrient levels. The variation with nutrient is of the form $\frac{N}{Km+N}$ where N is nutrient level and Km is Michaelis constant. We will assume that $N(\tau)$ is large, that is, $\frac{N}{Km+N} = 1$ for all time τ. We will lump the sunlight and temperature dependence into a single function of time by setting $r = C_kT$ where $T = C_3 + C_4 \sin (C_5\tau + C_6)$.

Since zooplankton are "grazers" they have negligibly small handling times so that we set $t = 0$. Since b is important for only very large values of P, we will also set $b = 0$ (Note that this assumption is compatible with a zero handling time. If $t \neq 0$ then the above system is unstable unless $b \neq 0$).

The zooplankton do not utilize all of the phytoplankton that they graze. Thus the utilization efficiency e is a function of phytoplankton concentration. We use the relationship $e = C_7P/Kmp + P$ where Kmp is the analog of a Michaelis constant with respect to the phytoplankton biomass. Finally, attributing the death rate of the phytoplankton to respiration we take $d = K_3T$.

We must now become more specific in regard to what lake we are investigating. For convenience we will take as our "lake" the Sacramento-San Joaquin Delta for which published data is available (see DiToro et al., 1972). We introduce a complication in using this data because of flow rates, but if we confine ourselves to the year 1966 in which the flow rate was low and nearly constant we may have a good approximation to a lake. The temperature distribution, phytoplankton concentration and zooplankton concentration for this year are reproduced from DiToro et al. (1972) in figures (2).

From the data plotted in Figure (2a) we obtain the constants

$$C_3 = 14.5°C \quad C_4 = 6.5°C \qquad (8)$$
$$C_5 = .01722/\text{day} \quad C_6 = 1.571$$

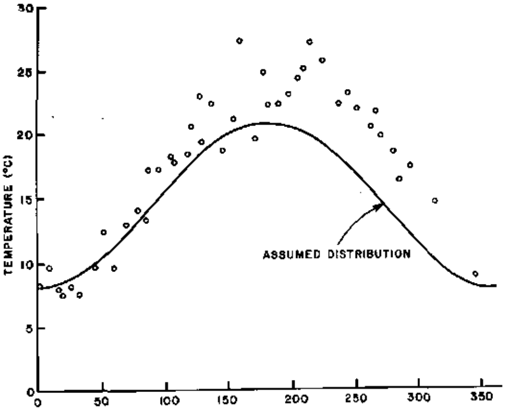

FIGURE 2a. 1966 TEMPERATURE DATA IN SAN JOAQUIN DELTA (AFTER TORO, ET. AL., BY PERMISSION)

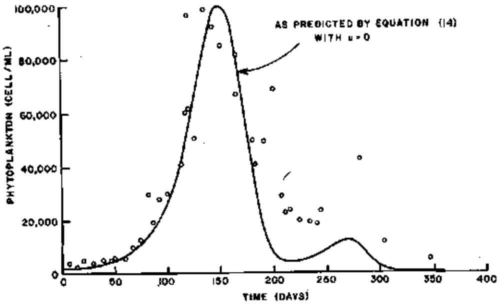

FIGURE 2b. 1966 OBSERVED DATA OF PHYTOPLANKTON IN SAN JOAQUIN DELTA (AFTER TORO, ET. AL., BY PERMISSION)

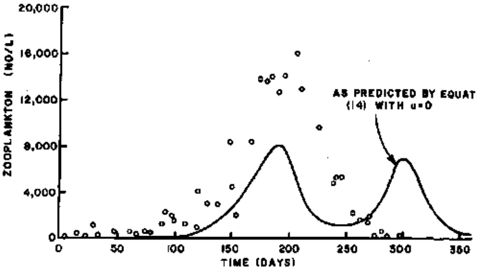

FIGURE 2c. 1966 OBSERVED DATA OF ZOOPLANKTON IN SAN JOAQUIN DELTA (AFTER TORO, ET. AL., BY PERMISSION)

DiToro et al. (1972) also gives the following values

Zooplankton grazing rate =
$$a = 1.69 \times 10^{-5} \text{ 1/No.Z day}$$
Phytoplankton Michaelis constant $\qquad$ (9)
$$Kmp = 3.42 \times 10^{3} \text{ cells/ml}$$
Zooplankton respiration coefficient
$$K_3 = .01/\text{day°C}$$

The constants C_k and C_7 are implied from the data given in figures 2b and 2c by noting definite maximums in the phytoplankton and zooplankton. At these points $\dot{P}$ and $\dot{Z} = 0$ and the right hand side of equations (7) can be used to evaluate the constants. The following values were obtained

$$C_k = 2.53368 \times 10^{-3}/\text{day } ^\circ C$$

$$C_7 = .250/\text{day} \tag{10}$$

We will assume that the phytoplankton will be kept under control by adding the algaecide copper sulfate. Figure (3) illustrates the effectiveness of this agent as a function of concentration.

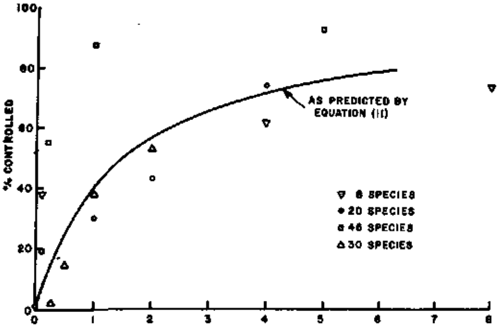

FIGURE 3. PERCENTAGE OF SPECIES OF ALGAES CONTROLLED.

Let u = % controlled. Then the data is approximated by the expression

$$u = \frac{PPM}{1.5 + PPM} \tag{11}$$

A gallon of copper sulfate costs approximately $17.00 and contains 7.1% active ingredient. Thus one gallon in a million yields 0.07 PPM or alternately to maintain 1 PPM of algaecide will cost about $242 per million gallons of lake water per day.

We may take u = % controlled as our control variable. Thus $0 \leq u \leq 1$ and the daily kill rate of phytoplankton is simply given by uP. Our cost of control must now be weighed against the cost of making the water fit for human consumption by other means. The filtering and chemical costs associated with a large scale water purification plant is about $24 per 100 cells/ml of phytoplankton for each million gallons treated. If we let X_0 = cost in dollars per day for each million gallons of lake water we have

$$\dot{X}_0 = .024P + (242)\,(1.5)\,\frac{u}{1-u} \tag{12}$$

Our optimal control problem thus becomes one of determining the control level u, $0 \leq u \leq 1$ such that the relative cost

$$X_0 = X_0/.024 = \int_0^f \left(P + \frac{cu}{1-u}\right) d\tau \tag{13}$$

over a years time is a minimum subject to the constants

$$\dot{P} = P(C_k T - aZ - u)$$

$$\dot{Z} = Z\left(\frac{C_7 P}{K_{mp} + P} - K_3 T\right) \tag{14}$$

$$T = C_3 + C_4 \, \text{SIN}(C_5 \tau + C_6)$$

where c = 15,140 and all other constants are as previously defined. The phytoplankton P is measured in cells/ml, the zooplankton Z in number/l and the temperature T in °C.

A necessary condition for optimality is that the control u satisfy a maximum principle (See Leitmann, 1966). Employing the methods of this reference we obtain the following control law

$$U(\tau) = \begin{cases} 0 \text{ if } \hat{\lambda}p > -a \\ 1 - \sqrt{\dfrac{-a}{\hat{\lambda}p}} \text{ if } \hat{\lambda}p < -a \end{cases} \tag{15}$$

where $\hat{\lambda}p$ is determined from the equations

$$\dot{\hat{\lambda}}p = P - \hat{\lambda}_Z C_2 \, Kmp \left(\frac{P}{(Kmp+P)^2}\right)$$

$$\dot{\hat{\lambda}}z = Z \, \hat{\lambda}pCg \tag{16}$$

(Note $\hat{\lambda}_p = P\,\lambda_p$, $\hat{\lambda}_z = Z\lambda_z$ where λ_p and λ_z are the usual adjoint variables. The abnormal solutions are contained within the normal ones so we have taken $\lambda_0 = -1$.) If we leave the final values for P and Z unspecified then $\hat{\lambda}_p(\tau_f) = \hat{\lambda}_z(\tau_f) = 0$ where τ_f for this problem is given by τ_f = 365 days.

