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OPENING SPEECH

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Interest in the long-term observation of vegetation dynamics is increasing and the focus is changing. Early research in Europe was concerned mainly with the history of species migration and vegetation development after the latest glaciation and in peatswamp succession. In German forestry silvicultural handbooks during the 19th century mentioned vegetation change only in connection with stand growth and increment. RUBNER(1952, p.524-525) in his book on the biogeographic basis of silviculture quotes examples of primary succession to forest given by FURRER (1923), AICHINGER and SIEGRIST (1930) and WALTER (1937) hinting their importance for forestry purposes. He concludes:"The dynamic concept which characterizes plant sociology, has much contributed to a deeper understanding of vegetation cover, especially of the forests, but it cannot be ignored, that it (- the concept of dynamics -) easily leads to speculation".

The number of titles in comprehensive cross-sectional reviews may be an indication of the intensity of research into forest succession and dynamics. In the rather comprehensively interdisciplinary review of "Ökosystemforschung" on the Symposium of the Deutsche Botanische Gesellschaft and the Gesellschaft für Angewandte Botanik in Innsbruck, 1971, ELLENBERG in the introductory paper covers succession studies only in a general reference to "Entwicklung von Ökosystemen" on one and a half page (p. 16-17) which concludes that:"not all adjacent ecosystems of gradually changing complexity, or of other features, are connected as parts of a successional series, but may have always been different. Particularly in the Anglo-Saxon and American literature the importance of the successional dynamics has often be overrated" (ELLENBERG, 1973). In the "Festschrift für Heinz Ellenberg" (1983), among 80 papers in parts I and II were only 2 papers devoted to succession in forests:

- the one was by Mueller-Dombois on the die-back in Hawaian forests,
- the other by Jeník on succession on the Polona balds.

Also among the 15 papers of the "IUFRO Urwald-Symposium", (MAYER, 1982) of the Virgin Forest Working Group only 2 papers specifically referred to vegetation development and forest dynamics. The one was by FANTA on the dynamics of forests on the sandy soils in the Netherlands. The other by BUECKING describes the long-time observation in forest vegetation study plots in the Black Forest. Among the 195 titles cited by BOSSEL et al. (1985) in "Dynamik des Waldsterbens" only 3 bore clear reference to the changes of the forest ecosystem and the secondary succession initiated by aerial pollution. The majority of cited papers treated isolated, single processes or referred only passingly to comprehensive change of structure and functioning of the ecosystem as a whole.

The ecological methods handbook by ELLENBERG and MUELLER-DOMBOIS (1974) treats succession, climax and stability in chap. 13 (p. 370-410) which apart from reference to earlier and more biographic or sociological work by AICHINGER, GAMS, TUEXEN, WALTER and WENDELBERGER (l.c. 1974) contains no references to European forest succession research. For some reason, ecological research and especially research into forest dynamics stagnated in Central Europe after a promising start in the 19th century. Static concepts continued to prevail and only recently, more dynamic and system-oriented approaches were adopted (e.g. BOSSEL et al. 1985). This is illustrated by the long survival of the concept of a homeostatic terminal climax state. It is therefore not surprising that the extensive and comprehensive literature review in SHUGART's (1985) recent book on forest dynamics contains only very few references to Central European sources.

One of the reasons for the failure to perceive the very dynamic nature of forest ecosystems lies in the fact that almost the whole of Central European forests are man-made in some way or another and the majority of the lowland forests are first or second generation plantations on formerly deforested, degraded and desolated land.

While research in primary forests showed convincingly the highly dynamic and thermodynamically open nature of the virgin forest ecosystems, the notion of a normal forest being in a sustainable equilibrium persisted among European foresters and ecologists. For example, ELLENBERG (1973, p. 16) assumes that once the climax stage has been reached through a series of instable developmental phases of succession the ecosystem of a virgin forest would eventually achieve a state of equilibrium, i.e. the climax ecosystem would not increase its biomass, but production and decomposition/consumption would be and remain in balance. On the other hand, however, ELLENBERG (l.c. p.26) also refers to the colonization of a clear-felling or wind-thrown area as an example of cyclical or secondary succession which occurs in many forest areas, including the tropics. He states that the primary succession in a forest climate is in basic principles similar to this secondary succession (that would mean, the ideal climax is an ideal and not real), but concedes that there are far too few exact observations on primary forest succession yet available. There has been a somewhat different development of more dynamic and generally more active ecological research in Great Britain, The Netherlands, Scandinavia, and in tropical countries, but this research was understandably more related to grassland, fields, sand dunes, heathland and moors than to forests, except in the tropics.

What are the problems, which have been and are still hindering progress in forest dynamics research?

Firstly, they are philosophical: The Clementsian and the Gleason's views are still not yet sufficiently reconciled in the minds of many natural scientists; forestry scientists in addition have been much preoccupied with the "Normality Concept" of a forest in a state of perpetual equilibrium.

Secondly, they are rooted in the traditional practice of forestry: The normal forest with sustained growth, increment and yield, conforming with yield table standards, is still the prevailing perception of a sustained forest, ignoring the fact that forests and forested landscapes are far from anything near stability and equilibrium, that the so-called "normality" is an ephemeral exceptional state, and that forests are largely indeterministic, highly dynamic and unfortunately unpredictable ecosystems under varied stresses.

Thirdly, there are the new threats: forested land is subject to pollution and destructive use and misuse, as a result to climatic, edaphic and biotic changes to which the forest trees and the forest ecosystems are not adapted and cannot adapt, making eventual catastrophic collapse inevitable, unless the man-made strains cease.

What needs to be done to cope with the problems?

Firstly, to stop drastically, rapidly and effectively the further destruction of resources, media and life support systems by curbing deforestation in the tropics and environmental pollution and degradation anywhere.

Secondly, to develop a better understanding of the natural dynamics of forest ecosystems and their reaction and performance under stress in a variable and changing environment, which does not mean necessarily more, but definitely better research.

Thirdly, to develop forests which are better adjusted, have better self-regulating capability and which can serve man better than many of our present forests, once pollution has stopped and its after-effects have been overcome.

Therefore, the aims of this workshop should be:

- to clarify among ourselves the meaning of succession and forest dynamics in their many facets;
- to discuss the ecological significance and management implications of forest dynamics, diversity in time and space, and biological self-regulation;
- to identify research need, and objectives at the various levels of
  - population dynamics
  - ecosystem dynamics

  and to discuss possible ways and means to achieve them;
- to establish a working group to work out a concept of a programme to guide and coordinate research activities in the field of forest dynamic studies in Western and Central Europe and to maintain contacts with other research groups elsewhere and in other fields;
- generally, to revitalize research into forest dynamics in Europe.

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Invited papers

FOREST SUCCESSION: THEORETICAL CONCEPTS

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Summary

Itself a living entity, the forest implies intrinsic changes and adaptive processes extended in time. Taken as either "the fourth dimension" or "an essential factor", time involves sequence, duration and direction. Within the multitude of scientific approaches, foresters and ecologists views prevailingly refer to the medium section of the respective time and space scales. Clements constituent processes still preserve their valuable message. Differentiation between endogenous and succession is seldom possible due to the combination of driving forces. Adoption of facilitation, tolerance and inhibition models can assist in the analysis of the integrated events. Population ecology elucidates the small-scale spatio-temporal changes, while plant sociology remains a basic tool in explanation and prediction of regional processes.

Keywords: Succession, dimension, driving force, classification.

Introduction

Both in forestry and ecology, definitions of even fundamental terms vary a great deal. This also refers to the two terms appearing in the title of this paper: forest and succession. Forest - conceived as (1) merely a stand of trees, or (2) a mixed biotic community,or (3) an ecosystem including physical factors of the habitat - is a living spatio-temporal entity, a living system par excellance.

Life, generally, implies intrinsic changes, such as birth, growth, life-form, development, life-cycle, death, evolution, life strategy and extinction. Natality and mortality are strictly determined by the gene pool of individual species and play a primary role in the success of the pertinent organism. Growth forms and life cycles decide the participation of forest species in the entire organisational pattern of the ecosystem. Obviously, the most complex tropical coral reefs cannot match a mature temperate or tropical forest in their structural diversity and functional complexity.

Life also implies adaptive reactions toward environmental changes, for example, diurnal and seasonal rhythms, or stochastic fluctuations of life-supporting resources and life disturbing factors. Only a minor part of the adaptive features is reflected in the morphological constitution of forest biota, while the much greater part is fixed at the level of biochemical processes within the cells, tissues and organs.

Perception of time

All changes and adaptations of forest biota occur in various space and time scales, acquire different spatial and temporal dimensions. This variety is reflected in many "organisational levels", e.g., in the molecular, cellular, organismic, population, community, ecosystem or geosystem level. Investigations into these organisational levels are covered by numerous branches of science, while forestry concentrates merely on the middle part of the pertinent time and space scales (see Fig. 1.).

An essential part of the intrinsic changes and adaptations within the forest is usually called "forest succession". Time is the predominant feature of succession and its various aspects must be taken into account. Foresters idea of time quite naturally implies three fairly distinct concepts: sequence, duration and direction. All foresters know that leaf fall follows flushing, decay follows growth, mature trees follow seedlings, spring follows winter, etc., and that they all "take their time". Sequence and duration entail directionality; even common sense assumes that the "arrow of time" has a direction. The film of life is never played backwards" (Kalmus, 1971).

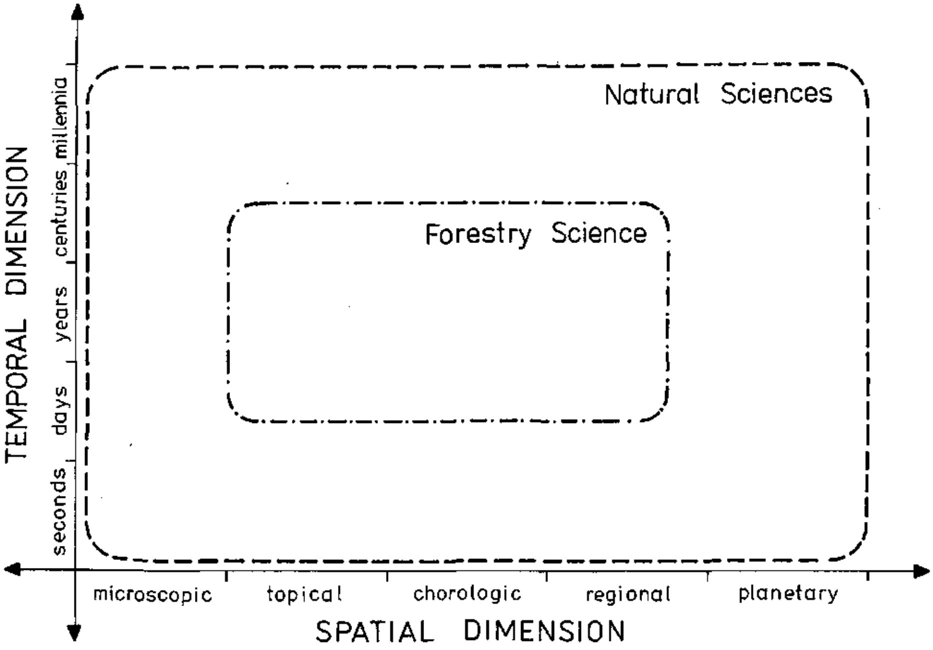


Fig. 1. Delimitation of time and space scales in natural sciences and forestry science.

Sequence, duration and direction of time have enabled a simple division to be made of the most important phenomena in forest dynamics. According to actual "progress" of change, and relevant successive, cyclic and/or fluctuation characters, several basic types of changes may be distinguished. Also the source of change, either exogenous or endogenous, can determine our classification. Duration of the stages, changes or cycles is another criterion that may be useful in basic classification of forest dynamics. In Fig. 2 classification of dynamic phenomena has been expressed both in iconic and mathematical way.

Perception of forest alterations belong to the common experience of inhabitants of primeval forests. Utilization of the forest plants, soils and animals necessarilly required destruction of a certain part of the forest, and induced its restoration and regeneration. The Mayan civilization rested upon the milpa system, a kind of agro-silviculture whose "successional phenomena" were incorporated in the whole management (Alcorn, 1984). Similar knowlege of forest succession is well anchored in the life of other tropical nations performing various kinds of shifting cultivation. Native people usually distinguish between forest biota related to regrowth of natural clearings or man-induced gaps, and biota belonging to the mature forest.

Search for unifying concept

A scientific approach towards forest dynamics developed only in the second half of the 19th century, and in the first decades of our century. Interest in the development and evolution was inspired by Darwin's "Origin of species ..." (first published in 1859) whose influence can be traced in all natural sciences. One of Darwin's chapters is called "On the geological succession of organic beings" and deals

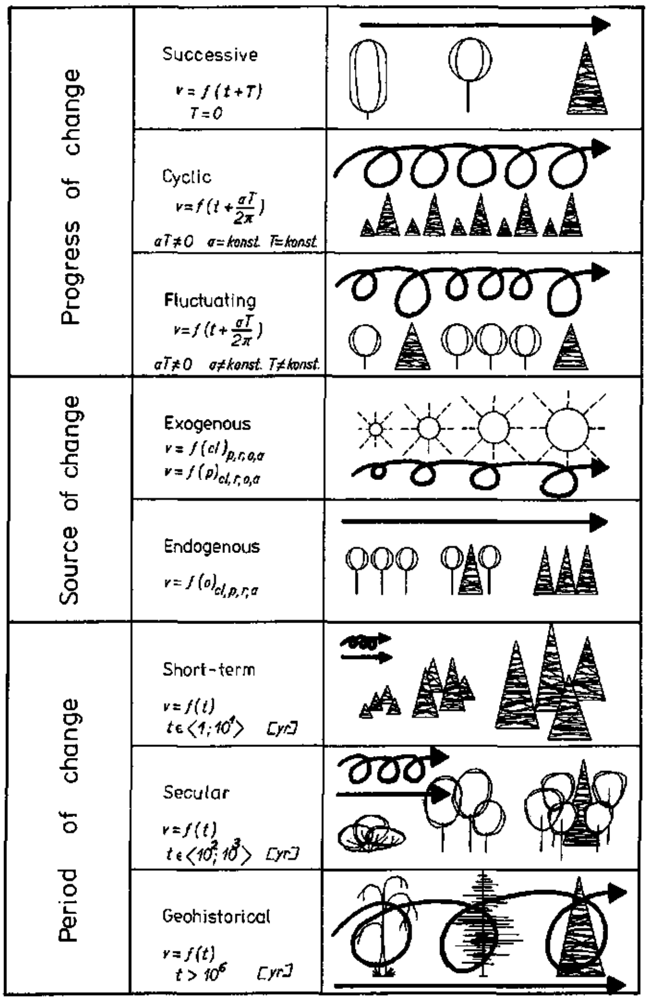


Fig. 2. Classification of changes in nature according to three criteria.

with general rules of appearence and disappearance of species within a geological time scale. The rigidity of natural phenomena was shattered, and scientists started searching for changes and their causes. Developmental aspects can be seen in the early monographs and textbooks of plant geography and ecology, e.g., in the works of M. Kerner, A. Grisebach, R. Hult and E. Warming. Towards the end of the 19th century, organic deposits found in peat bogs were used to define developmental stages of European vegetation. In the same period, silviculture and forest management achieved a notable progress reflected in the early textbooks by A. Cieslar, H. Mayr, K. Gayer and G.F. Morozov. These books treat in detail the processes and methods of stand regeneration, and contain a number of observations related to forest succession. Morozov, for example, clearly distinguished between the forest "pioneer species" (birch, alder, sallow) and forest "edificatory species" (spruce, oak, etc.). In his summarizing work "Utshenye o lese" (German edition only in 1928 Morozov discussed many details referring to internal driving forces of what he called "replacement of forest species".

The term "succession" definitely anchored in the ecological terminology only after the publication of two monographs compiled by F.E. Clements (1916, 1928) Clements idea that the mechanism producing succession was composed of six essential processes was accepted by numerous workers all over the world, the foresters included. His approach was so pervaded by orderliness and laced with biological intuition that it has remained represented, in essence, in basic papers analysing the present state of succession theory (MacMahon, 1980). The above mentioned six constituent processes of succession were called nudation, migration, ecesis, reaction, competition, and stabilization. The first four processes make the so-called initiation phase while competition represents the continuation phase, and stabilization equals the termination phase. With regard to our Fig. 1, the influence of Clements theory has covered mainly the regional and choric space scales, with minor influence on the detailed topic examinations. The climax theory, developed within the vast stretches of the North American continent, originally necessarilly neglected small-scale patterns encountered in detailed studies of Central and West European landscape. But the theory was immediately employed to explain the postglacial development of the broad and extensive zones in the northern part of Euroasia incorporating rather uniform lowland areas.

For a long period, the terms "succession" and "climax" functioned as unifying words in the tangle of ecological problems derived from dynamics and processes in nature. However, these terms have never gained a monopoly in ecology. It may be worth while of mentioning that the selection of Clements writings (compiled and edited by B.W. Alfred and E.S. Clements in 1949) was published under the more general title "Dynamics of vegetation". And to jump right into the present time, H.H. Shugart (1984) preferred a title "A theory of forest dynamics" leaving the term "succession" in the subtitle. This notable shift in the unifying term is also reflected in the name of our workshop, which enables its participants to treat forest processes and changes in a much broader way. Though Clements "succession" was never restricted to plants, in the minds of plant ecologists and foresters it usually shrank to developmental processes referring to woody plants and herbaceous vascular species.

Holistic approach

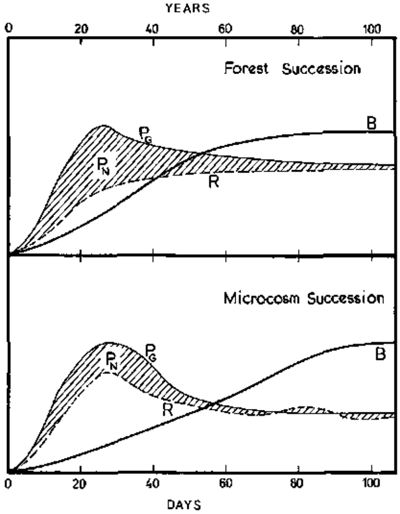
If applied to the whole forest ecosystem, succession must be treated as a holistic phenomenon covering all structural and functional phenomena, or as a set of successions referring to various life forms. For example, forest entomologists have described a well defined succession of flies invading the carcasses of forest animals; four stages of fly inhabitants are usually distinguished on a dead body lying on the forest floor. Complexity of structural and functional changes has brought about separate labelling of individual processes, stressing either structure or function. For example, the concept of "sylvigenesis", widely used by R.A.A. Oldeman in tropical forests, refers to morphological processes by which forest architecture is built, in other words, to the processes of forest-making corresponding to morphogenesis of individual plants (Hallé, Oldeman, Tomlinson, 1958). Though very much morphological, the approach of the above authors has proved to be very fruitful and surprisingly successful even in the period of sophisticated measurements and mathematical modelling.

In the studies of forest dynamics, foresters and ecologists can fortunately exploit the long-lived, sizable and immobile organisms called trees. Everyone that has studied eocystems of less bulky and more mobile organisms, such as spring-heads, lakes, streams, coral reefs, grasslands or steppes, will appreciate the chance provided by the tree growth-form and tree-ring anatomy. Of course, tropical foresters miss the annual rings that reflect the mid-term dynamics of the temperate forest in a spectacular way. On the other hand, mature forest requires decades and centuries for its differentiation and can hardly serve as a suitable experimental object. Therefore, many theoretical concepts for succession have been developed in short-term ecosystems such as old fields, river banks or sand dunes. Some of the comparisons have provided new insights into the obscurity of forest dynamics, but most of them can be even misleading.

Odum (1971) dared to compare the development of energetics in a forest described by Kira and Shidei and a laboratory microcosm studies by Cooke. This comparison (Fig. 3) shows certain general trends in production, respiration and biomass accumulation during both the forest succession and microcosm development. However, in greater detail, specific phenomena coupled with the forest composition will necessarily prevail. This can be clearly shown in Fig. 4 redrawing the results of observations from an oak-pine forest at Brookhaven National Laboratory, U.S.A., where succession had to be divided into the herb, shrub and tree stages that were clearly reflected in the production, biomass and species diversity. If all living components including micro-organisms and vagile consumers had been taken into consideration, the models of energy and information flows would have been still more complicated and would have been difficult to interpret adequately.

Driving forces

For many years, foresters and ecologists have been interested in the forces driving the gradual exchange of biota and causing the gradual alteration of physical features of the habitat. Two categories of forest dynamics are frequently distinguished under a number of parallel terms: (1) Endodynamic, autogenic or endogenous succession is supposed to be driven either by antagonistic or mutually positive relationships between biota occupying the site; within the forest community the biological role of dominant herbs, shrubs and trees is particularly



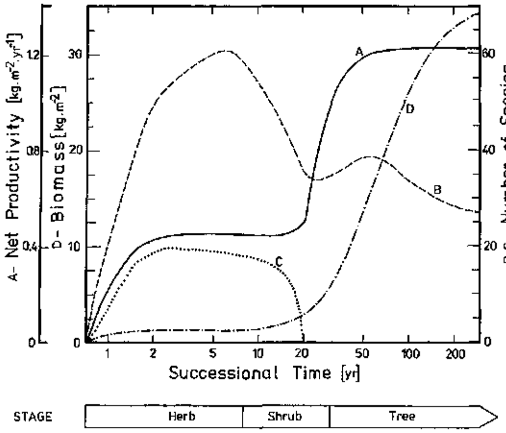


Fig. 3. Comparison of the energetics in ecosystem development of a forest and a laboratory microcosm (after E.P. Odum, 1971); P_G- gross production, P_N - net production, R - total community respiration, B - total biomass.

Fig. 4. Productivity (A), diversity of forest plant species (B), diversity of exotic species (C) and biomass (D) in the oak-pine forest Pinus rigida, Quercus ilicifolia, Q. coccinea, Q. alba at Brookhaven National Laboratory, Long Island, U.S.A. (after B. Holt and G.M. Woodwall sec. Whittaker, 1979).

appreciated. (2) Exodynamic, allogenic or exogenous succession is governed primarily by changes in external physical features of the habitat and effects of physical stressors of the environment.

In a detailed view and practical forest research, these two categories of succession could never be clearly separated, though the idea of complementary "biotic" and "abiotic" factors has been accepted as a comfortable approach. Some ecologists, e.g. Moravec (1969), have suggested that the term "succession" should be reserved to its very original meaning for the endogenous biotic processes only. The same author has proposed that all the other kinds of vegetation dynamics should be called "adaptive changes". Again, this proposal cannot be easily accepted in practical research of forest dynamics where various biotic and abiotic processes interlace. Obviously, any simplification of ecological phenomena produces difficulties in the incorporation of new details recognized within the integrated research of forest ecosystems. Recent models of driving mechanisms producing changes in ecosystems are becoming increasingly sophisticated and tend to distinguish between the driving and disturbing forces, and between mass-energy flows and information flows. Fig. 5 presents one of these iconic models.

Some of the models covering forest succession tend to emphasize the mass-energy budget, an approach greatly enhanced by the influence of E.P. Odum and H.T. Odum, and supported by the International Biological

Programme and Unesco/MAB projects. The classical studies of birth-death pattern in the course of regeneration and rejuvenation in woodlands to revive in contemporary population studies covering not only vascular plants and vertebrates, but also less known and inconspicuous life forms, such as soil micro-organisms, fungi, insects and other invertebrates.

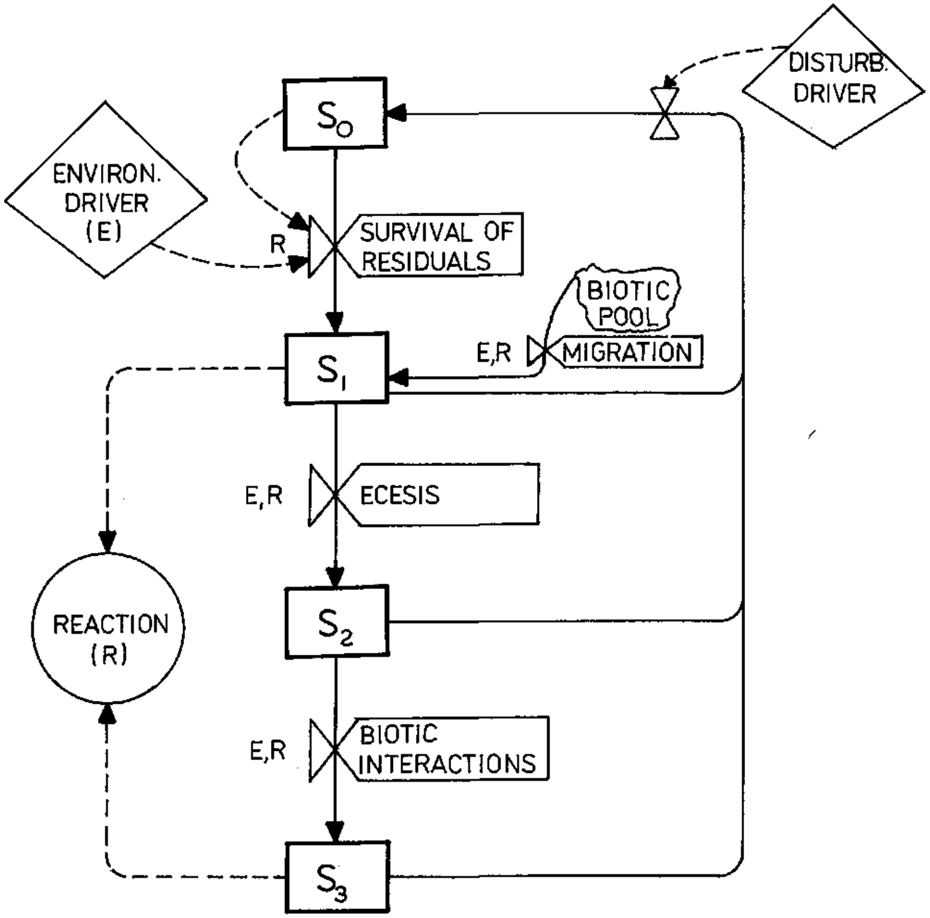


Fig. 5. Model of mechanisms producing the change of an ecosystem; S_o ... S_3 are states of the ecosystem at any instant; full line arrows show mass-energy flows, dashed arrows show information flows. Letters next to control gates replace dotted lines from that point to the control for the sake of graphic simplicity (adapted from MacMahon, 1980).

ebrates. The taxonomic approach towards forest dynamics is far from being overcome and obsolete. The species, as the best carriers of genetic information, still remain the best and straightforward indicators of forest dynamics, and their qualitative message can be easily translated into a quantitative record. Using the species composition, some models of forest succession have managed to predict successive replacement of species and the respective periods of their presence in areas affected by dominant physical factors. Fire as an important factor of this category, has brought several foresters to the elaboration of useful models that enable to predict both floristic and population changes in stands affected by fire. Fig. 6 is redrawn from Kessel and Potter (1980) and represents one of these floristically based models.

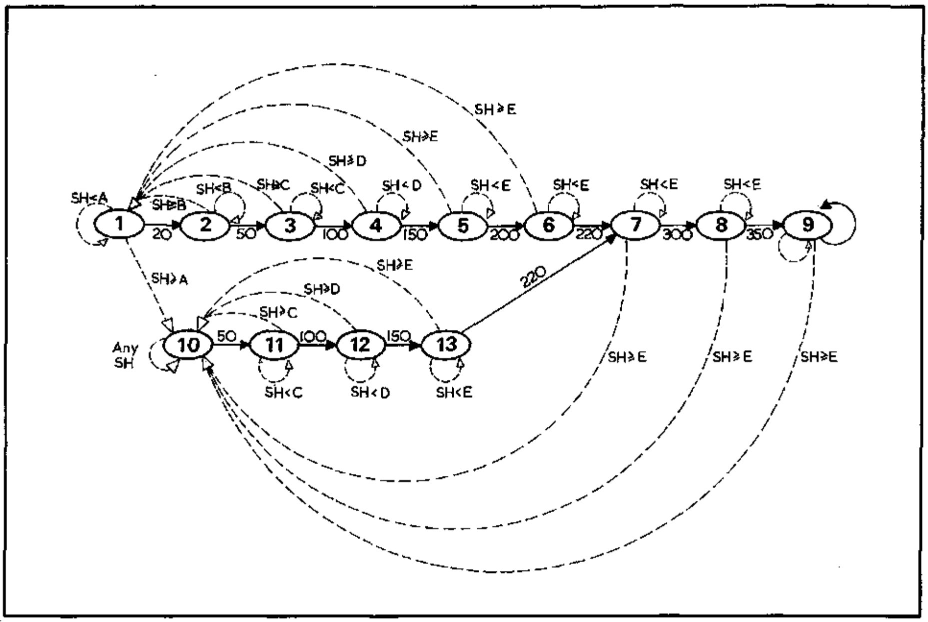


Fig. 6. Postfire succession model for Lewis and Clark National Forest, Montana, U.S.A. Transitions in the absence of further disturbance are determined by stand ages (years) shown on the solid arrows; transitions due to further disturbance are a function of stand age and fire scorch height; the critical scorch height values (A ... E) vary between 1.8 to 13.7 m and are given by the authors in a separate table. Also the species composition of each of the 13 successional states is defined for various habitat types in accompanying tables. After Kessel and Potter (1980).

Conceptual models

In order to explain the details of forest dynamics, some authors have diverted from Clements model of driving forces and have suggested a new approach. Connel and Slatyer (1977) explain the sequence of species in vegetation dynamics by three ways: (1) Facilitation model is a kind of dynamics based on "early succession" species and successive modification of the environment that is necessary for the following "late succession" populations. (2) Tolerance model explains the dynamics by parallel occurrence of set of species whose composition does not relies on preparatory work of the "early succession" species. (3) Inhibition model represents a case in which the site is occupied by certain early invaders that have retained their place and check the penetration of new invaders until their own individual decline or damage. In a chapter called "Competition versus facilitations" Shugart

(1984) reduced the number of the above mentioned models to two more or less opposing concepts. The forest reality strongly supports this reduction.

The present ecological literature seems to be divided into two main streams with regard to the ecosystem structure and succession theories. One of these streams emphasizes a holistic approach to biotic communities and ecosytems. The other stream stresses the individualistic population approach relying on detailed observations of life-forms, life-cycles and life strategies of individual components. In Europe, due to the influence of traditional plant sociology, the holistic approach seems to be more represented than in countries following the heritage of Clements in North America, and particularly in Great Britain remaining under the influence of J.L. Harper. Many compartmental models of forest succession, worked out by plant sociologists, leave aside that plant communities represent only a fraction of the ecosystem totality and thus are unsufficient for the prediction of the diverse large-scale phenomena and processes in which contemporary forestry seems to be involved. A fully integrated ecosystem approach still seems to be far from materialisation. We must, therefore, accept the methods stressing the role of individual populations of trees or other dominant organisms, as developed by Drury and Nisbet (1973), Glenn-Lewin (1980), etc. As shown by Shugart (1984), some computer models can simultaneously consider the role of individual trees within the context of the whole ecosystem.

Though more pragmatic in their views, foresters in Europe have developed many pioneer notions and sophisticated theories related to the forest dynamics and forest management. On the other hand, European ecologists have kept informing the foresters on the broader context of ecosystem research. Both branches of research have become complementary and will remain so, hopefully, in the future. Also, the experience with either temperate or tropical forest dynamics has reinforced each other and has rapidly expanded the common pool of useful information. The unidirectional stream of information from the temperate countries towards the Tropics has changed into mutual exchange of information and experience among foresters all over the world.

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METHODS OF FOREST DYNAMICS RESEARCH

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Summary

Forest dynamics research can be performed on different levels of complexity (population, community, ecosystem). A method cannot be designed to be appropriate on all levels. Examples of different methods of forest dynamics research are described and elucidated on case studies. Methods investigating man's past interactions with forest ecosystems are also included. It is an advantage when several levels of complexity are investigated in field studies and, consequently, more than one method is used.

Keywords: Methods, forest dynamics, written evidence, vegetation maps, air photographs, dendrochronology, demography.

Introduction

A forest is an ecosystem, with its characteristic organisms, soil properties and its own climate. The importance of the different organisms cannot be judged directly from the quantity in which they occur, or from their different sizes. Probably different organisms - ranging from soil micro-organisms up to the tallest trees - are of different importance during different successional stages. However, forest ecologists commonly concentrate on the trees. This bias is understandable from several points of view. Trees are long-lived. According to Harper and White (1974), tree individuals have been estimated to ages over 5000 years, though ages over 1000 years are exceptional. Even if there is evidence that grass species, herbs and vascular cryptograms can reach considerable ages (Oinonen, 1967; Tamm, 1972 a, b; Harper and White, 1974; Callaghan and Emanuelsson, 1985), trees are generally the oldest.

Ecologists focus on trees is also reasonable from the point of view that during their whole lifespan the trees change their roles in an ecosystem more than the field-layer species. A tree starts as a small shoot in the field-layer among thousands of other life-forms and grows into a large tree dominating the community. Even if field-layer species also reach considerable ages, few of them exert such an influence as the trees on the whole ecosystem. Lastly, in boreal, boreo-nemoral and nemoral (temperate deciduous) regions the annual growth of trees is distinguishable in the wood as annual rings or through budscars. In many herbs there are also possibilities to make age-determinations by counting annual parts of rhizomes or other parts (Persson, 1975; Callaghan, 1980; Backeus, 1985). However, dead material often disappears if it is not preserved in anaerobic environment, e.g. peat, which makes it impossible for scientists to use field layer species in retrospective investigations. Forest trees are a storehouse of information about their history, and the history of the ecosystem to which they belong.

Forest dynamic research can be performed on different levels of complexity - the population level, the community level or the ecosystem level - and the methods used can be grouped according to this division.

Other possible categories are a) historical methods including written sources, old maps and other historical material, b) retrospective methods including dendrochronology, pollen analyses, comparisons between vegetation maps and different kinds of photographs, c) prospective methods (simulations), d) dynamic methods, e) static methods and f) experimental methods. However, not all methods can be categorized simply. In this paper I have made a practical division based on the particular case-studies I have chosen to discuss. (Several further methods are not discussed e.g., analysis of micro- and macrofossils, architectural analysis (Hallé et al., 1978) and simulation modelling (see Prentice, this volume)).

Different research methods should preferably be used together. Ecosystem dynamics may depend not only upon the present state but also on "the memory" of the ecosystem (Van Hulst, 1980) as a result of, e.g., earlier disturbances, seed banks, age distributions, land use, etc. Methods investigating man's past interactions with the ecosystem are therefore included in this review. The main "disturbances" in Scandinavian forests have been tree-felling storms (Sernander, 1936), forest fires (Zackrisson, 1977), attacks by insects (Tenow, 1972) and changes in land-use by man. Nowadays forest fires are controlled and, instead, man's use of the forest has changed and will increasingly change the forested landscape to even-aged stands which are partly fertilized and where the natural processes are strongly controlled. Grazing by moose (Alces alces) (Bergström, 1981) has also increased during recent decades. The changed chemistry of the atmosphere and precipitation are other new factors. Forest dynamics, in a naturally and artifically changing environment, are highly complex and need to be studied with a wide range of techniques.

Discussion of methods

Written evidence

In his valuable book, Ancient Woodland, Rackham (1980) mentions place-names as "the earliest useful documentation" but also stresses that "their interpretation involves many pitfalls".

Important sources are different kinds of maps with attendant descriptions. In Sweden, maps are available from the early seventeenth century and onwards. The maps were prepared for several reasons, e.g. to assess taxes, to partition land in different ways or to solve disputes about boundaries. Fig. 1. shows an example of a map from Vardsätra nature reserve, a deciduous forest which has been wholly protected since 1912. Different parts of this forest have been used either as a hay-meadow, as arable fields, or as a woodland pasture. A superficial analysis of the forest cannot assess the different land-uses in the same way as a closer analysis. The former arable fields are now part of the forest and birch trees are more common here. Unexpectedly few trees have grown up on the abandoned fields. Instead, hazel shrubs are common. The descriptions on the map or associated with the map frequently include notes on the vegetation, especially about trees and shrubs. Other examples of maps from relatively small areas, only a few km^2, are given for instance by Ryberg (1971), Larsson (1971) and Haeggström (1983).

Other documentary studies have shown changes over larger areas. Malmström (1938) used material from different archives and was able to show forest changes from about 1650 up to 1920 in four different maps of Halland (area ca. 4700 km 2) in Southern Sweden.

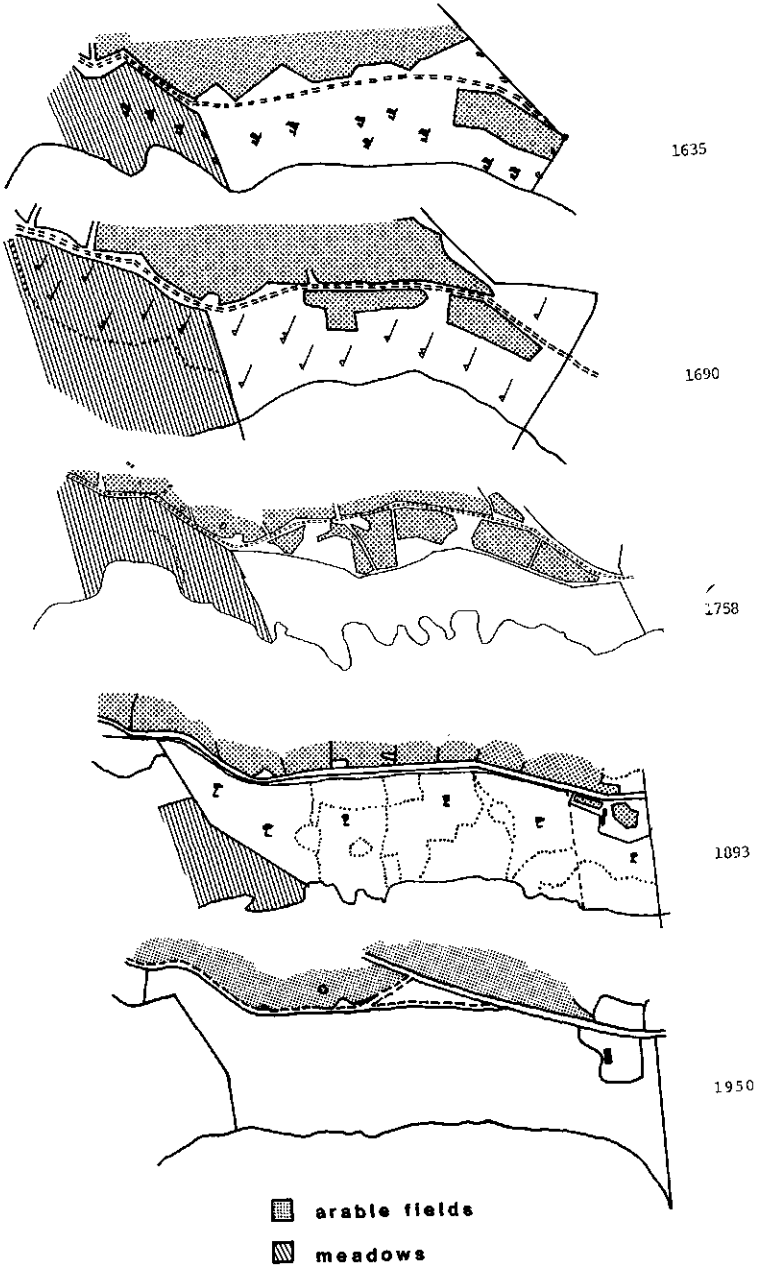


Fig. 1. Landuse maps of Vardsätra nature reserve from different times. The reserve was established in 1912. The area of the reserve is shown on the last map. The main area was probably a wooded pasture, the last grazing being in 1912.