An extremal solution (one which satisfies the necessary conditions for optimal control) requires satisfying a two point boundary value problem. The initial values for P and Z are known from our model. However the initial values of $\hat{\lambda}_p$ and $\hat{\lambda}_z$ are unknown and must be chosen so that at the 365th day $\hat{\lambda}_p = \hat{\lambda}_z = 0$. This was accomplished in the solutions shown in figures (4).

Note that control is used from the first day to initially decrease the number of phytoplankton present. The control is continuously decreased until the 273rd day when it is set equal to zero for the remainder of the year.

The effect on the phytoplankton is to decrease their numbers until about the 130th day when the effect of temperature is sufficient to increase their numbers in spite of the control level used. Except for the initial period, the lake is quite clean on the basis that serious pollution starts at approximately 1000 cells/ml.

Because of the relatively small numbers of phytoplankton, the zooplankton population is kept at very low levels and is not plotted. The levels are so low as to uncouple the zooplankton effect in the optimal control analysis.

It is evident from figure 4c that a substantial savings in overall cost is obtained

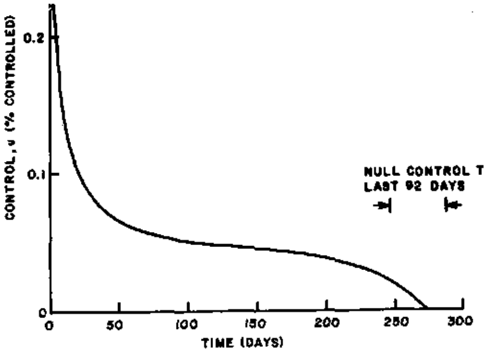

FIGURE 4a. CONTROL PROGRAM

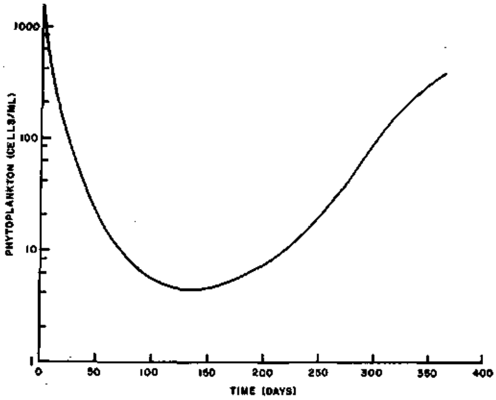

FIGURE 4b. PHYTOPLANKTON DISTRIBUTION FOR THE CONTROLLED MODEL.

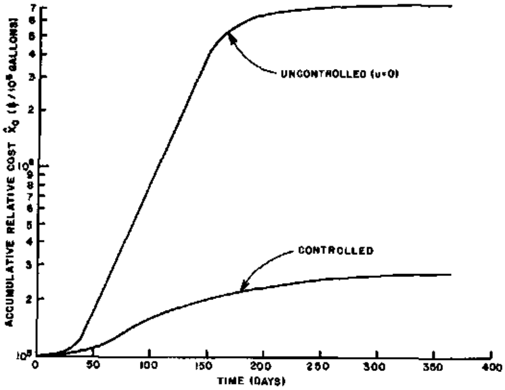

FIGURE 4c. COST OF THE CONTROLLED AND UNCONTROLLED MODEL

by employing control. It is of interest to note that the incremental cost due to the presence of phytoplankton is substantially less than the cost of control during the control cycle. This result might be upsetting to a control program manager, to him it would appear that a substantial investment in algaecide is being made to maintain a relatively clean lake. However, if less algaecide were to be used, then the phytoplankton growth would be greater at a latter time offsetting any short term gains in cost due to using less control.

It is also worth noting that the control levels are never a large fraction of what is available. This is simply because the magnitude of control available can easily dominate the natural growth rate of phytoplankton (compare C_kT with u). Greater control effort would be expected for certain other initial conditions however. It is also expected that the nature of the solution presented here may change substantially if the cost of control (e.g., the parameter c) were appreciably higher than the value used.

The results presented here are not complete in the sense that a control program for all starting conditions has not been synthesized. The synthesis problem obviously requires more computation but in principle can be done with the analysis presented here. The interested reader is referred to Vincent, 1972; Goh et al., 1974; and Vincent et al., 1974, where a complete synthesis has been performed but for a simpler model.

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INSTANTANEOUS (STATIC) VS LONG-TERM (DYNAMIC) OPTIMIZATION IN ECOSYSTEMS

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Summary

Dynamic optimization is distinguished from static optimization in that the former considers the effect of decisions at one time upon the condition (state) of the system at a later time, and optimizes a long-range objective, over a long time period, by choosing values of strategy variables changing throughout that long time period. Numerous examples are given of existing dynamic optimization formulations in biological resource management, life history theory, and foraging optimization. Two examples (one in fishery optimization and one in foraging optimization) each demonstrate the difference between static and dynamically optimal strategies. Use of computing methods on analytically (i.e., pencil and paper) intractable problems is briefly considered.

Introduction: Optimization approaches

Many ecosystem optimization models (including, for instance, many approaches to the question of harvest optimization by man, or foraging optimization by other animals) are static approaches. That is to say, a set of one or more decision variables is chosen to optimize (i.e., maximize or minimize) a performance index (i.e., a cost or benefit index) which depends on these decision variables. Typically, constraints apply to this choice of decision variables, due to the nature of the organism or system under consideration and due to impinging ecological pressures. The word static is applied to these approaches because only a single time period is considered, in the following senses.

1. The relationships defining the cost (or benefit) and those defining the constraints all apply on the average to this single time period, and do not change within that time period.
2. The relationship between this time period and other time periods is not considered.

Thus, a solution of a static optimization problem is a set of values of the decision variables, applicable only to the time period in question, rather than a long-term strategy, changing with time to optimize some long-range goal.

If one allows the performance index and/or the constraints (in a static optimization approach) to change from one time period to the next (due to changes in the ecosystem or in the impinging pressures), the result is a sequence of static optimization problems, each of which may have a qualitatively different solution from those of previous and succeeding problems in the sequence. (One might even consider infinitesimal time periods, as in Pearson (1974) and obtain a continuum of static optimization problems.) This removes part but not all of the disadvantage of the static approach, since the relationship between one time period and another (memory) is not considered.

For some optimization models, the static approach may be inappropriate, because the relevant objective (performance index) is a long range one and because the effect of past decisions on present condition may not be ignored. For example, consider an optimization model of a hypothetical species in which selective pressure is for maximum excess weight at breeding time, for conversion to eggs (provided, of course, that the adult survives to breed and lay eggs). At the same time, suppose excess weight is disadvantageous in escaping pre-reproductive mortality, and disadvantageous in terms of energy required for daily maintenance. In the face of a seasonally varying pattern of mortality risks and food abundance, a member of this hypothetical species might be ill-served by simply maximizing daily energy input, throughout the year (a sequence of static optimizations). The best policy in terms of maximizing the long range goal (excess weight at egg-laying time)X(probability of surviving to lay eggs) might consist of maintaining minimum weight most of the year, and then taking advantage of a period of increased food (and/or decreased mortality risk) to gain weight rapidly.

Another example can be hypothesized in resource management. Suppose a company has control of a biological resource which grows very slowly to an enormous size and value. From the standpoint of maximizing present value (in which future income is discounted in value, inversely to the "average" growth rate of money invested), waiting for such a resource to mature might be a very poor policy, and the company might be better served by harvesting the resource after a period of initial rapid growth, or perhaps by harvesting the resource immediately and investing in more rapidly growing capital (biological or otherwise).