Comparison between photographs from different time periods

Several publications have demonstrated how to analyse old pictures taken for other reasons than vegetation studies in comparisons with new photographs taken from exactly the same place.

Pettersson (1958) used this technique to show changes in the tree and shrub populations from several different localities on the island of Gotland. Kullman (1982) discussed the tree limit on a mountain and used photographs from 1919 to compare them with the situation today. This comparison clearly shows an increase in the number of trees above the former forest limit and up to the top of the mountain. Waldemarson Jensén (1979) used old photographs from 1899 and 1922 in evaluating successions in a delta area in North Sweden, including changes in shrub and tree communities. She was able to show both progressive and retrogressive successions.

Hastings and Turner (1966) used photographs from the end of the last century which showed changes in an arid and a semiarid region in the United States. They were able to count the numbers of individuals on some of the old photographs and, while comparing them with actual figures, they could estimate the reduction in numbers. In some instances they made a prognosis of further development.

To comment on the changes in Vardsätra nature reserve, Sjörs (1964) used photographs from two different occasions. This area was grazed up to 1912 and had the structure of an open deciduous woodland at that time. Ten years later the number of shoots in the hazel stools had increased considerably. Nowadays the hazels have decreased depending on the dense tree cover (Hytteborn, unpublished data).

Vegetation maps and air-photographs

Vegetation dynamics can be studied by remapping. In this situation air-photographs are a good help. This is probably more obvious in studying primary successions than secondary ones. If already the first map was made with the aim of studying vegetation dynamics, the precision may be fairly high. Otherwise there are limited possibilities to make a good comparison.

Table 1. Number of species in the field layer in 1904 and 1976-78 in three different plots on Skabbholen, Sweden. Plot I (see map from 1904) was an open meadow in 1904, but overgrown by trees in 1976-78. The figures from a nearby place, still open, are given in parentheses; In 1904 plot IV was a meadow with Sesleria coerulia, in 1977 it was covered by trees, mainly alder. At both occasions plot V was an ash stand.

	PLOT I	PLOT IV	PLOT V
Number in 1904	44	34	37
Number in 1976-78	18 (51)	31	30
Common both years	1 (14)	6	23
Disappeared since 1904	43 (30)	28	14
New in 1976-78	17 (37)	25	7

Fig. 2. shows two maps of an island in the Baltic, mapped and remapped with an interval of 80 years. The first map is rather sketchy. The second map was made by crossing the area on foot at regular distances and noting each time when a border between selected types was passed. On the reproduced map the number of types has been reduced in order to coincide with the map from 1904. In addition to this field investi-

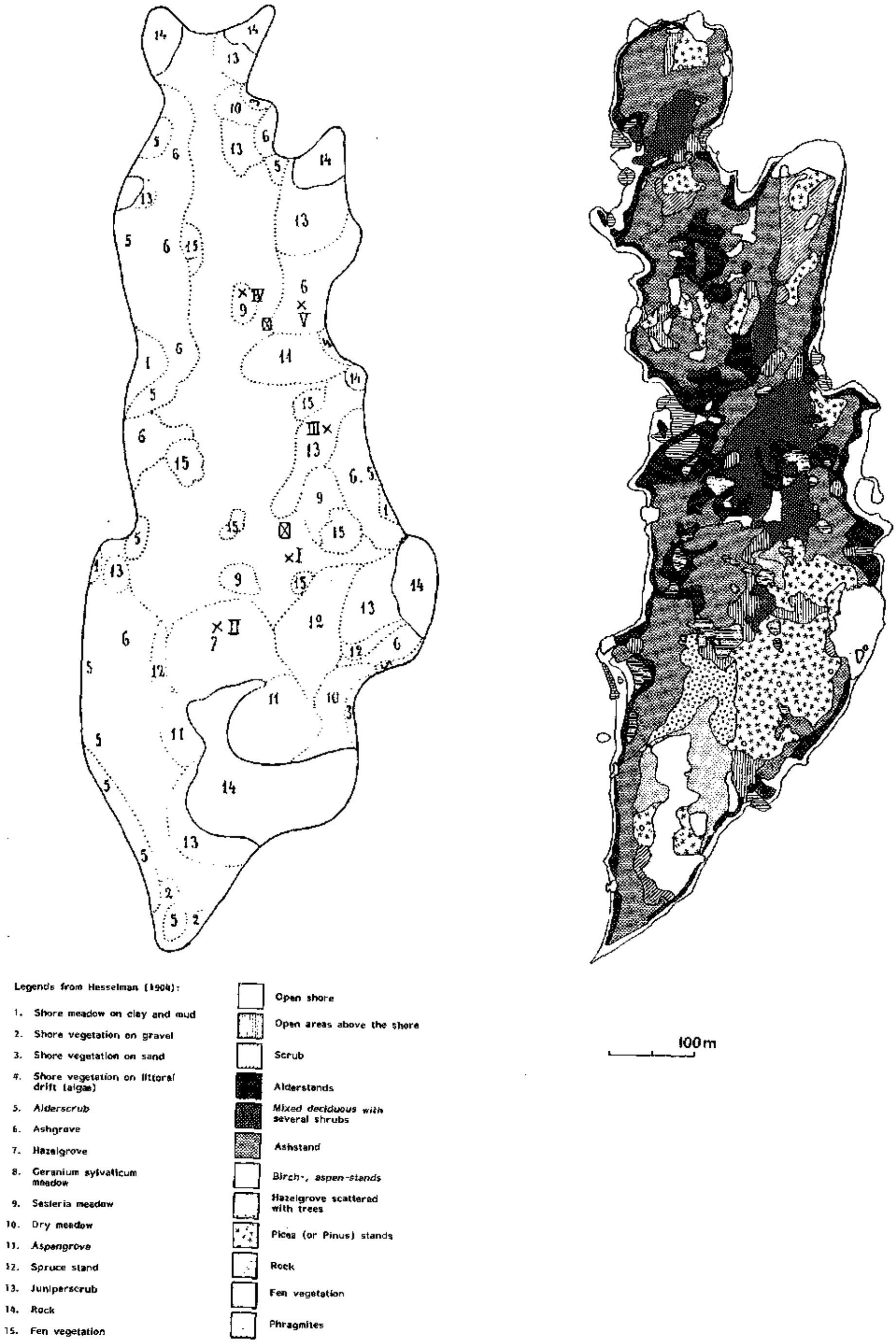


Fig. 2. Vegetation maps of Skabbholmen, an island in the Baltic. The first map from Hesselman (1904) is rather sketchy. The second is largely based on field investigations.

gation, air photographs from 1939 and onwards were also used. It was difficult to distinguish the different deciduous forest types in black and white air photographs.

Only a few open areas above the shore are left. These are dry places, mostly on sand, with thick grass cover. The hay-meadows with scattered trees have changed to either Fraxinus excelsior, Alnus glutinosa or mixed deciduous stands, depending on the groundwater conditions. Most of the Juniperus communis stands are now overgrown by spruce. The wet meadows with Sesleria coerulia have completely disappeared. Stands of spruce and ash are the most stable types. Table 1 gives some figures for changes in the field-layer in three plots recorded in 1904 and localized with high precision again in 1976-78. The time interval between the two recordings is obviously so long that it is difficult to draw general conclusions. In plots I and IV several different stages may have passed. These plots have changed considerably but the ash stands have remained fairly stable.

In a study of a dune system Van Dorp et al. (1985) used air-photographs from three periods and vegetation maps from two periods. From these, they reconstructed five vegetation maps on a uniform scale. They placed a grid system over these maps, calculated transition frequencies between the chosen vegetation types, and arrived at conclusions about the directions of the successions.

Dendrochronology

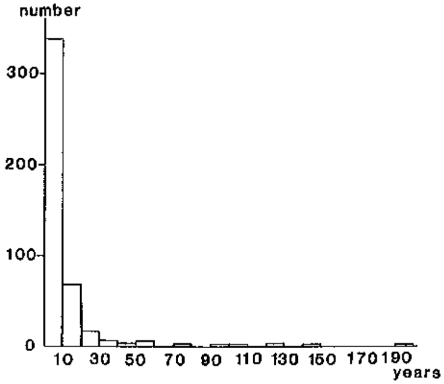
The history of a tree is partly inscribed in its annual rings. If the number of annual rings at the base of a tree are carefully counted, the germination year can be determined rather precisely (Zackrisson, 1978; Cramer, 1985; Van der Maarel et al., 1985a). Henry and Swan (1974) reconstructed the development of a forest stand from 1665 to 1967 in New Hampshire, using dead material such as fallen logs and stumps as well as core datings from living trees. Zackrisson (1977) used both dead and living trees to cross-data the fire-scars and established the former mean interval between forest-fires in a continental area in northern Sweden to ca. 80 years. These rather frequent fires have a decisive effect on the vegetation types which, according to Zackrisson, cannot be regarded as edaphic climax stages.

Measurements of the annual rings of all trees in an area over a longer period can show the development in a quantitative way. Whittaker and Woodwell (1969) combined such measurements with dimension analysis and were able to reconstruct the change in biomass of each species over a fifty-year period after a fire. The shrubs had a peak about 10-20 years after the fire after which the tree species took over.

Sernander (1936) showed that storm-gaps have an important role in the regeneration of forests. He estimated that the frequency of tree-felling storms in each forest stand in the county of Uppland was at least 5 per century. In gaps, Sernander showed that the regeneration could both occur from dwarf-trees - old but small individuals with a retarded growth in height and with very narrow annual rings - and from seedlings (see also Hytteborn and Packham, 1985). Sernander set up the hypothesis that the primaeval forest, Fiby Urskog, was severely damaged by a storm in 1795. Others were of the opinion that the forest had been a wooded pasture in the eighteenth century (Hesselman, 1935). The storm has been clearly documented in many forestry reports and also in paintings (cf. Rackham, 1980, p. 15). Timber from trees felled by the storm was used in building houses. Sernander showed that old trees had had a dwarf-tree stage with very narrow annual rings inscribed in the centre, and with a growth increase after 1795. Fig. 3. gives one example, where the increase in radial growth after 1795 is distinct.

Fig. 3. Increment core of a mature Norway Spruce (Picea abies). The tree was over 210 years old, 28 m tall and had a diameter at breast height (1.3 m) of 38 cm. Note the marked increase in radial increment values immediately after 1795, the year of the great storm.

Hytteborn et al. (manuscript) give an example where the age distribution of all individuals is used in a dynamic study. The age distribution of a nearby area in the sub-alpine birch region with a few scattered Picea abies shows a remarkable pattern with many individuals below 20 years (Fig. 4a.). A few of the older birch trees show a significantly reduced growth in 1965-1967 (see Fig. 4b.). No such reduced growth is found in the radial increment of spruces in the same plot. According to information in Tenow (1972), the start of an outbreak of Oporinia autumnata was observed in 1964. The larvae killed most of the birch trees. Only a few of the attacked trees survived but with reduced growth during the years of the outbreak. The regeneration of birches started after the attack.



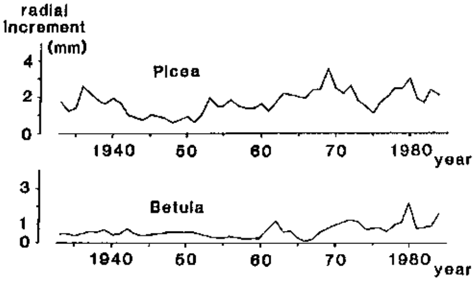


Fig. 4a. (left). Age class distribution from a 20x20 m plot in the subalpine birch forest near Kvikkjokk (unpublished data from Verwijst and Hytteborn).

Fig. 4b. (right). The mean radial increment in five birches and in two spruces. Note the reduced growth in 1965-1967 in the birch trees.

Static and dynamic approach; multivariate methods

To judge successional directions from recordings of different plots at one time is a common method, perhaps more common than a dynamic approach. Several authors have emphasized the difficulties with such a static approach, e.g. Austin (1977, 1981). There is an uncertainty whether the plots really represent the change with time because of heterogeneity in space, both biotic and abiotic. Van der Maarel et al. (1985b.) demonstrated a considerable multiple pathway between 1959 and 1980 for a dune system. Also Fig. 2. shows different successions from a common origin.

On a seashore with a steady shore displacement, there is great probability that the different zones upwards in a smooth topographical gradient also present the different stages in a primary succession. The vegetation change here is accompanied by a change in the abiotic environment, with decreasing ground water level and increasing content of organic matter in the soil. Fig. 5. is an example in which both the static and the dynamic methods have been used and these combined approaches are represented in an ordination (Hytteborn and Cramer, 1985). Twenty adjacent plots (1-20 in Fig. 5.) situated from the shoreline up to the forest were recorded. The samples in the ordination diagram are distributed along axis 1. The plots were recorded on two occasions with a six-year interval and the arrows in the diagram mark the change. The floristic composition in the lower quadrats has changed in the direction of the main successional sequence. In contrast, the upper quadrats have changed in another direction, probably due to a high water with erosion as a consequence. The method, detrended canonical correspondence analysis (DCCA) (Ter Braak, 1985), also gives the position of species in the diagram and the direction of the environmental gradients. Elevation has nearly, but not exactly, the same direction as the general gradient of floristic change.

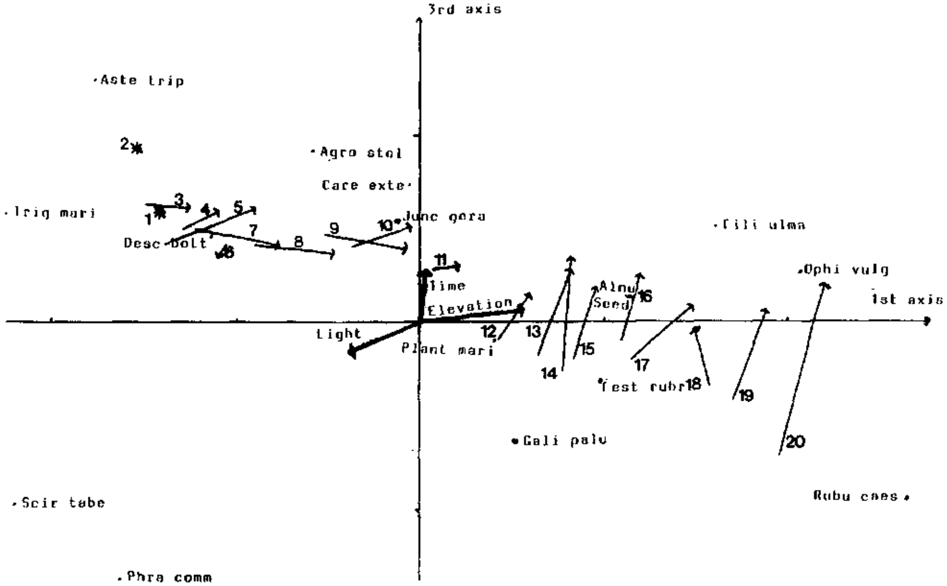


Fig. 5. Ordination biplot from DCCA showing the position of 20 vegetation samples. The same plots were recorded six years later and the floristic change is shown by arrows. The biplot also gives the position of a few major species and directions of environmental variables.

Demography, age-state and size distribution

During an individual's development from a seedling to a mature tree the requirement changes. Grubb (1977) emphasized the importance of the regeneration niche and this concept was widened by Cramer (1985) to the establishment niche, then including species with predominantly vegetative propagation. When regarding dynamics in forests as changes of numbers of individuals and changes in the share occupied by each species in the total population, it is necessary to investigate all stages in the development.

The chronological age is often considered as an important characteristic and is used in demographic studies. However, for many species it is not possible to age-determine individuals and for others the stages in the development are not simply correlated with age. Another possibility is then to use the concept "age state" (Rabotnov, 1969; Gatsuk et al., 1980), implying that different morphologically distinguished phases are used irrespective of age. In the example given below I have used different height-classes instead of age states. Height is one of the criteria given by Zaugolnova (in: Gatsuk et al., 1980) in distinguishing the different age states in *Fraxinus excelsior*.

The survivorship for cohorts of *Ulmus glabra* and *Fraxinus excelsior* show about the same shape. The seedlings have a rather high mortality during the first years (the four lowest curves, Fig. 6.). The curves are drawn from observations in permanent plots from 1978 and onwards in the dense deciduous forest at Vardsärta nature reserve. In 1978 all shoots of the two species below 0.5 m were age-determined. This was only possible up to five years of age. The survivorship of shoots over five years of age gives a straight line in both species (the two uppermost curves), indicating constant mortality. No differences can be seen between the two species. In both species, shoots in this height-class can reach considerable ages, between 50-100 years, and most of the shoots from 1978 were at least older than the five years and are thus now (1985) older than thirteen years.

A survey in plots regularly distributed over the forest show that ash is more common than the other species in the lower height-classes (Table 2.). *Ulmus* is represented by many individuals in the lowest height-class.

Table 2. The number of shoots per ha in different height classes in Vårdsätra nature reserve, Sweden.

	< 0.5m	0.5-1.3m	1.3- ca 4m	> ca 4m
Acer platanoides	5000	240	54	14.3
Betula verrucosa	0	0	0	34
Fraxinus excelsior	88000	2000	860	247
Populus tremula	160	60	12	0
Prunus padus	1100	940	680	65
Quercus robur	0	0	0	4
Sorbus aucuparia	0	4	29	56
Ulmus glabra	34000	770	696	374

Combining these facts with the dynamic survivorship curves for seedlings and small saplings with no differences between *Fraxinus* and *Ulmus* the hypothesis that ash should be the dominant in the future could be put forward.

Since the tree layer was investigated in 1912 and on several later occasions, it is possible to check whether this hypothesis is correct. Fig. 7. shows numbers and basal areas of the most common tree species in a 20x110m profile in the forest on four different occasions. Even if the number and the basal area of ash increased from the grazed situation in 1912, it is obvious that elm will be the dominant tree species in the future in spite of a much lower number in the field layer. Conclusions from size distributions alone must be very cautious and preferably supported by evidence obtained from other methods. The light requirement for Fraxinus excelsior in what Zaugolnova called "immature state", increases sharply (Zaugolnova, in Gatsuk et al., 1980). In a dense environment it gives a higher mortality of ash in the high shrub layer and also in the low tree layer than in elm.

Table 3. Some characteristics of small individuals <0.5 m of Fraxinus excelsior and Ulmus glabra in a dense stand. The length measurements are from a larger sample than the rest.

	Current shoots		Leaves per plant	
	length (mm) 1977	weight (g)	number	weight (g)
Fraxinus excelsior	8.7 ± 1.3	0.058 ± 0.018	4.12 ± 0.52	1.44 ± 0.29
Ulmus glabra	16.8 ± 1.2	0.073 ± 0.018	9.52 ± 1.53	0.77 ± 0.18

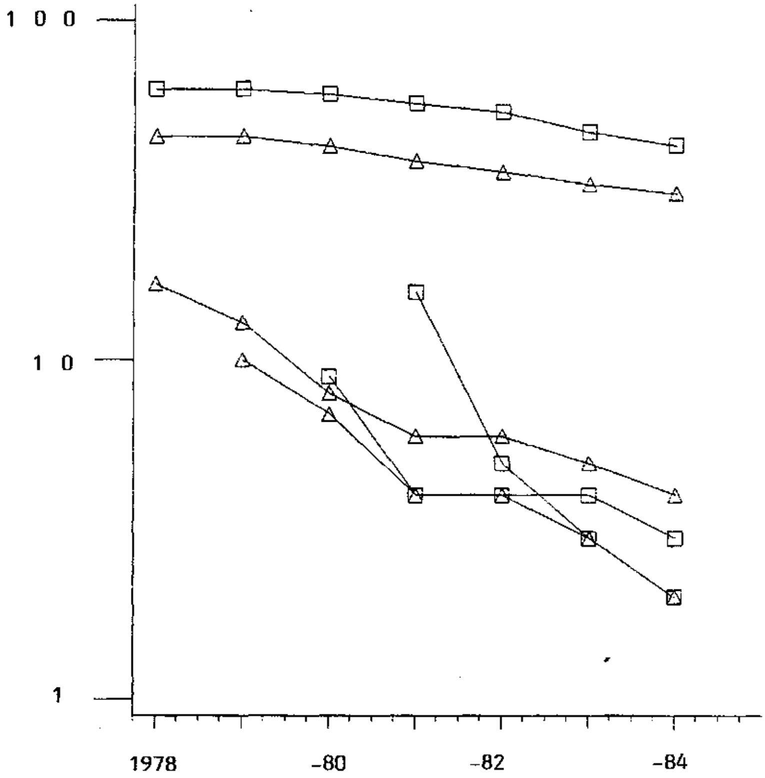


Fig. 6. Survivorship curves for cohorts of Fraxinus excelsior (triangle) and Ulmus glabra (square), Vardsätra nature reserve.

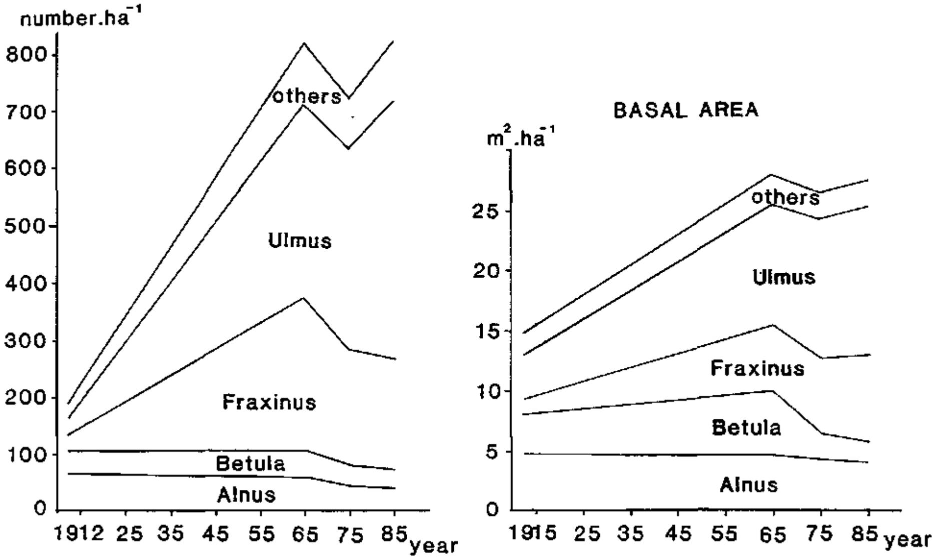


Fig. 7. Changes in numbers and basal areas from 1912 to 1985 in a profile (ca 110 x 20m) in Vardsätra nature reserve.

There are also differences in the growth characteristics between the two species below the dense crown cover (see Table 3). Both species allocate most of their production to the leaves but elm has about twice as long annual shoots as ash. In the long run the elm will overshade the ash.

Experiments

Many questions do not appear answerable on the basis of observations alone. Difficulties arise, for instance, in separating the effect of different factors on a vegetation type or on a population. In Harper's textbook from 1977 many examples are given on experiments on a population level. Austin (1981), discussing vegetation dynamics, also mentions the necessity of experiments. He especially asks for numerous treatment levels instead of a more traditional experiment with few treatment levels and many replicates. Many different types of experiments can be made, from simple enclosures preventing access by grazing animals to perturbations of the environment or the plant community.

A simple disturbance experiment on a wet meadow made by J. Skoglund (unpublished) can illustrate some points. He killed the vegetation in plots and looked for seedlings and their survivorship in control plots and in the experimental plots. When he destroyed the vegetation, unintentionally, the microtopography was destroyed. In the control plots the germination and the survivorship was correlated with the microtopography (Fig. 8.). The highest germination of Salix spp. occurred on an intermediate level, but the survivorship was best on the highest level. In that particular year the intermediate level had a suitable soil moisture during the germination period, but during other periods that level was too wet for seedlings. The destroyed plots were thought to have a higher germination than the controls because of the absent competition. Instead, they had a lower germination because of the excessively wet condition as the microtopography was lacking. The

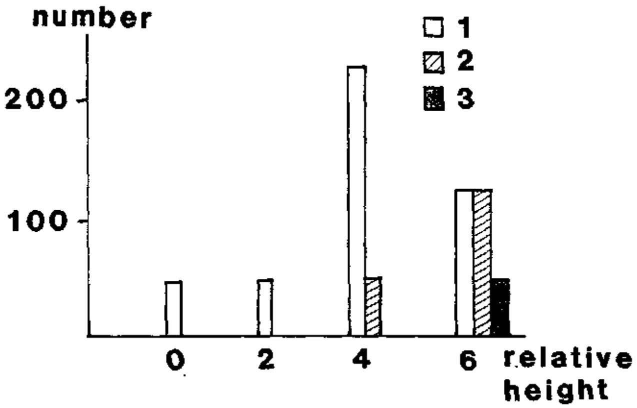


Fig. 8. Number of seedlings of Salix spp. per m^2 on a wet meadow in relation to the micro-topography (plot size 20 x 20 cm). 1= seedlings in 1982, 2= survivors in 1983, 3= survivors in 1984, (Skoglund, unpublished).

survivorship was also lower than in the control.

This experiment illustrates that there may be difficulties in interpolating results from experiments when not all acting factors are controlled. It does not mean that experiments should be avoided, only that the interpretation should be done with care and that the experiments should be performed on followed for more than one year in order to diminish the effect of the weather in an extreme year (cf. Austin, 1981).

Conclusions

Dynamics in forests are not simple unidirectoral changes but different pathways are possible from a common origin, both in primary successions and within an established forest. The research design must take this diversity into consideration and conclusions from a few observations must be restricted. Dynamics depend both upon past conditions and upon present circumstances. A study should therefore include an investigation both of historical factors and of factors actually exerting influence at present.

Dynamics occur on several different levels and no level can be regarded as more important than the others. A method cannot be designed to be appropriate on all levels. It is an advantage if several levels in a process are investigated and, consequently, that more than one method is used.

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SOME CONCEPTS AND OBJECTIVES OF FOREST DYNAMICS RESEARCH

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Summary

Forest dynamic theories can acquire predictive power through simulation modelling and sensitivity experiments. A theorie based on simplified tree physiology, life history and interaction processes is implicit in forest simulation models of the JABOWA type (gap models). Theories and models implying different simplifications may be appropriate to different hierarchical levels of organization, e.g., landscapes, forests, and trees.

Different types of observational data on forest dynamics have widely differing spatial and temporal scale characteristics. Phenomena observed on different scales may provide test data for different types of theories and models incorporating different approximations. Endogenous processes may dominate stand dynamics over tens to hundreds of years, while exogenous climate change effects may dominate changes in geographic patterns of forests over thousands of years.

Keywords: Gap models, hierarchy, scale, palynology, CO_2.

Introduction

Forests are a major component of the biosphere and their dynamics are central to the dynamics of the biosphere and its chemical components. An understanding of the processes involved in the dynamics of forests at several space and time scales is essential for the prediction of changes in forest ecosystem and biosphere characteristics in response to a regionally and globally changing physical environment.

A principal theme of this paper is that although forest dynamics has no single unifying theory, the development of predictive theories appropriate to particular space and time scales and levels of organization is necessary - for both basic and applied problems - and feasible. The paper is in five sections. The first is a general commentary on the objectives of a dynamical theory. The following three sections deal with general ideas from hierarchy theory, more specific rationales for simulation modelling, and the scale characteristics of different types of observational data. The final section brings together these various topics in the context of real-world climate change frequencies and forest response rates, and recommends some possible directions for research.

What are we trying to predict?

As an illustration, consider the problem of predicting changes in stand composition and structure over time scales of decades to centuries - i.e. forest dynamics on the space and time scales most commonly considered as "stand development" and "succession". The stands we are considering may have been disturbed or managed in various ways. They are not necessarily at equilibrium with the prevailing environmental conditions outside the forest.

The state of each forest stand at a point in time can be represented in a multidimensional state space whose axes are state variables representing (for example) the leaf biomass of each species, together with any further community or ecosystem descriptors that are necessary for a dynamically sufficient description of the stand (see e.g. van Hulst 1980). Dynamic sufficiency means that the position of the stand in this state space is all we need to know in order to predict the direction and rate with which the stand is moving through the state space. Thus with each point in state space there is associated a vector, which could be called a succession vector, describing how the stand is changing. Where succession vectors converge, there is a (local) equilibrium or climax state.

In this way the state of a forest system can be pictured as a point in an n-dimensional space and the direction and rate of spontaneous change in the system as a vector of particular orientation and length. These vectors completely specify the possible behaviours of the system, provided the parameters or boundary conditions remain constant - in other words, they specify the possible pathways and rates of endogenous change, such as might be observed after a variety of different perturbations to the stand's composition and structure. But if the parameters of the system change then potentially all of the succession vectors change. The forest stand can therefore be imaged as a particle moving through a space whose dynamic structure is constantly changing in response to changes in the environment.

The utility of this state space/vector field metaphor for ecological dynamics was discussed by Lewontin (1969), who used it as a framework for definitions of stability. It is an abstract metaphor which can accommodate many of the complexities of real-world ecological systems. For example, it includes the concept of climax without implying that such a state is ever maintained for long, or even reached at all; environmental variation may ensure that the "particle" is always in motion, simply because the dynamic structure of the space is changing (directionally, or back and forth) in time. There can be more than one co-existing equilibrium state for a given set of environmental boundary conditions (Sutherland, 1974), and a shift in these boundary conditions may induce either smooth changes in the position of equilibrium, or "catastrophic" changes of the type described by Grimm (1984) and discussed by Ritchie (1986) and Prentice (1986).

Ideally, we should be able to specify the dimensions of state space and predict all possible succession vectors under all possible boundary conditions. Now a sceptic might reasonably object that the amount of data required to construct succession vectors for any forest system is more than we could hope to collect; that many of the required combinations of environmental conditions and forest states may not be observable; and that the experimental manipulations needed to create these combinations would be out of the question, because of the amount of work involved, and because of the length of time needed to observe change. These objections are valid and support Harper's (1982) argument that understandig of community dynamics cannot emerge from observational data alone - nor even from experiments, if the experimental manipulations are carried out on whole communities. We should focus on developing a mechanistic understanding of community function, using information from observations or experiments pertaining to processes within the community. Harper characterized this insight as the most fundamental scientific contribution of the late A.S. Watt, whose investigations of how "process" determines "pattern" provided the necessary conceptual basis for plant community ecology as a predictive science.

Harper (1982) described Watt's approach as "reductionist", but the meanings of "holism" and "reductionism" are not quite as clear as in usually implied. McIntosh (1981) pointed out examples where avowed holists used apparently reductionist modes of reasoning, and vice versa. Significantly, McIntosh singled out forest dynamic models of the JABOWA class (Botkin, Janak and Wallis, 1972; Shugart, 1984) as constructs which defied classification as holistic or reductionistic. Shugart (1984) noted that the "special theory" of forest dynamics implicit in these models has its origins in Watt's mosaic-dynamic view of plant communities, and that this view is consistent with the idea of hierarchy as an organizing principle in the analysis of complex systems.

Hierarchy theory is a dialectical synthesis which shows holism and reductionism to be complementary rather than opposing modes of scientific investigation. The idea of hierarchy was popularized in ecology by Allen and Starr (1982) and explored more deeply in an ecological context by Allen, O'Neill and Hoekstra (1984). At its simplest, hierarchy theory implies that complex systems can only be understood through a conceptual stratification into "levels of organization"; phenomena observed at one such level can only be understood in terms of processes operating at the next lower level. The nature of complex systems allows quite complex phenomena to "emerge" at a given level through the interactions of components observed at the level below. Thus the complex dynamics of forest composition becomes understandable in terms of the physiological and life history characteristics of individual trees, and their interactions with one another through their effects on and responses to their local environment. There is no mystery about emergent properties; they are predictable; but they are not necessarily trivial or obvious. Oliver (1982) noted that the inference of stand dynamics from tree physiological characteristics "has been abused where attempts were made to explain forest development patterns on the basis of one or two physiological characteristics", but that models of the JABOWA type "take into account a multitude of physiological factors interacting to lead toward various stand development patterns" (Oliver, 1982, p. 106). According to Allen and Starr (1982), it is the implicit hierarchical nature of these models that makes them useful in predicting the emergent properties of forests. Hierarchy theory lets us see the wood as well as the trees.

Acceptance of the idea of hierarchy could avoid certain misunderstandings that can arise among biologists with different orientations and backgrounds. For example, a forest ecologist may legitimately use models of tree growth which a tree physiologist would consider oversimplified. The reason for this is that the forest ecologist is interested in how complex phenomena at the forest stand level can be predicted from the most fundamental physiological and life history characteristics of trees. She will therefore be using the simplest, most generalized formulations of processes at the level of individual trees. Her colleague, the physiologist, has an entirely different task: to understand the complexities of tree growth in terms of simple models of the behaviour of cells and tissues. What is irrelevant noise to the forest ecologists may be interesting phenomenology to the tree physiologist.

A wider awareness of hierarchical principles should lead to peaceful coexistence, and constructive discussion, among scientists concerned with adjacent levels of organization. Forest ecologists should use the best available generalizations from work connected with the next lower (physiological) level of organization to construct theories of how forests work. Similarly, generalizations emerging from theoretical and predictive investigations of forest stand dynamics should be available as basic tools in the development of models for the vegetation dynamics of landscapes and regions.

Rationales for simulation in forest dynamics

In general, scientific theories acquire their ability to make testable predictions from the application of mathematics. Mathematical models make explicit the real-world consequences of theories, in ecology as in other sciences.

Physical and engineering models of complex systems often take the form of sets of differential equations which can be solved and analysed using the mathematical techniques of dynamical systems theory. These techniques allow insight into overall system properties such as stability and response times without recourse to large computer simulation. For example, Ågren (1982, 1983) has derived general equations for the linked dynamics of carbon and nitrogen in conifer forest ecosystems and used this theory to predict overall ecosystem responses to perturbations of various kinds. The elegance of Ågren's approach is both a strength and a limitation: generality is achieved (necessarily) at the expense of realistic detail (Harper, 1982). Such general theoretical approaches to ecosystem dynamics complement less abstract approaches based on computer silumation and model sensitivity experiments which rely on the power of modern computers. Simulations and sensitivity experiments using large computer models have become standard in atmospheric science. Simulation models are less developed in vegetation science, but progress has been made with stochastic models of the dynamics of vegetation composition and structure over "successional" time (Shugart, 1984; van Tongeren and Prentice, 1986). Shugart (1984) and Prentice (this workshop) give special attention to the JABOWA class of forest dynamics models, also known as "gap models". These are stochastic models which simulate the structure, composition and production of forest stands. Their design allows them to be used to predict directions and rates of change in particular forest systems as a function of a constant or varying environment.

Many other more specialized computer-based models have been developed to forecast stand development, mostly in an economic forestry context. There is a critical distinction however between models based on theory (deductive models) and descriptive statistical models, which in their purest form have no theoretical content but rely on fitting empirical functions to data. The descriptive statistical approach has been successful in predicting forest yields from present stand structure, composition, site factors, and management alternatives (e.g. Hägglund, 1981). Today's complex descriptive models are a logical extension of traditional yield tables and have similar strengths and weaknesses. Undoubtedly, the way to maximum precision in yield prediction under fixed environmental conditions is through such statistical approaches, underpinned by a suitably large data base obtained from the full range of conditions for which predictions are to be made. But the use of such data-hungry models is limited to that range of conditions; such models can simulate forest stand development, but only so long as the environment remains within bounds determined by the data base. Outside these bounds the models become useless. On the other hand, deductive models based on mechanisms within the forest should be capable of simulating forest changes under a much wider range of environmental conditions, including possible (past or future) conditions not encountered at present.

The testing of deductive (analytical or simulation) models requires some ingenuity, and like the testing of any scientific theory, it is never complete. The predictions may be subject to much greater uncertainty (both about the model's structural reliability, and about the exact numbers it computes) than the predictions of statistical models; nevertheless, deductive models are an important part of the development of ecological theory, and may also tell us things about forests' possible responses to a changing environment which there is no other way to guess. For example, Solomon et al. (1984) used a JABOWA type simulation model to project the effects of a simulated climate change resulting from raised atmospheric carbon dioxide on forest biomass and composition in eastern North America. This study was used by Shugart et al. (1985) in their assessment of effects of raised carbon dioxide levels on forest ecosystems. Shugart (1984) discusses other comparable applications of gap models in deducing possible large-scale effects of environmental changes acting on individual trees, including direct effects of raised CO_2 levels on forest growth. The results of such model experiments provide good examples of the phenomenon of emergence in contexts that are of more than academic interest.

Scale properties of different data types

The idea of hierarchy is closely connected with the concept of scale. The development of theory and models of vegetation dynamics requires scale to be considered explicitly. Biospheric phenomena, like atmospheric phenomena, can be conveniently categorized according to the space and time scales of observation required to observe their dynamics. Commonly the processes requiring the largest spatial scales of observation have the greatest inertia and therefore demand long time scales of observation; the resulting simultaneous nesting of phenomena according to spatial and temporal scales allows the definition of hierarchical levels of organization at which different types of process predominate (Delcourt, Delcourt and Webb, 1982). These levels may allow useful simplifications for the development of different types of models (Prentice, 1983). Gap models simulate stand dynamics in discrete patches on the order of 0.1 ha in area and with a timestep of 1 year; global processes taking thousands of years cannot be simulated directly using such models, but should be simulated using more highly aggregated models in which high-frequency phenomena simulated by gap models are averaged out and other, low-frequency phenomena come into play.

Sets of observational data can be characterized in terms of their spatial and temporal "grain" (Allen et al., 1984) or "resolution" (Prentice, 1986), and "extent" (Allen et al.) or "frame" (Prentice), in space and time. Grain and extent are linked in the sense that coarsed-grained data are no use for observing fine-scale phenomena while fine-grained data are commonly unsuitable for building extensive data sets. Temporal and spatial scale properties of data are independent, however; the various sources of observation data can be cross-classified by these two properties.

The most detailed information on the state and change of forests can be obtained from permanent plot studies. The field investigation is free to choose among a very wide range of compositional, structural, and abiotic ecosystem characteristics. But the spatial scale of direct field observation is obviously limited, and the length of time over which direct observations can be carried out is equally obviously limited. Fortunately, data at the spatial scale of the sample plot or forest stand can be obtained with a greater temporal extent by various indirect means (e.g. review by Oliver, 1982). Analyses of age structure and fire-scar investigations on extant forests allow a retrospective study of stand development, which can sometimes be strengthened or extended by the use of historical documentation (e.g. review by Hytteborn in this workshop). Time series of air photographs have been used to reconstruct spatial patterns of forest change over decades, at a slightly larger spatial scale (e.g. van Dorp, Boot and van der Maarel, 1985). Pollen analysis from raw humus accumulations on the forest floor is another promising technique for investigating forest dynamics at the stand scale. The source radius for most of the pollen arriving at a point under a tree canopy is on the order of 20 m only (Prentice, 1985). Raw humus preserves pollen grains in stratigraphic sequence. Humus profiles often date back to the last hot fire, but occasionally may be protected from fire and give a longer record. The technique is discussed by Jacobson and Bradshaw (1981).

The other extreme of spatial scale in forest data is exemplified by satellite remote sensing data. A radiometric method has been used to sense broad-scale patterns in the seasonal dynamics of vegetation using NOAA satellite information (Goward, Tucker and Dye, 1985). This approach is promising for investigating seasonal and short-term interannual changes in green biomass at broad spatial scales. But many broad-scale properties of forests, such as regional and global patterns in species composition and standing crop, are not prone to change on the time scales over which satellite data have been available. Standard palynology is the main source of data on the dynamics of geographic patternsin species composition (Solomon and Webb, 1986) and has been used in conjuction with a forest simulation model to study the long-range dynamics of geographic patterns in standing crop (Solomon and Shugart, 1984; Solomon and Tharp, 1985). Pollen samples from moderate-sized lakes or bogs have source radii at least three orders of magnitude larger than within-forest sites, and therefore integrate information over entire landscapes. Standard pollen analysis provides macro-scale sensing of vegetation in space and time (Webb, Laseski and Bernabo, 1978; Delcourt et al., 1982).

Allen and Starr (1982) suggested that ecologists are often unjustifiable prejudiced towards thinking of the spatial and temporal scales of direct field observation as being somehow more real than the macro-scales that are accessible only via indirect methods, such as satellite data and palynology. There are good reasons not be prejudiced in this way, because there are major problems of scientific and societal importance that require an understanding of forest dynamics on these macro-scales. A similar prejudice is involved when "contemporary" plant communities (studied by "contemporary" ecologists!) are dinstinguished from "past" plant communities, studied by "palaeoecologists". The distinction is one of scale only. Observational data on the dynamics of communities always include the past; there are only different time scales of dynamics, which require different lengths of historical observational record.

"Special theories" and modelling approaches for different observation scales

The observation scale determines what phenomena are observed, and therefore also what processes are most important in causing the observations. This consequence of hierarchy was discussed in a geomorphological context in the classic paper of Schumm and Lichty (1965); it has equally important implications for forest dynamics.

Prentice (1986) and Webb (1986) consider how vegetation change can appear to be endogenously or exogenously controlled, according to the time scale of the observation set. We considered vegetation changes driven ultimately by climatic variation, but limited by the possible rates at which vegetation can respond to such variation. Climate varies with many different, superimposed frequencies and vegetation can respond to environmental variation through several processes with different time constants.

But climatic variation does not have a "white noise" spectrum. The frequency spectrum of natural climatic variability is very approximately U-shaped with the greatest power concentrated in frequencies that have astronomical causes - at the high-frequency end the daily and seasonal cycles, and at the low-frequency end the Milankovitch orbital cycles (with periods of 20 to 100 ka) which drive the glacial/interglacial alternation and the changing geographic extent and strength of the monsoons, vegetation responds in different ways to different frequency bands in environmental variation, as indicated by Ritchie (1986), Prentice (1986), and Webb (1986). Three types of response can be distinguished:

(1) Perennial plants are adapted (through phenology, cold and drought protection systems, and so on) to "ride out" the seasonal cycle and also, once established in the vegetation, tolerate considerable interannual variability. The high frequencies of climatic variability are strong but forest composition and structure remain unaffected by them. Variation over such short time scales is "perceived" by the forest as part of its static environment, and may even contribute to maintenance of some of the forest's steady-state characteristics, such as species diversity (e.g. Fagerström and Ågren, 1980).

(2) Forests can respond to intermediate frequencies, for example to climatic trends like the change from Little Ice Age conditions to present conditions. Such changes are on a similar time scale to the lifetimes of trees, and so to many processes affecting structure and composition. But these intermediate frequency signals are relatively weak. Therefore when observing forests on this time scale we may see most clearly endogenous vegetational responses to natural episodic disturbances. Climatic variation on this intermediate time scale may act on forest composition and structure through direct effects on tree reproduction and growth, or indirectly through effects on the natural disturbance regimes (Grimm,1983; Zackrisson, 1977). But these effects may be subtle and to some extent masked, damped, or lagged due to their interaction with natural frequencies of stand-scale response (Davis and Botkin, 1985).

(3) Forest composition also responds to low frequency climatic change. These changes are of long period compared to the time required for endogenous vegetation response, which over a time frame of (say) 10 ka may be too fast to observe. Likewise, natural disturbances may occur so often as to seem part of the state of the vegetation, which to a first approximation may be considered in equilibrium with the low frequency component of climatic change (Webb, 1986).

These considerations motivate the development of different "special theories" applying to different observation scales:

(1) The "special theory" of forest dynamics incorporated in gap models (Shugart, 1984), with its basis in tree growth physiology, life history characteristics and competitive interactions, allows tests with observational data on the composition, size distribution, and age structure of existing forest stands (most usefully, old-growth forests). Such test data can be extended where possible by permanent plot studies and raw humus palynology. To an approximation, tests of models designed for these spatial and temporal scales can often disregard environmental change (Van Tongeren and Prentice, 1986). This approximation would also allow chronosequence studies to provide test data for models.

(2) A "special theory" for the regional-scale dynamics of forest composition on a Late Quaternary (10 to 20 ka) time scale might have quite a different basis, in the climatic tolerance surfaces of species (Bartlein, Prentice and Webb, 1985). Tests of such a theory would use continental-scale maps from standard pollen analysis (e.g. Huntley and Birks, 1983). To simulate such data, it may be sufficient to map time-averaged equili-

brium states of forest composition into a space defined by climate variables; then apply regional scenarios for low-frequency climate change constrained by the response of the atmosphere to global boundary conditions (radiation patterns, ice sheet configuration and CO_2) (Prentice, 1983; Bartlein et al. 1985). Such a test would not explicitly consider demographic and competitive processes; in fact, the endogenous aspects of forest dynamics which are so important on shorter time scales would be ignored, while the driving force of environmental change would be emphasized.

Such apparently incompatible theories for different observation scales may coexist provided it is recognized: (1) that neither is universally true; (2) that there may be situations for which neither is adequate. In the Late-Quaternary pollen record of forest dynamics, Davis et al. (1986) and Ritchie (1984) among others have focused on the early Holocene as a period when the response of mid- and high-latitude forests to exceptionally rapid climatic changes 13 - 10 ka ago may have been limited by the rate of endogenous successional processes and/or intrinsic limitations on species migration rates. Human-caused climatic changes in the future may also prove large enough to induce major geographic shifts in potential forest composition (Emanuel, Shugart and Stevenson, 1985) yet occur over a short enough period to make stand-scale dynamic processes rate-limiting (Delcourt et al., 1982). Forecasting the impact of such changes will require consideration of different kinds of information on forest dynamics, applying to various space and time scales. Scientists and working groups concerned with the environmental issues related to forest dynamics should not confine their awareness of techniques and information to one particular theory, modelling approach, or observational scale.

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SOIL DYNAMICS AND FOREST SUCCESSION

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Summary

In this review some concepts of forest and soil successions are discussed in terms of climax, steady state and open systems, and some basic principles of irreversible thermodynamics are presented within this framework.

Additionally, nutrient cycling in relation to succession is treated and some important aspects of chemical weathering, especially of silicates with respect to their structural stability, and its soluble products is discussed.

Finally, the role of phosphorus as a master variable during the various soil- and forest succession stages is considered.

Keywords: Chemical weathering, nutrient cycling, phosphorus, system theories, succession.

Introduction

In 1935, the botanist Tansley defined the ecosystem as the aggregate of plants, animals, and microbes plus the environment in which they live. The term "ecosystem" has gained great popularity and the ecosystem-approach has been very successful in environmental studies.

The advantage of an ecosystem approach when studying nature is that the interrelationships between and the dynamics within the distinguished spaces or subsystems are closely connected, resulting in a better insight in the total system and its various compartments.

Within terrestrial ecosystems we can distinguish subsystems or compartments e.g. the soil and the vert (green) space (Jenny, 1941, 1980). Vert space comprises all above-ground parts of the terrestrial system, the plants, the animals and the voids between them. Soil space includes soil horizons with their mineral and dead organic materials, the gas- and water-filled pores, but also all organisms inhabiting it. Consequently, soil is not a purely abiotic system, but a mixture of biota and abiotic matter.

Tracing the exact boundary the soil space and vert space may become rather frustrating, due to the extreme complexity of both these spaces. Conventionally, the soil is taken as beginning with the forest floor at the base of a tree, but this distinction is only an operational one.

Already in 1941, Jenny developed a concept in which time (age) is one of the state factors of the ecosystem. Applied to ecosystem genesis in time, the chronosequence, he postulated that properties of the whole system and consequently properties of the subsystems, vegetation, fauna and soils are a function of time, given the state factors climate, topography (hydrological regime) and parent material.

Concepts of forest and soil successions

In 1899, Cowles formulated the idea of a temporal plant succession that culminated in Clement's visionary construction of the vegetation climax in a mature (soil) landscape (Jenny, 1980).

Whittaker (1953, 1957) and later several others reviewed the literature in the climax concept. Two main approaches with respect to this concept exist. One is mainly based on the floristic and physiognomy of vegetation and its relation to climate. The other approach centres on the problem of population and productivity in relation to all environmental factors. Both approaches are largely restricted to vegetation. Whittaker compromised between the several ideas of climax and formulated the climax pattern hypothesis: Climax vegetation is a pattern of population corresponding to the pattern of environmental gradients and more or less diverse according to the diversity of the environments and kinds of population in the pattern. In terms of species populations, the climax, like the phytosociological associations, is a concept which does not stand up to critical examination (Whittaker, 1953). He also stated that his definition of climax vegetation as a self-maintaining system of interacting populations was far from absolute. His definition emerged from his ideas on species individuality and time space continua, but neglects the whole ecosystem characteristics of nutrient availability, productivity, structure etc., that should form the basis of any concept of ecological dynamics. Whittaker suggested that the climax condition may be better defined by the term "steady state", defined as vegetation of changing and developing character, incompletely stabilised, with the balances gradually shifting. With this definition the usual distinction between climax and succession, based on relative stability and directional change, breaks down.

Whereas the concept of climax pertains mainly to vegetation, maturity has a similar meaning, but pertains to the soil space of the ecosystem. The concept of soil maturity has developed from being strictly morphological, referring to descriptive field criteria, to being dynamic and based on soil forming processes (Jenny, 1941). A mature soil is normally defined as being in "equilibrium" with the environment of a soil. In terms of a soil property - time function, soil maturity is reached when the curve becomes flat and remains so, indicating zero change. Not all soil components reach maturity at the same rate or simultaneously. According to Jenny, at the particular conditions of dynamic equilibrium: steady state, the change in a sub-property during a time interval will be zero; so time can be neglected since it has no further effect. It has to be mentioned that, in contrary to the vert space, very slow rates of change within the soil may be mistaken on the human time scale for apparent steady state.

In studies involving vegetation/soil system development the parameters of time and the associated concept of adjustment become chief considerations. The concept of adjustment is termed "dynamic equilibrium" or "quasi-equilibrium" (Leopold and Langbein, 1962). This concept includes the condition of "steady state" which refers to the tendency for a constant state to develop (Abrahams, 1968) and has been successfully used in irreversible thermodynamics, biology, pedology and geomorphology. It defines certain conditions of an open system, where the emphasis lies on the continuous interactions of processes and the system components. Highlights of the steady state are the constancy of the system as a whole and in its phases, although there is a continuous flow of the component materials.

The classical (equilibrium) thermodynamics depict that all closed systems will move towards a state of minimum free energy (G) (maximum entropy (S) and/or minimum energy) given by the equation (at constant temperature and pressure):

$$\Delta G = \Delta H - T \Delta S \qquad (1)$$

were H denotes the enthalpy. For any open system, the concept of entropy can be equated with a measure of randomness or disorder of a system. As entropy increases, disorder of systems also increases. Thus, the drive toward maximum entropy implies a tendency toward system disorder. However, living systems represent both an energetic and a configurational improbability since living systems are highly ordered and energy-rich (Morowitz, 1971). This is only possible by the import of energy and matter into the system. The same reasoning can be applied to soil development. The ordening of parent materials into pedons by horizonation is due to fluxes of energy and matter leading to a decrease in entropy.

According to Prigogine (1961) the total change in entropy of open systems can be written as:

$$\Delta S = \Delta S_e + \Delta S_i \qquad (2)$$

ΔS_e denotes the change of entropy due to interactions with the surroundings and ΔS_i denotes production of entropy due to irreversible processes within the system; ΔS_i is always positive, ΔS_e may either be negative or positive. Therefore, depending on the magnitude of ΔS_e, the total entropy change in an open system can be negative as well as positive. For biological and soil systems, entropy will decrease as a result of cell and profile development (more ordening). Consequently, the entropy of the surroundings must increase and entropy flows from such open systems to the surroundings. Prigogine (1961) has shown that at steady state, entropy production within in open system reaches a minimum which just equals entropy flow from the system. Thus, at steady state, entropy as well as other state variables of the system become constant (fig. 1a). A steady state will be maintained through negative entropy flow which is caused by the system receiving more energy than given off or by influx of matter with less entropy than that of matter leaving the system. It should be apparent that entropy levels of the steady state can be less than that of preceding states (fig. 1a).

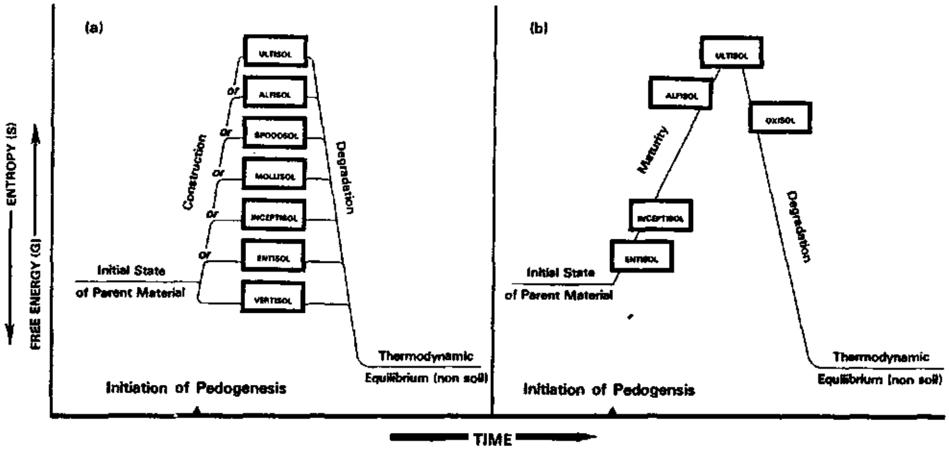


Fig. 1. A schematic representation of free-energy and entropy content of soils in selected orders as a function of time: a) assumes the existence of steady states; b) represents the continuous evolution of soils towards equilibrium (after Smeck et al., 1983).

Summarizing it can be concluded that, at steady state, energy and/or matter influx is just sufficient for maintenance of the properties of the (soil) system; in other words, aggrading processes just balance degradational processes. From figure la it can also be seen that not all steady states of soils occur at similar energy nor entropy levels. The characteristics of a system at steady state are dependent upon the initial state and the fluxes of the system. Parent materials subjected to the high energy influxes will attain steady state at higher free-energy or lower entropy levels than those subjected to low levels of energy influxes. Intense leaching of the soils gives more highly ordered soil. According to Prigogine (1961) a system cannot leave a state of minimum entropy production by spontaneous irreversible processes. If a system deviates from the steady state due to change in external flux, spontaneous internal changes take place which cause the system to return to the steady state. However, it has been emphasized that not all soils have attained a condition at steady state and there are soil scientists who say that all soils are in a state of continuous evolution (fig. lb). Undoubtedly many soils represent transient states whereas others represent steady states. Both states play a role in soil formation and soil development can best be depicted as a combination of both figures presented in figure 1 (Smeck et al., 1983).

Ecologically, steady state can be defined as a temporary state of dynamic equilibrium in an open system. Whittaker (1953) referred to this state as the levelling-of the time distribution of any parameter such as productivity. The distiction from climax can be immediately seen. The vegetation component of the ecosystem considered to be climax, in the sense that it is self-maintaining, may appear to be constant with time. However, within the whole ecosystem, there can be a simultaneous and continuous imbalance between input and output of materials. This imbalance is a function of loss of nutrients from the soil by leaching in excess of nutrient release by weathering, loss by erosion, lateral and surface runoff of water, uptake by plants, input by rainfall and dry deposition and other atmospheric processes, all of which contribute to the open nature of the ecosystem. Inherent to the steady state concept is the "considerable" scope for fluction within the ecosystem.

Finally, it can be concluded that steady state adequately defines a temporary state of dynamic equilibrium in an open system such as the vegetation/soil system. It employs "dynamic equilibrium" as denoting adjustment in a non-reversible sense tot a state of mineral change with time. Fundamental to the meaning of steady state is a minimum continuous variation within and between all parts of the ecosystem.

Within forest successions during steady state conditions considerable fluctions with respect to the vegetation may exist resulting, among other things, in various biomass accretion models (Peet, 1981; see fig. 2): 1. the simple asymptotic increase of biomass towards an upper limit, fixed by site conditions (Odum, 1969),2. a stochastic version of the logistic yield model, resulting in a shifting mosaic model, which accounts for a dip in biomass (Bormann and Likens, 1979) and 3. the model which predicts initial increase followed by a decrease and then a subsequent recovery. Here, rather than a simple dip to an asymptotic "steady state", level biomass shows a series of damped oscillations around an equilibrium level. Even the concept of a cyclic succession for forest development fits within certain limits well within these oscillating steady state models.

Finally, it has to be emphasized that the successional time to enter the steady state stage for the various subsystems of the ecosystem can vary considerably (fig. 3). This figure is taken from Jenny (1980) and gives a hypothetical chronosequence of soils and vegetation during a

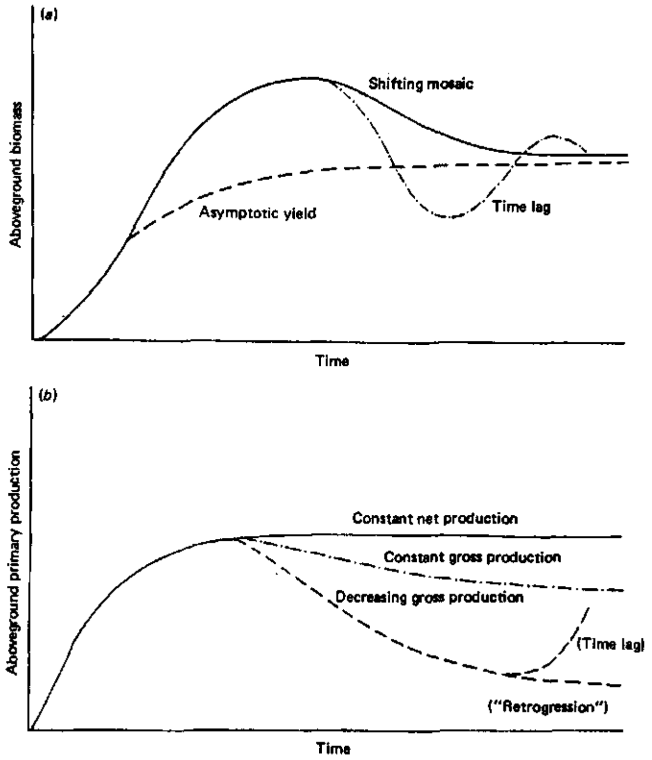


Fig. 2. Successional changes in biomass (a) and production (b) as predicted by various models described in the text (after Peet, 1981).

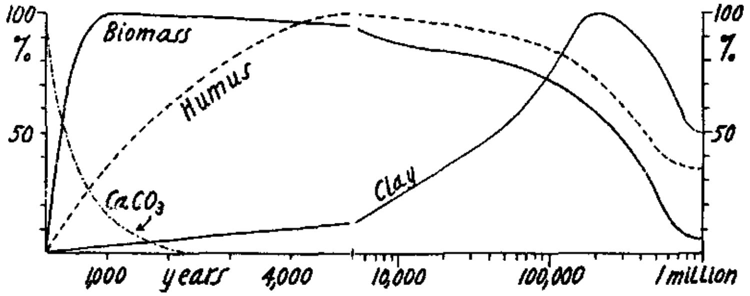


Fig. 3. Hypothetical chronosequence of soils and vegetation during a "million" years on level topography (after Jenny, 1980).

"million" years on level topography and humid climate. Vegetation "steady state" arrives first, humus maximum later and some characteristics of the mineral part od the soil e.g. the clay content last. For other soil characteristics like the CaCO$_3$ content, steady state conditions arrive relatively rapidly. In this figure also the "real" edaphic plant steady state is indicated, although it can be wondered of this stage will be reached at all, due to major alterations of the state factors such as

climatic changes, tectonic tilting followed by severe erosion.
To my opinion a lot of misconceptions with respect to forest- and soil succession interrelationships exist due to an insufficient notion of the different time scales for the various compartment stages of the ecosystems.

Forest succession and nutrient cycling

Forests and woodlands of the world occupy slightly more than one-third of the earth's land area and they contain major fractions of the terrestrial stocks of C, N, S and P. Today, carbon and nitrogen budgets are available for a variety of forest ecosystems, although most are incomplete (Melillo and Gosz, 1983); on the contrary, the sulphur and phosfor budgets are less common and/or fragmentary.
However, at this time a gap still exists in the knowledge of the mechanisms that control cycling rates of an element; this requires consideration of element interactions. Studying nutrient cycling fluxes on an ecosystem level base, even when ecosystem components are inadequately known, is valuable because study of this ecosystem level can help to elucidate which components and processes require further study. Patterns of nutrient availability and fluxes generally strongly affect plant succession.

Vitousek and Reiners (1975) have suggested that change in net ecosystem production is major determinant of the balance between inputs and outputs of elements in terrestrial ecosystems (fig. 4). They argued that in the course of primary succession element outputs are initially relatively high (approximating inputs), following by a drop to a minimum because of element accumulation biomass and detritus due to higher ecosystem production. In late succession stages, when net ecosystem production approaches zero, output rates rise again approximately to equal inputs (steady state stages). In most cases of secondary succession, net ecosystem production is negative immediately following disturbance and in such cases output rates can exceed input rates (fig. 4).

However, also other processes can systematically affect chemical budgets in the course of terrestrial ecosystem succession, resulting in different, although still balancing, levels of inputs and outputs. The processes controlling changes in nutrient inputs and outputs in primary and secondary succession, were recently reviewed by Gorham et al. (1979).

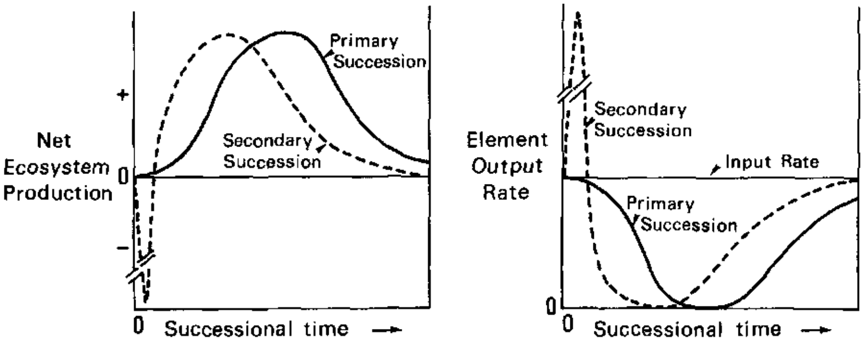


Fig. 4. Patterns of change in net ecosystem production (NEP) during primary and secondary succession of terrestrial ecosystems (a); patterns of output rates for a limiting element in primary and secondary succession, assuming that changes in storage are controlled principally by NEP and that input rates are constant (b) (after Gorham et al., 1979).

In table 1 processes are shown which affect element inputs to systems, including rock and soil weathering, nitrogen fixation, particle impaction and gas absorption; those that change with alterations in hydrology, including losses of dissolved substances, erosion and oxydation/reduction reactions; and those biological processes directly or indirectly affecting the balance between input and output, including net ecosystem production, element mobilisation or immobilisation, cation/anion balance, the production of allelochemic substances, and changes in element utilisation by the biota (Gorham et al., 1979). Only those processes which are intrinsic to ecosystems are present here, ignoring external factors such as changes in precipitation or atmospheric deposition amounts. However, these external factors are at the moment important in nutrient cycling, especially in the industrial countries. Each of these processes varies systematically in the course of succession, though the magnitude of each change may be difficult to predict in the course of any particular succession.

Table 1. Intrinsic varying ecosystem processes due to successional development*

1. Processes affecting inputs
   a. Rock and soil weathering
   b. Nitrogen fixation
   c. Particle impaction and gas absorption
2. Hydrologic processes affecting outputs
   a. Loss of dissolved substances
   b. Erosion
   c. Regulation of redox potential
3. Biological processes affecting the balance of inputs and outputs
   a. Net ecosystem production
   b. Decomposition and element mobilisation
   c. Regulation of solution chemistry
   d. Production of allelochemics
   e. Variability in utilisation of elements

* After Gorham et al., 1979

Chemical weathering

In this paragraph some information will be given of weathering and soil formation processes, which deliver the nutrients for the ecosystem. Also some remarks will be made on the reciprocal interactions of ecosystem-level nutrient fluxes and vegetational changes.

Weathering entails both physical and chemical processes, but within our subhumid climate chemical weathering is much more important. Chemical weathering includes the processes by which environmental agents are acting within the zone of influence of the atmosphere, produces relatively stable new mineral phases as clay minerals and pedogenic oxydes. In these processes dissolved substances are produced and removed. Chemical weathering rates are strongly controlled by climate, i.e. temperature and water flux, parent material (rocks), relief and biota.

Within a climatic region the patterns and rates of chemical weathering are highly dependent upon parent material. Its texture, structure and mineralogical composition will have an influence on rate of percolation, surface area affected and chemical reactions. For silicate rocks weathering characteristics can be differentiated into four classes: basic crystalline, acid crystalline, alkaline igneous and argillaceous sedimentary rocks. During primary succession especially the amount of easily weatherable minerals will control the chemical element level, while during secondary succession the degree of prior weathering, e.g. the mineral assemblage of primary and secondary minerals will influence subsequent weathering rates (Gorham et al., 1979).

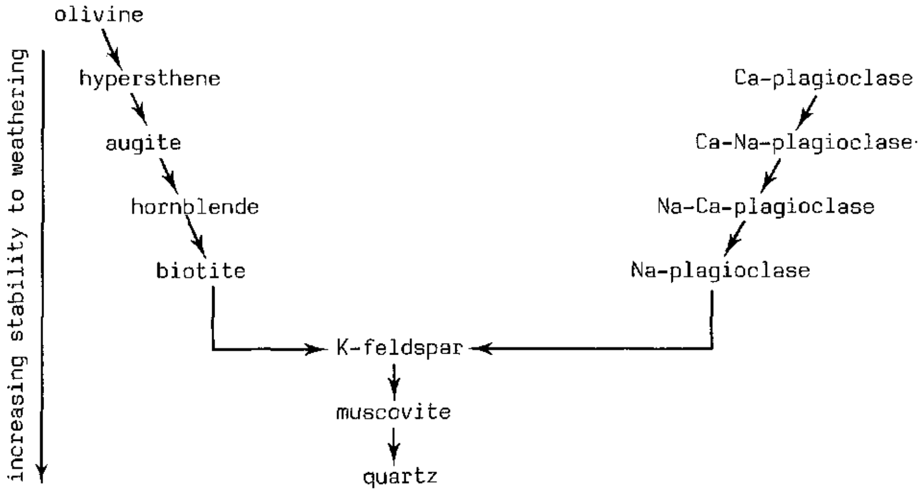
The following section will review some basic principles governing the character and speed of chemical weathering of silicates, the most important rock forming and consequently the main source of nutrients with the exception of nitrogen and carbon, e.g. the silicate reaction with water or acids. It should be emphasized that during succession the amount of acids produced within the soil system can be fluctuating, mainly due to changes in biological activities. The reactivity of silicate minerals to water or acid is largely a function of the silicate polymerization inherent to the mineral structure (table 2).

Table 2. Classification of Silicate Minerals*

SiO_2 Polymer Configuration	Percent Si-O-Si Linkages	Anion Formula	Si/O	Example
Isolated Tetrahedra	0	SiO_4	1/4	Mg_2SiO_4 (forsterite)
Tetrahedra Doublet	25	Si_2O_7	1/3.5	$Ca_2Al_3O(SiO_4)(Si_2O_7)OH$ (epidote)
Single Chain	50	SiO_3	1/3	$MgSiO_3$ (enstatite)
Closed Chain	50	$(SiO_3)n$	1/3	$Be_3Al_2(SiO_3)_3$ (beryl)
Double Chain	69	Si_4O_{11}	1/2.75	$Ca_2Mg_5(Si_4O_{11})_2(OH)_2$ (tremolite)
Sheet	75	Si_4O_{10}	1/2.5	$Mg_3(Si_4O_{10})(OH)_2$ (talc)
Framework	100	SiO_2	1/2	SiO_2 (quartz)

* After Johnson (1984)

Table 3. Stability of minerals to weathering.



The primary structural unit in silicate minerals is the SiO_4 tetrahedron, which polymerise in various ways through a Si - O - Si covalent bond. Silicate minerals are conveniently classified on the basis of their silicate polymer configuration (table 2).

Generally, the more Si - O - Si linkages present in a mineral, the more difficult it is to dissolve the mineral in water or acid, and to deliver nutrients. In table 3 the most water-soluble minerals are listed at the top and the most insoluble are at the bottom. The dissolution of a silicate mineral is conventionally called hydrolyses weathering. In strictly chemical terms hydrolysis is the dissolution of a salt in water, which produces an excess of H^+ or OH^- (acid or basic hydrolysis). Because most minerals are basic salts their hydrolysis generally leads to an excess of OH^-. However, there is one notable exception: the hydrolysis of pure quartz yields a weak acid, silicic acid ($H_4SiO_4^0$), as an end product, which imparts a slightly acid character to reaction (3):

$$SiO_2(s) + 2H_2O \rightleftharpoons H_4SiO_4^0, \text{ with a pK value} = 4.00 \qquad (3)$$

It is significant that the quartz structure represents the highest possible level of silica polymerization i.e. a Si:O ratio of 1:2. The hydrolysis of quartz requires that a three-dimensional Si - O - Si network be broken down into a set of discrete SiO_4 tetrahedra. This depolymerization reaction is bimolecular, involving the breaking of a strong Si - O - Si bond and a simultaneous presence of an anion, in this case OH^-, to complete the new bonding arrangement. The quartz dissolution amount and rate increases at higher pH values (increasing OH^- concentration) due to dissociation of silicic acid. It is evident from the above that one of the most dominant minerals found at the earth's surface, quartz, is not vulnerable to acids.

At the other extreme from quartz (see also table 3) there are silicate minerals that are relatively reactive to acids. A good example is the mineral forsterite, an magnesium silicate. The hydrolysis of this mineral is given by reaction (4):

$$Mg_2SiO_4(s) + 4H_2O \rightleftharpoons 2Mg^2 + 4OH^- + H_4SiO_4^0, \ pK = -27.13 \qquad (4)$$

This reaction is obviously acid-dependent, which is shown by reaction

$$Mg_2SiO_4(s) + 4H^+ \rightleftharpoons 2Mg^{2+} + H_4SiO_4^0, \ pK = 28.87 \qquad (5)$$

For this reaction no Si - O - Si bonds need to be broken due to the fact that the silica configuration in forsterite, a SiO_4 anion, is already that of silicic acid. Consequently, in this case only the relatively weak ionic bond between Mg - O needs to be broken.

The majority of the silicate minerals, however, is somewhere between quartz and forsterite with respect to both their structural complexity and their hydrolysis properties. Consequently, in theory relatively high concentrations of OH^- for the fissioning of the Si - O - Si bonds, combined with a high concentration of H^+ would optimise the amount of the hydrolysis taking place and presumably its kinetics too.

With respect to the primary minerals with an aluminosilicate structure, for instance feldspars, the following can be said on their reactivity. In these structures, which are double chain, sheet and framework structures, it is common for aluminium to systematically substitute for silicon. This substitution effects strong changes in the physical and chemical properties of the resulting structure. Generally, aluminium substitution gives a silicate structure more susceptible to hydrolysis and acid attack, because each AlO_4 tetrahedron represents a weak link in the silica polymerization network. This can be seen in reaction (6) as the acid dissolution of an idealised SiO_4 - AlO_4 anion complex:

$$O_3Si\text{-}O\text{-}AlO_3^{7-} + 3H^+ \rightleftarrows SiO_4^{4-} + Al^{3+} + 3OH^- \qquad (6)$$

This reaction indicates that H^+ is an active agent in the decomposition of a Si - O - Al bond and it is in contrast to the Si - O - Si bond decomposition, where OH^- is the active agent.

Summarizing it can be said with respect to the crystal structure of silicates that the relative stability of these minerals to weathering appears to be related to the degree of basicity, degree of linkage of the tetrahedons, relative number of aluminium and silicum tetrahedons and other factors that induce a lowering of the basicity of the mineral and a destruction of bonds linking the tetrahedons (Barshad, 1964). From the point of view of chemical composition, the larger the number of independent tetrahedons, the more basic is the mineral which is the larger in the ratio of basic cations to silicium. Similarly, the larger the number of aluminium tetrahedons, the more basic the mineral.

The relative stability of silicate minerals to weathering follows a close order of crystallization, that is, the less basic the mineral the more stable it is (Bowen, 1928; Goldlich, 1938; see also table 2).

The soluble products of chemical weathering

Soil solution is essential to chemical weathering. Minerals desintegrate because of their constituent atoms and ions are dissolved and (partly) removed from the soil system resulting in an unstable environment for (primary) minerals and a formation of new (secondary) minerals as clay minerals and pedogenic oxides. The main local feature of soil solution lability is the continuous transformation of dissolved constituents into different chemical species over a broad range of reaction time scales. This persistent, but kinetically complex process, controlled by interactions involving solar energy and biota, is the essential driving force for soil profile development which governs the pattern of chemical weathering (Sposito, 1981). Chemical thermodynamic models of soil and rock weathering have been successfully developed (Helgeson et al., 1969; Fritz, 1975 and 1984), and they are mainly focussed on solubility control, usually through the dissolution-precipitation reactions of hydrous oxides and alumino-silicates constrains by the Gibbs phase rule (Verstraten, 1980; Lindsay, 1979). In order to avoid conceptual errors in the interpretation of the soil solution composition data, some quidelines have to be presented. One of the most important of these quidelines is the Gay-Lussac-Ostwald (GLO) step rule. In the context of the ion-association model this empirical rule can be summarized as follows (Sposito, 1984):

"1) If the initial activity of a ion in the soil solution and attendant soil conditions make several solid-phase states potentially accessible to the ion, the solid phase which forms first will be the one for which the activity of the ion would be nearest below its initial value in the soil solution.

2) Thereafter, other accessible solid phases will form in order of decreasing activity of the ion in the soil solution and the rate of formation of each solid in the series will decrease as the corresponding ion activity decreases. In an open system any one of the solid-phase steps may be maintained "indefinitely" on the time scale of the weathering experiments".

The GLO step rule provides a conceptual framework for the observed sequence of feldspar weathering (Stumm and Morgan, 1981; Fritz, 1984);

it gives good results for secondary mineral formation (clay minerals and pedogenic oxides) and also gives good productions for successions of clay minerals with a various degree of crystallinity (Karathansas and Hajek, 1983).

In figure 5 an example taken from Sposito (1984) is presented, where chemical thermodynamics, incorporating the GLO step rule has been used on soil weathering, involving some secondary minerals. In this figure an activity-ratio diagram for Al^{3+} in Bt and C horizons of Ultisols is presented. The data point represents the average and range of pAl and PH_4SiO_4 of the soil solutions for the Bt and C horizons. The soil solution composition indicates that, at the pH, pFe(III) and pMg values an association between Al-beidellite and kaolinite of varying disorder is likely. This prediction was confirmed by X-ray diffraction analysis. The log K_{so} values for the soil kaolinites ranged between 7.3 and 10.4, spanning the kaolinite continuum completely, with the larger values tending to be found in C horizons, where smectite predominated.

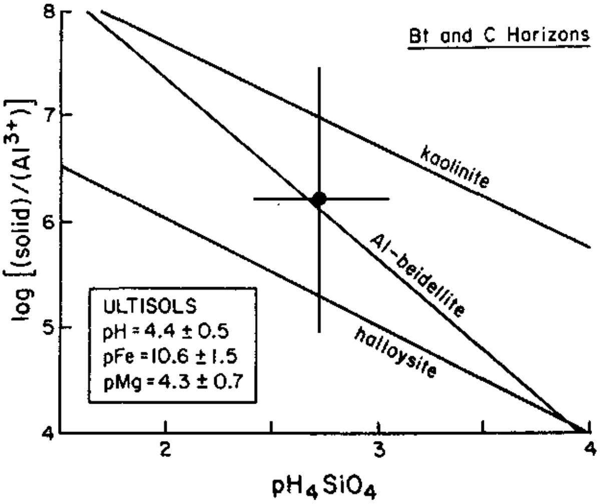


Fig. 5. Activity ratio diagram for Al^{3+} (aq) in Bt and C horizons of four Alabama Ultisols (after Sposito, 1984).

Summarizing with respect to chemical weathering it can be said that within a climatological region the mineralogical composition of the parent material and parent rock often plays a dominant role on the chemical weathering rate and together with the weathering products on nutrient levels and nutrient availability.

The biota can also affect chemical weathering in several ways. Roots can have a physical action on parent material by fracturing rocks. Plants and detritus will retard runoff and promote slow percolation. These effects will enhance chemical weathering. Increasing transpiration will decrease water available for weathering reactions to some extent. The most important effect of biota on chemical weathering is probably through its generation of acidity. Biological respiration by roots and soil biota adds carbon dioxide to the soil atmosphere, thus tending to maintain or even increase the supply of hydrogen ions to the parent material. Organic acids resulting from litter decomposition or root exudation may also play a important role in soil and rock weathering, especially in cool humid environments or in soils with poor parent materials in the temperate humid climates. Sometimes, some of these organic acids, i.e. the fulvic acids, may act as a powerful chelator and play a leading role in mobilisation of metals like iron and aluminium and the alteration of primary and secondary minerals.

Variability is to be expected in chemical weathering rates. Such variability makes prediction of changes in rate over the course of terrestrial succession most difficult. Nevertheless the following tentative generalisation comes from Gorham et al. (1979): "To a large extent the rate of chemical weathering and its changes during succession will be determined by climate, parent material and relief. The biological effects associated with succession will be modifiers of fundamental trajectories set by these physical factors". Changes in weathering rates are likely to be greater during primary succession than during secondary succession - given the same climate, parent material and relief. This fundamental contrast between primary and secondary succession is due to the chemically unstable nature of fresh parent material in a new site due to many easily weatherable minerals. Weathering will last longer to reach a steady state during primary than during secondary succession. However, one has to bear in mind the remarks already given with respect to different time scales for the vert space and the soil space. A good deal of weathering may be independent of the biota, especially in the primary succession, so that changes in weathering rates through succession are not wholly or necessarily biotically induced by succession itself.

Both primary and secondary succession probably exhibit an initial increase in weathering rate with time, because factors change together in ways that promote chemical weathering. These factors may include physical weathering, increased water percolation into physically weathered material, and increased acid-generating capacity through the accumulation of biomass (Gorham et al., 1979). This acid potential could be especially important in those cases of secondary succession where acidity is increased by nitrification following cutting. This was established for the devegetated watershed at Hubbard Brook (Dominski, 1971).