In general, an optimization formulation appropriate to situations such as the two exemplified above must include the following aspects:

1. A single long time period is considered.
2. The performance (cost or benefit) index is global in the sense that it is a single number based on the condition of the individual animal, ecosystem, or biological resource, and on values of the decision variables, in that entire period. (Examples of global performance indices are probability of survival until the end of the time period, accumulated yield over the time period with or without time discounting, or total combined cost of pest control and crop losses to pests over the time period.)
3. The present condition (state) of the organism or system, at any time in the long period, is the result of all past and present values of decision (control or strategy) variables during that long time period, and of the condition at the start. Commonly, a set of (coupled) differential or difference equations (one equation for each condition variable) describes this dependence of present upon past. (For example, the condition of a forest in any year might be the total standing biomass, or the set of standing biomasses of all individual age classes. The decision variables during any year might be total biomass cut, with or without differentiation by size of age.)
4. The constraints, due to characteristics of the animal or system being considered, and to impinging pressures, may apply to the condition (state) of the ecosystem or to the decision (control) variables. These constraints may be the same throughout the long time period, they may vary with time (e.g., with the seasons) throughout that time period, or they may apply to specific instants (such as the beginning and end) of the time period. (In the forest management problem, equipment availability might dictate an upper limit on cutting, and political regulations might dictate that no more than a given fraction of trees may be below a certain age.)

In the dynamic approach, a strategy consists of values of the decision variables <u>at all times</u> within the long time interval (i.e., the decision variables as functions of time). An optimum strategy (i.e., one which maximizes or minimizes the performance index) for such an optimization problem must be, by the definition of the problem as in 1-4 above, a strategy which takes into account the effects of past behavior on present condition, as well as (possibly) time-varying constraints, to achieve a long range (global) objective.

Examples of dynamic optimization

Dynamic optimization has been applied to a variety of ecosystem management problems such as pest management and fishery yield maximization, and to natural selection problems such as life history optimization and foraging optimization. With no claim to completeness, a sampling of such formulations will now be described.

Fisheries optimization

Two distinct models are commonly used for the population dynamics of fisheries, namely the logistic model in which all age-classes are lumped together into a single population, and the Beverton & Holt (1957) model which accounts for year-classes individually (beginning with an assumed recruitment for each year class). Since the latter is considered in the next section, only dynamic optimization approaches to the former will be considered here. In these (Clark 1973a, 1973b; Cliff & Vincent, 1973; Goh, 1969/70), the overall time period is at least long enough to allow repeated fluctuations in the fish population (perhaps infinitely long, for mathematical purposes). The goal is maximization of total catch over that period (with or without inclusion of an economic discount factor over time), the condition (state) of the system at any time is the total number of fish, the decision (control) variable at any time is the rate of catching fish (except in Cliff & Vincent, 1973 where the control is fishing effort, a quantity multiplied by number of fish to give catch rate). Constraints dictate that at all times both the number of fish and the catch rate (or fishing effort) must be non-negative.

Pest management

Goh, et al. (1973) provide an interesting and fairly general formulation of the optimal pest management problem, using a standard Lotka-Volterra predator-prey model modified to include artificial release of either species (pests and/or natural predators upon them), as well as artificial mortality (chemical spraying) to pests and/or predators. The overall time period under consideration is not fixed a priori, but is the time necessary to achieve a desired equilibrium level of pests and predators. The goal is to minimize the total cost of the pest control program prior to reaching this equilibrium. Condition variables include population size of both pests and predators, with the possibility of including current concentration of chemical residue if a persistent chemical is used. Decision variables are rates of application of chemical and of pest and/or predator release. An optimal strategy, then, is the best (vis-a-vis the cost index) <u>combined</u> schedule of the three. The constraints simply dictate upper limits for each strategy variable (and eliminate biologically impossible negative strategy variables).

Life history optimization

This problem, in which the goal is maximization of an individual's contribution to the population size over the long term, has been considered by Cole (1954), Hamilton (1966), Mertz (1971) and others. Two recent works best pose this as a dynamic optimization problem. Gadgil & Bossert (1970) consider the entire lifetime of the animal as the underlying long time period, over which the single benefit index is the ultimate rate of increase m, (i.e., the rate of population growth whenever a stable age distribution is reached. At any age x in the animal's lifetime the animal's condition (state) is described by body weight w_x and probability l_x of surviving to age x. These are related (via difference equations) to all past and present values of the decision variable θ_x, which is reproductive effort at age x. Predation and resource scarcity appear in the difference equations via age-dependent parameters (not considered as decision variables, but rather as "givens"). The decision variable θ_x is constrained to be nonnegative and may not exceed a maximum reproductive effort. One might easily include an (age-dependent) lower limit on body weight, as well.

Taylor, et al. (1974) extend and modify the above approach. Over the animal's lifetime, they demonstrate that maximizing ultimate rate of increase m is equivalent to maximizing (Fisher's 1958) reproductive value at age zero, which is in turn equivalent to maximizing reproductive value at every age, taking into account the organism's development up to that time. They characterize the animal's condition at age x entirely by weight s_x of reproductive tissue (e.g., eggs, embryos) and weight w_x of other tissues. The strategy variables at age x are not merely reproductive effort, but energy allocations to ongoing maintenance, current reproduction, growth of reproductive tissue, and growth of other tissue. Age dependent birth rates and age-to-age survivorships are included as mathematical intermediates, but not considered directly as condition or strategy variables. The energy allocation decision variables are constrained by an upper limit on total energy uptake (dependent on age x, condition s, w), and by a zero lower limit on some of the individual allocations.

Foraging optimization

Much of the extensive work on foraging optimization has involved the static approach. Cody (1974) optimizes a measure of overall fitness, in the presence of a mix of two resources, as a function of similarity and abundance of those resources, and of a minimum level of allowed fitness. Schoener's (1971) review also includes his own approach to maximizing net energy/feeding time. Emlen (1966) maximizes the same goal by trading (in the mean) energy gained from taking a food item against energy gained from going on to the next item. Pearson's (1974) energy/feeding time static optimization similarly introduces probabilities of taking each food, and uses a multi-food "disc" equation to determine total energy per unit time. He converts this approach to dynamic optimization by considering expected energy gain over the predator's lifetime, based on mean survival probability and mean energy accumulation as condition variables at each time in the animal's lifetime. These condition variables, in turn, depend on the strategy variables (food-taking probabilities) of his static model, applied at each time. The next section will discuss a dynamic optimization model (Katz, 1973, 1974a) for scheduling of feeding in the presence of predictable time-variations of resource availability.

Contrast between strategies

To emphasize the differences between the static and dynamic approaches, two examples will each be considered in some detail using both approaches.

Beverton-Holt fishery model

Clark, et al. (1973) consider the Beverton-Holt (1957) model of fishing a single year-class of a fish species, assuming given recruitment R to that year class at initial time zero. Per capita mortality consists of constant natural mortality M and a term F(t) proportional to fishing effort. (The units of fishing effort are chosen so that this proportionality is unity.) If x is the number of fish in the year-class at time t, then

$$\frac{dx(t)}{dt} = -[M+F(t)]x(t), \quad x(0) = R. \qquad (1)$$

Assuming (average) weight of a fish of age t to be a known function w(t) (so its derivative w'(t) is also known), rewrite equation (1) as follows in terms of fish biomass $B(t) = w(t)x(t)$:

$$\frac{dB(t)}{dt} = B(t)[\rho(t)-M-F(t)], \; B(0) = w(0)R \quad (2)$$

where $\rho(t) = w'(t)/w(t)$ (the growth rate per unit body weight) is known and assumed to decrease with age. Thus the condition (state) of the year class is its biomass and the strategy variable is fishing effort.

Clark, et al. assume a fixed price p per unit weight of fish, and fishing cost $cF(t)$ proportional to fishing effort, so that the (instantaneous) revenue/unit time is $R(t) = F(t)[pB(t)-c]$. (Hence fishing will be unprofitable whenever biomass drops below threshold c/p.) Finally, they assume a very large upper limit F_{max} on fishing effort, so that non-negativity of fishing effort is the only effective constraint.

Static maximization of net revenue dictates simply letting the fish grow (no fishing) until the time t_o of maximum biomass, then rapidly fishing them out until biomass falls to the profitability threshold c/p. (Equations 7 and 8 of Clark, et al. show that biomass of the year class will thereafter never exceed threshold.) Figure 1a shows the strategy dictated by this static criterion.