Because by definition secondary succession takes place on previously occupied sites, the amplitude of response should be small and weathering rates will be quickly resumed to their original levels.

The role of phosphorus during successions

The reciprocal interactions of nutrient fluxes and vegetational change on ecosystem level will be discussed here. The clearest examples of the probable influence of such fluxes on vegetation derive from studies of primary succession and soil development in New Zealand (Walker, 1964; Walker and Syers, 1976).

Walker and coworkers have hypothesized that in terrestrial systems phosphorus is the master element, regulating the accumulation of carbon, nitrogen and organic sulphur in soils. They have shown that both the total amount and the chemical forms of phosphorus change irreversibly and predictably during soil development (fig. 6a).

In their scheme the total soil phosphorus pool is divided into four components: 1) easily weathered (primary) minerals such as apatite, indicated as Ca-P; 2) available P or non-occluded P; 3) difficultly weathered (mainly secondary) minerals or occluded P, and 4) organically bound P.

Phosphorus is present in weatherable minerals at the beginning of soil development, in a range of forms including presumably plant-available forms in early and mid-development, and bound in organic matter with a wide C:P ratio or in highly inaccessible mineral forms in the final stage

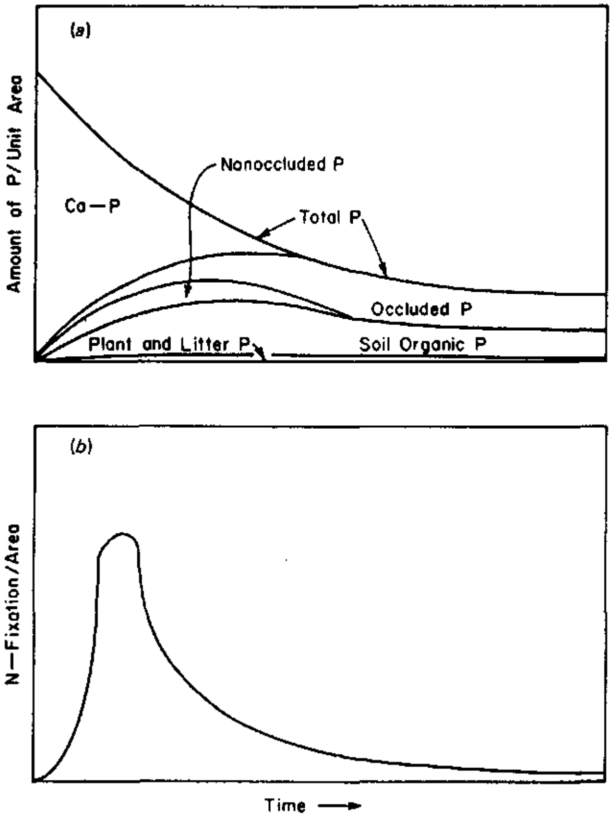


Fig. 6. Changes in total phosphorus and phosphorous fractions in the course of soil development (a); hypothesized changes in nitrogen fixation during soil development (b) (after Vitousek and White, 1981).

of development. The total amount of phosphorus present declines through soil development as a consequence of phorphorus leaching losses. In extreme cases, plant biomass and production can drop markedly late in soil development, probably in response to the low phosphorus levels.

The time scale of the processes shown in this figure is variable from tens of thousands to millions of years, depending on the climate (leaching intensity), the initial phosphorus level and the phosphorus adsorption capacity of the soil material. The time scale for this soil development is always very long with respect to that of the secondary succession. Consequently, the fractions and forms of phosphorus can be regarded as reasonably constant for any single secondary succession event.

Phosphorus exerts control over nitrogen accumulation by influencing nitrogen fixation. Nitrogen fixation rates are controlled partly by an adequate phosphorus supply, partly by available N:P ratios and to a lesser extent on pH, especially for rhizobia (Granhall, 1981). Nitrogen fixation increases in primary succession to a relatively early peak and declines as the N:P ratio in the system increases (allowing the growth of non-nitrogen fixers) and as available P decreases (fig. 6).

The net result of these processes is a system with in the very early stages of soil formation on parent material devoid of nitrogen, nitrogen fixation as an important process. With high phosphorus availability and increasing nitrogen availability, plant production increases and organic matter begins to accumulate in the soil. In the middle steps of soil formation, losses of P are equalled by P input from weathering, the N:P ratio increases and non-N fixers compete successfully for the N and P being mineralised from soil organic matter. The amounts of available N and P are in the optimum range for maximum plant production and organic matter continues to accumulate in the soil. Late in the soil development, soil organic matter begins to decline. This occurs when Ca-P has disappeared or fallen to such a low value that the rate of release of P by dissolution of apatite is less than the loss of P from the system, either by leaching or conversion to unavailable forms or both (fig. 6). Further development of the ecosystem in climates where leaching occurs causes additional loss of P and leads to declining levels of unavailable inorganic P and organically bound P as well as organically bound C, N and S (Walker and Syers, 1976); Melillo and Gosz, 1983).

Finally, it has also to be mentioned that, to the extent that N supply limits biological activity, it can, in turn, influence weathering rates by limiting acid production resulting in a mutual feedback between weathering (P status) and N fixation under these conditions (Reiners, 1983).

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FOREST SITE AS A FRAMEWORK FOR FOREST SUCCESSION

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Summary

An attempt is made to adapt the chronosequence concept of Jenny (1941, 1980) to research on forest succession. By applying forest site as a stable complex of environmental factors and forest community as a stable pool of organisms to the chronosequence concept, the assumption of constancy of independent ecosystem factors can be fulfilled, so that the change in vegetation (succession) can be considered as being a function of time in its relation to stochastic elements.

An example of a graphic model of forest succession on sandy soils in central Netherlands is given and the concept of iterative, alternative, and deflective strategies in forest succession is described. The model enables development trends of the potential natural (climax) forest communities as related to particular sites to be defined. Using the model, communities related to each other can be put on one common successional line and arranged in a system as development stages.

Keywords: Chronosequence concept, forest succession, forest site, iterative, alternative, deflective strategies in forest succession.

Introduction

An appropriate general concept to serve as a theoretical basis for the forest succession research, should fulfil the following criteria:

a) it should be based on the ecosystem theory;
b) it should be easily applicable to the given forestry conditions.

The ecosystem concept developed by Jenny (1941, 1980) seems to fulfil these demands. According to this concept, system properties (as related to the whole system, vegetation, animals, soil) are dependent on or are a function of the state factors (such as climate, pool of species, topography, parent material, time):

$$l, v, a, s = f(cl, \phi, r, p, t, \ldots) \qquad (1)$$

In this relation, time plays a special part. Young ecosystems are strongly controlled by the state factors. In older systems, system properties develop interrelations, forming the content of ecosystems. The autonomous self-regulative processes play a more important role. They cannot, however, exist and function outside the framework of the ecosystem-independent state factors (cf. Gigon, 1975).

Application to succession: the chronosequence concept

The state factors can play different parts in the development of ecosystem properties. One or more of them may be dominant, the others subordinate. When time is dominant, a chronofunction or chronosequence develops:

$$l, v, a, s = f(\underline{t}, cl, \emptyset, r, p, \ldots) \qquad (2)$$

According to Jenny, this chronosequence equation can be understood as a general formula expressing the development of the ecosystem.

If the subordinate factors are invariant or if they vary considerably but with little effect, the equation changes into the following form:

$$l, v, a, s = f(t)_{cl,\ \emptyset,\ r,\ p\ \ldots} \qquad (3)$$

This equation expresses the ecosystem genesis and development in time under a fixed combination of climate, pool of organisms, relief, parent material and dot effects. In other words: succession of a system is a function of time when other variables are constant, or when their changes influence the development of the system hardly or not at all.

Major (1951) applied Jenny's general ecosystem concept to vegetation and its succession. His chronosequence formula has principally the same form and interpretation as Jenny's:

$$V = f(t)_{cl,\ \emptyset,\ r,\ p} \qquad (4)$$

meaning that the succession of the vegetation can be interpreted as a function of the change in time if the independent factors climate, organisms, relief, parent material (and dot factors) are constant or of relatively little importance in determining differences in the vegetation development.

This statement gives rise to the following question:
under what circumstances may the influence of the independent factors be assumed to be constant, so that the vegetation change in question (succession) could be considered as being caused by a change in time only?

The constancy of the independent factors is, of course, a somewhat hypothetical assumption. In fact, such conditions can only occur in climate chambers, within which artificial environments with a given pool of organisms can be created and kept constant.

Under field conditions, the forest site concept seems to approach the concept of constancy of independent factors the best. Below I shall try to develop this hypothesis and to discuss its possible application to research on forest succession.

First, however, three particular aspects of constancy (or non-constancy) should be mentioned:

a) The constancy of a factor does not mean non-fluctuation. In certain factors, constancy seems to have different dimensions: parent material may be seen as a more constant and stable factor than, e.g., climate or water table. Fluctuation in a factor can be diurnal, or seasonal, or short-term, - causing fluctuations in vegetation development but having only little or no influence on the general course of the succession.

b) The non-constancy of a factor has to be understood as a systematic, irreversible shift in the basic characteristics of that factor over a long period (at a scale of decades or centuries) which, at the least, leads to a new quality of the factor in question (e.g. long-term change in the climate; changes in relief e.g. caused by severe erosion; decalcification of parent material etc.).

c) Extreme fluctuations produce a special situation. Because they reach outside the common range of fluctuations of the factor in question, extremes cause drastic, unexpected changes in ecosystems. They can be designated as disturbances or errors. The common feature of these phenomena is stochasticity.

To give non-constancy explicit recognition, Jenny (1980) included the stochastic term $\underline{u}$ in his chronosequence equation. The equation then becomes:

$$l, v, a, s = f(t, u)_{cl,\ 0,\ r,\ p,\ \ldots} \qquad (5)$$

We may assume that, analogous to other factors, stochastic elements can play a dominant or subordinate part in ecosystem development. There is a special relation between time and stochastic elements: when $\underline{u}$ becomes dominant, the role of $\underline{t}$ is unimportant. And vice versa. This relation expresses the very important role of disturbance and stochasticity in the development of ecosystems: during a serious perturbation development in time is broken off: after that, a new development in time can take place, time being dominant and stochastic elements being subordinate factors, until a later perturbation occurs.

Applying this change to Major's approach to vegetation succession, we obtain the following basic equation for the chronosequence:

$$V = f(t, u)_{cl,\ 0,\ r,\ p} \qquad (6)$$

which says that, under a fixed combination of independent environmental factors and stable pool of organisms (in this case reduced to the vegetation), the succession could be considered as a function of time in its relation to stochastic elements.

Application to forestry and forest succession

Forest succession is the pattern of changes in species composition of a forest community during or after an important change in the physical environment or in the community itself. This change opens new ecological niches that can be filled up or colonized by new invadors.

All items in equation (6) can be translated into and interpreted by conventional forestry terms, using forest site as an expression for the complex of independent environmental factors, forest community as the pool of organisms, and time and stochastic elements as factors directly affecting the course of the succession. The equation then expresses forest succession as a development in time (t) in its relation to stochastic elements (u), as related to forest site and forest community.

This interpretation enables the concept of ecosystem genesis and formation to be applied to forestry in concrete forestry terms and with familiar tools. Forest site is understood as being more or less stable complex of environmental factors affecting the composition, structure, development, growth and productivity of a forest community. Forest site types are collections of localities with the same combination of site factors, the same type of relations between the site and forest community and the same silvicultural possibilities. A forest community (here understood as vegetation community) is a complex aggregation of plants, dominated by trees, which develops and exists in a close relation with the physical environment. Under the given site conditions, a forest community has its own development trends, features of inter- and intraspecies competition, regeneration ecology in particular species, etc.

Central to this concept is the relation "forest site - forest community", in Europe better known as "Standortsbezogenheit der Waldgesellschaften" (cf. Jahn, 1969; and others). We may see this relation as a forestry interpretation of Whittaker's "climax pattern concept" (Whittaker, 1953, 1974). According to this concept, the climax is to be interpreted as a steady-state community adapted to the characteristics of its own, particular habitat. We may assume that, logically, Whittaker's concept is valid and applicable not only to the climax community, but also to the preceding succession stages/communities that can develop on particular habitats. This implies that forest site is of essential importance for the succession, defining the framework, limits and gradients within which and along which succession - from the initial up to the climax stage/community - takes place. In this way, the whole ecosystem development gradient can be defined.

Based on this assumption, models of the succession of particular climax communities - or types of the potential natural vegetation - as related to their sites can be developed.

Example of a forest succession model

Using data from research on the spontaneous regeneration of forests on the Veluwe hills, central Netherlands, various types of succession have been distinguished on different sites which, however, could be integrated in a common model (Fanta, 1982, 1983). The model has been given a simple graphic form. It involves both primary and secondary succession with their progressive and retrogressive developments and succession strategies after perturbation (fig. 1).

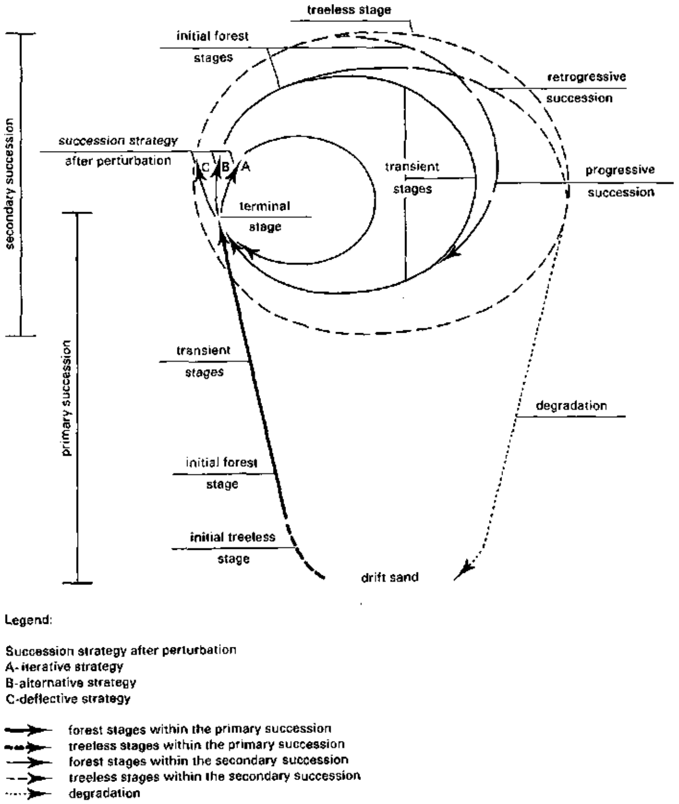

Fig. 1. Model of the forest succession on the lowland sandy soils.

A primary succession takes place on recent and former drift sands. These sands have to be considered as raw, undeveloped substrates which have never before supported any vegetation (substrates without any soil profile, soils in development). The primary succession is considered to be directional, involving various treeless stages and initial, transient and terminal stages of forest.

The secondary succession takes place on soils with a well developed, perhaps even degraded profile. It is considered to be a cyclic process involving both progressive and retrogressive developments in their initial, transient, terminal and treeless stages.

The concept is based on the relationship of successive stages and on the same relationship of forest and herbaceous communities that can develop successively on particular sites. Each community represents one stage in the succession. The entire process can be described as a pattern of stages (dynamic approach) or as a pattern of forest communities (phytosociological approach). Together, the stages or communities form a "succession mosaic" which can be considered as representing the potential natural vegetation in all its development stages.

The way in which forest-tree regeneration and the herb layer react to perturbations in forest communities plays an important role in forest succession. Three succession strategies are possible:

A - iterative strategy: when the same stage/community reappears after perturbation;

B - alternative strategy: when an earlier succession stage/community appears after the perturbation (e.g. pioneers regenerate after decay of a terminal stage);

C - deflective strategy: forest community falls into decay without any tree regeneration; a treeless stage (i.e. a community with herbaceous vegetation) develops as "Ersatzgesellschaft" instead of the forest. This treeless stage can hardly be considered to be a gap in the forest succession; it is a natural part of the succession of the forest.

This threefold concept can be regarded as being analogous or supplementary to the "facilitation - tolerance - inhibition model" of Connell & Slatyer (1977).

The type of disturbance or decay of a forest community and the accompanying circumstances (e.g. whether or not seed fall occurs before or after disturbance) play a very important part in the course of succession following perturbation. In the model, perturbation is not meant to relate to the terminal stage only. At any moment, regardless of its successional stage, the forest community can be disturbed or decay may be caused by elements that have a stochastic character (e.g. hurricanes, floods, landslides, insect plagues), resulting in the start of new developments, either progressive or retrogressive in character. The same situations are well know from the analyses of primeval forests (cf. e.g. Zukrigl et al., 1963; Mayer & Neumann, 1981).

Application of the model

The model has been developed in and tested in lowland conditions. According to Tüxen & Diemont (1937) and Westhoff (1956), substratum and soil are important factors affecting forest communities in this area, resulting in differences in their development. Westhoff even questioned whether in lowlands the climax as a steady state community can develop at all. To date, these problems have rarely been investigated in the field, first of all because of the severe impact of man on forests and soils and secondly because of the absence of natural forests in this area. The model presented here, although simple and only in a preliminary graphic form, might possibly help to overcome the disadvantages of the real situation and help to explain forest development trends in this area.

So far, three different succession sequences have been distinguished and described in the area investigated in the Veluwe. They occur in three different sites with different types of potential natural vegetation (potential climax communities).

We have discovered that the application of the model to forest succession research on particular sites provides much information about regeneration ecology of particular tree and plant species, succession strategies, site properties etc. Using the model, we hope to elucidate development trends of the potential climax communities as related to particular sites (fig. 2). Communities related to each other can be put on one common successional line and arranged in a system as development stages.

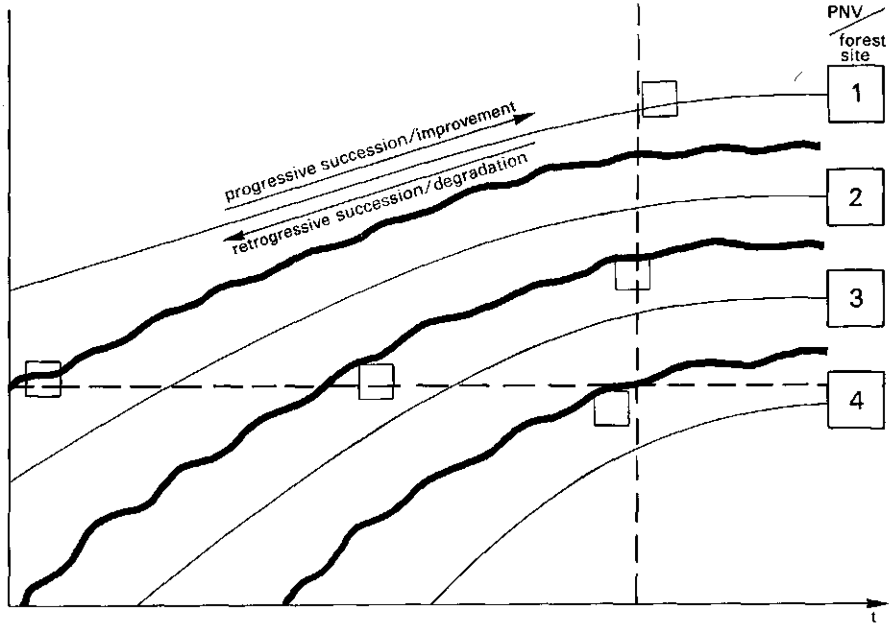

Fig. 2 Scheme of the successional series of the potential natural forest communities and their Ersatzgesellschaften as related to forest sites.

For many years, forest ecologists have been interested in research on development trends of forest communities on particular sites. E.g. Aichinger (1951, 1954, 1974) developed his system of "forest development types" (Waldentwicklungstypen); Mikyška (1964, 1971) introduced the term "fazielle Degradationsphasen" - degradation phases of the natural forest communities caused by applying different silvicultural measures in forests.

The model described above could be a valuable contribution to the solution of this problem. Both degradation and improvement phases as well as progressive and retrogressive successional stages and other phenomena can be incorporated in the system given above. In this way, complete successional series of the potential natural forest communities as related to their sites and their man-made modifications (Ersatzgesellschaften) can be defined. Such a system will supply much useful ecological information and will have a high predictive value, enabling the repercussions of different management decisions and treatments of forest stands on particular sites to be forecast.

Similar models could be developed for different conditions, or maybe this model could be applied to different conditions. I believe that further research in this direction will be of great importance to forest geobotany, forest site doctrine and to both silviculture and forest management practice.

This approach also enables forest succession data to be quantified, e.g. using the Markovian chains method. Horn (1975) applied this method to predict forest development in a mixed forest in the USA. Stratifying the basic data according to sites will undoubtedly provide more exact information. In this way, the predictive value of graphic succession models can be checked, improved and adapted to concrete situations.

Conclusions

Forest site seems to be vitally important for research on forest succession defining border lines of forest ecosystems and forming a framework within which succession takes place. Stochastic elements can play an important part in forest succession, but succession by itself does not happen arbitrarily. Within the site boundaries, succession has its own elementary rules and strategies. These rules and strategies must be known if forest ecosystems are to be understood as dynamic entities.

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Voluntary papers

Section 1: Humus Layer annd Soile Development during Succession

CHANGES IN VIRGIN SOILS CAUSED BY PINUS SYLVESTRIS

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Summary

A preliminary investigation was made of the accumulation and breakdown of amounts of organic matter, total nitrogen, phosphorus and potassium and of soil acidity in the litter (LFH) horizon, in the A horizon and in the C horizon of inland stabilized sand dunes located in the National Park de Hoge Veluwe, The Netherlands.

The study included sites, representing five stages in the development of natural stands of Pinus sylvestris: 1. bare sands, 2. ± 30 years old trees, 3. ± 55 years old trees, 4. ± 70 years old trees, 5. wind blown trees. The organic matter in the litter compartment in the five stages was found to amount to 20-30, 40-70 and again 0 $ton.ha^{-1}$ organic matter respectively. In the litter and A horizon a significant decrease of the pH was found with increasing age of the stands. For instance, the pH H20 in the A horizon decreases from 4.6 in the bare sands to 4.1 in the 70 years old stand. In stage 5 most of the accumulated organic matter in the litter compartment is mineralized, but only about 19% of the organic matter in the litter layer is transferred to the mineral soil. Also most of the nitrogen in the litter compartment is lost after the trees have fallen over. The nature of the changes in vegetation and soil conditions is discussed.

Keywords: Pinus sylvestris, litter accumulation and decomposition, sandy soils, initial soil development.

Introduction

Little factual information is available about effects of a given vegetation on soil properties and soil processes. Especially pertinent information about soil modification by different tree species is scanty (Stone, 1985).

The absence of reliable data is comprehensible since they should be collected by direct observation of the effect of vegetation on soil development through time. The indirect method, by examination of spatial comparison of trees of different ages will only work if the underlying proposition of the method that spatial variation between soils is absent, can be at least substantiated. Subrecently stabilized aeolian sand deposits may be expected to represent rather uniform soil conditions, at least at sites that have not yet experienced spatial diversification by foregoing generations of trees or by differences in landuse in the past. Therefore, using the indirect method, sites were selected in stabilized blown out sands without substantial soil development. The sites included nearly bare sands, sites occupied by spontaneously invaded Pinus sylvestris of different age classes and sites with wind blown trees. It is assumed that the sites represent a chronosequence, which allows to study the effect of Pinus sylvestris growth on initial soil development.

Materials and methods

Site description

Five sites were chosen in an area of approximately 8 ha in stabilized blown out sands in the Otterlose Zand area of the National Park de Hoge Veluwe in the centre of The Netherlands as follows:

I. bare sands with some Corynephorus canescens and bryophytes
II. ± 30 years old trees of Pinus sylvestris
III. ± 55 years old isolated trees of Pinus sylvestris
IV. ± 69 years old Pinus sylvestris trees, scattered within site II
V. trees of Pinus sylvestris of site III, blown over in 1972

The age of the trees was determined with an increment borer. Eight trees were measured in site II and four in sites III and IV. Mean age and standard error are given in table 1.

Table 1. Mean age and standard error of Pinus sylvestris trees in different sites.

Site	II	III	IV
Age	30(4)	55(4)	69(8)

Within the 8-ha area the bare sands (site I) and part of the wind blown sites (site V) were selected on the basis of a vegetation of similar floristic composition: Corynephorus canescens, Polytrichum piliferum, Campylopus flexuosus and Cladonia species. In the other sites the herbaceous layer was absent.

The soil development in the area is rather weak. Only a shallow A horizon has developed and no groundwater is present within several meters of the surface. The soils can be classified in the order to entisols, i.e. mineral soils with very little development. Owing to climate and absence of groundwater these sandy soils belong to the large group of Udipsamments.

Methods

In all sites the litter layer (LF(H) horizon), the A horizon and the C horizon up to 15 cm below the surface of the mineral soil were sampled. The layer was sampled by removal of the litter over a surface of 0.25 m^2. Volumetric samples were taken from the mineral soil by a 'root auger' with a diameter of 0.08 m to a depth of 0.15 m of the mineral soil. In the field, the mineral sample was divided into an A and C horizon. The litter of 0.25 m^2 was weighed wet in the field and a subsample was taken to the laboratory for dry weight determination and chemical analyses. In sites I and V, four samples were taken at random. Four trees were selected in the sites III and IV each, and eight in site II. Below each tree crown, samples of soil compartments were taken at various distances of the trunk; 0-0.5 m, 1-1.5 m (sites II, III, IV), 2-2.5 m, 3-3.5 m and 4-4.5 m (sites III, IV).

All samples were air dried ($90^{\circ}C$) and the bulk density of all mineral soil samples was calculated. Next, prior to further chemical work, the samples of four trees, belonging to the same soil compartment and taken at the same distance to the trees, were mixed in sites III and IV. The same procedure was followed in site II, but those eight trees where split in 2x4 trees before mixing. The samples of site I and V were not mixed. Chemical analyses included pH(H_2O, KCl), organic matter (by loss of ignition), total nitrogen (N-Kjehldahl), total phosphorus (digestion by 1:1 H_2SO_4 (96%), and HNO_3 (65%), molybdate reagent, measured optical densitity at 680 nm and total potassium (destructed in the same extract as phosphorus and measured by AAS).

Calculations

So far, four chemical analyses of mixed samples in the sites III and IV were available, representing the four distances sampled toward the tree. In site II only two distances were sampled but mixed samples here comprised only four trees (out of eight) providing four analyses as well. The four samples of site I were not mixed prior to analysis. So in site I also four analyses of each horizon were available. Therefore, the standard errors or coefficients of variation in the paper are calculated from four analyses each. Because of the variability of the depth of the A horizon in and between sites, the amount of organic matter and N, P, K in the mineral soil (kg.ha-1) was calculated for the A and C horizon to a depth of 0.15 m of the mineral soil.

Results

Changes in the litter layer

Litter accumulation (LF(H) horizon) is absent in the bare sands with only some mosses (I). In the wind blown site (V) all litter had disappeared in the period 1972 - 1982.

A general account on the amounts of accumulated litter and N, P, K (LF(H) horizon) in sites II-IV is given in table 2.

Table 2. Mean values of amounts of litter (LFH) and N, P, K below Pinus sylvestris in different sites. (Estimate of the coefficient of variation in brackets).

Site	mean age trees	O.M. $ton.ha^{-1}$	N $kg.ha^{-1}$	P $kg.ha^{-1}$	K $kg.ha^{-1}$
II	30 (4)	6 (1)	130 (20)	5 (1)	6 (1)
III	55 (14)	77 (29)	1380 (500)	60 (18)	79 (22)
IV	69 (8)	40 (18)	790 (290)	34 (10)	46 (11)

Between site II and sites III-IV the differences, also in tree age, are significant (T-test, P<0,05), but not between sites III and IV.

Depth of the A horizon

In all sites hardly any development of soil horizon can be found, but an initial A/C profile has developed within 10 cm depth of the mineral soil. A significant difference in colour and depth was noticed between the bare sands (I) and the sites with Pinus sylvestris. The colour (Munsell Colours) in site I is black (10 R2/1) and dark grey (10 R4/1-10 R5/1) in the sites with Pinus. Also the depth of the A horizon in site I (table 3) has increased compared to the Pinus sites, but within the Pinus sites no significant changes are seen.

Table 3. Mean depth of the A horizon in the sites. (Standard error in brackets).

Site	Depth A-horizon (cm)
I	3(1)
II	8(1)
III	8(3)
IV	7(2)
V	5(3)

Soil acidity

The acidity of the litter layer, A and C horizon (up to 15 cm of the mineral soil) for the sites I-V which are assumed to form a chronosequence, are given in figure 1 (pH H_2O) and figure 2 (pH-KCl). Both figures show trends for a decrease of the pH of all soil horizons, proceeding from site I to site IV.

Changes in the mineral soil

Volumetric soil samples of the mineral subsoil were taken to asses the amounts of organic matter, nitrogen, phosphorus and potassium in the mineral soil compartments. The amount of organic matter in the upper 15 cm of the mineral soil of the sites is given in figure 3.

The increase of organic matter in site V compared to site IV must be attributed to a transfer of organic matter from the litter layer (which disappeared after the Pinus trees were blown by the wind) to the mineral soil. The large variations indicated for site IV and V are mainly due to the bulk densities within these sites; the trends indicated in figure 3 are only partly reflected on a percentage of weight base (table 4).

Table 4. Mean values (x) and standard erros of the organic matter content on a dry weight base (%) in the A and C horizons of the sites.

	sites	I	II	III	IV	V
A horizon	x	1.6	1.7	1.6	1.3	2.5
	s	1.2	0.6	0.6	0.1	1.1
C horizon	x	0.7	0.9	0.9	0.9	1.4
	s	0.1	0.1	0.2	0.1	0.5

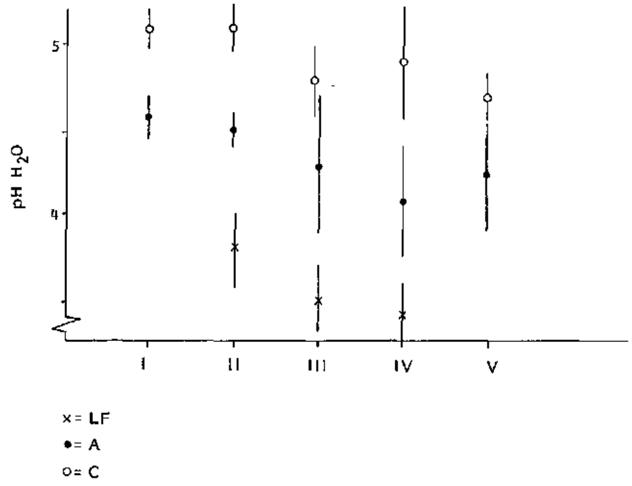

Fig. 1 pH H_2O in the litter layer, A and C horizons of sites 1-V. Standard deviations originate from different sampling distances to the trees within a site.

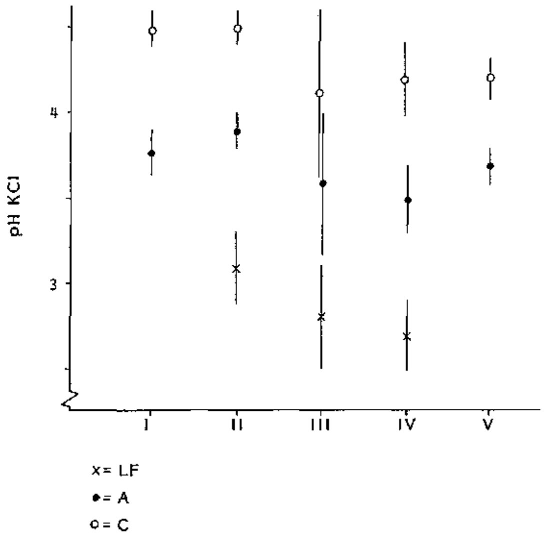

Fig. 2 pH-KCl in the litter layer, A and C horizon of sites I-V. Standard deviations originate from different sampling distances to the trees within a site.

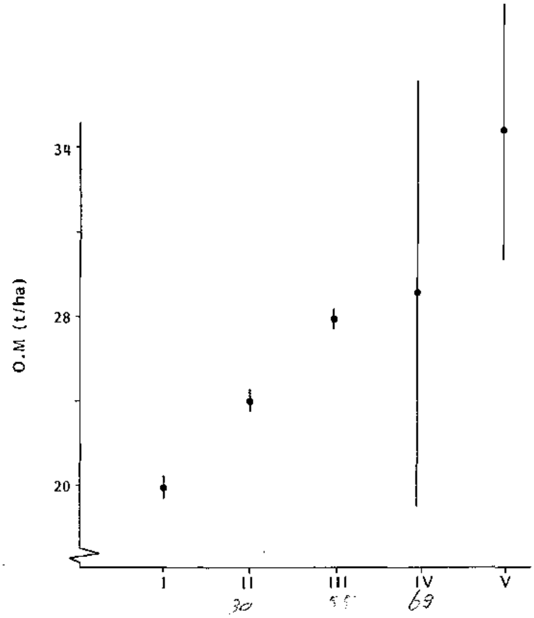

Fig. 3 Amounts of organic matter (O.M. $ton.ha^{-1}$) in the upper 15 cm of the mineral soil in sites I-V. Standard erros comprise the variation originating from the sampling distance to the trees within a site.

The trends in organic matter in the upper 15 cm of the mineral soil (fig. 3) are not found in the amounts of nitrogen, phosphate or potassium (table 5).

Table 5. Amounts ($kg.ha^{-1}$) of total nitrogen, phosphorus and potassium in the upper 15 cm mineral soil (Standard error in brackets).

Site	O.M. $ton.ha^{-1}$	N	P $kg.ha^{-1}$	K
I	20	486 (7)	127 (36)	2003 (20)
II	24	396 (60)	98 (20)	1673 (18)
III	28	555 (15)	117 (22)	1896 (14)
IV	29	479 (18)	91 (18)	1405 (11)
V	35	516 (22)	167 (20)	2221 (23)

Discussion and conclusions

An interesting fact in the wind blown site V is the reappearance of a ground vegetation of Corynephorus canescens and mosses, a vegetation also found in the blown out sands (site I) not yet colonized by Pinus sylvestris.

The cyclic change in the vegetation is also seen in the litter layer. Like in the open sands, no litter was observed in the selected 'wind blown' site, which explains probably the reappearance of the ground flora of bare sands in the wind blown site.

Despite the cyclic change in litter accumulation after falling over of the trees in site V, transfer of organic matter from the litter compartment to the mineral soil in time is evident from figure 3. Especially the wind blown site V shows an increase of about 6 ton.ha^{-1} organic matter, compared with site IV. At the time of the wind blowing event the trees in site V were about 57 years old (the trees have the same age as those in site IV: 69 years in 1982; wind blowing occurred in 1972). If we assume a linear relation between age and litter accumulation as suggested by the data in Ovington (1961, table 1), interpolation of the data of sites II and IV suggests (table 6) that at the time the trees fell down about 32 ton.ha-1 organic matter was available in the litter layer.

Table 6. Assumed (see text) total amounts of organic matter, nitrogen, phosphorus and potassium in the litter horizon below the trees of the wind blown site at the time of falling over (1972).

O.M. ton.ha^{-1}	N kg.ha^{-1}	P kg.ha^{-1}	K kg.ha^{-1}
32	639	27	37

In that case, about 19% (6 ton.ha^{-1}) of the litter was transferred to the mineral soil (up to 15 cm depth). In table 7 the mean amounts of N, P and in the mineral soil K in site I-IV are calculated from data in table 5.

Table 7. Mean values of N, P and K (kg.ha^{-1}) in the upper 15 cm of the mineral soil of sites I-IV and in site V.

Site	N kg.ha^{-1}	P kg.ha^{-1}	K kg.ha^{-1}
I-IV	479	108	1744
V	516	167	2221

If we compare the amounts of phosphorus and especially of potassium in the mineral soil with the relatively low amounts of these elements in table 6 it is obvious that a transfer of P and K from the litter horizon to the mineral soil cannot be detected. With regard to nitrogen, however, it can be seen that the amount of nitrogen in the litter compartment (table 6) is of the same magnitude as the amount of nitrogen in the mineral soil (compartment) (table 7). However, hardly any more nitrogen is found in the mineral soil of site V compared to sites I-IV. Therefore, it should be concluded that most of the nitrogen stored in the litter compartment is lost from the soil system, after falling over of the trees.

With respect to soil acidity it can be concluded from figures 1 and 2 that the pH drops in the litter horizon and A horizon as trees grow older. This observation is in line with the literature (Dickinson & Pugh, 1974). After the trees fall down (site V) the pH tends to increase. An increase of the pH is also found after clear-felling of the forest (Nykvist & Rosen, 1985).

Acknowledgement: We thank the Director of the Hoge Veluwe for permission to work in the National Park. Chemical analyses were made by the Chemistry Department of the Research Institute of Nature Management.

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STUDIES ON ORGANIC SOIL PROFILES I : METHODOLOGY AND ITS APPLICATION IN THE HULSHORSTERZAND

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Summary

In this paper the general context and characteristics of studies on organic soil profiles, as carried out by the University of Amsterdam are discussed.

First, attention is paid to the specific position and development of the organic profiles and the role of soil forming factors are described. The study has been carried out in five first generation Scots pine stands of increasing age 15, 30, 55, 90, and 130 years, all on recent drift sands without antecedent soil formation.

It was found that evident differences exist between soils within the chronosequence related to the various stands. Within the time-span the increase of thickness of the organic profile and differentiation between and development of new organic horizons together with development of new organic horizons together with development of a micropodsol are most prominent.

Keywords: Organic profiles, humus profiles, humus, sandy soils, Veluwe, Netherlands, multivariate analyses, Twinspan, succession, *Pinus sylvestris*, micropodsol.

Introduction

In the past, organic profiles (humus profiles) have long been neglected by pedologists, in particular in The Netherlands, although studies on humus and its role in plant nutrition and soil structure are old topics in soil science. However, it is increasingly understood that knowledge about their characteristics and genesis is essential for pedogenetic and ecological studies of non-agricultural soils.

Organic profiles hold a position, which is intermediate between mineral soil and edaphon. Its properties are strongly controlled by the input and characteristics of the biomass (litter) and by the soil fauna and flora. The system, as compared to mineral horizons, rapidly adapts to changes in conditions.

Research on organic profile development and its pedological implications is hindered by the fact that organic profiles, as observed in the field, largely owe their characteristics to processes active in the past. These processes were dependent on factors such as vegetation and drainage, which may have rapidly changed in time, as well as on the antecendent soil formation.

In general the number of factors and variables is too large to allow quantitative statements on the genesis and characteristics of organic profiles as dependent on substratum and vegetation. Such data are essential prerequisites for genetic classifications of soil profiles, applicable in the field.

The research of the FGBL of the UvA concentrates on the genesis of organic profiles as dependent on the factors parent material, time and vegetation, with the aim to develop a genetic classification. Our approach is to study field situations in which the number of variables is limited and all relevant factors are well known. This implies that the research is carried out on organic profiles, developed in recent parent materials, without relevant antecedent soil formation, with a vegetation of which management and age are exactly known and with a well defined hydrology.

Current research projects

Thus far four situations have been studied.

Hulshorsterzand (Central Veluwe): recent eolian sands of uniform composition with first generation Scots pine stands. The stands are of different age. The herbal layers in the stands represent a distinct vegetation succession.

Petrea (North Veluwe): pre-glacial sands of ice-pushed ridge.
Variables are:
- vegetation differentiation in a thirteen years old natural vegetation;
- substratum characteristics, i.e. uniform parent material with a strongly disturbed podzol (variable antecendent soil characteristics).

Bremerbergbos (Oostelijk Flevoland): recently reclaimed polder, calcareous marine-lacustrine deposits. Only one variable:
- vegetation (plantations of Robusta and Balsem Poplar, 27 years old).

Lepelaarsplassen (Zuidelijk Flevoland): recently reclaimed polder, calcareous clays and sludge deposits under natural willow stands.
Only one variable:
- parent material.

This paper deals with the research on organic profile development during the forest succession in the Hulshorsterzand area (Central Veluwe).

Data collecting and statistical approach

Both semi natural and planted forests in The Netherlands are divided into parcels and often one or two species are planted or sowed in one parcel. For decades this has been common practice in forestry. This means that one might expect uniform development of the organic profile under a uniform stand in one parcel. However, studies on organic profiles, like those in the Hulshorsterzand, face three major problems:
- variability in composition of the input of biomass produced by different trees and different herbal layers;
- variability in quantity of biomass input related to the distance of major litter sources (distance towards stem and canopy);
- variability in ecological conditions such as microclimate.

These together results in a high variability of organic profiles at microscale. This means that the study on the overall habitus of the organic profile under different vegetation types e.g. parcels with different stands and/or different species has to be carried out, using statistical methods.

In the Hulshorsterzand this approach was as follows:

In five first generation Scots pine stands of increasing age (15, 30, 55, 90, and 130 years), all on recent drift sands without antecedent soil formation, sites were selected at random. At these sites soil profiles were extensively described, using the Guidelines for Soil Profile Description (FAO/UNESCO, 1975) for the mineral profile and the system of Klinka et al. (1981) for the organic profile. Klinka's descriptive system is basically similar to that of the FAO/UNESCO. Vegetation at the sites was also recorded. Data of the organic profile were statistically analyzed, using standard methods as well as Twinspan, which is a computer-programme for multivariate analyses currently used in ecological studies.

The collected data consist of:

- numerical properties like thickness of the horizons. These were analyzed using statistical methods like determining mean values of thickness and standard deviation of recorded values within one stand;
- non numerical morphological properties like horizon designation, character of boundaries, kind of material, fabric, roots, biota and soil flora. These were described and/or scaled into classes.

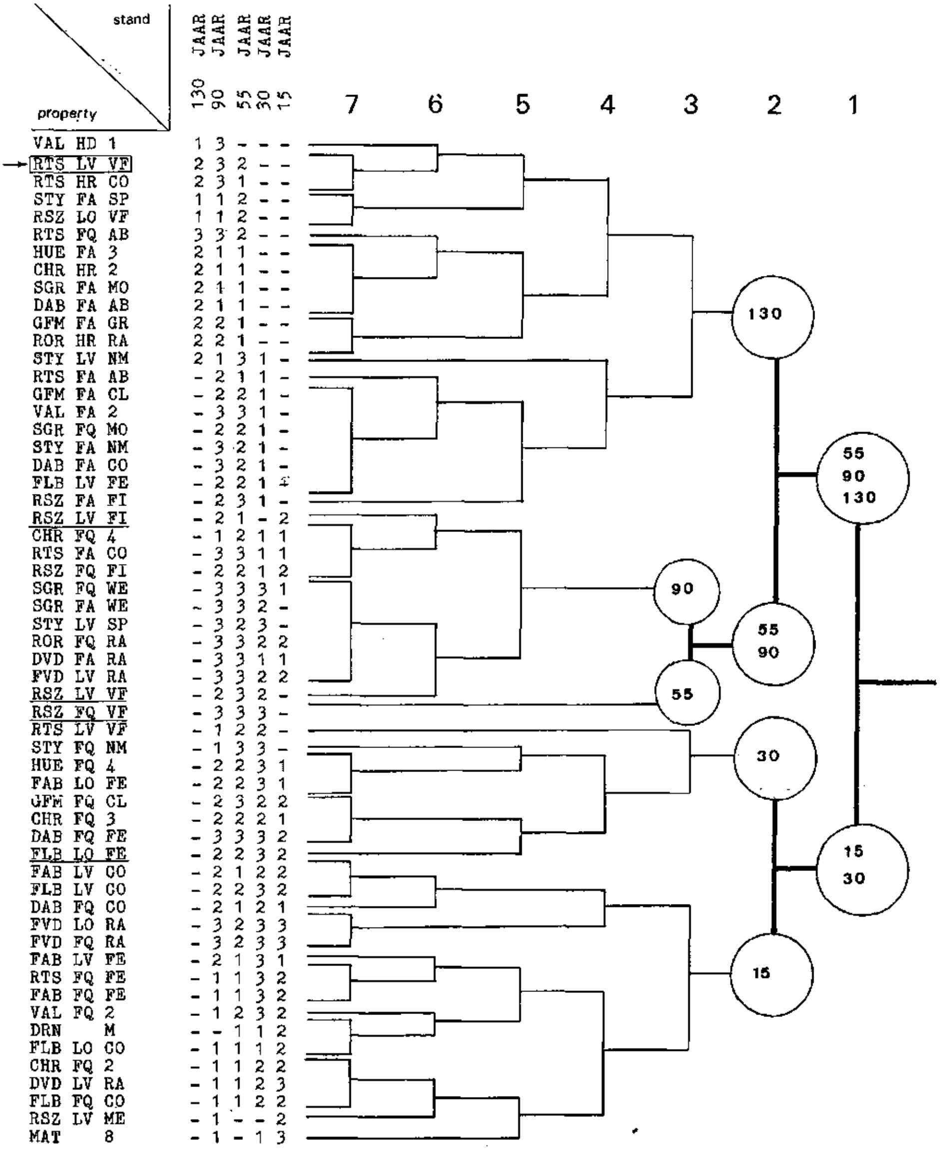
Here most attention will be paid to the statistical approach to the non numerical properties.

The non numerical morphological field properties scaled in classes were converted into coded data, in order to use these as input for Twinspan. Property, class of the property (sub-property) and the horizon symbol were combined in one binary code which is related to field conditions in one of the five stands. This means for instance that a descriptive property like the form of a boundary of the F-horizon, scales into smooth, wavy, irregular or broken. The use of classed properties results in a strongly increasing number of sub-properties in the Twinspan programme.

The Twinspan programme has been used to identify relations between morphological characteristics and organic profile succession. It compares all properties with the five stands. To do so frequencies for each sub-property are calculated for each stand. This means that the initial number of site characteristics is reduced to a new set of attributes for each of the different stands. The frequences of the sub-properties are split up into three 'cutlevels': 0-25%, 26-50%, 51-100%, giving a high and stable quality of classification. The cutlevels are retrieved as 1, 2, 3 in the output of Twinspan (see figure 1). The structure of the output resembles that of the Braun Blanquet method.

Figure 1 shows a dendrogram of the output of Twinspan. At each level preferential and non preferential properties, e.g. the differentiating criteria, were determined and resulted in a split up into 7 levels. The first three levels show the ranking of the five stands. The other 4 levels show the grouping of properties within one stand.

The ranking of the stands, although obvious in the field, is done without the numerical data on the sites as well as without data on sub-properties occurring in less than three stands. This means that there are also certain morphological properties which are exclusive for one stand.



property	130 JAAR	90 JAAR	55 JAAR	30 JAAR	15 JAAR
VAL HD 1	1	3	-	-	-
→ RTS LV VF	2	3	2	-	-
RTS HR CO	2	3	1	-	-
STY FA SP	1	1	2	-	-
RSZ LO VF	1	1	2	-	-
RTS FQ AB	3	3	2	-	-
HUE FA 3	2	1	1	-	-
CHR HR 2	2	1	1	-	-
SGR FA MO	2	1	1	-	-
DAB FA AB	2	1	1	-	-
GFM FA GR	2	2	1	-	-
ROR HR RA	2	2	1	-	-
STY LV NM	2	1	3	1	-
RTS FA AB	-	2	1	1	-
GFM FA CL	-	2	2	1	-
VAL FA 2	-	3	3	1	-
SGR FQ MO	-	2	2	1	-
STY FA NM	-	3	2	1	-
DAB FA CO	-	3	2	1	-
FLB LV FE	-	2	2	1	4
RSZ FA FI	-	2	3	1	-
RSZ LV FI	-	2	1	-	2
CHR FQ 4	-	1	2	1	1
RTS FA CO	-	3	3	1	1
RSZ FQ FI	-	2	2	1	2
SGR FQ WE	-	3	3	3	1
SGR FA WE	-	3	3	2	-
STY LV SP	-	3	2	3	-
ROR FQ RA	-	3	3	2	2
DVD FA RA	-	3	3	1	1
FVD LV RA	-	3	3	2	2
RSZ LV VF	-	2	3	2	-
RSZ FQ VF	-	3	3	3	-
RTS LV VF	-	1	2	2	-
STY FQ NM	-	1	3	3	-
HUE FQ 4	-	2	2	3	1
FAB LO FE	-	2	2	3	1
GFM FQ CL	-	2	3	2	2
CHR FQ 3	-	2	2	2	1
DAB FQ FE	-	3	3	3	2
FLB LO FE	-	2	2	3	2
FAB LV CO	-	2	1	2	2
FLB LV CO	-	2	2	3	2
DAB FQ CO	-	2	1	2	1
FVD LO RA	-	3	2	3	3
FVD FQ RA	-	3	2	3	3
FAB LV FE	-	2	1	3	1
RTS FQ FE	-	1	1	3	2
FAB FQ FE	-	1	1	3	2
VAL FQ 2	-	1	2	3	2
DRN M	-	-	1	1	2
FLB LO CO	-	1	1	1	2
CHR FQ 2	-	1	1	2	2
DVD LV RA	-	1	1	2	3
FLB FQ CO	-	1	1	2	2
RSZ LV ME	-	1	-	-	2
MAT 8	-	1	-	1	3

Fig. 1. A dendrogram showing differentiating properties of the organic profile related to the different stands of Scots Pine in the Hulshorsterzand area. On the left side the codes of the properties are listed. RTS LV means that Roots abundance (RTS) in the Lv horizon in the 130 year old stand is very few (VF).

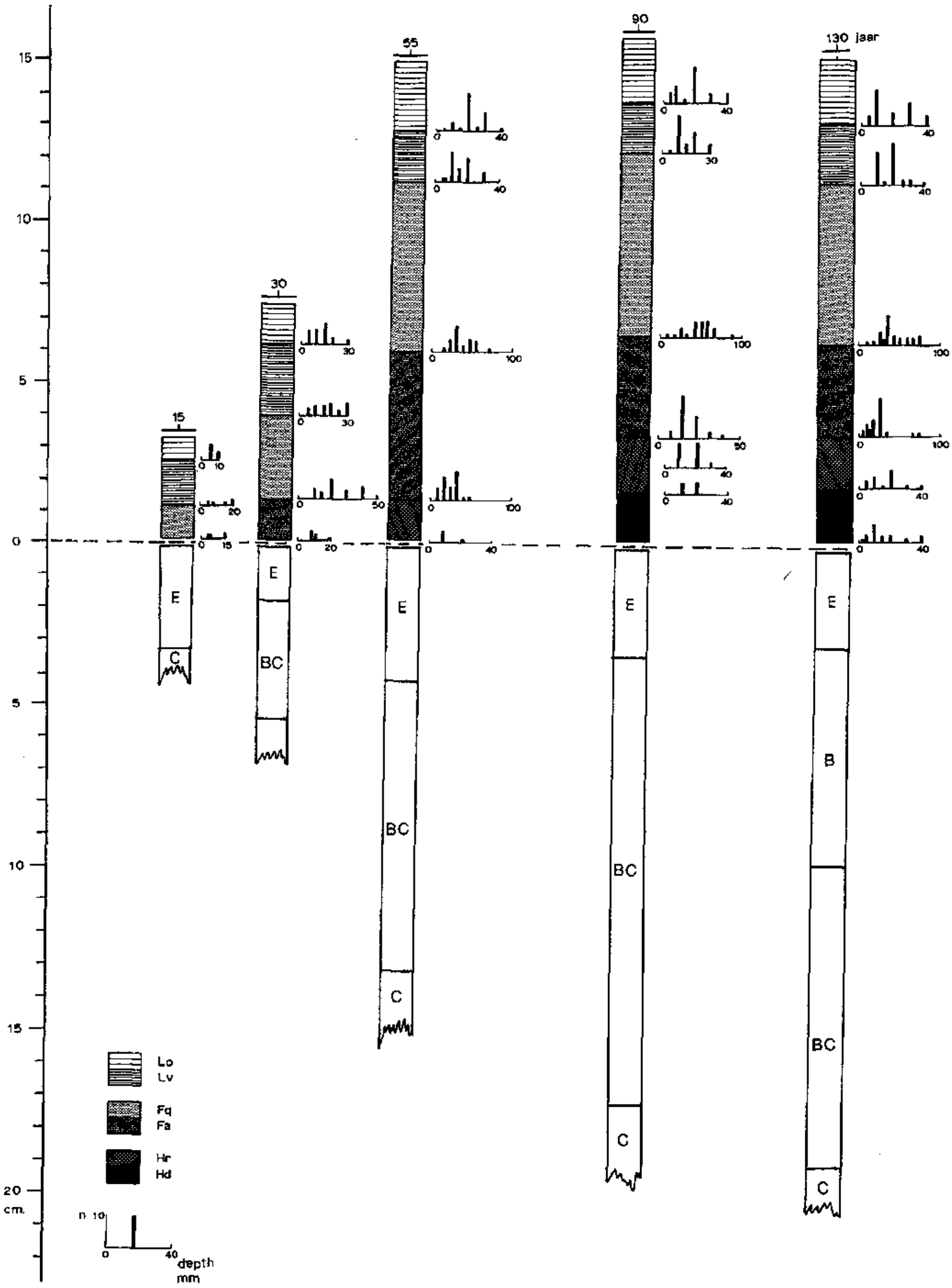


Fig. 2. Standard soil profiles including frequency diagrams of thicknesses of organic horizons for each of the Scots pine stands.

Discussion of results

The Twinspan analyses show that clear differences in non numerical properties exist between the various stands, closely related to differences in age. These results, which will not be dealt with in detail here, are in conformance with the results of the statistical analyses of the numerical properties. The latter are as follows:

The chronosequence exhibits a strong increase in thickness of the organic horizon as well as a clear differentiation in time. Soil horizon development and differentiation in the mineral profile is less pronounced and is restricted to the development of a micropodzol.

The organic profile:

In fig. 2 the "standard soil profiles" for each of the stands studied are indicated, with mean thicknesses of specific horizons within a stand. To the right the thickness of the various organic horizons at the sites studied is presented in a frequency diagram. This diagram provides essential information on the variations in thickness of the horizons within the parcels. Mean thickness of the various organic horizons is also indicated in table 1 with, in addition, the standard deviation and the number of profiles studied.

Table 1. Mean thicknesses of the organic horizons with their standard deviation of the various Scots Pine stands.
n* = number of soil profiles.

	n*	Lo	Lv	Fq	Fa	Hr	Hd
15 years	(12)	7 (3)	14 (7)	10 (6)			
30 years	(20)	13 (6)	22 (16)	26 (13)	11 (5)		
55 years	(26)	21 (8)	15 (7)	52 (23)	45 (8)	13 (5)	
90 years	(29)	20 (10)	15 (7)	56 (22)	31 (32)	17 (7)	15 (5)
130 years	(29)	20 (13)	18 (8)	49 (22)	28 (19)	16 (10)	16 (12)

The first conclusion which can be drawn is that the thickness of the organic profile strongly correlates with the age of the stand. Its strong increase from 30 to 55 years, however, needs some comments. The 15 and 30 years old stands are spontaneous pine stands, whereas the 55 years old stands has been planted. In its initial stages the latter stand had a denser tree stand and a higher biomass production, which may have resulted in a more rapid development of the organic profile. Secondly, *Deschampsia flexuosa*, when abundantly present as is the case in the older stands, seems to induce the development of a relatively thick organic profile.

As regards the thickness of the litter layer, equilibrium seems to be reached in about 55 years. It should be stated that in the younger soils (15 and 30 years) the thickness, compositon and bulk density (related to the composition) are quite variable, whereas in the older soils these are rather uniform.

The thickness of the fermentation layer, discontinuous in the 15 years old stand, rapidly increases with increasing age. Its considerable and rather uniform thickness in the 55 years stand is probably connected with the abundance of *Dechampsia flexuosa*. The slightly decreasing thickness of the F horizon in the older stands might be connected with a lowered vitality (lower litter production) of Deschampsia with increasing age, in combination with the introduction of species with a biomass production, which is lower and/or of a different composition. Vegetation in these older stands becomes more differentiated. Frequency distributions of thickness in the 55 and 90 years old stands are close to normal. However, in the 130 years old stand a bimodal distribution was found, strongly correlated with the rather differentiated herbal vegetation: thinner under Deschampsia and thicker under Empetrum and Vaccinium.

H horizons were first encountered, as discontinuous pockets, in the 30 years old stand. In the 55 years old stand locally a thin Hr horizon was found, mainly in pockets, but Hd horizons were not observed. In the older stands (90 and 130 years) the H horizon is continuous and its thickness only slightly increases in time. Observations in 300 years old pine stands elsewhere in The Netherlands show that equilibrium will only be reached after a very long period of time.

The mineral profile:

All soils studied are well drained and can be classified as vague soils ("*duinvaaggronden*").

In fig. 2 the "mean mineral profile" in the various parcels has been indicated. With respect to the horizon designation used the following needs to be stated:

- The E horizon

The drift sands contain a small amount of iron, which is present, together with a little clay, as thin coatings around the sand grains. Horizons, immediately underneath the organic profile, which lack these coatings and have a bleached appearance, have been described as E horizons. Whether iron indeed has been eluviated or is still present, but bound to organic matter, has not been established.

- The B and BC horizons

Underneath the E horizon a weakly developed B horizon is present. When having a slightly redder hue and stronger chroma than the parent material, due to slight illuviation of iron (together with organic material), but lacking soil structure, this horizon has been described as a BC horizon. In case that soil structure, although weak, is observed which is accompanied by a more distinct difference in hue and chroma, such horizon has been described as a B horizon.

Figure 2 shows that with increasing age the thickness and development of the mineral profiles increases. The thickness of the E horizon, however, hardly increases with age. Contrasts between the various horizons, not indicated in this figure, on the contrary, regularly increase with age. This indicates that the presence of an E horizon, as defined above, not necessarily implies a vertical transport of iron c.q. slight podzolisation. In fact mineral profiles with a B horizon, which represent distinct micropodzols, were only encountered in the 130 years old stand.

Conclusions

Each of the stages in a vegetation succession has a specific impact on the environment and therefore strongly determines the development and character of organic profiles. However within a stand which represents a specific succession stage the effect of other factors such as geomorphology, exposition and local vegetation becomes prominent and causes a large variability in organic profiles characteristics. This means that it is difficult to identify those properties which characterise a specific stage within a vegetation succession.

The results show that horizon sequences together with thicknesses of individual horizons differentiate, to some degree, for soil profiles in stands of different age. For profiles with a similar horizon sequence, the Twinspan programme allows the identification of properties of individual master horizons, which characterize the individual stands.

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STUDIES ON ORGANIC SOIL PROFILES II: SUCCESSION OF ORGANIC MATTER PROFILES IN THE HULSHORSTERZAND

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Summary

Changes in soil profile morphological characteristics related to stand age of Scots pine, on well drained recent active eolian sand dunes, were found to be closely correlated with a number of relevant soil chemical and soil physical properties.

The conductivity (Ec) of water extracts within the various horizons decreases with time and depth. A sharp boundary exists between the organic horizons with high Ec values and mineral horizons with relatively low Ec values. This Ec pattern has a striking coincidence with the distribution of rootmass and thus with the uptake of nutrients in time and space, by Deschampsia flexuosa. The various pH curves clearly indicate that a steady state equilibrium is not yet reached within the upper organic horizons and that in near future pH values will further decrease.

The decrease of C/N ratio of the organic horizons with time must be ascribed to the resultant of a) residual accumulation of primary organic matter with high C/N values and b) the overruling effect of fixation of nitrogen in secondary newly formed organic substances with relatively low C/N ratio.

Keywords: Organic profiles, humus profiles, humus, Veluwe, Netherlands, multivariate analyses, succession, Pinus sylvestris, humification, mineralization, rootmass, biomass, sandy soil.

Introduction

As described in the paper "Studies on organic profiles I" morphological properties of organic profiles under Pinus sylvestris stands in the Hulshorsterzand were found to change strongly in time and to be closely related to the age of these stands, which form a vegetation succession.

Although the characteristics of organic profiles are related to vegetation succession, it is clear that the profile itself exerts considerable influence on the nature of the succession of (semi) natural vegetation. Most seeds for example, germinate in the organic horizons and changes in ecological conditions within these horizons will have effect on their germination. Of particular interest is therefore what changes occur in physical and chemical properties of organic profiles and for what reasons and, furthermore, how plants react on these changes.

One of the aims of our research on organic profiles is to establish whether a relation exists between the morphological properties, as observed in the field, and the ecological characteristics. Some results of such research in the Hulshorsterzand are presented here.

In order to prevent confusion the terms used in this paper for the description of organic matter will be briefly elucidated. "Biomass" comprises all organic matter present in the profile and consists of living organic matter (fauna, flora and roots) and of dead organic matter. The latter comprises the litter and all kinds of transformed organic material, generally referred to as humus. Several authors use the therm humon for the dead organic matter in the soil profile and, in analogy, the term "humomass" is used.

Analyses and results

In each of the Pinus sylvestris stands (30, 55, 90 and 130 years old) one soil profile has been sampled. To cope with the internal variability of the different stands and the related variability in soil properties, sampling sites were located under the middle of the largest branch of a tree. Care was taken to sample sites with similar exposition and geomorphology. The profiles thus selected, with respect to their morphology, strongly resemble the "standard profile" of the stand. Organic horizons were sampled by collecting all material within a square, of which the surface area is known, thus enabling the calculation of their bulk density and dry weight per unit surface area. Mineral horizons were sampled by normal methods (bulk samples and pF rings).

The following analyses have been carried out:
Total biomass of the organic horizons (figure 1) and within each horizon: Biomass and rootmass, pH (H_2O) and pH ($CaCl_2$) in 1:5 solutions (figure 4), conductivity (Ec 25° C) and dissolved $NH_4{}^+$ and $NO_3{}^-$ in 1:10 extracts of organic horizons and conductivity (Ec 25^0C) in 1:2 extracts of mineral horizons. Total nitrogen and carbon of the organic matter (figure 7) and loss of weight by 500^0C.

Discussion

In figure 1 total biomass of the profiles analyzed is plotted against the age of the stands. The curve flattens after 90 years, which implies that the accumulation of organic matter slows down after this period. The decrease in biomass accumulation after 90 years, in so far as biotic factors are concerned, can be due to 1) changes in the quality and quantity of the litter input, and 2) changes in the quality and quantity of the biomass input by roots.

As can be seen in figure 2, biomass expressed in kg/m^2 and horizon thickness in cm, the biomass of the litter horizon is rather constant or even slightly increases, which indicates that quantity of litter input remains rather constant. Its quality, which is reflected by the C/N ratio of the litter, ranging from 30 in the youngest stand, via 30 and 29, to 28 in the oldest stand, seems rather constant too, see figure 7. Apparently, changes in the input of biomass by roots and their quality are at least partly responsible for the decrease in biomass accumulation after 90 years. This is strongly supported by the analytical data, as will be discussed below.

Rootmass of each horizon in g/m^2 together with biomass in kg/m^2 is presented in figure 3a. The density (I) of the rootmass, for Fa and Fq horizon, expressed as the ratio rootmass/biomass versus age is presented in figure 3b. It must be stated that, for some L horizon, the separation of herbal vegetation from the rootmass is problematic. The high rootmass of such horizons is partly due to these problems and therefore not plotted in figure 3b.

The overall rootmass of the organic profiles, table 1, shows that, within the organic profile, an optimal rootmass within the whole soil profile occurs in the 55 and 90 years old stand, and that rootmass

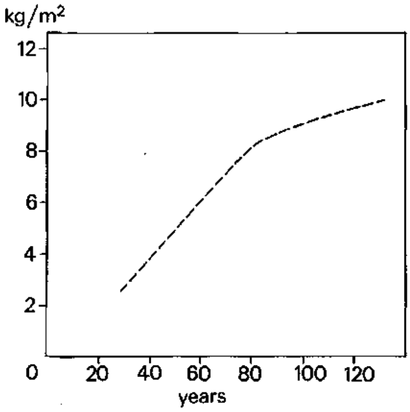

Fig. 1. Total accumulated biomass (kg/m^2) of four profiles under <u>Pinus sylvestris</u>, related to the age of the stands.

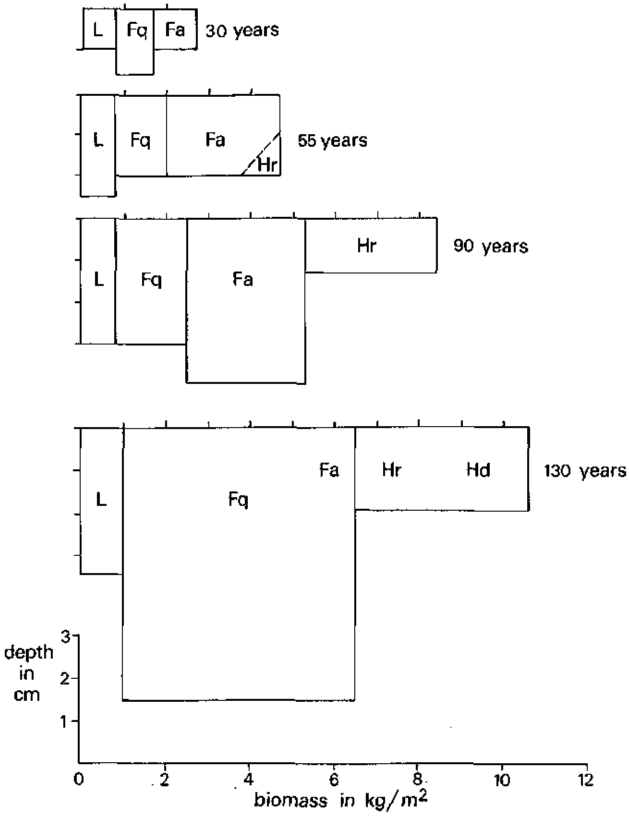

Fig. 2. Biomass (kg/m^2) and depth (cm) of the different organic horizons within four profiles under <u>Pinus sylvestris</u>, related to the age of the stands.

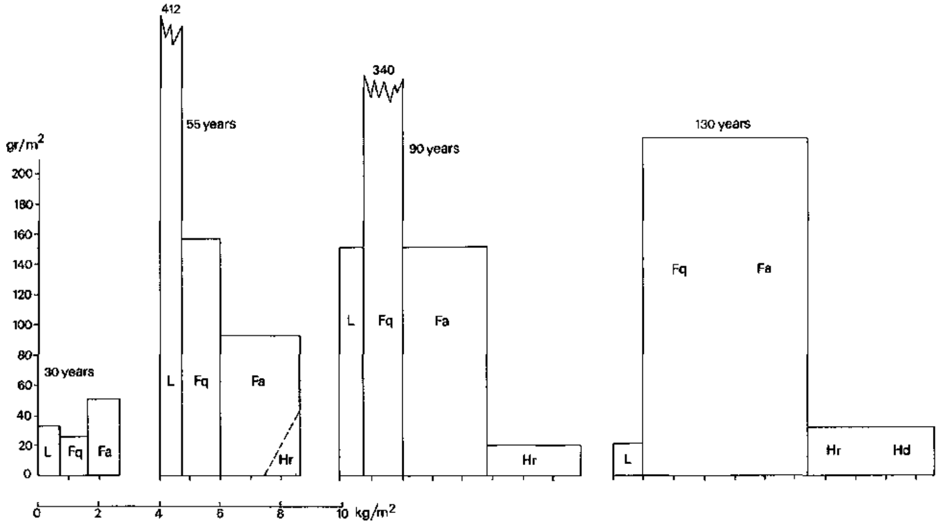

Fig. 3a. Biomass (kg/m^2) and rootmass (g/m^2) of the different organic horizons within four profiles under Pinus sylvestris, related to the age of the stands.

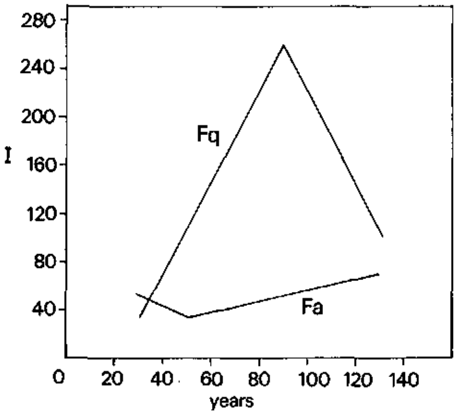

Fig. 3b. Rootindex (I) : Rootmass/biomass of the Fq and Fa horizon related to the age of the Pinus sylvestris stands.

spectacularly decreases in the 130 year old stand.

Table 1. The overall rootmass of the organic profiles.

30 years	135 g/m^2	
55 years	754 g/m^2	
90 years	762 g/m^2	
130 years	289 g/m^2	with a relatively high rootmass in the B horizon

The distribution of rootmass over the different horizons, figure 3a, shows that the depth of the optimal rootzone increases with time. With regard to the individual horizons, the pattern in the Fq horizon is most striking. As can be seen from figure 3b and table 2 root density within the Fq horizon varies the most. Root density as well as rootmass increases with age until approximately 90 years. After that period, within the Fq horizon, rootmass decreases and biomass strongly increase. Roots, in the 130 years old stand, are randomly distributed through the Fq, Fa, Hr and mineral horizons.

Table 2. Rootmass and biomass of the Fq horizon.

	age of stands	30	55	90	130	years
rootmass	Fq horizon	29	170	378	239	g/m^2
biomass	Fq horizon	823	1323	1819	8944	g/m^2

The vitality of the dominant herb, Deschampsia flexuosa, in the 90 years old stand has already diminished and this herb, in the 130 years old stand, is replaced by a much more varied herb vegetation with abundant Empetrum nigrum. This coincidence, in the Hulshorsterzand is striking!

To which extent the change in vegetation can be ascribed to a gradual change in organic profile characteristics, in favour of the development of a more varied and deeper rooting herbal vegetation, or is an autonomous process in the vegetation is not clear. However, the chemical data, to be discussed later on, are strongly in favour of the first.

The statistical analyses of the field data (see table 3) confirm the tendencies observed in the profiles analyzed. This table shows the root abundance at random sites within the five different stands in the Hulshorsterzand. The classes represent counts of roots within a fixed area (Klinka, 1981).

Table 3. Roots abundance. no=none/ fe=few/ co=common/ ab=abundant

	15	30	55	90	130 year
L	fe	fe	fe	fe	fe
Fq	fe	fe	co/ab	ab	ab
Fa	no	co	co	co	ab
H				co	co

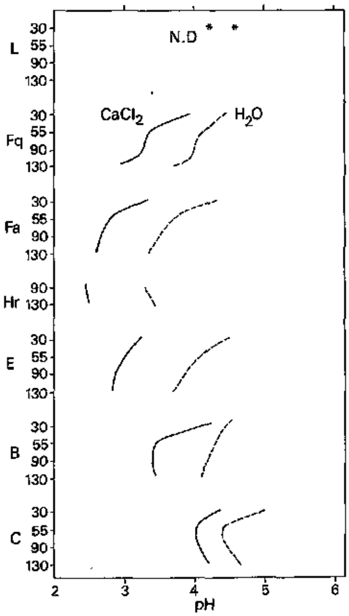

Fig. 4. pH (H_2O) and pH ($CaCl_2$) of the various horizons within four profiles under Pinus sylvestris, related to the age of the stands.

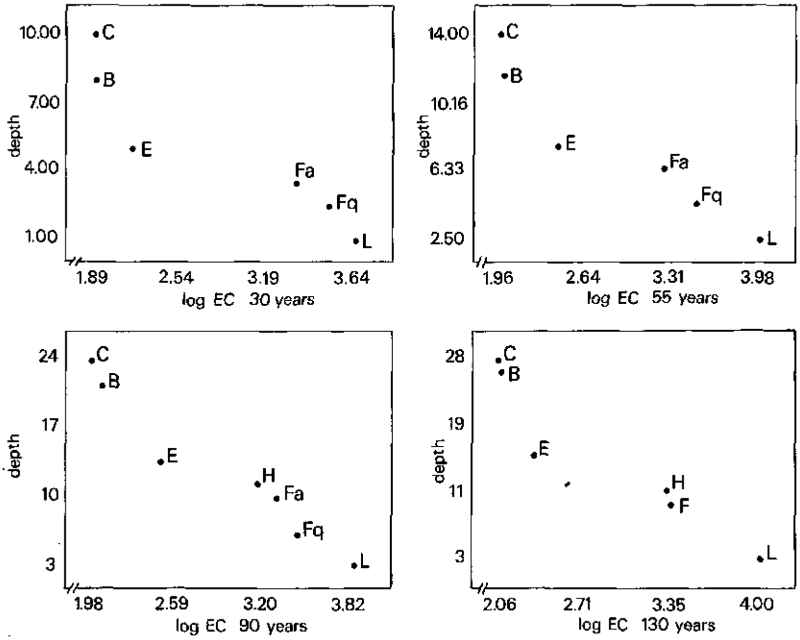

Fig. 5. Log Ec 25°C plotted against horizon depth of the various horizons, of the four profiles under Pinus sylvestris, related to the age of the stands.

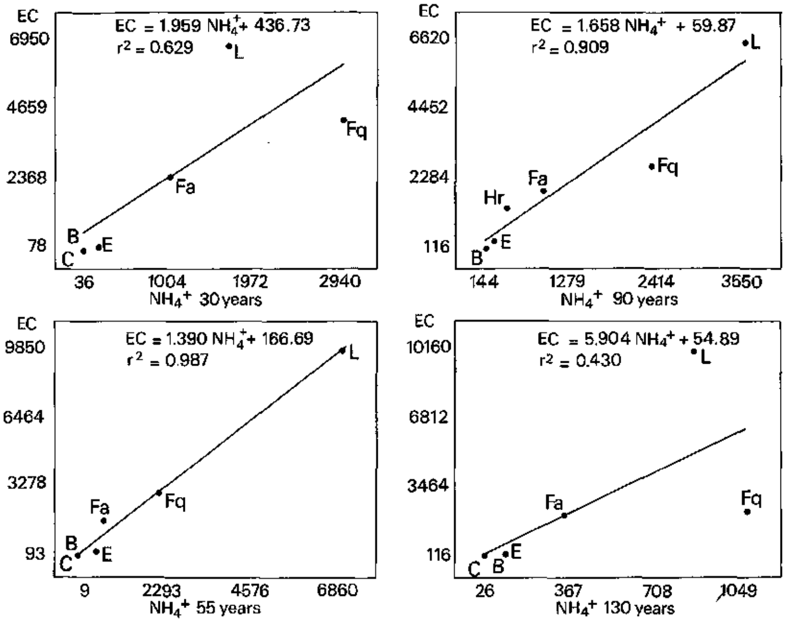

Fig. 6. Ec 25°C plotted against NH_4^+ concentration (umol/l) of the various horizons, of the four profiles under Pinus sylvestris, related to the age of the stands.

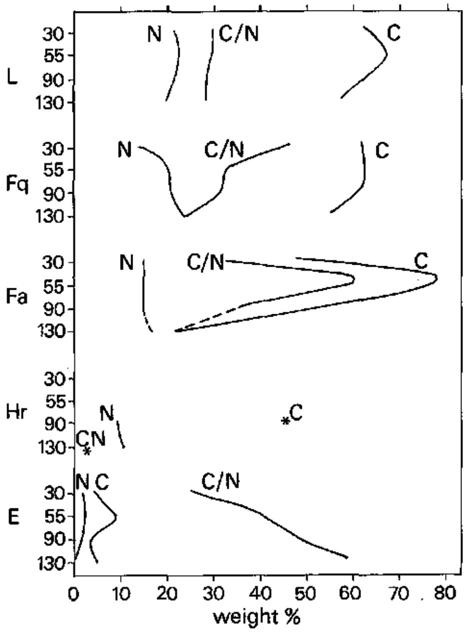

Fig. 7. C, N (weight %) and C/N ratio's of the various horizons, of the four profiles under Pinus sylvestris, related to the age of the stands.

The conductivity (Ec) is a measure for the availability of nutrients to plantgrowth. It is dependent on the mineralization and humification of organic matter. Figure 5 clearly shows a decrease of Ec with depth and a sharp boundary between the organic horizons, with relatively high Ec values, and the mineral horizons with relatively low Ec values. These figures illustrate that within the soil profiles two totally different zones exist: The organic zone with a high rootmass (uptake of nutrients) and the lower mineral zone. This chemical zonation is reflected, in the field, by sharp boundaries between the mineral and organic horizons.

As stated before, the C/N values of the litter horizons are rather invariable. However, the differences in Ec 25 values between the various litter horizons suggest that some changes in the chemical composition of the litter occur. This can be expected in view of the changing composition of the herbal layer.

In figure 6, the Ec 25°C is plotted against NH_4^+ concentration in mmol/liter. It clearly shows that Ec is positively correlated with the NH_4^+ concentration. NO_3- is low and slightly increases with depth to a maximum of 16 micromol/liter within the B and C horizon. In these horizons the ratio NH_4^+/NO_3- roughly equals one. The data indicates that mineralization of organic matter results in the production of NH_3, which reacts with H+ to NH_4^+. This explains the relatively high pH and Ec of the litter horizons, see figure 4. The uptake of NH_4^+ by roots, together with nitrification (relatively insignificant), produces H^+ ions. This uptake happens in the lower organic horizons (see root distribution discussed above) and results in lowered pH and Ec values of these horizons (see figure 4 and 5).

In the mineral soil pH increases with depth, as can be expected because of its low rootmass, its balanced NH_4^+/NO_3- ratio and its acid buffering capacity.

Figure 4 shows the change of pH within similar horizons, related to the age of the stands. The curves clearly indicate that a steady state equilibrium is not yet reached and that in near future pH values of the upper organic horizons will further decrease. The coincidence of the relatively strong decrease in pH and the disappearance of <u>Deschampsia flexuosa</u> between approximately 90 and 130 years, indicates that further acidification strongly reduces competitive vigour of <u>Deschampsia</u>!