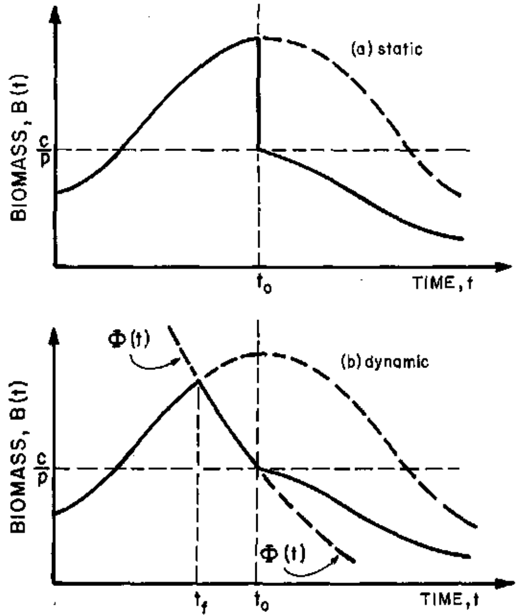

Figure 1 (Clark, et al., 1973). Optimal fishing: (a) maximum net revenue (static); (b) maximum present value (dynamic). Solid = actual biomass; dashed = extension of unfished biomass curve or Fisher curve.

On the other hand dynamically maximizing the total present value of all (present and future) profits

$$PV = \int_0^{\infty} e^{-\lambda t} F(t)[pB(t)-c]dt \qquad (3)$$

(where λ is the instantaneous discount rate) dictates an optimal fishing strategy (fishing effort with time) shown in figure 1b. This strategy is based on the "Fisher curve" $\Phi(t)$ (Fisher, 1930; equations 9, 12 of Clark, et al.). Respectively below (above) this curve, the "net biovalue" $V(t) = pB(t)-c$ is instantaneously increasing faster (slower) than the discount rate. The equation of this curve (Clark, et al.) depends upon c, p, λ, m, and w(t). The optimal strategy calls for periods of: (1) non-fishing until time t_f when biomass reaches the Fisher curve; (2) fishing so that B(t) remains exactly on the Fisher curve until biomass falls to the profitability threshold (which occurs exactly at time t_o of "maximum natural biomass"); (3) ceasing to fish while biomass declines. Clark, et al. show that initial fishing time t_f always satisfies $t_\lambda < t_f < t_o$ where t_λ is the time at which net natural growth rate per pound of biomass ($\rho(t)$-M, cf. equation 2 above) falls below discount rate λ.

Figure 1 reveals that the dynamically optimal strategy obtains its advantage (in terms of present value) by beginning to fish earlier, namely at the time t_f when the fish are ceasing to increase in value as rapidly as a comparable amount of money invested at the prevailing discount rate. Less total fish biomass is taken (figure 1b) despite the increased present value. The dynamic strategy differs inherently from the static strategy by taking into account not only the value of the catch, but the time when this value is obtained (via the discount rate) and the relationship between past actions and present biomass (via inclusion of fishing effort and fish biomass in both the fishery dynamics equation (2) and benefit index (3)).

Optimal foraging by Quelea quelea

Katz (1973, 1974a) models foraging strategy and weight change of the African Weaver Bird Quelea quelea (documented by Ward 1965, 1971) in response to predictable food-availability and breeding cycles. Condition (body weight w) and strategy (fraction x of the daylight day spent feeding) are related by the following differential equation, over total time period T = 1 year.

$$\frac{dw(t)}{dt} = -cw(t)-d(t)+(au(t)-q)x(t) \qquad (4)$$

when c and q respectively model the weight and foraging effort dependence of respiration, u(t) is a (given) time-varying parameter modeling food availability, and d(t) (normally zero, positive when nestlings are being fed) models excess respiratory demands of the breeding cycle. Constraints include nonstarvation $w(t) \geqq w_{min}$ (minimum weight documented Ward 1965) and limits $0 \leqq x(t) \leqq x_{max}(t)$ on feeding effort. Given parameter $x_{max}(t)$ is 1 except during feeding of nestlings, when its drastic reduction models the corresponding reduction in time available to adults for feeding themselves.

Food conditions (bar graph, figure 2; Katz, 1973, 1974a; Ward 1965, 1971) begin with normal food availability, followed first by food scarcity and immediately thereafter by lush, plentiful food. The entire breeding cycle takes place in this short lush season, culminating in feeding the nestlings. Finally, food conditions return to normal.

Selection pressure (via the hot midday sun and the competing activity of water-getting) is for minimization of total annual feeding effort, expressed (within a constant factor) as

$$\mathrm{AFE} = \int_0^T x(t)dt \qquad (5)$$

This must be minimized, while avoiding starvation, in the face of two annual crises, each of which forces a weight loss (cf. Ward, 1965) and thus dictates a prior buildup: (1) the period of extreme food scarcity; (2) the time and energy stresses of feeding nestlings.

One might suspect equivalence between minimizing AFE (above) and minimizing feeding effort each day (static optimization each day) with a provision forbidding $w(t) < w_{min}$ (starvation). This would result (cf. figure 2a) in feeding slightly above the minimum maintenance level at the beginning of the year, in order to gradually gain weight just sufficient to survive the food scarcity. After the scarcity one would expect a similar slight excess (over minimum maintenence) feeding and gradual weight buildup, prior to feeding nestlings.

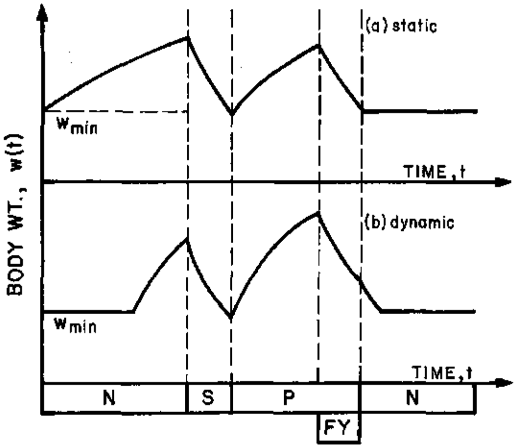

Figure 2 (Katz, 1974a). Optimal foraging: (a) minimum daily feeding effort (static); (b) minimum annual feeding effort (dynamic). Conditions: N = normal food; S = scarce; P = plentiful; FY = feed young.

This sequence of static optimizations fails to consider: (1) possible overeating when food is plentiful (more food in less time) to save feeding effort later; (2) the penalty (in terms of increased feeding necessary to "break even" - cf. $cw(t)$, equation 4) for increased weight.

When these are taken into account, the dynamic optimal foraging and weight gain histories (Katz, 1973, 1974a) entail: (1) rapid weight gain (maximum feeding effort for a short time) just prior to the food scarcity; (2) maximum feeding throughout the lush season (with a weight excess at the end of it). In fact, the dynamically optimal strategy entails only periods of maximum weight gain (minimum weight loss) $x(t) = x_{max}(t)$, periods of complete non-feeding, and periods of pure starvation avoidance (feeding at minimum maintenance level) occurring only at minimum weight. Thus something (but not necessarily instantaneous feeding effort minimization) is always done as strongly as possible, with scheduling dictated by the long-range goal.

Computing methods

Practical dynamic optimization problems tend to require numerical methods. This is easily obscured by the numerous analytic (i.e., obtainable by "pencil and paper") solutions to simple example problems which appear as demonstration cases in the literature. Introduction of realistic complications, however, often destroy the analytic tractability.

For example, Clark, et al. (1973) were able to extend their optimal solution of the Beverton-Holt fisheries model (cf. previous section) to sequential year classes by assuming negligible fishing costs. Without that assumption, there is every indication (Clark, pers. comm.) that an analytical solution is impossible.

A more complicated (and even less analytically tractable) problem arose recently in discussions with Daniel Huppert and David Somerton concerning crab fisheries in Alaskan coastal waters. Modeling these species requires distinction between males and females, due to differing growth rates, and because the crabs' shape requires males to be larger (thus older) than females when mating. Extending the Clark, et al. (1973) sequential year class formulation to such a species would require two condition (state) variables (numbers or biomass of males and females) for each age class. Furthermore ensuring sufficient breeding stock to allow the desired recruitment would require minimum thresholds (constraints) on numbers of large (old) males and small (young) females.