An interesting phenomenon within the Fq horizon is the positive correlation between the Ec 25 and the C/N ratio, which decrease with increasing age of the stand (see figure 8). In the 30 year old stand

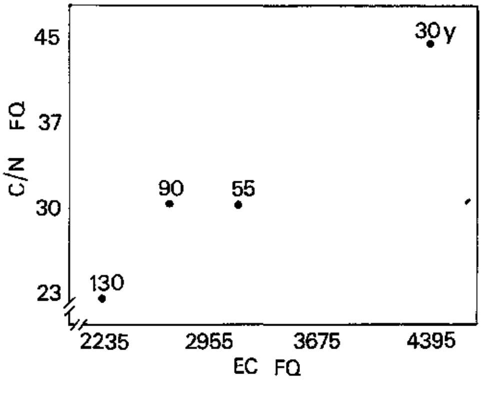

Fig. 8. The relation between C/N ratio and Ec 25 within the Fq horizons related to the age of stands.

biological and root activity is low; fixation of nitrogen within newly formed organic material therefore must be in time, as biological and root activity increases, nitrogen fixation increases proportionally. The overall result is a decrease in the C/N ratio. The concurrent decrease in Ec, as stated before, must be ascribed to the uptake of nutrients by the vegetation and by newly formed humic substances.

These conclusions are in accordance with data on droppings abundance of random sampled soils within the different stands (table 4). Droppings abundance is known to be correlated with biological activity and thus with the uptake of nutrients. Droppings abundance clearly shows an increase in faunal activity in the Fq, Fa and H horizon with time as well as from the upper to the lower horizons.

Table 4. Droppings abundance. no=none/ fe=few/ co=common/ ab=abundant

	15	30	55	90	130 year
L	fe	no/fe	no	no	no
Fq	fe	fe/co	fe	fe	fe/co
Fa	fe	co	fe/co	co	co
H				ab	ab

Conclusions

Changes in profile morphological characteristics were found to be closely correlated with a number of relevant soil chemical and soil physical properties. These properties are indicative for the nutrient cycling and uptake and for the mineralization and humification of organic matter. Most indicative appeared to be the root system and the faunal activity in the soil. These are frequently neglected in pedological and biological studies.

Field surveys on root systems, faunal activities and related soil properties were found to be usefull to establish the changes in the ecological conditions in soils within a vegetation succession. These may provide the essential basis for an ecological organic profile classification.

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STUDIES ON ORGANIC SOIL PROFILES III: SOIL DIFFERENTIATION UNDER POPLAR AND WILLOW STANDS IN THE FLEVOPOLDERS

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Summary

Forest plantations in the Flevopolders, reclaimed during the fifties, offer very good possibilities for studies on the relationships between the factors vegetation, parent material and time and the initial soil formation, in particular the development of the organic profile.

Preliminary research was carried out on two poplar stands (Robusta and Balsam), both 27 years old and on similar parent material, and on two natural willow stands, both 17 years old, but on different parent materials (sandy versus clayey). The soils, although very recent, shows marked differences in profile morphology as well as in chemical characteristics. "Robusta soils" and "clayey willow soils" exhibit for example less accumulation of organic matter, stronger nitrification and a higher nutrient status. These phenomena can be ascribed to differences in the rate of mineralisation/humification of the litter.

In case of the willow stands, the differentiation is most probably due to the less favourable soil physical conditions in the sandy soils. The differentiation in the "poplar soils", however, seems to be due to differences in litter characteristics, in particular their edibility.

Keywords: Humus profiles, marine deposits, nutrient cycling, poplar stands, willow stands.

Introduction

East Flevoland has been reclaimed in 1955 and South Flevoland in 1968. It is therefore not surprising that soil development in these polders is still in its infancy: Leaching, weathering and accumulation of organic matter have only just started and soil ripening is often still incomplete.

The Flevopolders are particularly suited for studies on the effects of vegetation, parent material and time on initial soil development, in particular on the development of organic soil horizons. The main reasons for this are that the vegetational history is exactly known and that a large variety of forest plantations and parent materials occurs. Drainage, furthermore, is strongly controlled and antecedent soil formation is completely lacking.

Preliminary investigations on the organic profile development, of which the first results are presented below, have been carried out at two sites: the Bremerbergbos and the Lepelaarsplassen. A more systematic study into the organic profile development of forest soils in the Flevopolders started in summer 1985.

Site characteristics

In the Bremerbergbos soils on similar parent material and with similar drainage, but under different types of poplar plantations (Robusta and

Table 1. Organic matter contents in weight % (upper part) and densities in kg/m^3 (lower part).

Bremerbergbos Poplar				Lepelaarsplassen			
Robusta		Balsam		Willow 1		Willow 2	
L	58.9	L	77.4	L1	79.0	L	84.3
Ah1	10.2	F	50.0	L2	38.7	Ah1	25.5
Ah2	5.0	F+A	22.5	A	5.8	Ah2	9.4
Bw1k	2.1	Bw1	2.3	Bw	5.8	Bw1	9.8
Bw2	4.5	Bw2	2.2			Bw2	8.3
		Bw3	4.1				
L	67	L	37	L1	99	L	32
Ah1	100	F	41	L2	91	Ah1	174
Ah2	1190	F+A	212	A	784	Ah2	167
Bw1k	1310	Bw1	1240	Bw	870	Bw1	n.d.
Bw2	1310	Bw2	1240			Bw2	n.d.
		Bw3	1240				

Balsam), were studied. Both stands are 27 years old. The soils are developed in calcareous silt loams (top soil) to silty clay loams (deeper than 30 cm), overlying coarse sands (see also figure 1). Subsequent on its reclamation, but prior to being planted, the parcels have been used for agriculture for a period of 5 years and at that time have been fertilized (mainly N-fertilizer). In the same period the "balsam parcel" has once been treated with insecticides.

In the Lepelaarsplassen soils under two natural willow stands, about 15 years old, but on different parent materials were studied. The stand "willow 1" is on a thin sludge deposit with a texture of sandy clay loam, overlying deposits with a texture of clay loam. "Willow 2" lacks the sludge deposit and is directly on the clay loam (see also figure 1).

Field observation showed that marked differences exist in profile development, in particular of the organic profile, between the different stands in both Bremerbergbos and Lepelaarsplassen: Balsam poplar and "willow 1" exhibit a stronger accumulation of organic material and a more pronounced horizon differentiation. In each stand a characteristic profile was described and sampled for further analyses.

Analyses and results

In figure 1 the soil horizons of the four profiles analyzed are schematically indicated. The soil horizons are according to the Guidelines for Soil Profile Description (FAO/UNESCO, 1975) and to the system of Klinka et al. (1981).

General data on the soil profiles are presented in figure 1 (carbonate contents and grain size distribution) and in figure 2 (C and N contents, C/N ratios and pH values). Organic matter contents and bulk densities are listed in table 1. Compositions of soil water extracts are presented in table 2 and are expressed in mmol/100 g dry sample. The amounts of water soluble Ca, Mg and K, expressed in mmol/m^2 per cm soil as well as total amounts per soil horizon are presented in figure 3, 4 and 5. In figure 6 values for water soluble NO_3-, NH_4 + and org. N are presented.

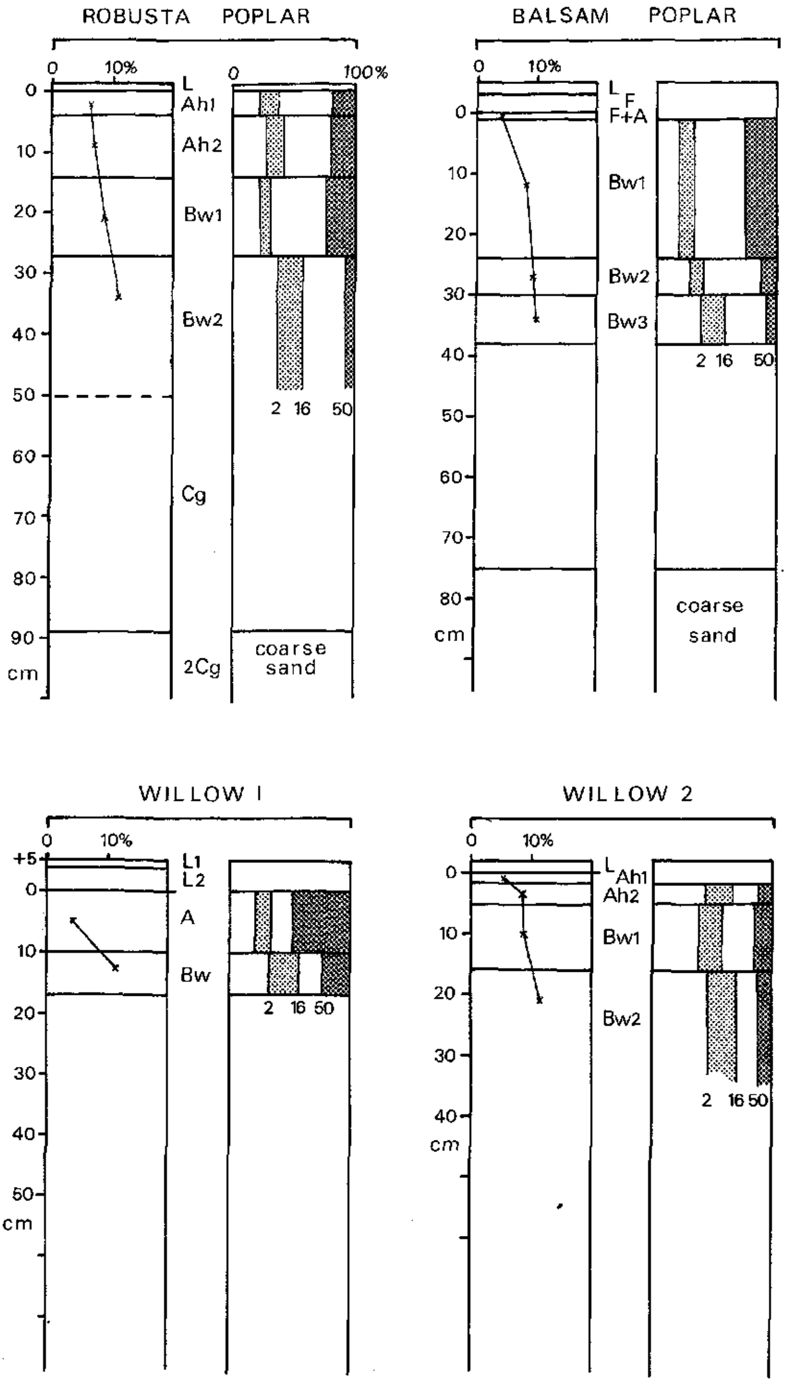

Fig. 1. General data on the soil profiles studied:
Left: Soil horizons and carbonate contents.
Right: Grain size distribution (fractions <2 , 2-16 , 16-50 and >50).

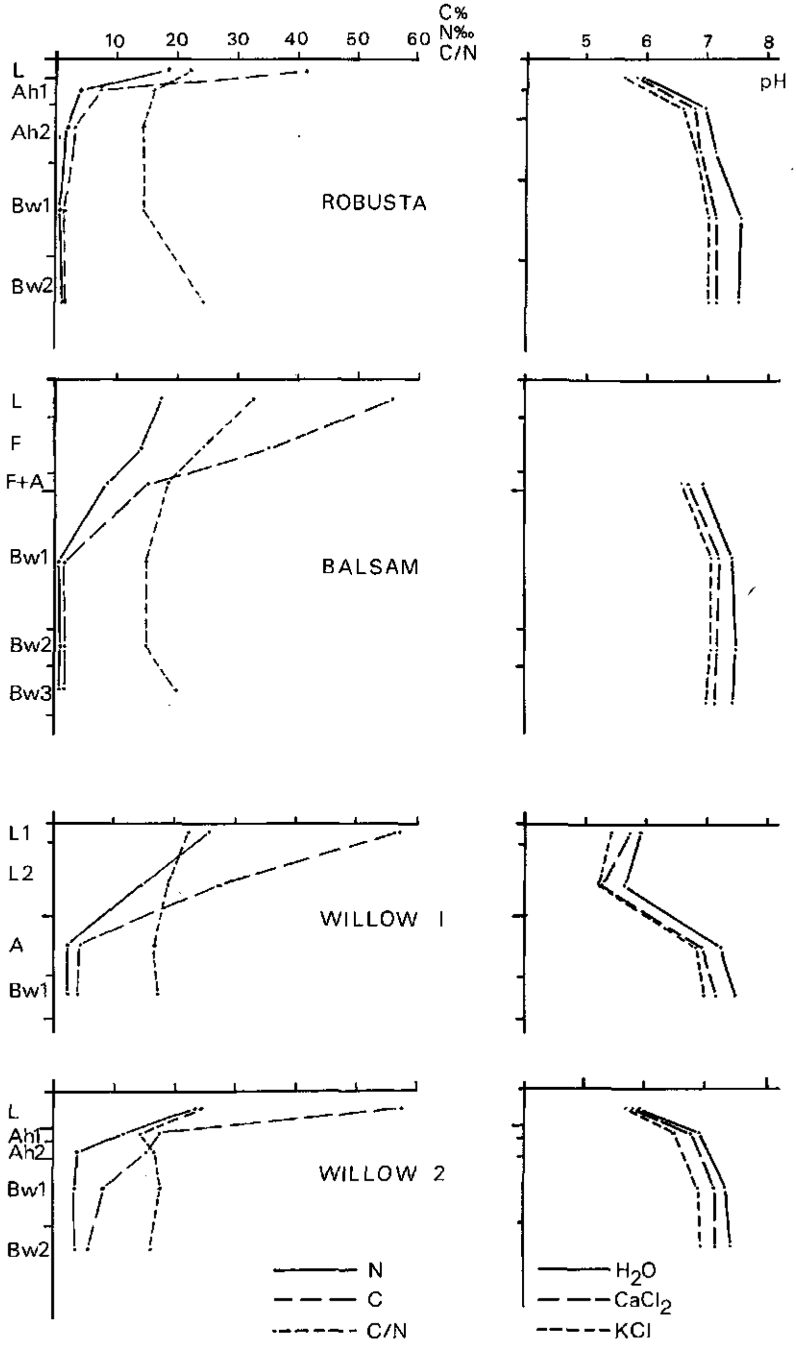

Fig. 2. Chemical data
Left: Total C and N and C/N ratios.
Right: pH values in 1:5 extracts (organic horizons) and 1:2.5 extracts (mineral horizons).

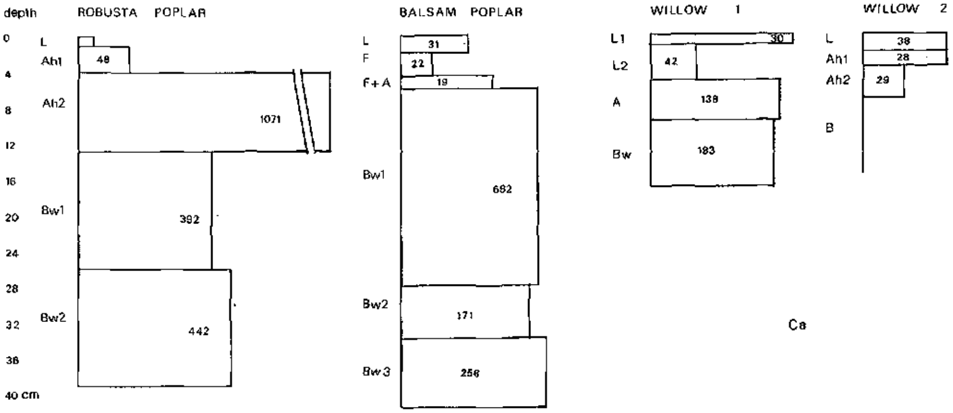

Fig. 3. Water soluble Ca^{2+} expressed in mmol/m^2 per cm soil and total amounts in mmol/m^2 per soil horizon.

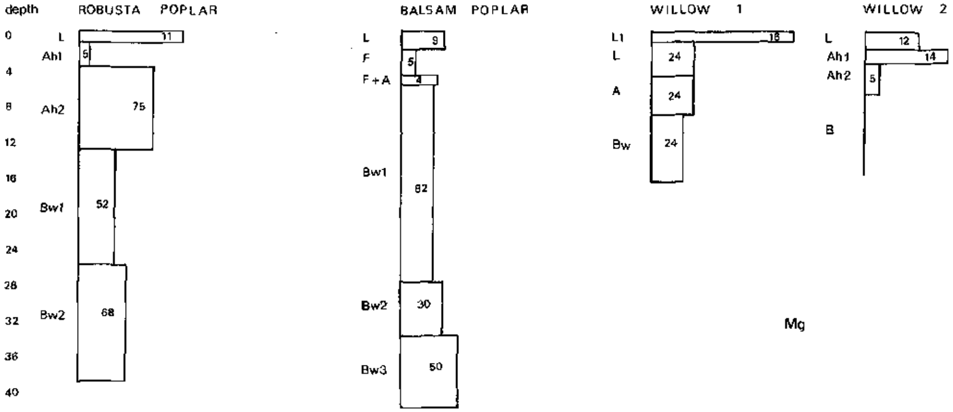

Fig. 4. Water soluble Mg^{2+} expressed in mmol/m^2 per cm soil and total amounts in mmol/m^2 per soil horizon.

Discussion

The general data confirm the field observations: The soils with stronger developed organic horizons (Balsam and willow 1) indeed exhibit a more pronounced accumulation of C and N and, under poplar, a distinctly higher C/N ratio.

The poplar stands

The Balsam poplars, as compared to the Robusta poplars, exhibit a more vigorous growth. However, although some related differences will exist in biomass input and in elemental composition of the input in the poplar stands, these cannot account for the observed differences. These must primarily be ascribed to differences in the rate of mineralization and humification as well as in the faunal and microbial activities connected with these processes.

Field evidences for a stronger faunal activity under Robusta poplar are the weak horizon differentiation and well developed fine crumb structure of the Ah horizons , which in the soil under balsam is, respectively, strong and weak coarse angular blocky.

Indications for a more retarded breakdown of litter into humus and a lower level of nutrient cycling under the Balsam poplar are also found in the soil water analyses: Water soluble N, K, Ca and Mg (i.e. kg/m^3) are lower. Furthermore, organic N is the dominant N species and NO_3- is low, indicating that N-mineralization and nitrification are somewhat retarded. These data also point, for the Robusta poplar, to a massive mineralization and release of nutrients in the Ah2 horizon, which in fact is the main rooting horizon, whereas under the Balsam poplar a much more regular distribution and lower level are observed.

Lower rates of mineralization and humification under the Balsam poplar should lead to stronger accumulation of organic C and N, i.e. to higher total amounts of organic C and N, expressed in kg/m^2. Unfortunately the initial organic matter content of the sediment is relatively high and as a result only a rough estimate of the amount accumulated can be obtained. Taking as a measure all organic matter in the L and Ah1 horizons of the "Robusta profile" and in the L, F and F+A1 horizons of the "Balsam profile", these values are 0,65 kg C and 0.034 kg N per m^2, and about 1.2 kg C and 0.048 kg N per m^2 respectively.

As regards the water soluble P contents, these are clearly controlled by their solubility in calcareous media and thus, except for the organic horizons, are invariably low.

The poplar parcels, prior to being afforested, have been managed in different ways (fertilization and insect control). It is, hoewever, extremely unlikely that these differences in management practices had more than very temporal effects, i.e. only on the very initial organic profile development. The atmospheric input of N over the past 27 years, for example, exceeds by far the amounts added as fertilizer. Furthermore, levels of water soluble phosphate show little variation between the stands, except for organic P content, which is controlled by the characteristics of the organic matter. It is therefore concluded that the differences in preafforestation management played an at most very insignificant role in the genesis of the soils studied. Lastly, in the field no indications

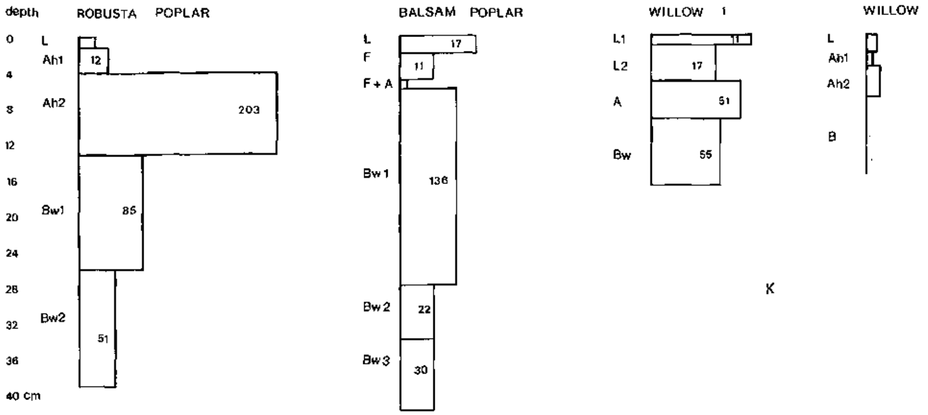

Fig. 5. Water soluble K$^+$ expressed in mmol/m^2 per cm soil and total amounts in mmol/m^2 per soil horizon.

were found for differences in soil fauna composition, other than related to differences in soil conditions, earthworms being present at both sites.

Given the constancy of all soil forming factors, but the vegetation, the already quite considerable differences (in 27 years) in humification, mineralization and nutrient cycling can only be ascribed to differences in litter characteristics, in particular in their edibility for the soil fauna. It is not excluded that such lower edibility has to do with the "exotic" origin of the Balsam poplar.

The willow stands

The soils under the willow stands exhibit similar phenomena: C and N accumulation, horizon differentiation and soil structure are closely related to each other and are most expressed in Willow 1. Estimation of

Table 2. Composition of soil water extracts expressed in mmol/100 g dry sample.

Horizon	K	Ca	Mg	NH_4	NO_2 NO_3	org N	ortho P	org P	SO_4	HCO_3
Robusta poplar, Bremerbergbos										
L	0.28	5.48	1.71	5.30	0.00	6.56	1.49	1.17	0.85	6.76
Ah1	0.29	1.21	0.13	0.10	0.31	0.24	0.03	0.03	0.01	1.47
Ah2	0.19	1.00	0.07	0.05	0.08	0.12	0.00	N.D.	0.01	0.10
Bw1	0.05	0.23	0.03	0.00	0.00	0.03	0.00	0.00	0.02	0.42
Bw2	0.03	0.26	0.04	0.00	0.00	0.03	0.00	0.00	0.04	0.48
Balsam poplar, Bremerbergbos										
L	2.30	4.18	1.27	2.29	0.02	3.74	1.40	1.29	0.69	3.51
F	0.91	1.76	0.41	0.76	0.47	0.98	0.21	0.31	0.18	3.51
F+A	0.04	0.97	0.19	0.29	0.17	n.d.	0.02	n.d.	0.04	1.96
Bw1	0.05	0.25	0.03	0.01	0.01	0.06	0.00	0.00	0.01	0.47
Bw2	0.03	0.23	0.04	0.00	0.00	0.03	0.00	0.00	0.03	0.40
Bw3	0.03	0.26	0.05	0.00	0.00	0.04	0.00	0.00	0.05	0.32
Willow 1, Lepelaarsplassen										
L1	1.15	3.02	1.61	3.21	0.81	3.36	1.19	0.50	0.29	5.25
L2	0.81	1.15	0.52	0.60	0.79	1.19	0.38	0.07	0.27	1.38
A	0.13	0.34	0.06	0.01	0.14	0.08	0.00	0.00	0.02	0.57
Bw	0.09	0.30	0.04	0.00	0.10	0.07	0.00	0.00	0.03	0.52
Willow 2, Lepelaarsplassen										
L	0.46	5.88	1.92	8.29	0.07	9.94	2.45	1.27	0.87	6.36
Ah1	0.05	1.09	0.53	0.23	0.00	0.55	0.02	0.06	0.07	2.24
Ah2	0.11	0.50	0.09	0.01	0.18	0.13	0.00	0.00	0.03	0.79
Bw1	0.66	0.44	0.08	0.00	0.15	0.15	0.00	0.00	0.05	0.60
Bw2	0.05	0.52	0.08	0.01	0.13	0.14	0.00	0.01	0.07	0.70

the amount of C and N accumulated leads to the following values: 1.7 kg C and 0.082 kg N per m^2 for the L horizons of "Willow 1" and 0.8 kg C and 0.045 kg N per m^2 for the L + Ah1 horizons of "Willow 2".

The contents of water soluble elements expressed in mmol/m^2 c.q. mmol/m^3 not only depend on mineralization and humification rates but also on texture (for example adsorption by clay) and biomass input and as a consequence are difficult to interprete. The data in table 2, combined with those in the figures 3-6, however, rather clearly indicate that mineralization and nutrient cycling is more prominent in the soil of willow 2, in accordance with tendencies discussed above.

As can be seen in figure 1 strong differences exists in texture of the superficial parent material. Therefore some quantitative differences in biomass production between the two stands is to be expected. The sludge deposits characteristically have very poor physical properties, such as low porosity and low penetrability for soil fauna, which are due to their mode of deposition. It is therefore highly probable that the differences in development and characteristics between the two soils are due to the rather adverse conditions for soil fauna in the sludge deposits, rather than to differences in biomass production.

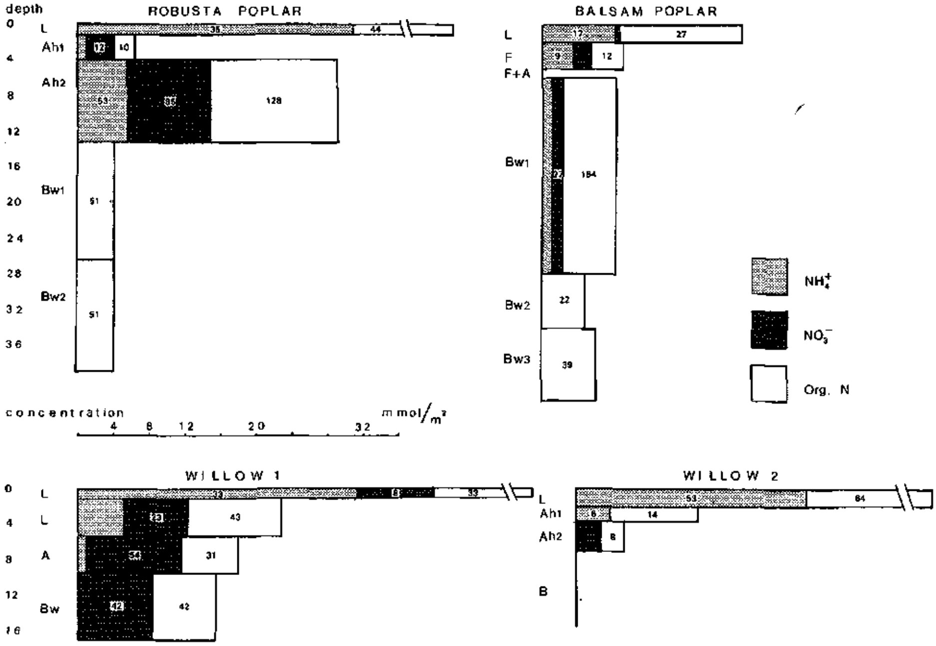

Fig. 6. Water soluble NH_4^+, NO_3^- and organic N expressed in mmol/m^2 per cm soil and total amounts in mmol/m^2 per soil horizon.

Conclusions

The research showed that within a few decades minor differences in vegetation or parent material may already lead to clear differences in development and nutrient status of soils. Further research should be carried out on the effects of such differentiation on soil genesis and on forest succession and production, and its results could be applied in the management of forest plantations in the polders.

The differentiation is clearly reflected in the organic profiles, as observed in the field. Therefore, field surveys of organic profiles can serve to rapidly establish major trends in soil development and in nutrient cycling.

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CHEMICAL INFLUENCES OF TREE LITTERS ON HERBACEOUS VEGETATION

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Summary

The effect of freshly fallen litter of beech, oak, birch, pine or larch added to soils on the establishment and growth of herbs and grasses was investigated under experimental conditions. Mortality during the first four weeks was high on many of these litter-soil mixtures, but was lowest in humus rich soil. Growth was also severely affected. Litter of beech completely inhibited growth of the plants and litter of oak, birch and pine caused growth reduction to a certain extent. Litter of larch had no inhibiting effects. The two grass species Milium effusum and Holcus lanatus were less severely affected than the two herbaceous species Scrophularia nodosa and Senecio sylvaticus. After 4 months most of the growth inhibiting effects had diminished. Inhibition persisted only on beech litter. Soil analyses strongly suggested that inhibition could be explained by release of organic compounds from litter material. These results are discussed in view of their significance for processes in forest dynamics.

Keywords: Litter-fall, decomposition, phenolics, herbaceous vegetation.

Introduction

In forest ecosystems trees highly influence site characteristics, not only physically in terms of light, temperature and water but also chemically. They produce large amounts of litter material which is deposited on the soil. By processes of decomposition and humification these substances are broken down and recycled in the form of nutrients, or are changed into more stable humus compounds. In general this signifies an amelioration of soil properties such as nutrient status and soil structure (Scheffer and Ulrich, 1960). However, there are indications that litter deposition can have negative effects on the ground vegetation (Bublitz, 1953; Winter und Bublitz, 1953; Rice, 1974; Leibundgut, 1976; Blaschke, 1979). During the first stage of decomposition many organic compounds are released from litters (Kuiters and Sarink, 1985) that can highly diminish plant growth. There are indications that phenolic compounds, precursors in the forming of humic substances, are highly responsible for these effects (Lohdi, 1978; Blaschke, 1979; Fisher, 1980). Many authors have stressed the importance of chemical interference by the release of inhibiting substances from the litter of trees and ground vegetation for succession processes in woodlands (Rice, 1974; Schütt et al., 1975; Zukrigl, 1983; Ernst, 1983). In this study we compare the capacity of different tree species for the release of organic substances from their litter and how this influences herbaceous vegetation.

Materials and methods

Freshly fallen litter material was collected in autumn (8 november, 1984) at a woodland site near Baarn (The Netherlands) on an acid, strongly podzolized sandy soil with pH 3.0-3.5. The material was collected randomly in more or less homogeneous plots of beech (Fagus sylvatica L.), oak (Quercus robur L.), birch (Betula pendula Roth.), pine (Pinus sylvestris L.) and larch (Larix decidua Mill.). The litter was dried, roughly ground and mixed through soil. To determine the influence of humus content, two soil-types were used: a mixture of gardensoil/sand, ratio 4/1 or 1/4 (v/v), here being defined as an organic soil resp. a mineral soil. Pots of 600 ml were used which finally contained 2/3 soil and 1/3 litter material. In the control pots no litter was added. Six germinated seeds of the plant species Scrophularia nodosa L., Senecio sylvaticus L., Milium effusum L. or Holcus lanatus L. were transplanted into a pot. Each treatment was replicated four times. The pots were placed 'at random' in a greenhouse with controlled conditions (20 +5 °C; a light/dark regime of 12/12 h; a light intensity of ca. 50 W. m^{-2}; 70% r.h.).Several soil characteristics were determined at the begin and end of the experiment. Total C- and N-content were determined by a Carlo Erba elemental analyzer and the total water soluble phenolic content with Folin-Ciocalteus reagens. Tannic acid was used as reference compound and the phenolic content was expressed as tannic acid equivalents (TAE). After 4 weeks no more seedlings died and the mortality was determined. After 14 weeks the shoots of the plants were cutted, dried and weighted. In a second experiment the pots in which almost no growth had occurred were replanted with germinated seedlings of Scrophularia nodosa L. and Senecio sylvaticus L. and mortality and biomassa production were determined after resp. 4 and 8 weeks. Mortality data were tested with analysis of frequencies and dry weights were tested with two-way analysis of variance after testing homogeneity of variances. Each species was tested seperately.

Results

Soil properties after addition of litter material

Initial conditions

In table 1 the initial soil conditions are presented. Without addition of litter, the organic soil and the mineral soil only slightly differed in pH. The C-content and especially the total N-content differed significantly, indication that the mineral soil had a relatively poor nutrient status as well as a low humus content. Addition of litter slightly decreased the pH of the mixtures. The C- and N-content strongly increased, except in pots where pine litter was added. The phenolic content of the pots was strongly increased as well, especially in the mineral pots. This can be explained by the relatively less adsorption of phenolic acids on humus material in the mineral soils, leading to higher concentrations of phenolics in the soil solution.

Changes in soil conditions during decomposition

At the end of the first experiment the soil properties were determined again. The results are presented in table 2. The phenolic contents of the soils are dramatically reduced during the four months of decomposition. This is the result of oxidation, microbial breakdown and polymerization to humus matter. In the organic rich soil, the C-content is also lowered, due to C-assimilation by micro-organisms. In the beech and pine-mixtures the microbial activity was relatively low.

Mortality and growth of seedlings

Experiment 1

During the first weeks after transplantation some mortality occurred (table 3), except on birch litter in organic soil. On organic soil mortality for S.sylvaticus was high on beech and pine litter and for S.nodosa on oak and pine litter. On mineral soil mortality was higher in comparison with organic soil, except for S.sylvaticus on beech litter. Most of the grass species seedlings survived all treatments. Mortality was positively correlated to the phenolic content of the soil. The above ground biomass production after 14 weeks growth on the soil litter mixtures is presented in fig. 1. There were large differences in response to litter types. Beech litter completely inhibited growth of all seedlings. Oak, birch and pine litter also inhibited plant growth, but to a lesser extent. Larch barely inhibited plant growth. On this litter type there was a strong species-specific difference between the soil types. H.lanatus was usually less inhibited on the mineral soil than on the organic soil. Both grass species were less severely inhibited than the dicotyledonous species.

Experiment 2

As previously mentioned, the pots in which inhibition was most severe were replanted after 4 months. In this experiment the seedlings of both dicotyledonous species were used to investigate the persistence of inhibition in the course of time. The mortality of seedlings after 4 weeks growth in this experiment was considerably diminished compared to the first experiment. However it was still high, especially for S.nodosa (table 4). Among the various litter types, birch caused the highest mortality, while almost no seedlings died on pine litter. Mortality was still positively correlated to the phenolic content of the litter-soil mixtures.

The results op biomass production 8 weeks after transplantation are presented in fig. 2. On beech litter the growth of plants was still completely inhibited. Pine litter still inhibited growth to a certain extent but the strong inhibition on oak and birch litter had disappeared. On a mineral soil with birch or oak litter S.sylvaticus is even strongly stimulated compared to the controls. This may indicate that decomposition of the litter material has made more nutrients available and that a woodland-clearing species as S.sylvaticus can take advantage of this situation.

Table 1. Some soil properties immediately after addition of litter to an organic and to a mineral soil. Litter material was mixed through soils in a ratio of 1 : 2.

	ORGANIC SOIL				
litter type	pH	% C	% N	C/N	phenolics µg TAE/pot
control	5.0	18.4 ± 1.7	0.40 ± 0.05	46	25
beech	5.0	24.0 ± 7.7	0.52 ± 0.09	46	42
oak	4.7	20.4 ± 1.4	0.65 ± 0.02	31	97
birch	4.9	24.8 ± 6.9	0.77 ± 0.25	32	26
pine	5.1	9.1 ± 3.3	0.25 ± 0.04	37	56
larch	4.7	22.9 ± 6.9	0.64 ± 0.20	36	27

	MINERAL SOIL				
litter type	pH	% C	% N	C/N	phenolics µg TAE/pot
control	5.3	0.8 ± 0.0	0.03 ± 0.01	27	7
beech	5.1	3.6 ± 0.8	0.10 ± 0.03	36	49
oak	4.2	7.5 ± 1.4	0.31 ± 0.03	24	199
birch	4.7	14.0 ± 2.1	0.43 ± 0.04	33	52
pine	4.7	3.0 ± 0.9	0.08 ± 0.01	37	50
larch	4.6	5.6 ± 0.0	0.17 ± 0.00	33	57

Table 2. The soil properties 4 months after the addition of the litter material.

	ORGANIC SOIL				
litter type	pH	% C	% N	C/N	phenolics µg TAE/pot
control	5.0	7.2 ± 1.7	0.19 ± 0.04	38	12
beech	5.5	18.7 ± 0.3	0.52 ± 0.09	46	14
oak	3.9	6.4 ± 0.3	0.26 ± 0.01	25	18
birch	4.8	13.5 ± 0.9	0.44 ± 0.03	31	9
pine	5.3	8.8 ± 2.0	0.17 ± 0.07	52	15
larch	4.0	10.2 ± 0.5	0.36 ± 0.03	28	0

	MINERAL SOIL				
litter type	pH	% C	% N	C/N	phenolics µg TAE/pot
control	5.1	1.1 ± 0.0	0.05 ± 0.01	22	2
beech	5.7	4.6 ± 0.9	0.13 ± 0.04	36	20
oak	4.1	6.6 ± 0.2	0.26 ± 0.00	25	51
birch	4.9	3.9 ± 0.1	0.20 ± 0.03	20	56
pine	5.4	3.0 ± 0.3	0.11 ± 0.01	27	10
larch	3.6	7.5 ± 0.7	0.28 ± 0.02	27	0

Table 3. Percentage mortality (mean and standard deviation) of the seedlings, 4 weeks after planting on the litter-soil mixtures.

ORGANIC SOIL				
litter type	Senecio sylvaticus	Scrophularia nodosa	Milium effusum	Holcus lanatus
control	8 ± 16.7	0	0	0
beech	46 ± 25.0	8 ± 9.6	0	0
oak	25 ± 9.6	54 ± 21.0	0	0
birch	0	0	0	0
pine	46 ± 28.5	42 ± 28.9	0	0
larch	13 ± 16.0	21 ± 16.0	0	0

MINERAL SOIL				
litter type	Senecio sylvaticus	Scrophularia nodosa	Milium effusum	Holcus lanatus
control	4 ± 8.3	13 ± 16.0	0	0
beech	4 ± 8.3	46 ± 34.4	4 ± 8.3	4 ± 8.3
oak	88 ± 16.0	88 ± 16.0	0	0
birch	17 ± 13.6	29 ± 28.5	0	0
pine	58 ± 21.5	54 ± 16.0	0	13 ± 16.0
larch	25 ± 9.6	17 ± 23.6	0	0

Table 4. *Percentage mortality of the seedlings, 4 weeks after planting on the* 4 months old litter-soil mixtures.

ORGANIC SOIL		
litter type	Senecio sylvaticus	Scrophularia nodosa
control	0	0
beech	4 ± 8.3	8 ± 9.6
oak	0	8 ± 9.6
birch	4 ± 8.3	29 ± 47.9
pine	0	13 ± 16.0

MINERAL SOIL		
litter type	Senecio sylvaticus	Scrophularia nodosa
control	0	25 ± 21.5
beech	50 ± 13.6	50 ± 23.6
oak	0	88 ± 16.0
birch	33 ± 45.1	58 ± 21.5
pine	0	0

Fig. 1. Mean shoot dry weight of the plants, expressed as percentage of the control after 14 weeks growth on the soil-litter mixtures. Controls are 100%. Vertical lines represent standard deviations.

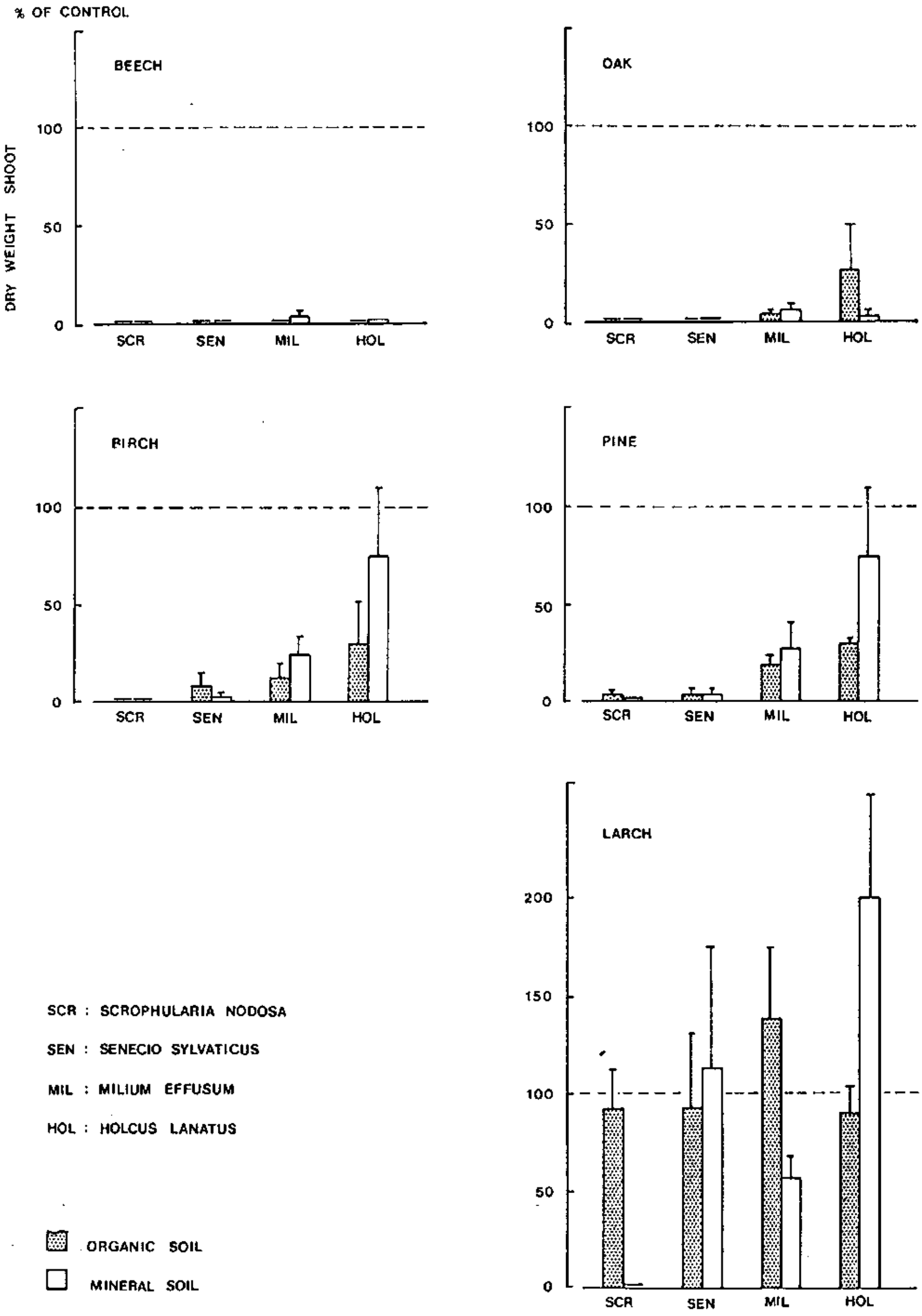
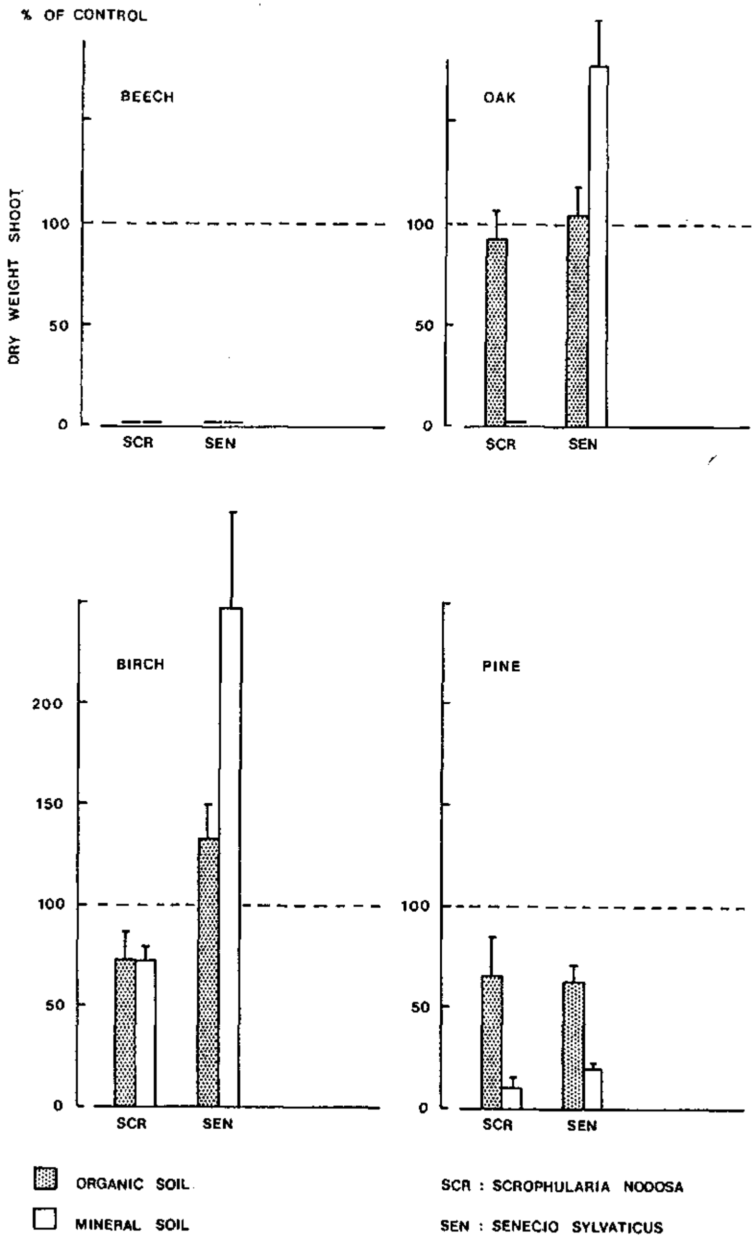


Fig. 2. Mean shoot dry weight of the plants, expressed as percentage of the control after 8 weeks growth on the 4 months old soil-litter mixtures. Controls are 100%. Vertical lines represent standard deviations.



Conclusions

The annual deposition of large amounts of litter on woodland soils does not only mean a nutrient enrichment stimulating plant growth, but can also have severe inhibiting effects due to the release of organic substances. The chemical influence of litter has two components, a mineral component and an organic component. Which component dominates is seasonally dependent. During the early phase of decomposition the influence of organic substances is large, often resulting in negative effects on plant growth. Presumably phenolic compounds play an important role but certainly other compounds are also involved. During decomposition water soluble organics in the soil solution disappear by microbial breakdown, by polymerization to more stable humus compounds, or by leaching into deeper soil layers (Scheffer und Ulrich, 1960). The experiments of Winter and Bublitz (1953) revealed that after winter, leaves are less inhibitive to plant growth. This conforms our results.

Under field conditions the potential inhibiting effect of litter will depend on the amount of litter deposited, but also on site conditions such as annual precipitation, microbial activity, and the presence of adsorbing clay or humus particles. The inhibition by beech litter seems to be more persistent than other litter types. This possibly indicates that the dominant status of beech in many woodlands in western- and central Europe results from an organic soil factor that strongly inhibits plant growth. Establishment of other tree species or herbaceous vegetation often does not take place in such woodlands.

The potential inhibiting effects of litter has special implications for plant-species that germinate in autumn, like Digitalis purpurea, Senecio sylvaticus, Silene dioica, Galium aparine, Milium effusum and Holcus lanatus. For autumn germinators, litter can have selective influences. Our experiments further reveal that the responses are strongly species-specific. S.nodosa proves to be a species that is very sensitive for organic compounds in a mineral soil, whereas H.lanatus is less sensitive in a mineral soil compared to an organic soil. In general, grass species are less severely inhibited than herbaceous species. This may be an explanation for the often grass-dominated vegetation in many species-poor woodlands. Although we only tested herbaceous species, it seems likely that seedlings of shrubs and trees also may be affected by the organic compounds in litter leachates (Rice, 1974; Leibundgut, 1976; Fisher, 1980). In situations where the undergrowth produces large amounts of litter we can also expect inhibiting effects of herbs on tree-seedlings, as suggested by the results of Schütt et al.(1979).

For a better understanding of forest dynamics the chemical interference between trees and herbaceous vegetation should be taken into consideration.

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DYNAMICS OF SHEATHING (ECTO-) MYCORRHIZAL FUNGI IN WOODLAND

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Summary

Some mycorrhizal fungi (eg. Heleboma, Laccaria and Inocybe) are characteristic of young birch stands whereas others (eg. Russula, Tricholoma and Amanita) are associated with more mature stands. It is probable that spores are the prime agents for mycorrhizal infection on tree seedlings colonising new sites.

Within naturally regenerating forest the situation may be different. When the roots of regenerating birch seedlings are linked to those of old trees, they appear to be infected with late-stage fungi. However, when isolated from the older tree roots, the seedlings develope mycorrhizas of early-stage fungi. The type of infection seems to be essential for the development of different species of mycorrhizal fungi.

Up to now, there is ample evidence about this phenomenon in birch. Similar phenomena, however are known in other tree species such as Pinus radiata, P. monticola, Pseudotsuga menziesii and Picea abies.

Further on, some other problems of the mycorrhiza research as related to forest succession (host specificity of mycorrhizal fungi in pioneer and climax species; nutritional requirements in mycorrhizal succession) are discussed, based on literature.

Keywords: Dynamics, succession, sheathing mycorrhizas, ectomycorrhizas, Betula.

Background

The wide range of fungi which live within the forest ecosystem form a dynamic interacting community. One of the groups within this community consists of the mycorrhizal fungi which have an important role in nutrient cycling. Terrestrial plant communities tend to be dominated by either endomycorrhizal or sheathing (ecto-) mycorrhizal plants (Moser, 1967). During ecosystem succession tot climax forest in northern temperate regions the fungal association of higer plants change from endomycorrhizas in herbaceous and scrub communities to sheathing mycorrhizas associated with trees (Rose, 1980). Sheathing mycorrhizal associations involve a broad spectrum of fungi, over 2000 fungal species worldwide being potential or proven sheathing mycorrhizal symbionts (Trappe, 1962).

Little is known about the changes in sheathing mycorrhizal species composition which occur as forests develop, nor of the processes within the forest ecosystem which may control or be affected by such changes. This paper sets out to document the current information regarding changes in the mycorrhizal flora of birch and other tree species as they age and to consider the implications of mycorrhizal succession for forest development.

Mycorrhizal dynamics in ageing birch stands

Evidence from fruitbody observations

In the literature, a number of fungal genera are listed as being associated with birch (Trappe, 1962; Watling, 1973). These include Amanita, Boletus, Cantharellus, Cortinarius, Hebeloma, Inocybe, Laccaria, Leccinum, Paxillus, Russula, Scleroderma and Tricholoma. However, little information is available about the soil conditions, climate and age and size of the trees with which the fruitbodies were observed. Consequently, only a general impression has been gained of the distribution and role of mycorrhizal species within birch communities.

Recently, however, Watling (1984) observed that Laccaria laccata (Scop.:Fr.) Cooke was often the only agaric present in pioneer communities of birch on shale waste and margins of scree slopes. By contrast, other agarics (Russula spp. and Lactarius spp.) and some boletes were usually associated with mature woodlands. He also noted that although Lactarius torminosus (Schaeff.:Fr.) S.F. Gray was found in mature and remnant birch stands, the closely related L. pubescens (Fr.:Krombh.) Fr. was usually recorded as a pioneer species in association with young, often isolated, trees.

Mason et al. (1982) have recorded the occurrence of fruitbodies during the first 10 years after planting a mixed stand of birches (Betula pendula Roth and B. pubescens Ehrh.) at the Bush Estate, Midlothian, Scotland and have obtained evidence of both a temporal and spatial succession of mycorrhizal fungi (Table 1). An ordered sequence of fungi was observed, although some (eg. Hebeloma crustuliniforme (Bull.: St. Amans) Quelet) were transient, whereas others persisted. It is interesting to note that, so far, species of Tricholoma and Amanita, characteristically associated with mature birch (Watling, 1973) have not yet fruited at this site.

Observations of mycorrhizal fruitbodies by Miles (1985) at 4 woodland sites formerly under heather moorland, also confirm the occurrence of mycorrhizal successions with birch. Although trees of a considerable age range (from 15 years upwards) were examined, Amanita muscaria (L.:Fr.) Pers.: Hooker and Tricholoma columbetta Fr. Kummer fruitbodies were only found with B. pendula trees of at least 29 years and 72 years old respectively.

Thus it appears that some mycorrhizal fungi (eg. Hebeloma, Laccaria and Inocybe) are characteristic of young birch stands whereas others (eg. Russula, Tricholoma and Amanita) are associated with more mature stands. This sequence of fungi can, however, be modified by soil type and environmental factors; for examble Paxillus involutus (Batsch:Fr.) Fr. was found to be dominant on young birch growing in coal spoil but not present on young trees growing in a brown earth soil (Mason et al., 1982).

Host-related factors are also of importance. The fruitbody data from the Bush Estate showed that the number of fungal species associated with Betula pendula and B. pubescens increased from 4 species in year 3 to a total of nearly 30 species by year 10, with a consistently greater number of fungal species associated with B. pendula (Mason et al., 1982). Differences between clones were also observed. Three years after planting 4 clones of Betula pubescens on a groundwater gley close to Bush Estate (Last et al., 1984), significantly more fruitbodies of Inocybe petiginosa (Fr.:Fr.) Gillet were associated with clone C than with clone D. Conversely, more fruitbodies of Laccaria tortilis ((Bolt.) S.F. Gray) Cooke developed near D than with clone C.

Fruitbodies tended to occur in rings; species appeared first close to the tree and progressively moved outwards, being replaced near the tree

Table 1. Succession of fruitbodies of proven, or suspected, sheathing mycorrhizal fungi appearing in a stand of birches (*Betula* spp.) planted at Bush Estate, near Edinburgh (Last et al., 1983).

Years after planting	Fungi
1	Nil
2	*Hebeloma crustuliniforme* (Bull.: St. Amans) Quelet
	Laccaria sp.
3	*Thelephora terrestris* Ehrenb.:Fr.
4	*Hebeloma fragilipes* Romagnesi
	H. sacchariolens Quelet
	H. mesophaeum (Pers.:Fr.) Quelet
	Inocybe lanuginella (Schroet.) Konrad and Maublanc
	Lactarius pubescens (Fr.:Krombh.) Fr.
6	*Cortinarius* sp.
	Hebeloma leucosarx P.D. Orton
	Hymenogaster tener Berkeley and Broom
	Inocybe petiginosa (Fr.:Fr.) Gillet
	Leccinum roseofracta Watling
	L. scabrum
	L. versipelle (Fries and Hök) Snell
	Peziza badia Persoon ex Merat
	Ramaria sp.
7	Other *Cortinarius* spp.
	Other *Hebeloma* spp.
	Lactarius glyciosmus (Fr.:Fr.) Fr.
	Leccinum subleucophaeum Dick and Snell
10	*Hebeloma vaccinum* Romagnesi
	Russula betularium Hora
	R. grisea (Pers.: Secr.) Fr.
	R. versicolor J. Schaeff.

by the next fungus in the succession. Thus around a tree of 6-8 years old, 3 or 4 concentric rings may be observed, with the first fungus in the temporal succession being furthest from the stem and the most recent species being closest to the stem.

Evidence from mycorrhizas

Although the occurrence of fruitbodies does not give a comprehensive insight into events below ground-level, Warcup (pers. comm.) while working at the Bush experimental site, was able to relate fruitbodies in the stand of *Betula* spp. to their own distinctive types of mycorrhizas (Mason et al., 1983). Further supporting evidence has been presented by Deacon et al. (1983) who examined the distribution of mycorrhizas in soil cores taken at 0.25 m intervals outwards from the base of an 8 years old *B. pubescens*. *Hebeloma*-type mycorrhizas were most frequent in the outer sampling positions while *Leccinum*-type mycorrhizas were found mostly in the inner positions. *Lactarus*-type mycorrhizas, although located in all positions, peaked in frequency in the middle samples. This pattern closely reflected the distribution of fruitbodies observed round the tree and therefore provided support for the concept of mycorrhizal succession.

Experimental investigations

Deacon et al. (1983) began to explore the significance of these observations by growing birch seedlings in a set of soil cores taken from beneath fruitbodies of a range of mycorrhizal fungi surrounding 8 years old birch trees. Seedlings grown in cores removed from beneath fruitbodies of fungi occurring early in the succession, Laccaria and Inocybe, always developed mycorrhizas attributable to these fungi. However, when Lactarius and Leccinum cores were tested the only mycorrhizas that developed were attributable to Hebeloma and other early sequence fungi. This demonstrates differences in the abilities of fungi which occur early and late in the succession to establish mycorrhizas on seedlings in field soils - a difference, which has led to their division into "early" and "late-stage" fungi. This distinction is not apparent in sterile soils in which both these groups readily form mycorrhizas (see Table 3) (Deacon et al., 1983).

This difference between early- and late-stage fungi was investigated by Fox (1983) who found that birch seedlings, planted into an unsterile soil supplemented with spores of one of a range of fungi, readily developed mycorrhizas with species of Hebeloma, Inocybe and Laccaria (early-stage fungi) but not with Cortinarius, Lactarius, Leccinum or Russula (late-stage fungi). This may be an ecologically important distinction between these groups as it is probable that spores are the prime agents for mycorrhizal infection on tree seedlings colonising new sites.

The situation within naturally regenerating forests may be different. Here, there is ample evidence, especially from fungal foray records, to indicate that mature birch possesses a stable microflora of mainly late-stage fungi (Watling, 1973; 1984). However, the roots of regenerating tree seedlings also appear to be infected with late-stage fungi (Fleming, 1983) such as Lactarius, Cortinarius, Russula and Amanita. Fleming (1983) suggested that a common feature of these fungi was their ability to fo strands which could act as sources of infection for seedlings. When birch seedlings were planted into the soil close to the trunk of an 11 years old Betula pubescens, late-stage Lactarius pubescens mycorrhizas formed on the seedlings' roots. However, when soil was isolated, by coring, from the parent tree roots, the seedlings developed mycorrhizas of early-stage fungi. This suggests that L. pubescens, and possible other late-stage, strand-forming fungi, can form mycorrhizas with seedlings only if the fungus is linked to an older tree. For example, 73% of a naturally ocurring population of 1 year old birch seedlings growing in a chestnut coppice in southern England were found to have late-stage, bolete-type mycorrhizas (Fleming, 1983). However, when birch seedlings were grown in samples of the coppice soil which had been removed from the site, only early-stage mycorrhizas developed (Fleming, 1983). Separation of late-stage fungi, like other root-infecting fungi, from a well-established food base appears to reduce their infection potential (Garrett, 1951; Fleming, 1983). Thus the range of fungi forming mycorrhizas on seedlings growing within the woodland environment is likely to differ from that associated with seedlings colonising primary sites because of the types of infection processes that can occur.

Changes in mycorrhizas associated with other tree species

Sequences of mycorrhizal fungi have also been observed with other tree species. Observations with Pinus radiata (Chu-Chou, 1979) indicate that the sequences of mycorrhizal fruitbodies associated with birches and pine have many species in common (Table 2). Similarly, in other studies with Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) in which Chu-Chou and

Grace (1981) made isolations from mycorrhizas, they were able to confirm that *H. crustuliniforme* was associated only with seedlings whereas *A. muscaria* could only be isolated from trees 13 or more years old. Based on fruitbody observations, Mosse et al. (1981) reported a distinct succession of mycorrhizal fungi in stands of Norway spruce (*Picea abies* (L.) Karst.) in the French Jura mountains, while Miller (1983) observed 5 and 78 potential mycorrhizal fungi fruiting under young and mature western white pine (*Pinus monticola* Douglas ex D. Don). Similar increases in the number of fungal species with a single ageing host were noted by Lamb (1979) and Thomas, Rogers and Jackson (1983).

Successional trends in host specificity of mycorrhizal fungi

Some trees have a broad range of fungal associates whereas others are more restricted. This appears to influence the success of a particular host and its relation with other tree species. For instance western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) usually grows in mixed stands, frequently having become established as a climax species under the canopy of seral overstory species (Kropp and Trappe, 1982). The fungi associated with hemlock are mostly not host-specific. Clearly, it is advantageous to invading tree species to be adapted to whatever mycorrhizal system is already established in a forest. Conversely, it will be to the benefit of pioneer tree species that tend to grow in pure stands (eg *Alnus rubra* Bong.) to be much more fungal specific (Kropp and Trappe, 1982).

Table 2. Succession of sheathing mycorrhizal fungi associated with *Pinus radiata* D. Don growing in New Zealand (Chu-Chou, 1979).

Time (years) after outplanting	Fungi observed
1	*Hebeloma crustuliniforme* (Bull.: St Amans) Quelet
1 - 5	*Laccaria laccata* (Scop.: Fr.) Cooke
	Rhizopogon luteolus Fr.& Nordh.
	Rhizopogon rubescens (Tul.) Tul.
5	*Inocybe* spp.
	Suillus spp.
10	*Amanita muscaria* (L.: Fr.) Pers.: Hooker

These views are supported by the observations of Malajczuk et al. (1982) who concluded that the success of eucalypts and *Pinus radiata* D. Don in the establishment of exotic plantations and as invaders of indigenous tree communities could be attributed in part to their compatibility with broad host-ranging fungi existing within these communities. They further suggested that not only did a natural succession of mycorrhizal fungi occur in native stands of eucalypts and *P. radiata* as they matured but that this succession tended over time from broad-host-ranging towards dominance by host-specific fungi. This reduction in the diversity of fungi associated with older stands corresponds with data from root assessments made in 250 year-old Douglas fir/larch forests (Harvey et al., 1976) which indicated that fir and larch at this stage were only associated with a single dominant mycorrhizal fungus.

Nutritional requirements in mycorrhizal succession

A number of factors thought to be involved in determining mycorrhizal successions were proposed by Dighton et al. (1981) (Table 3).

The supply of carbohydrates (phosynthates) from the tree host to the fungal symbiont is of paramount importance to the development and functioning of mycorrhizas (Hacskaylo, 1983). Nutritional experiments have shown that early-stage fungi are less glucose-demanding than late-stage fungi and, in addition, early-stage fungi tend to produce smaller fruit bodies than late-stage fungi (Deacon et al., 1983). This adds support to the views of Dighton et al. (1981) that early-stage fungi have a lower demand for, or reduced access to, host-derived carbohydrate.

Table 3. Possible factors influencing the succession of mycorrhizal fungi on tree roots.

Fungal attributes	Stage in succession	
	Early	Late
Energy demand (supplied by host)	Low	High
Ability to supply nutrients to the tree	Supplies nutrients from labile inorganic pool	Supplies nutrients from inorganic and organic pool
Competetive ability of fungus:- Ability to compete in:		
(a) Sterile soils	+	+
(b) Unsterile soils	+	-

As stands mature it would appear that a greater proportion of photosynthate is allocated to mycorrhizal production in order to satisfy the host's mineral nutrient demands (Vogt et al., 1983). This is suggested from data which shows that mycorrhizal biomass increases with stand development, reaching a maximum at canopy closure, especially on nutrient-poor sites where a significantly higher mycorrhizal biomass is maintained than on nutrient-rich sites.

At canopy, however, temperature and moisture conditions become less favourable for decomposition (Swift et al., 1979) and litter breakdown declines (Vogt et al., 1983). It is therefore interesting to note that early-stage mycorrhizal fungi that develop on seedlings appear to favour mineral rather than organic soils (Alvarez et al., 1979) while late-stage mycorrhizal fungi of mature forests prefer the organic fractions (Harvey et al., 1976). It may be speculated that within mature forests, late-stage fungi produce a range of extracellular enzymes which afford them the advantage of being able to derive mineral nutrients and also possibly supplement their carbohydrate pool directly from the accumulating organic matter. Although direct evidence is not available, Bartlett and Lewis (1973) have demonstrated phosphatase and phytase activity of mycorrhizal beech roots while Giltrap (1982) showed that a number of mycorrhizal fungi were able to produce polyphenoloxidases.

Conclusions

Mycorrhizal succession is a widespread phenomenon. Although the mechanisms controlling it are far from clear, several factors are emerging which appear to influence the successional changes observed. These include the ability of mycorrhizal fungi to infect plants of different ages including competitivity with other microbes, host specificity, the soil type, and the nutritional requirements of the host and the fungus. However further knowledge is needed before we can ascertain (a) the relationships between mycorrhizal succession, plant succession and soil development and (b) the implications of mycorrhizal succession for successful forest development during first and subsequent rotations.

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Posters

STUDIES ON HUMUS PROFILES

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Theme

Study of genesis and characteristics of humus profiles in relation to vegetation, parent material and time and the impact of these soil forming factors on soil forming processes, in non-agricultural (semi natural) areas.

The distinction between "humus profiles" and mineral soil profiles is connected with the speed of adaptation to changes in external soil forming factors. The humus profile is strongly influenced by and adapted to present environmental conditions. The mineral soil profile, in contrast, is the expression of soil forming processes active over a much longer period.

Changes in the environment almost directly alter the development and character of the humus profile, which is also influenced by the mineral soil profile and the previous developed humus profile. This means that it is extremely difficult to separate the effects caused by vegetation and by antecedent soil formation, on the genesis of humus profiles.

The field studies therefore were carried out on profiles without antecedent soil formation. In this situation the effect of vegetation, parent material and time on the genesis of humus profiles can be studied.

In practice, in the Netherlands, this means: Studies on humus profiles within stands of different age on eolian sands and on recent marine deposits.

Once the above mentioned relations are clear, the surveys on humus profiles can be extended to more complicated situations involving more soil forming factors, for instance antecedent soil formation.

The survey as carried out by the University of Amsterdam comprises the following main research aspects:

1) Development of a more detailed typology of horizon characteristics of humus form profiles.
2) Development of a classification of humus form profiles.
3) Humus profile succession studies within stands of different age on identical parent materials and their implication for the classification.
4) Pedogenesis: Correlation of macroscopic and microscopic characteristics of humus profiles with pedogenetic processes such as nutrient cycling, eluvation, leaching and bioturbation.
5) Methodology and general structure of surveys on humus form profiles. focused on variability and the statistical application.
6) Field survey methods.
7) Data handling.

The examples on the poster are connected with some of the above mentioned research aspects.

BIOGEOCHEMICAL BALANCE STUDY OF A FOREST ECOSYSTEM

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Introduction

The general aim of the project is to establish water and element budgets of a forest ecosystem in order to quantify the effects of atmospheric deposition on soil/water acidification.

The study site is a forested area located in the rural eastern part of the Netherlands. In this area two catchments were chosen for detailed hydrological, chemical and biological investigations. Jurassic clays (70% clay, 30% silt) constitute the lower watertight boundary of the basin. Above the surface of this deposit a 1.15 to 4 m thick layer of sandy (clay) loam glacial till is found with a 50 cm thick sandy weathering residue on top of it. The sandy layer and the top of the boulder clay are distinctly acid (pH 3-4) with pH values increasing further down in the profile. The catchments are almost completely covered with forest (85%): oak, beech, spruce and pine, the remainder of the area being occupied by grassland.

The study is based upon the distinction of compartments within the forest ecosystem such as: the atmosphere, the vegetation, the soil and the hydro/lithosphere. In these compartments the elements are accumulated in fluctuating amounts which can easily by measured. Exchanges between the compartments will exist in which water will generally serve as the transport medium. The magnitude of these water and element fluxes exhibits large fluctuations as a function of the season and metheorological conditions. As a consequence measurements are carried out for several years.

In the forthcoming pages attention is paid to three main topics of the general research programme, successively: the hydrology, the chemical fluxes and the nitrogen budget of the forest ecosystem.

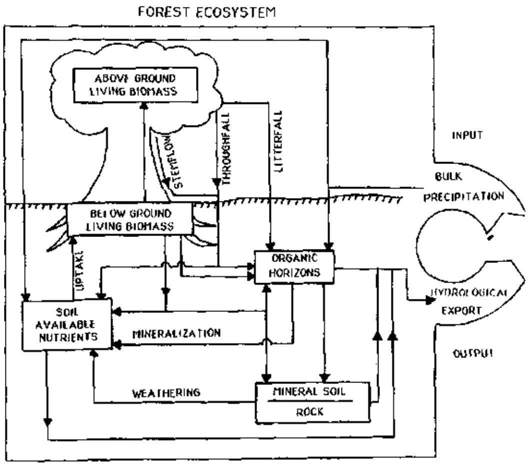

Fig. 1. Compartments and fluxes of a forest ecosystem.

Hydrology of a forest ecosystem

Hydrological processes are of primary importance in biogeochemical balance studies of forest ecosystems. They are studied in order to quantify water fluxes, as water is the most important transporting agens, but also because hydrological conditions can influence dry deposition, biological activity, chemical reactions and plant physiological processes.

The atmospheric element input is controlled by the time-distribution and the amount of rainfall. Wet deposition is highly correlated with the amount of rainfall, while dry deposition strongly depends on the period that leaves are wet and thus on the rainfall distribution. Leaf wetness and interception are studied by detailed measurements of rainfall and throughfall intensity, windspeed, vapour pressure deficit and canopy structure.

Soil water fluxes are controlled by the input of throughfall water, by drainage and by the uptake of water by roots. Figure 2a shows that the input of water to the soil is strongly reduced by interception. Overall this "waterloss" equals 17% in leafless periods and 27% in leaf growth periods. It is partly compensated by transpiration reduction as long as leaves are wet due to interdepted water. Drainage of water, and thus the element output, depends on the soil water conductivity. Because of the impermeable jurassic clay and the rather low conductivity of the glacial till, discharge is only found at very high groundwater tables within the sandy topsoil (Figure 2b and 2c). The uptake of water by roots induces characteristic soil water suction fluctuations (Figure 3). These are a result of root distribution, a low capillary rise and an abrupt change of physical properties within the soil profile. Numerical simulation models are used to calculate soil water fluxes and water uptake by roots. Daily measurements of tensiometers at different depths (Figure 2) are used for model calibration and validation.

Chemical fluxes in a forest ecosystem

The chemical approach of the ecosystem study is predominantly based upon the hydrological balance of the forest as water is the major transport medium of the elements concerned.

Solute input in the catchment mainly occurs in precipitation and is dominantly controlled by amount of precipitation and wind direction (source area). Four main sources can be distinguished: seaspray (Na, Mg and Cl), industrial activities (SO_4 and Cl), rural activities (NH_4, NO_3) and local dust (K, Ca, Na, Mg).

The magnitude of the various ion inputs in precipitation is subsequently altered during the passage of rainfall through the forest canopy. The variety of processes operating in the canopy may cause both increased input rates - related to e.g. leaching (Mn, K, figure 4) and dissolution of dry deposited compounds (HN_4, SO_4, figure 4) - and decreased input rates related to exchange reactions on the leaves (H). Some ion species exhibit almost no canopy effects (Cl, Na, NO_3).

Ion deposition in stemflow has been studied for several years but showed to be of only minor importance: 1-5% of the ion deposition in throughfall.

Upper soil horizons are very acid (pH 3-4) and the composition of the soil solution is controlled by throughfall input (K, NH_4), litter decomposition products (NH_4, NO_3), uptake by the forest vegetation and the congruent dissolution of clay minerals, pedogenic oxides and primary silicates (Al, Fe). Deeper in the soil profile where pH values are between 5 and 7 the composition of the soil solution is dominantly controlled by incongruent dissolution of primary silicates and clay minerals generating high concentration levels of Ca, Mg and K.

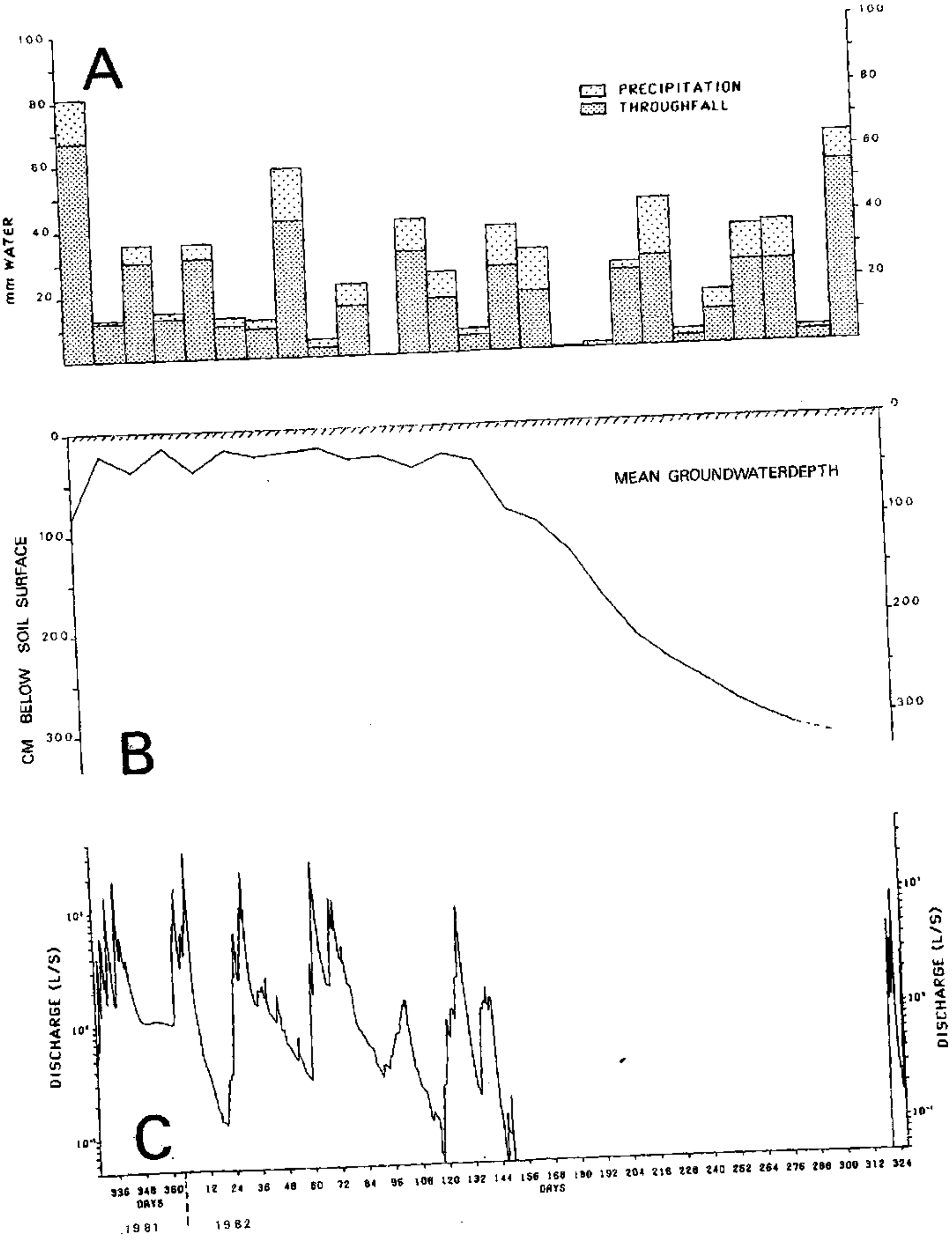

Fig. 2. Waterfluxes in a forest ecosystem.

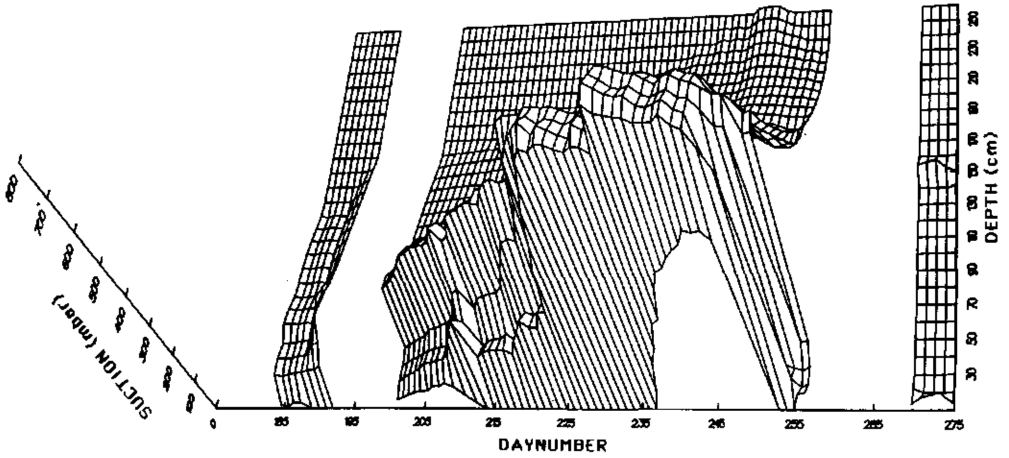

Fig. 3. Soil water suctions 1984.

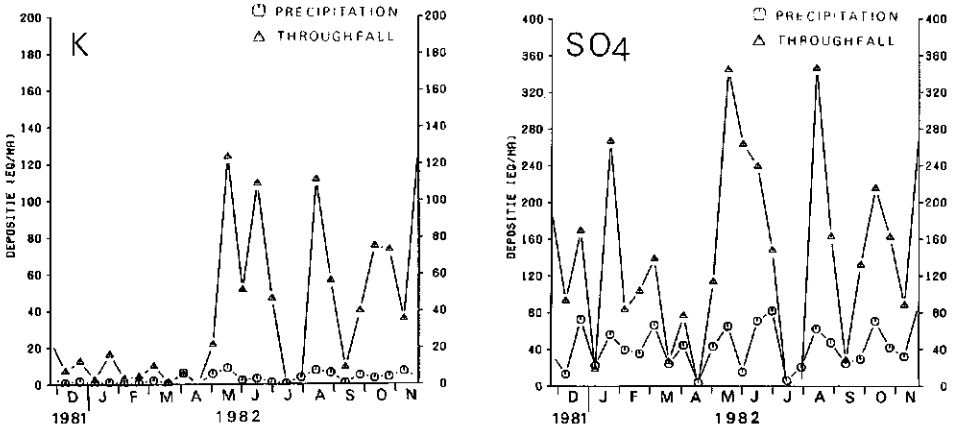

Fig. 4. Canopy effects on ion deposition of potassium (K) and sulphate (SO_4).