Now, recent years have seen extensive research in computing algorithms for dynamic optimization problems, generating many classes of methods, each having advantages for certain classes of problems. Although some excellent compendia exist (e.g., Polak, 1971) an "amateur" is well served by wariness, first because of the aforementioned complexity and diversity of methods and problem classes, secondly because the algorithms most readily comprehensible to the novice are rarely the ones which work the best in complicated problems, and thirdly because aspects of realistic biological problems are likely to have nonstandard mathematical expressions and thus to require modifications of existing computing algorithms.

For this reason, the authors recommend

collaboration with a "practicing expert" in computing algorithms. While one of the authors has limited computing methods experience (Katz, 1974b), his narrowness of experience easily disqualifies him from the "expert" category. However, he volunteers his services as a broker in such matters.

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ON THE EVOLUTION OF HABITAT SELECTION[1]

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Summary

Although it is possible to define an optimum phenotype in any given mixture of two habitats, the optima for different mixtures are unequal in their absolute fitness. In fact, if the evolutionary demands of two habitats are discordant, then the average fitness of members of optimal populations is directly proportional to the dissimilarity of the optimum phenotype from the generalized phenotype. (The generalized phenotype is the one whose fitness is the same in both habitats.) Because of that, if habitat selection is cost-free, the single, fine-grained optimum is always replaced by the two extreme specialists, each of which is restricted to its own better habitat.

Even if there is a cost to habitat selection, a phenotype should elect to ignore its poorer habitat completely, provided the ratio of its fitness in the better habitat to its fitness in the poorer exceeds 1 plus the ratio of the time it spends in traveling within one patch of each of the two habitats to the time its spends exploiting one patch of the better habitat. Under no circumstances of the model is an intermediate amount of habitat selection optimal--a patch type is either never used or used whenever encountered. An extreme habitat specialist is almost certain to succeed if its fitness in its own best habitat is as much as twice as large as the fitness of the generalist. Usually even this much advantage is not required. Habitat selection is more likely to be a successful strategy in territorial organisms and in situations where there is high discordance between the demands of the two habitats.

If the two habitats are about equally represented, then each is likely to be inhabited by its extreme specialist. In this case, the two specialists ignore each other; if they are different species, their competitive alpha value should evolve to be zero (although it remains zero owing only to the continued threat of competition).

If one of the habitats is rather more common than the other, the two successful phenotypes should often be (1) the common habitat's most extreme specialist and (2) the fine-grained optimum for that particular mix of habitats. Here, the fine-grained form will use both habitats, the specialist only one, and competition between the two should be strong.

Introduction

Levins (1962) indicated that fine-grained species could subdivide environments in only rare situations. However, MacArthur & Levins (1964) suggest that if species or phenotypes preferentially exploit those habitats in which they are most fit, then each habitat type can support its own specialist. But under what circumstances is habitat selection an optimal strategy? In this paper, I attempt to expand the partial answer of MacArthur & Pianka (1966) to this question. In doing so, I shall present several new conclusions which may help population ecologists to design more meaningful investigations of competition and species packing phenomena (May & MacArthur, 1972).

An overlooked property of fitness-sets: the fine-grained habitat generalist is the poorest possible optimum phenotype

Assume that there are two environments, 1 and 2, which occur in proportions, p and q, respectively. Array the fitnesses of all possible phenotypes in a two dimensional graph whose axes, W_1 and W_2 are the fitnesses of each phenotype in pure patches of environments 1 and 2 (Levins, 1962); this is the fitness set. Define its outer margin as the set of points such that each point has the largest value W_2 of all points sharing its particular ratio of W_1/W_2. Since this is clearly the set of phenotypes from which natural selection must choose the optimum, we shall restrict ourselves to it. Finally, we shall agree that the interesting case to study is where the outer margin has negative slope; i.e. where the environments produce discordant demands on the phenotype so that improvement in fitness in one environment means diminished fitness in the other.

The generalist phenotype is the one with $(W_1/W_2) = 1$. Regardless of p or precisely how the adaptive function is constructed, the adaptive function is a weighted average of W_1 and W_2. Hence, the generalist's mean fitness is independent of p or the form of the adaptive function; it is a constant equal to the generalist's fitness in either environment: W_F.

Now let there be an environment, p_F, where

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[1]

the generalist has the optimum phenotype. The average fitness of the members of this monotypic population is simply W_F. As p is increased, the generalist will be replaced as the optimum by a specialist whose $(W_1/W_2) > 1$ (Levins, 1962). But at this value of p, the generalist maintains fitness W_F. Hence, its replacement always entails improvement in fitness for the population as a whole.

<u>The most extreme habitat specialists are always the best possible phenotypes in a fine-grained environment</u>

Let there be an environment, p_E, in which a particular phenotype with $(W_1/W_2) = E > 1$ is the optimum. Regardless of the form of the adaptive function, as p increases beyond p_E, the fitness of this phenotype will rise. Yet Levins (1962) points out that it is soon replaced by a new optimum phenotype, a more extreme specialist, whose $(W_1/W_2) > E$. Hence, replacement of a less extreme specialist by a more extreme one always entails an increase in the average fitness, $\overline{W}$, of the members of the population.

<u>Optimum phenotypes if habitat selection is free of costs</u>

If individuals can adjust their own personal experience of the environment to any value of p, they may be said to be capable of cost-free habitat selection. The reason for this is that the real cost of habitat selection will be seen below to be the time wasted in traversing unsuitable habitat; if p can be adjusted to 0 or 1, no time is wasted. Organisms which are small enough to reside for life in one single patch of their favored habitat, approach (or even achieve) cost-free habitat selection.

Because of the fact that the most extreme habitat specialist is always the best fine-grained optimum, it is clear that if it can indulge in cost-free habitat selection, it will achieve that highest fitness, just as if it were in an environment composed purely of its special habitat. It constitutes the optimum phenotype in that environment, and its counterpart, the extreme specialist in the other habitat, is the optimum in the other. Both these forms will survive as ecotypes (or different species) each restricted to its own special habitat and reaching a population density set by the resources within it (Fretwell, 1969).

<u>When should a specialist select habitats if a cost is involved?</u>

Let t_G be the average amount of time a phenotype spends in exploiting one patch of its good habitat type before it enters a patch of the poorer habitat. Let t_X be the average amount of time it spends exploiting a single patch of the poorer habitat. Let t_M be the time it spends not exploiting, but merely traveling through both the patches. These time symbols are summaries of a complicated set of variables including: p; the average size of patches; and the amount of resources contained in each patch.

While the phenotype exploits each patch, it profits. Its profit could be reckoned in fitness (net rate of reproduction), but it is more general to calculate it in rate of increase of reproductive value. Let the average rate of increase of reproductive value be $\ln W_G$ in the good patch, and $\ln W_B$ in the bad patch. These rates are defined as averages in order to allow for the depletion of resources that may occur in a patch as it is used by the phenotype. Finally, to be tidy, let us assume that the rate of metabolic cost incurred is a constant, M, in all patches and during all activities. (M is also calculated in units of the rate of increase of reproductive value.) From these considerations the average rate of increase of reproductive value is: $\ln \overline{W} = \left\{(t_G \ln W_G + t_X \ln W_B)/(t_G + t_X + t_M)\right\} - M$ (1)

Habitat selection is a good strategy only if $d \ln \overline{W}/dt_X$ is negative; that is, only if: $(\ln W_G/\ln W_B) > 1 + (t_M/t_G)$ (2)

From this simple expression, we obtain the intuitively obvious conclusions that: (1) For a phenotype to select a habitat, it must be better at exploiting it; (2) The greater its advantage at the good habitat, the more likely it will need to habitat select; (3) The more time it can spend exploiting the good habitat compared to traveling within it and within the poorer habitat, the more likely it is to need to habitat select. The latter conclusion is totally analogous to MacArthur & Pianka's (1966) conclusion that environments which cause phenotypes to spend a high proportion of their time searching compared to pursuing, produce generalistic opportunists.

A more novel conclusion also may be deduced from (2). Since (2) does not contain the variable t_X, then if some habitat selection is a good strategy, more is even better and the optimum is to reduce t_X to zero. In other words, a phenotype either exploits a habitat fully or doesn't exploit it at all. Recently Pulliam (1974) has produced the identical conclusion with respect to the resources with a habitat.

Clearly, of all those which are required to habitat select, the optimum is the one with the largest $\ln W_G$ since the fitness of all habitat selectors is: $t_G \ln W_G/(t_G + t_M)$

When is a specialist better than the fine-grained optimum?

Since the success of one of the extremely specialized habitat selectors completely frees its poor patch from exploitation, and therefore allows the empty patch to be exploited by a second phenotype, it is the success of the extreme specialist which generates polymorphism (or two successful species). The habitat selector succeeds in that environment where the generalist is the fine-grained optimum if: $t_G \ln W_G/(t_G + t_M) > t_F \ln W_F/(t_F + t_M)$ (3a)

where $\ln W_F$ is the average reproductive accumulation rate of the generalist and t_F is the time it spends exploiting two patches--one of each habitat type. Assuming that the generalist is the fine-grained optimum at p = 0.5 (which is probably nearly true in most cases), and thus, that $t_F = 2t_G$, inequality (3a) can be manipulated to:

$$\ln W_G/\ln W_F > 1 + \{t_M/(2t_G + t_M)\} \qquad (3b)$$

Since the limit of the right side of (3b) is 2 as t_G approaches zero, a habitat specialist which is twice as good in its habitat as the generalist, should always succeed. Moreover, a twofold advantage is only rarely necessary, and lower advantages should very often be successful.

Inequality (3) becomes easier to satisfy *in territorial organisms* because they can minimize t_M. Also, since a more concave fitness set implies a larger tradeoff than a less concave one, habitat selection is a better prospect with more concave fitness sets (which is really the central point of MacArthur & Levins, 1964).

Only one of the extreme specialists need succeed to produce stable phenetic diversity in a system. Since each specialist, by its habitat selection, needs to overcome less and less of a fine-grained fitness deficit as p changes to favor its special environment, satisfying (3) is about the most difficult criterion for the success of habitat selection. Therefore, as p moves away from the value which allows the generalist to be the fine-grained optimum it is easier and easier for one of the extreme specialists to succeed. Clearly, when p is large (or small) enough so that the fine-grained optimum phenotype also needs to select only its best habitat, then the most extreme specialist is going to replace it in that habitat.

The pattern of habitat use as p varies

When p is in the vicinity of 0.5 and habitat selection is the successful strategy, it is quite possible that both extreme specialists will succeed. If so, they should evolve to ignore completely each other's special habitat. The reason for this is that when each has filled its patch to carrying capacity, a foray into the other's patch type brings a phenotype into an environment in which its ln W is negative, whereas in its own, its ln W is zero. Thus, strong intraphenotypic (or intraspecific) territoriality should evolve, but there should be *no intertype territoriality* nor intertype competition. Precisely this situation has been observed in two similar species of kangaroo rats (*Dipodomys*) by Schroder & Rosenzweig (in prep.); these two rodent species have a competitive alpha of zero although they travel in each other's habitats; they are strongly intraspecifically territorial; they do not respond to each other at all in the field. In contradistinction to this data and the present theory, May & MacArthur (1972) predicted that such potentially close competitors were likely to show an alpha between 0.5 and 0.6. The discrepancy results because they considered what similarity a competitive system can tolerate, whereas I am asking what similarity is optimal.

When p is far from 0.5 only one of the extreme specialists is likely to be able to habitat select (because of inequality 2). However, the rarer habitat would not be empty. A second successful phenotype, the one that fills it, will be the one that can best exploit the given mixture of patch types, i.e. the fine-grained optimum. Thus there will be two successful phenotypes: the fine-grained optimum and the extreme specialist in the common patch type. When this happens, intertypic territoriality may evolve and intertypic competition should be substantial.

In the latter case, the two types will have nested niches: one will restrict itself to the common patch, the other will use both. This will occur even if, in the absence of the extreme specialist, the fine-grained optimum would, itself, have been forced to specialize on the common habitat. Density-dependent selection (Fretwell & Lucas, 1970) forces it to use both habitats. In such a case, the apparent generalist, is really a specialist too! And it specializes in dealing with the same (common) patch-type that the extreme specialist uses so well.

As p nears zero or 1.0, the fine-grained *optimum nears the phenotype of the extreme* specialist and competition intensifies. If the two morphs are different species, the rules of limiting similarity (May & MacArthur, 1972) apply. Hence when p is sufficiently far from 0.5, only one species can be supported.* But, since each can be generated from the other if both are in the same species, there is no limiting similarity of ecotypes. (Limiting similarity is caused by the probabilistic extinction of one of the species.) Instead, although occasionally one morph may disappear momentarily, usually both will be present, optimizing their species' utilization of the environmental heterogeneity by appropriate habitat selection.

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*Ordinarily, it is optimal for the morphs to be in different species until limiting similarity is reached, because separate gene pools can better match the exact morph ratios required to optimize the utilization of the environment, and because separate gene pools are unburdened by the strictures of additive inheritance (such as production of intermediates or the need to evolve developmental switch mechansims.)

A METHOD FOR FORMULATING SUBOPTIMAL POLICIES FOR CRUDELY MODELLED ECOSYSTEMS

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Summary

Our method is similar to what a bush walker does when he has only a rough map of a region. The map provides a basis to plan tentative routes from various points in the region to his destination. The points on such tentative routes plus their associated distances from the destination provide him with some intermediate targets. His actual decisions, optimal or otherwise, are based on an intermediate target together with empirical assessment of the terrain within his visual range. The proposed method is applied to a problem in pest control and a problem in fisheries.

Introduction

There are two common problems in the management of ecosystems. One is, how to harvest one or more species so that the yield is maximized and yet no irreversible damage is caused to the ecosystems, e.g. management of a fishery. The other problem is, how do we manipulate available control variables so that we stabilize the ecosystem, e.g. management of a pest.

Modern optimal control theory was developed in the last two decades and was motivated by problems in programming rocket flights (Leitmann, 1965) and in automatic control (Athans, 1966).

Suppose an ecosystem can be described by a set of first order differential equations

$$(1) \quad \dot{x}_i = f_i(x,\ u,\ t),\ i = 1,\ 2,\ ..,\ n,$$

where x_i stands for a species density or a resource level or some other state variable. u_r $(r = 1, 2, .., m)$ is a control variable, e.g. fishing effort or rate of application of insecticide. Typically the control variable must satisfy constraints like $0 \leqslant u_r(t) \leqslant a_r$ where a_r are constants. The problem is to choose admissible control variables which will drive the system from the initial state $x(0)$ to a terminal target, usually defined by $\psi^s[x(T), T] = 0$, $s = 1,2,..., p \leqslant n + 1$, and so as to minimize the pay off

$$g[x(T),T] + \int_0^T L\ (t,x,u)\ dt\ .$$

If $S(x,t)$ is the optimal value function, the optimal feedback control $u(x,t)$ is obtained by minimizing, for admissible u ,

$$(2) \qquad L(t,x,u) + \sum_{i=1}^{n} \frac{\partial S}{\partial x_i} f_i(t,x,u)\ .$$

This optimality principle is from Dynamic Programming. Unfortunately it can be very difficult to obtain $(\partial S/\partial x_i)$.

The proposed method

The steps in the method are as follows: (i) Build an analytical model of the ecosystem. (ii) Employ this model and optimal control theory to deduce optimal feedback control or representative optimal trajectories. (iii) Experimentally measure the rates of change of the state variables of the uncontrolled system at as many points in the state space as possible. Store this information. (This gives an incomplete picture of a velocity field in the state space. It is a crude but empirical model. The analytical model in step (i) helps to some extent in completing the picture. This is the type of modelling developed by Rosenzweig and MacArthur (1963). Their use of isoclines partition the state space into regions. Each region has its own pattern of velocity vectors.) (iv) Employ this empirical model and synthesise a feedback strategy by choosing the control variables so as to move in the best possible manner to the terminal target or an intermediate target which is tentatively provided by the optimal feedback control and its optimal value function in step (ii). This feedback control should be synthesised backwards from the terminal target. (v) Examine the sensitivity of the controlled system to errors in the empirical model.

An example in pest control

Let an insect pest (prey) live in a region with an insect predator. Assume that they only interact with other species which remain

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relatively constant in the time scale for their dynamics. Let $u_1(t)$ be rate of release of predators bred in laboratories, $u_2(t)$ be rate of application of nonresidual insecticide which kills only prey, $u_3(t)$ be rate of application of a nonselective and nonresidual insecticide, $u_4(t)$ be rate of application of insecticide which kills only predators and $u_5(t)$ be rate of release of pest bred in laboratories. Let N_1 be prey density and N_2 be predator density.

Let the analytical model be

$$(3) \quad \dot{N}_1 = g_1\ (N_1,N_2) - u_2N_1 - c\,u_3N_1 + u_5$$

$$(4) \quad \dot{N}_2 = g_2\ (N_1,N_2) + u_1 - u_3N_2 - u_4N_2$$

Let g_1,g_2 be as in the Lotka-Volterra model i.e. $g_1 = N_1 - N_1N_2$, $g_2 = N_2N_1 - N_2$. Let the control variables be subjected to constraints: $0 \leq u_r(t) \leq a_r$; $r = 1,2,3,4,5$. Let a_r be a constant. Finally we have to specify the target to drive the system to, and an index to measure the performance of the control policies. In pest control the performance index should be some weighted sum of (i) time to get to the target, (ii) total pest damage and (iii) cost of the control program.

A simplified version of the optimal policies for this problem is displayed in Figure 1 (Goh et al., 1974a). P is the equilibrium state of the uncontrolled system and has been chosen as the target for controlled trajectories. The state space is divided into five sectors if the constants $\{a_r\}$ are relatively large. In each sector a particular control variable is especially effective and should be applied at the maximum rate.

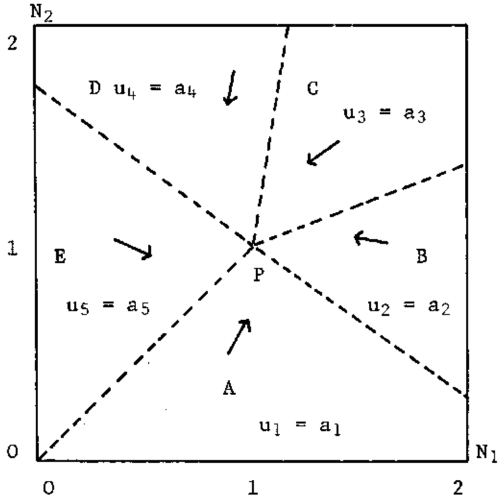


Fig. 1. Feedback control policy

In step (iii) we experimentally measure the rates of prey and predator densities at as many points in the state space as possible. Let these data at (N_1,N_2) be $h_1(N_1,N_2)$ and $h_2(N_1,N_2)$. Thus we have an empirical model with h_1 and h_2 in place of g_1 and g_2 in equations (3) and (4) and let $f_1 \equiv h_1 - u_2N_1 - c\,u_3N_2 + u_5$ and $f_2 \equiv h_2 + u_1 - u_3N_2 - u_4\,N_2$.

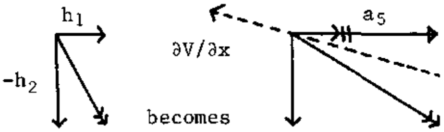
In step (iv) of the method we choose the control variables from the admissible set so as to minimize

$$\text{(A)} \quad \sum_{i=1}^{2} \frac{\partial V}{\partial N_i} f_i \quad \text{or} \quad \text{(B)} \quad \sum_{i=1}^{2} \frac{\partial V}{\partial N_i} \frac{f_i}{||f||} \ .$$

In this example we can choose $V = (N_1 - N_1^*)^2 + (N_2 - N_2^*)^2$ where $(N_1^*,N_2^*) \equiv P \equiv (1,1)$, the equilibrium. Criterion (A) says that the control variables should be chosen so that the projection of the vector f along the vector $\partial V/\partial x$ is minimized. This condition is similar to the optimality condition in (2) if $L(t,x,u) = 0$. This minimum projection should be negative. If not we choose a different target (N_1^*,N_2^*) . The choice should be guided by the feedback control strategy for the analytical model. Criterion (B) says that the control variables should be chosen so that the angle between f and $(-\partial V/\partial x)$ is minimized. $||f||$ stands for the norm of f .

In the general case, the suboptimal principles embodied in (A) and (B) by themselves, can only provide short term suboptimal policies. The long term optimality of the feedback control depends on how the intermediate targets (N_1^*,N_2^*) are chosen. For this, we must emploit the information obtained in steps (i) and (ii). If we complete the synthesis with only one target, then V is none other than a Liapunov function. If the control variables are continuous functions of the state variables and (A) or (B) is negative then we have sufficient conditions that the controlled system is stable.

Let us consider what happens at a point in region E in Figure 1 where $h_1 > 0$ and $h_2 < 0$. If u_5 is applied at the maximum rate a_5 , what happens is we are superimposing a vector on the natural velocity components and swing the resultant vector towards the target P .
Thus



If a_5 is large, it dominates h_1 at this point. If h_2 is an accurate measurement of the rate of change of the predator, the real rate of change of the prey could be equal to $-h_1 - a_5$ at this point without destroying our stabilization scheme. h_1 is the measured rate of change of the prey. This explains why our feedback control strategy is robust. More generally at (N_1, N_2) the feedback policy can tolerate errors δh_1 and δh_2 where

$$\sum_{i=1}^{2} \frac{\partial V}{\partial N_i} \delta h_i + \min_{u} \sum_{i=1}^{2} \frac{\partial V}{\partial N_i} f_i < 0 .$$

This is step (v) of the proposed method. It is a conservative estimate of δh_1 and δh_2. Better estimates may be obtained if a more appropriate Liapunov function V is employed. [There are mathematical technicalities. In the operation Min with respect to u, we ought to restrict u to continuous functions of the state variables. We should have feedback control synthesis on a connected region containing the target. Such conditions assure we have used the Liapunov stability theorem legitimately].

In this manner we obtain (Goh et al., 1974b) for the empirical model a feedback control policy very similar to that displayed in Figure 1.

An example in fishery management

Let us suppose a fishery can be described by a single first order differential equation. Let us approximate it by the logistic model $N = rN - (r/N_s)N^2 - u$, where u is the rate fish is caught and r, N_s are parameters. Let $0 \leqslant u \leqslant a$ and $0 \leqslant t \leqslant T$. The problem is to choose $u(t)$ so as to maximize the total yield $z(T) = \int_0^T u\,dt$ and such that $N(T) \geqslant e > 0$. If $a > r\,N_s/4$, the optimal policy is as displayed in Figure 2 (Goh, 1969, Cliff and Vincent, 1973).

The synthesis of a suboptimal policy based on empirical data for the natural rate of change of the fish population, is best made in the state-cost space (N,z). The empirical data for the natural rate of change at various population densities is displayed in the lower half of Figure 3. Denote this function by $h(N)$. Guided by the policies in Figure 2 we develope a suboptimal policy for the empirical model and display it in the upper part of Figure 3. A broken line is an isochrone for time to go, $(T - t)$.

Consider what happens at the point R. If $u \neq 0$ then

$$R \underset{h}{\longrightarrow} \qquad \text{becomes} \qquad \overset{u}{\uparrow}\!\!\longleftrightarrow$$

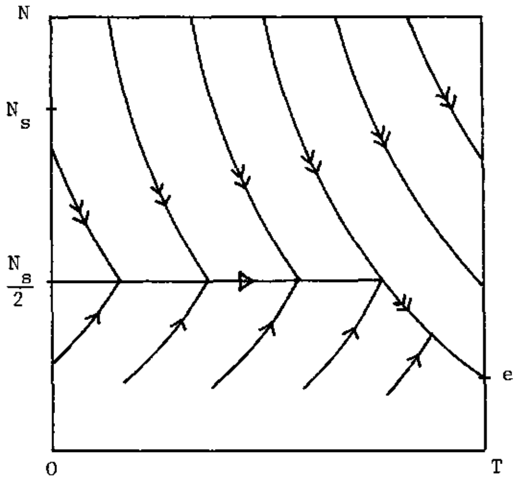


Fig. 2 $\longrightarrow u = 0$, $\twoheadrightarrow u = a$, $\longrightarrow\!\!\triangleright\ u = rN_s/4$

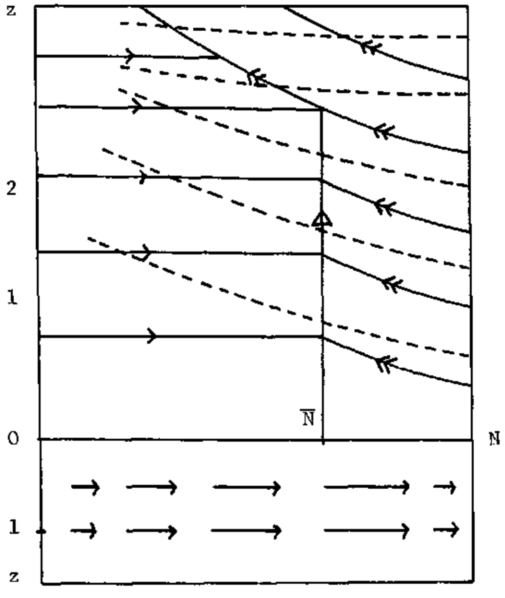


Fig. 3 $\longrightarrow u{=}0$, $\twoheadrightarrow u = a$, $\longrightarrow\!\!\triangleright\ u = h(\bar{N})$

Thus simultaneously, two vectors are superimposed on the natural velocity vector. In this example the choice of the intermediate target is crucial. If the target is (z^*, N^*) where z^* is very large and u is chosen to minimize $(z - z^*)\dot{z} + (N - N^*)\dot{N}$, then at R, u should be equal to a. But this will drive the system towards the extinction boundary $N = 0$. Let maximum of $h(N)$ occur at $\bar{N}$. Figure 2 suggests at $R \equiv (N,z)$ we should drive the trajectory towards $(\bar{N},z)$. If $h(\bar{N}) < a$ the suboptimal feedback control is not sensitive to differences between the actual natural rate of change of the fish population and the measured rate $h(N)$. Usually T is very large and we can ignore the distortion at the top part in Figure 3. Thus the maximum sustainable yield policy, widely used as a guideline in fishery, can be made into a robust policy if it is implemented in a feedback manner as displayed in Figure 3.

Conclusions

Our proposed method is an adaptive approach for formulating policies in the management of ecosystems. It employs two models, an analytical model for developing guidelines and an empirical model for the actual decisions. We have chosen simple examples so that we can focus on the ideas in the method. There are many difficulties in the application of this method to complex ecosystems. One is that, if there are more state variables than control variables, it is difficult to use the control variables to dominate the rates of change of the state variables, in the absence of a good model of an ecosystem. If we have a good analytical model of an ecosystem, we may be able to use controllability theorems (Lee and Markus, 1967) which guarantee that we can manage a system of n state variables by means of a single control variable.

Acknowledgement

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Closing session:

The significance of ecological principles for society

RURAL ECOLOGY IN DEVELOPMENT

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Summary

In as much as environmental problems in Indonesia primarily stem from poverty and from lack of development, these problems can only be overcome by development to increase the standard of living of the people. Since about 80% of the people live in rural areas, more emphasis should be laid on rural development and due considerations be given to rural ecology to prevent undesirable side-effects from arising in the development process.

Some characteristics of the rural ecology are:

1. Energy flow.
There is more or less equal distribution of energy and consequently also an equitable distribution of income. Introduction of energy subsidies to the village should take this into account in order to prevent the creation of the social gap between the rich and the poor.

2. Cycling of matter.
Man is part of the food web and is directly involved in the cycling of matter, which seems to be an efficient method of waste disposal and protein production. Rural development programs should endeavour to keep the cycling of matter intact, which improving the hygienic conditions.

3. Diversity of the ecosystem.
The home garden is planted with many species of plants which efficiently occupy the space in several layers. The people also obtain their living from diverse sources. These diversities give stability to the village ecosystem. Economic development should as far as possible maintain this diversity.

THE PROGRAMME ON MAN AND THE BIOSPHERE (MAB)

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UNESCO's Man and the Biosphere Programme can, to some extent, be regarded as a follow-up to the International Biological Programme. A number of scientists who participated in IBP have played an important role in the conceptual elaboration of MAB. Furthermore, MAB has been able to take advantage of previous IBP experience - both the achievements and the relative failures - in planning its own structure, content and action procedures.

Nevertheless, from the very beginning several characteristics have differentiated MAB from IBP. First of all, MAB is intergovernmental in structure; secondly, MAB is clearly problem-oriented and the priority areas of research are defined by countries themselves, with special emphasis on the ecological effects of man's manipulation of ecosystems and on the repercussions on human populations and societies of the resulting environmental changes; thirdly, MAB aims to be truly interdisciplinary, integrating such disciplines as geography and sociology in a broad sense with the natural sciences.

Officially launched in 1970 at the 16th General Conference of UNESCO, the MAB programme was outlined in general terms in November 1971, when the International Co-ordinating Council of MAB held its first session and proposed 13 projects of research. After almost three years of international activity and thinking, it appears evident that MAB, now in its implementation phase, is faced with problems of gaps and interfaces: gaps (or semantic and methodological barriers) between fundamental science and applied science, between natural and social science interactions, between research and decision-making processes, between academic and governmental structures; interfaces between natural and man-modified ecosystems, between rural and urban systems, between terrestrial, fresh-water and marine ecosystems. It is in these areas of interfaces that our scientific knowledge seems particularly scanty at present; it is the integrated study of interacting ecosystems in geographic units (watersheds, islands, coastal zones including land and water, landscapes with gradients of progressive man-induced modifications up to man-built environments) which should constitute the basis for management guidelines.

More specifically, the main challenges to be faced and the main goals to be reached by MAB are:

1. To set up a truly world-wide, international programme. While global in scope, this programme should take into account regional and national differences of sociological, cultural and economic character. More explicitly, it should arouse the interest, obtain the support and allow the participation of both developed and developing countries. From an operational viewpoint, mechanisms are envisaged which will facilitate bilateral, multinational, regional and international co-operative efforts. Methodologically, it is indispensable to define research levels of differing complexity and sophistication, so that countries with differing resources and manpower can collaborate and integrate their contributions at different interlinked phases.

2. To relate research to decision-making by a continuous feed-back process. In other words, the areas of research should be influenced by the real priorities in terms of regional and national planning; on the other hand, the research should provide planners with valuable elements on which to base their decisions concerning possible resource management alternatives.

3. To achieve an acceptable degree of comparability of research results, through the adoption of common methodological principles. This tends to be the main shortcoming of any international enterprise. Special attention is being given to this problem during the extensive planning phase of MAB, which includes the preparation of preliminary syntheses of existing knowledge and the pinpointing of crucial topics for research.

4. To integrate different disciplines from the initial phase of conceptualization of the problems, and then in planning and implementing the research and training activities. This does not mean that MAB aims, for instance, to set up well-defined projects of human geography, demography, human biology or sociology; rather, it implies the pervasiveness of this human approach throughout the programme.

5. To strengthen the research programme and make it feasible through the establishment of a parellel programme of training of

specialists in these fields. This requires a new approach to the preparation of scientists able and willing to participate in multidisciplinary research teams. As regards training of tropical ecologists - one of the highest priorities - activities in MAB are concentrated in tropical countries themselves, as a necessary step towards stimulating the building-up of their own scientific expertise and their own conceptual framework for research.

6. To facilitate the flow of data among participating countries and scientists, considering ways and means for overcoming linguistic, cultural and economic barriers. Special emphasis is given to the exchange of information, including the exchange of personnel, in transversal trends, such as among countries of the intertropical belt, to take advantage of the greater ecological and sociological similarities of their problems.

7. To provide an effective mechanism for international cooperation among governments, among intergovernmental and non-governmental organizations, as well as among scientists of different countries and disciplines. The need to avoid undue overlap or competitive efforts with other environmental programmes is strongly felt in MAB.

A number of promising results have already been achieved in the aspects outlined above, some gaps are being bridged and the long-term strategies proposed appear to be feasible. Most of the way, however, remains to be opened. Final success depends partly on actions still to be carried out by governments and coordinated by international organizations, but primarily on the extent to which the scientific community appreciates its involvement and its own responsibility in this challenging enterprise.

AUTHOR INDEX