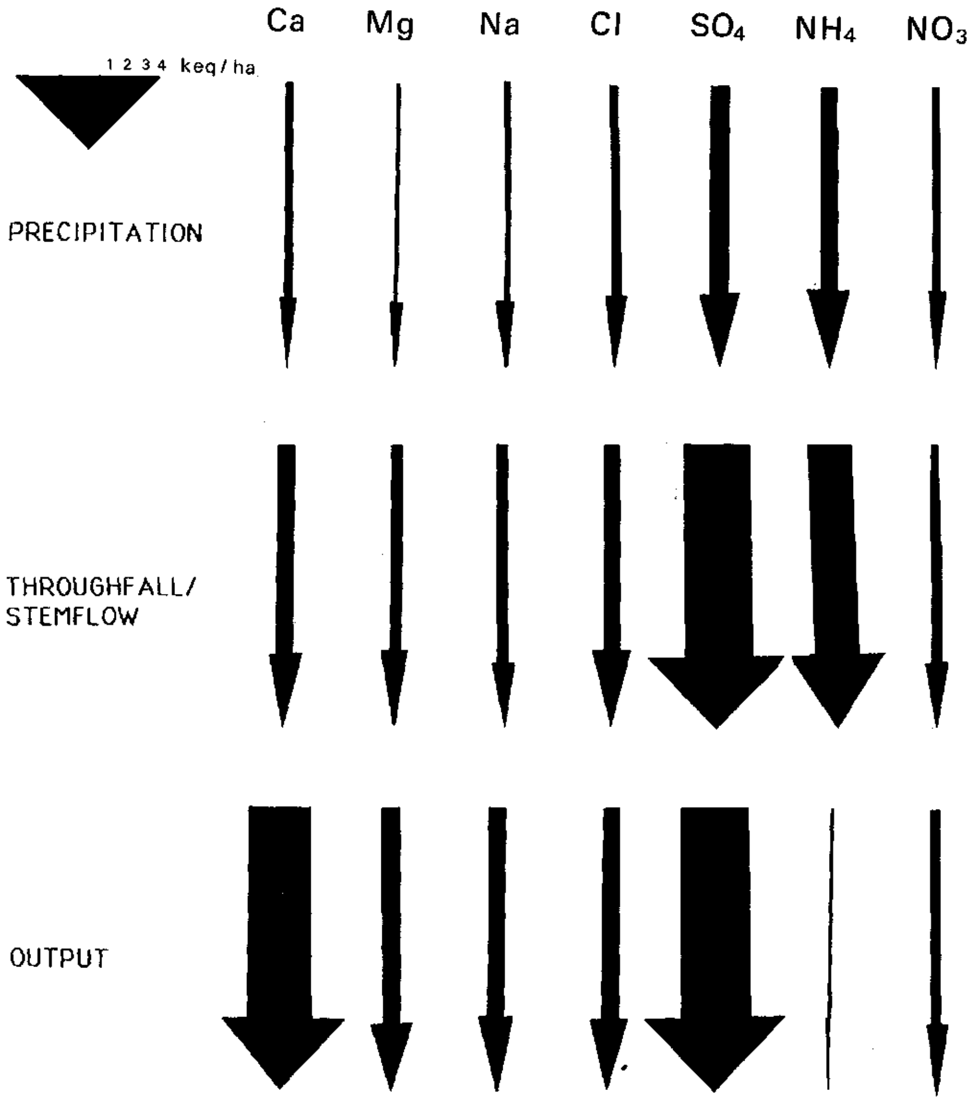

Fig. 5. Chemical fluxes through the forest ecosystem.

The nitrogen of a forest ecosystem

During the last decades the amount of ammonium in atmospheric deposition in the Netherlands has increased, associated with the increased bio-industrial production and use of manure.

Soil nitrogen transformations strongly effect the acidity of the soil and may result in chemical and biological alterations in the soil.

In order to quantify the nitrogen transformations, a nitrogen budget is being established of a mixed forest located in the eastern part of the Netherlands, consisting of beech, oak, spruce and pine.

The nitrogen cycle of a forest ecosystem is shown in figure 6. Some preliminary data have lead to an estimate of some of the transformations.

The annual amount of nitrogen in litterfall consists of 60-65% of nitrogen in beech- and oak leaves. To study the decomposition of this material a litterbag experiment was carried out with litter of oak and beech in a more or less constant ratio.

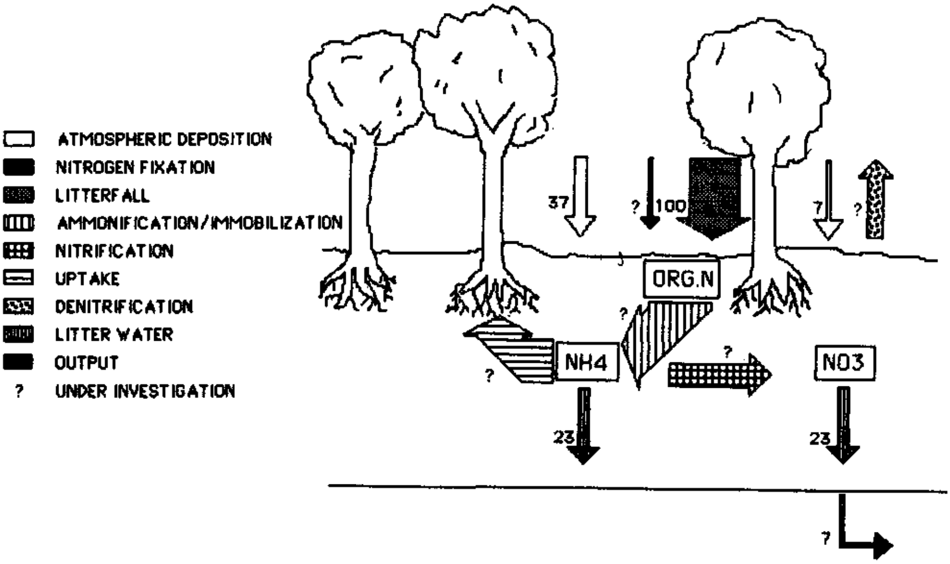

Fig. 6. The nitrogen cycle of a forest ecosystem, with some preliminary results (kg N/ha yr).

The experiment lasted for 39 months and will end after 48 months. In figure 7 the dynamics of the absolute amount of nitrogen in the bags (calculated as a percentage of the initial amount), as well as the percentage remaining dry-mass are shown as a function of time of incubation in the forest.

The results indicate a nitrogen immobilization of about 60% of the initial amount of nitrogen in the leaf-litter, during the first 9 months of the decomposition process. After 9 months, when the C/N-ratio has reached a value of about 20, the nitrogen is being mineralized. It takes about two and a half year before a net mineralization occurs in the leaf-litter.

Increases in the amount of ammonium and nitrate in oncubated soil cores will give an estimate of the rate of ammonification and nitrification.

The cores are closed (except for a hole for aeration) to prevent uptake

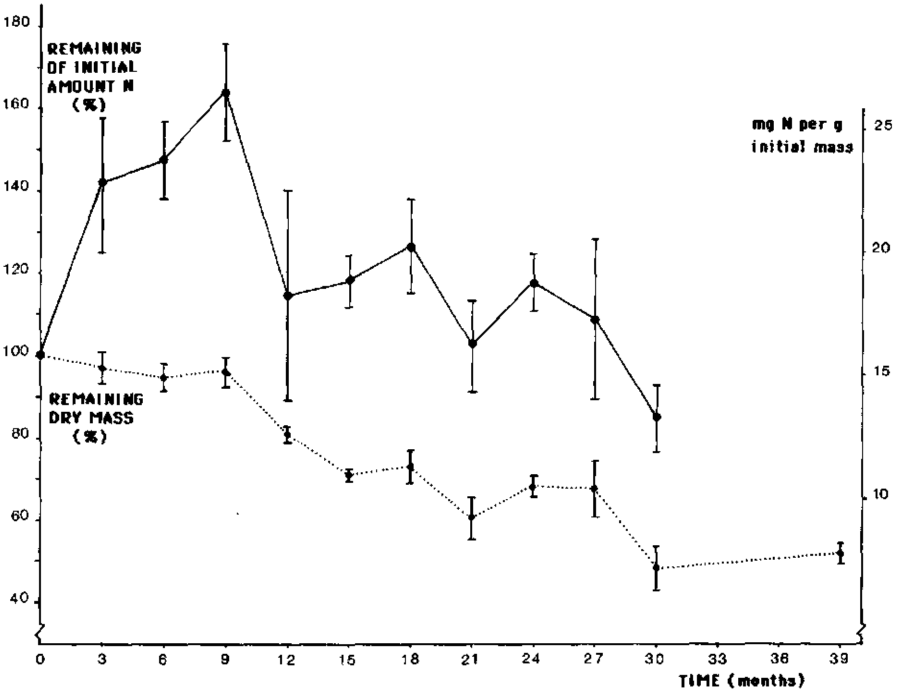

Fig. 7. The dynamics of the absolute amount of nitrogen in the litterbags and of the remaining dry-mass, in time.

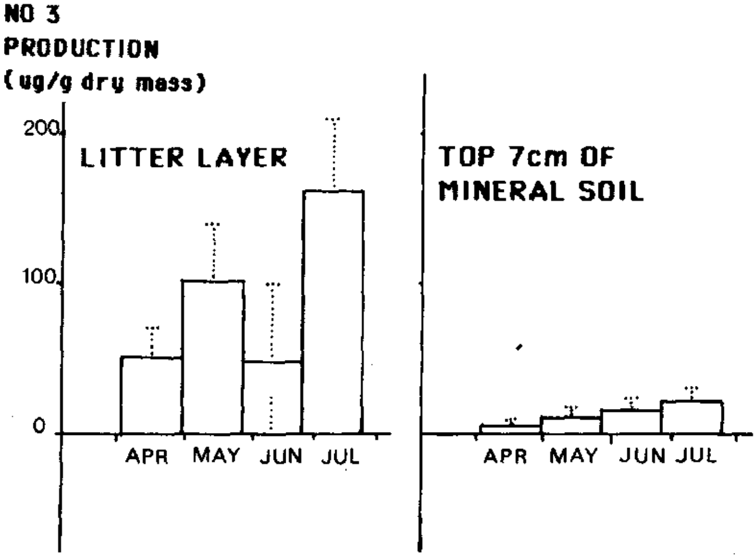

Fig. 8. Increases of the nitrate concentration in time.

by the vegetation, leaching of nitrate and input by throughfall and litterfall. The duration of each incubation period is four weeks. Some results are shown in figure 8.

Denitrification is quantified by means of a gas diffusion simulation model, which calculates the nitrous oxide flux fitting the nitrous oxide concentration gradient in the soil.

The assumption is that in a soil of this acidity (pH=3-4), nitrous oxide is the main product of denitrification. This assumption will be tested in a laboratory experiment, using acethylene to block the final step in the denitrification process of nitrous oxide to dinitrogen.

The nitrous oxide gradient will be measured using gas chambers on different depths in the soil.

Section 2: Primary and Secondary Succession in Different Forest Types

SUCCESSION IN FEN-WOODLANDS IN THE DUTCH HAF DISTRICT

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Summary

Succession in fen-woodlands on floating peat layers in the western parts of The Netherlands was studied. The vegetation types found could be ordered in time series in which the tendency to increasing dependence on rainwater was obviuous. In permanent plot studies in two woodland reserves several sub-associations of the Carici elongatae-Alnetum were found to be linked in time. In the most oligotraphentous communities Betula pubescens often gains dominance over Alnus glutinosa. Recent developments point to a reversal of the line of increasing dependence on oligotrophic conditions, possibly due to increased atmospheric nutrient input.

Keywords: Succession, permanent plots, Carici elongatae-Alnetum, Betula pubescens.

Introduction

Fen-woodlands in the western parts of The Netherlands developed commonly in old peat cuttings where the peat was taken from below the groundwater level. The rectangular ponds that resulted from the peat cutting became at first colonized by aquatic vegetation and were later on overgrown by a floating swamp of fen vegetation. This vegetation was commonly exploited for the production of reed for thatching purposes. Seedlings of shrubs and trees may establish in these fens and progressively impede the mowing management. Once mowing is abandoned the woody species may develop quickly due to the fact that they are not seedlings any more and possess a well-developed root system. Closed woodland vegetation may then establish within a few years. The most outstanding feature of these woodlands is that in many cases they are not in direct contact with the mineral subsoil. The peat layer that developed during the succession generally has not filled the water body completely with sediment.

Due to the fact that these developments occurred widespread and over a period of more than 50 years now, woodlands of different age and species composition as well as various stages of fen and shrub vegetation may be found in many nature reserves. Now that the eldest woodlands of this type have reached an age of almost 70 years it was decided to study succession patterns in these woodlands in order to be able to evaluate the developmental stages of woodlands for management or conservation purposes.

Two ways for the study of the succession from fen to fen-woodland and in the woodland phase were exploited. Firstly separate relevés from fens and woodlands in a number of reserves were used to describe vegetation types and rank them in a time series in order to construct a succession scheme. Secondly relevés from permanent plots were used to get more insight in the succession process in two woodland reserves.

In the small reserve "De Suikerpot" (just West of Hilversum) eight permanent plots were marked by J.H. Smittenberg in 1970 (Smittenberg, 1976). The vegetation of these plots was described almost every two years.

In the eldest nature reserve in The Netherlands, the "Naardermeer", the

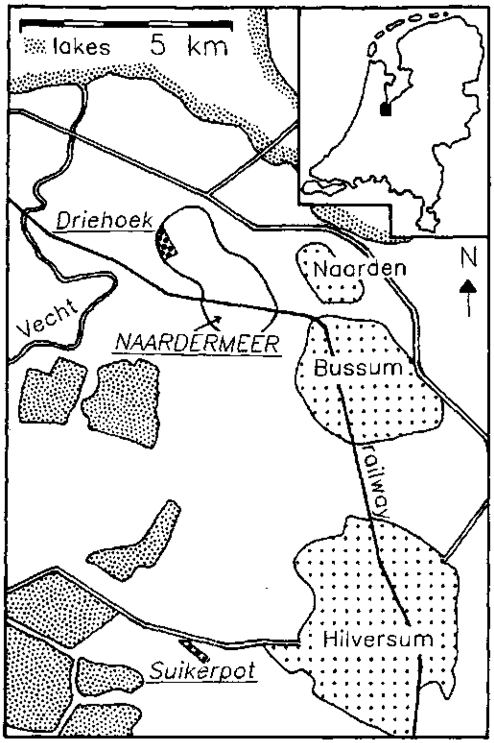

Fig. 1. Location of the fen-woodlands "De Suikerpot" and "De Driehoek" in the province of N-Holland (The Netherlands).

area called "De Driehoek" had been designated a strict reserve in 1919 and E.M. van Zinderen Bakker started in 1931 a series of 70 permanent plots covering a gradient from open swamp to incipient woodland (Van Zinderen Bakker, 1942). Over a 50-year period three complete surveys of all the plots in this transect are available. Both sites are marked in Fig. 1.

The succession scheme originating from the survey of fen and fen-woodland vegetation types will be taken as a starting point in this paper and refinements to this scheme that could be made based on the study of the permanent plots will be given detailed attention.

Methods

Relevés were made following the French-Swiss tradition (Braun-Blanquet, 1964). In most cases the depth of the groundwater as well as its pH and Electric Conductivity was assessed using portable field instruments. Samples from the superficial groundwater were collected and analysed at the laboratory of the Hugo de Vries-Laboratorium (Amsterdam) following standard methods referred to by Wiegers (1984).

The vegetation data were both processed according to the principles of Ellenberg (1956) and subjected to cluster analysis and a Principal Components Analysis following a routine from Orloci and Bowles (1982). The results of the groundwater analyses were used to characterize the different vegetation type discerned.

Nomenclature of higher plants follows Heukels-Van der Meijden (1983), of bryophytes Margadant and During (1982), and of syntaxa Westhoff and Den Held (1969) and Smittenberg (1976).

Results

The 151 relevés collected from fens, fen-carr, and fen-woodland were ordered in three separate tables (Wiegers, 1985) that were combined to a synoptic table (Table I). The temporal relations between the syntaxa to which the ten types discerned in this table belong are given in Fig. 2. Two main lines of development are discerned, one starting under oligo-mesotrophic conditions and one starting under more nutrient-rich conditions. As a result of peat formation and increasing insulation from the nutrient-rich groundwater shrub communities of the Alno-Salicetum cinereae may develop into less nutrients demanding types of the Carici elongatae-Alnetum.

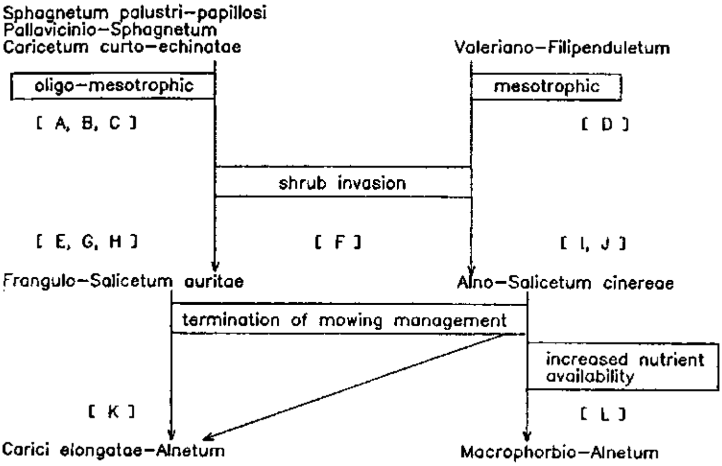

Fig. 2. Scheme of the succession to fen-woodland in some fens in the Dutch Haf District (prov. of N-Holland). The place of the relevé groups from Table I is indicated in this succession scheme. (from Wiegers, 1985).

From each of the permanent quadrats in "De Suikerpot" eight relevés were available. A synoptic table of the six syntaxa discerned is given in Table II. A cluster analysis of all the relevés revealed a separation into the groups at a dissimilarity level of 0.70. These ten groups could be ordered into six syntaxonomical units, of which five were subassociations of the Carici elongatae-Alnetum. The remaining one could be placed in the Alno-Salicetum cinereae. Principal components analysis suggested a straightforward temporal relation between five of the syntaxonomical groups (Fig. 3). This time-series runs from the Alno-Salicetum cinereae through the subassociations thelypteridetosum, caricetosum acutiformis, lysimachietosum, and sphagnetosum of the Carici elongatae-Alnetum. The subassociation betuletosum pubescentis obviously develops along a different line.

In the transect in "De Driehoek" the distribution of the vegetation types found in 1931, 1966, and 1981 is given in Fig. 4. The differential species of the types discerned are presented in Table III.

Combination of the succession scheme based on the transitions found in

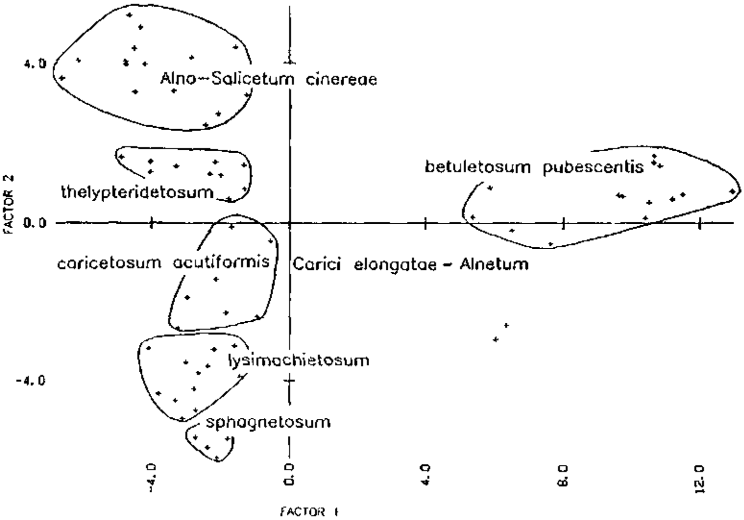

Fig. 3. Projection of the 64 relevés from the permanent plots in the fen-woodland "De Suikerpot" on the first two axes of a principal components analysis. Four subassociations of the Carici elongatae-Alnetum are found in a contiguous row with the Alno-Salicetum cinereae and one subassociation of the Carici elongatae-Alnetum is clearly separated from that group. The differentiating species from the syntaxa are given in Table II. (from Wiegers, 1985).

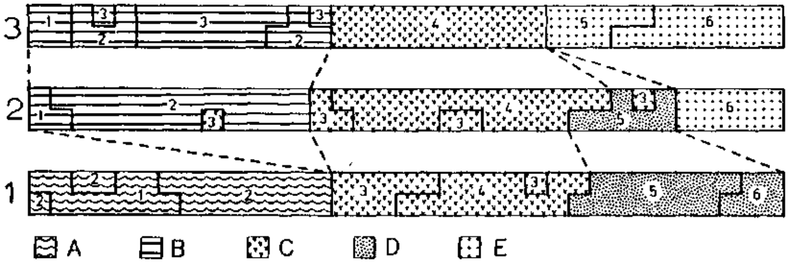

Fig. 4. Zonation in the vegetation in the transect in the fen-woodland "De Driehoek" in the Naardermeer. The differentiating species of the types are given in Table III. The numbers on the left side indicate the years (1= 1931, 2= 1966, 3= 1981) and are the first digit in the type numbers. The numbers inscribed in the transect are the second digit in this type numering.

A.1.1 : Caricetum paniculatae thelypteridetosum and Scirpo-Phragmitetum caricetosum pseudocyperi
A.1.2 : Scirpo-Phragmitetum caricetosum pseudocyperi and Thelypterido-Phragmitetum
B.2.1 + B.3.1 + D.1.6 : Alno-Salicetum cinereae
B.2.2 : Carici elongatae-Alnetum thelypteridetosum
B.3.2 : Carici elongatae-Alnetum lysimachietosum
B.3.3 + C.2.4 + C.3.4 + D.2.5 + E.3.5 : Carici elongatae-Alnetum betuletosum pubescentis

C.1.3 : *Thelypterido-Phragmitetum* and *Pallavicinio-Sphagnetum*
C.1.4 : as C.1.3, but with *Frangulo-Salicetum auritae*
C.2.3 : *Frangulo-Salicetum auritae*
D.1.5 : *Pallavicinio-Sphagnetum*
E.2.6 : *Carici elongatae-Alnetum caricetosum acutiformis*
E.3.6 : *Carici elongatae-Alnetum*, dry variant
(from Wiegers, 1985)

the fen-woodland of the Naardermeer with the succession lines presented in the Figs. 2 and 3 renders Fig. 5.

The subassociations of the *Carici elongatae-Alnetum* that may either develop immediately from shrub communities or evolve gradually from one another constitute a line of progressive peat formation, more aerated conditions in the upper substrate layer, and a lower availability of nutrients (especially nitrogen, sulphate, and magnesium), coupled to a lowering of the pH of the superficial groundwater. Data supporting this view are presented by Wiegers (1985).

Although the peat layer under the strongest oligotraphentous communities (the subassociations *sphagnetosum* and *betuletosum pubescentis* of the *Carici elongatae-Alnetum*) is more stable than in the communities developing immediately from the *Alno-Salicetum cinereae* (the subassociations thelypteridetosum and caricetosum acutiformis of the *Carici elongate-Alnetum*) and shows a smaller vertical displacement during the growing season caused by excess evaporation or rainfall (Jorna, 1984), the amplitude of the groundwater level, probably due to the different structure

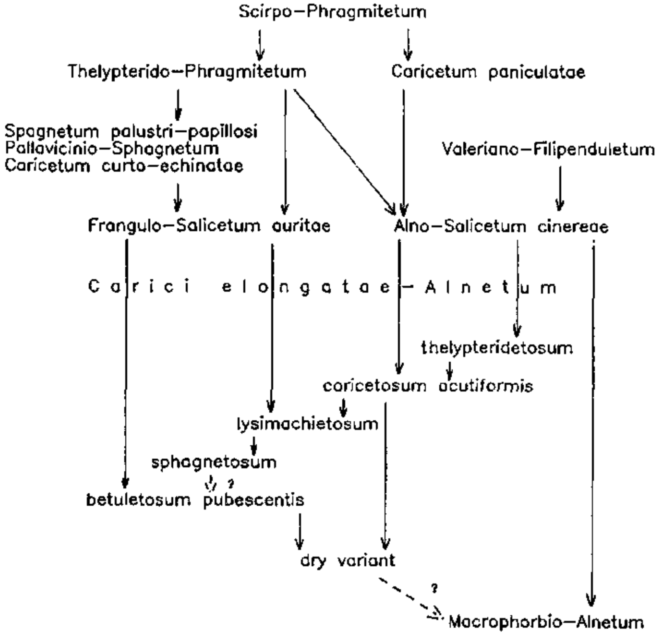

Fig. 5. Scheme of vegetation succession in fens and fen-woodlands in the Dutch Haf District, composed from the results presented in Fig. 2, 3 and 4. Two transitions that were not actually observed in the field but that possibly could occur are marked with a question-mark. (from Wiegers, 1985).

of the peat, is greater in the less oligotraphentous communities.

Next to the development to progressively oligotraphentous communities a succession from Betula-dominated types towards types in which Alnus glutinosa is of increasing importance can be seen in the scheme of Fig. 5. The return of Alnus in formerly Betula-dominated communities that is taking place in the last 15 years may be attributed to the higher nutrient input by atmospheric deposition, which enhances the chances for establishment of Alnus glutinosa.

Conclusions

The vegetations developments in small peat cuttings in the western parts of the Netherlands commonly leads to fen-woodland vegetation that becomes in time progressively insulated from the nutrient-rich surface waters. Rainwater stored in the peat body may give the ecosystem certain ombrogenic characteristics after a period that may vary in length from c. 30 to c. 60 years. Transition to fully ombrogenic peat bog may be hampered nowadays by increased atmospheric nutrient input. Reversal of the line of development towards increasing dependence on rain water was found in some cases. Under natural and unpolluted conditions the subassociation betuletosum pubescentis of the Carici elongatae-Alnetum seems to be a fairly stable phase in the succession.

Table I. Synoptic table of the vegetation types in some fens and fen-woodlands in the Dutch Haf District in the province of N-Holland. Only *Betula pubescens* and the differential species are shown.

A : *Sphagnetum palustri-papillosi*
B : *Caricion curto-nigrae*
C : transition between *Caricion curto-nigrae* and *Valeriano-Filipenduletum*
D : *Valeriano-Filipenduletum*
E + G : transitions from *Sphagnetum palustri-papillosi* towards *Frangulo-Salicetum auritae*
I : *Alno-Salicetum cinereae*
J : transitions from *Filipendulion* towards *Alno-Salicetum cinereae*
K : *Carici elongatae-Alnetum*
L : *Macrophorbio-Alnetum*
(table XV from Wiegers, 1985)

Type	L	K	I	D	J	C	B	A	E/G	F/H
number of relevés	4	17	27	13	7	9	26	7	17	24
mean number of species	21	15	17	18	12	11	10	9	12	17
Betula pubescens	2	V	IV	.	.	.	III	V	V	V
Brachythecium rutabulum	3	II	III	IV	.	.	.	.	.	.
Calystegia sepium	1	I	I	IV	.	.	.	.	.	.
Stellaria media	1	IV	I	I	.	.	.	.	.	.
Solanum dulcamara	4	III	I	I	.	.	.	.	.	+
Iris pseudacorus	4	+	II	II	+	.	.	.	.	.
Poa trivialis	1	II	I	II	.	.	.	.	.	+
Eupatorium cannabinum	3	I	+	II	+	.	.	.	.	.
Plagiothecium denticulatum	2	I	I	I	.	.	.	.	.	+
Dryopteris dilatata	1	II	II	.	.	.	.	.	.	+
Urtica dioica	3	II	I	.	.	.	.	.	.	.
Sambucus nigra	1	II	I	.	.	.	.	.	.	.
Crataegus monogyna	1	+	I	.	.	.	.	.	.	.
Ribes nigrum	1	+	I	.	.	.	.	.	.	.
Hedera helix	1	+	+	.	.	.	.	.	.	.
Thalictrum flavum	2	.	+	III	.	.	.	.	.	+
Filipendula ulmaria	4	.	I	II	.	+	.	.	.	.
Angelica sylvestris	3	.	II	I	.	.	.	.	.	.
Stachys palustris	1	.	I	II	.	.	.	.	.	.
Mentha aquatica	3	.	I	I	+	.	.	.	.	.
Carex riparia	.	+	I	IV	.	.	+	.	.	.
Rumex acetosa	.	I	III	II	.	.	.	.	.	.
Valeriana officinalis	.	II	II	II	.	.	.	.	.	.
Rumex hydrolapathum	.	+	+	II	.	.	.	.	.	.
Rhytidiadelphus squarrosus	.	+	+	I	.	.	.	.	.	.
Alnus glutinosa	4	III	.	.	.	.	.	.	.	.
Phalaris arundinacea	.	.	+	II	.	.	.	.	.	.
Cardamine pratensis	.	.	I	I	.	.	.	.	.	.
Viola palustris	.	.	I	+	.	.	.	.	.	.
Cirsium palustre	.	I	II	II	+	II	.	.	.	.
Dactylorhiza majalis	I	.	I	II	.	.	.	+	.	.
Lysimachia thyrsiflora	.	+	I	II	.	.	I	.	.	.
Eriophorum angustifolium	.	+	.	.	+	.	I	V	III	I
Oxycoccus macrocarpos	.	.	.	.	.	.	.	II	I	I
Polygonum amphibium	.	.	.	.	+	+	+	.	.	I
Scirpus lacustris	.	.	+	.	.	II	I	.	+	.
Danthonia decumbens	.	.	.	.	.	.	I	+	.	.
Erica tetralix	.	.	.	.	.	.	.	.	III	+
Potentilla anglica	.	.	.	.	.	.	+	.	+	I
Osmunda regalis	.	.	+	.	.	.	.	.	+	I

Table II. Synoptic table of vegetation types in permanent quadrats in the fen-woodland "De Suikerpot" near Kortenhoef. Only differential species are shown. T : tree layer, S : shrub layer, H : herb layer.

A : Carici elongatae-Alnetum betuletosum pubescentis
B : Carici elongatae-Alnetum sphagnetosum
C : Carici elongatae-Alnetum lysimachietosum
D : Carici elongatae-Alnetum caricetosum acutiformis
E : Carici elongatae-Alnetum thelypteridetosum
F : Alno-Salicetum cinereae

Group		A	B	C	D	E	F
number of relevés		16	9	7	5	11	16
mean number of species		30	28	25	33	27	32
Betula pubescens	T	V	.	.	.	.	.
Quercus robur	S	IV	.	.	.	.	.
Carex curta		IV	.	.	.	.	.
Campylopus fragilis		III	.	.	.	.	.
Phalaris arundinacea.		II	.	.	.	.	.
Campylopus flexuosus		II	.	.	.	.	.
Cephaloziella elachista		II	.	.	.	.	.
Sphagnum flexuosum		III	.	.	+	.	.
Betula pubescens	S	III	.	.	II	.	.
Quercur robur	H	IV	II	+	.	.	.
Pohlia nutans		IV	II	.	.	+	.
Dicranum scoparium		III	.	+	+	.	.
Frangula alnus	H	IV	+	II	III	I	.
Cephalozia bicuspidata		V	II	+	+	II	I
Sphagnum palustre		IV	IV	.	.	.	.
Amelanchier lamarckii	H	IV	IV	+	+	II	.
Plagiothecium curvifolium		+	II	.	.	.	.
Calypogeia fissa		IV	III	III	.	+	+
Holcus lanatus		V	IV	III	+	+	I
Dryopteris dilatata		II	V	V	III	III	III
Juncus effusus		.	V	III	.	.	.
Sparganium erectum		.	III	+	.	.	.
Rubus fruticosus s.l.		+	III	+	.	.	.
Pallavicinia lyellii		.	II	+	.	.	+
Salix aurita/cinerea	T	.	II	V	.	III	III
Carex elongata		.	V	.	.	.	V
Carex paniculata		.	IV	+	.	II	V
Eurhynchium praelongum		I	IV	III	V	V	V
Salix aurita/cinerea	S	I	II	V	V	V	V
Calliergonella cuspidata		.	.	III	II	III	IV
Plagiothecium denticulatum		.	II	II	V	IV	V
Polytrichum longisetum		+	.	II	.	.	.
Thelypteris palustris		.	.	II	V	V	V
Carex acutiformis		.	II	.	V	V	IV
Solanum dulcamara		.	+	II	V	IV	V
Lythrum salicaria		.	.	.	II	III	III
Potentilla palustris		.	.	.	II	+	I
Carex riparia		.	II	II	V	I	.
Salix capraea	S	.	.	.	II	.	+
Equisetum fluviatile		.	.	.	.	II	I
Galium palustre		+	.	.	+	III	V
Iris pseudacorus		.	+	+	II	.	V
Poa trivialis		.	.	+	.	II	V
Peucedanum palustre		.	.	.	.	+	V
Lycopus europaeus		.	.	.	.	.	V
Cirsium palustre		.	.	.	.	.	V
Lemna minor		.	.	.	.	.	IV

zone		A	A	B	B	B	B	B	C	C	C	C	C	D	D	D	E	E	E
type		1.1	1.2	2.1	3.1	2.2	3.2	3.3	1.3	1.4	2.3	2.4	3.4	1.5	1.6	2.5	2.6	3.5	3.6
number of quadrats		10	18	3	4	22	9	15	9	14	7	21	20	14	5	7	10	8	14
mean number of species		25	26	24	20	23	18	16	15	22	12	8	14	20	21	16	18	19	14
Sparganium erectum		V	V	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eupatorium cannabinum		V	V	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex hydrolapathum		V	V	1	1	II	.	.	.	.	.	.	.	.	.	.	.	.	.
Lycopus europaeus		V	V	.	1	I	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium palustre		V	V	.	1	I	.	.	.	.	.	.	.	I	.	.	I	.	.
Carex pseudocyperus		IV	IV	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mentha aquatica		III	III	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dactylorhiza majalis		II	III	.	.	.	.	.	.	I	.	.	.	I	.	.	.	.	.
Berula erecta		V	II	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scutellaria galericulata		III	I	.	.	I	.	.	.	.	.	.	.	.	.	.	.	.	.
Caltha palustris		.	IV	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sium latifolium		I	III	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dactylorhiza praetermissa		.	II	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sphagnum squarrosum		I	III	3	3	V	IV	II	.	.	III	.	.	.	.	I	I	.	.
Iris pseudacorus		V	II	1	4	I	.	I	.	.	.	.	.	II	.	.	.	.	.
Calliergonella cuspidata		I	II	3	3	II	I	.	.	.	.	.	.	.	.	.	.	.	.
Salix capraea	S	.	.	1	1	II	II	II	.	.	.	.	.	.	.	.	.	.	.
Calystegia sepium		.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex rostrata		.	.	.	.	III	.	.	IV	V	II	IV	II	I	.	I	I	I	.
Polytrichum juniperinum		.	.	.	.	I	.	.	I	I	II	I	I	.	.	.	.	.	.
Carex echinata		.	.	.	.	.	.	.	I	I	.	I	.	.	.	.	.	.	.
Drosera rotundifolia		.	II	.	.	.	.	.	IV	V	.	.	.	I	.	.	.	.	.
Agrostis stolonifera		.	.	.	.	.	I	.	.	II	.	I	.	I	I	III	III	V	III
Rubus fruticosus s.l.		.	.	1	1	II	I	.	I	II	.	.	III	I	V	.	IV	V	V
Sorbus aucuparia	T	.	.	.	.	.	.	.	.	I	.	.	.	.	I	I	III	.	I
Corydalis claviculata		.	.	.	.	.	.	.	.	.	.	.	.	I	.	.	III	.	II
Sorbus aucuparia	S	.	I	.	.	I	.	.	I	I	I	.	.	I	.	II	III	IV	V
Amelanchier lamarckii	S	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I	II	I
Stellaria media		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	II	.	II

Table III. Synoptic table of the differential species in the relevés from the permanent quadrats in "De Driehoek", Naardermeer. A, B, and C are the main vegetation zones. Each type has a number composed of two digits, the first indicating the time series (1= 1931, 2= 1966, 3= 1981) and the second the type within each series. The syntaxonomical units corresponding with these types are given in the legend of Fig. 4. Aquatic species, mainly present in 1931, are not included.

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AGE STRUCTURE OF WOODY SPECIES IN PRIMARY SUCCESSION ON A RISING BOTHNIAN SEA-SHORE

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Summary

This paper deals with the establishment and regeneration strategies of Acer platanoides L., Alnus glutinosa (L.)Gaertn., Fraxinus excelsior L., Hippophae rhamnoides L., Juniperus communis L., Picea abies (L.)Karst., Pinus sylvestris L., Populus tremula L., Quercus robur L. and Sorbus aucuparia L. in various stages of forest succession following sea shore displacement on a Bothnian Sea shore. Age determinations of more than 1000 individuals in three transects were used to reconstruct the establishment history of the populations following sea shore displacement caused by land uplift.

The relatively undisturbed woodland and sea shore plant communities of the same shore were analyzed using 59 releves. Successional trends in these data were analyzed with multivariate methods and compared with the results from the demographic study.

The lower woodland vegetation zones conformed to a simple model of undisturbed primary succession driven directly by sea-shore displacement. Regression analysis of age against elevation showed that the establishment rate of Hippophaë rhamnoides and Alnus glutinosa conformed to the rate of sea-shore displacement. Age structure of the higher parts of the forests reflected other influences on vegetation dynamics, mainly edaphic factors and former human impact.

Topographic and edaphic differences between the transects had a clear influence on the succession of plant communities. On exposed shores with a convex topography woodland communities developed with species more adapted to nutrient-poor and dry conditions than on sheltered shores with concave topography.

Keywords: Succession, population dynamics, land uplift, classification, ordination.

Introduction

Primary succession seres have often been inferred from the study of spatial sequences (zonations) in vegetation, assuming that they reflect different stages in a temporal sequence (Miles, 1979, Mueller-Dombois and Ellenberg, 1974). This concept has been used widely for shore vegetation (Cowles, 1899, Westhoff, 1947, Olson, 1958, Pierce and Kershaw, 1976) and the vegetation of recessional glacial moraines (Cooper, 1923b).

The interpretation of existing spatial variation as representing different stages of a temporal sequence is putative, however, and may lead to erroneous conclusions (Austin, 1977), because

- environmental gradients can interfere with the successional trend, e.g. microclimate near to a glacier front (Lindroth, 1965), edaphical and topographical heterogeneity (Olson, 1958) or salt spray gradients (Oosting, 1954);

- the directions of transitions between stages are hypothetical (Walker, 1970) and a successional trend should therefore be sustained by quantitative data on site age and population structure (Lawrence et al. 1967, Peet and Christensen, 1980);
- human activities may disturb the sequence (Schreiber, 1980).

We present here data on vascular plant response to changes in environment due to land uplift of a Bothnian sea shore. The rising shores of the Bothnian and Baltic Sea offer an excellent opportunity for the study of primary succession, because
- land uplift, being the main force underlying the environmental changes during primary succession on these shores, is well documented and can be quantified for each site;
- long-term studies have elucidated the relation between the zonation of vegetation and temporal change in the environment (Luther, 1961, 1979, Ericson, 1973, 1981a, 1981b, Ericson and Wallentinus, 1979);
- a variety of sites with only limited human impact is available.

We used two static approaches to analyze successional trends on these shores:
- the age structure of tree populations was used to reconstruct the establishment history of woody species in three transects. Tree age data have occasionally been used for studies of succession (Salisbury, 1925, Crocker and Major, 1957), but the age structure of such populations has only recently been shown to reflect changes in environment during the individual tree's life-span (Heikkinen, 1984, van der Maarel et al., 1985, Cramer, 1985, 1986). In our study area, trees and shrubs are lifted 50 cm or more above their location of establishment during less than 100 years. We determined tree age and site age (defined as number of years the site has been above mean zero level) and related them to each other;
- we also collected phytosociological data to analyze the response of plant communities to the major gradients on the shores, including the site age gradient.

From these two data sets, we inferred a successional sere. We considered also sites outside the transects and we used air photographs and historical records as a source of information about human impact and sea shore displacement in the area.

Study area

The nature reserve 'Häverö Prästäng' (60^{o} 07'N, 18^{o} 42'E) on the coast of Uppland, Eastern Central Sweden, is a peninsula in a relatively sheltered part of the Swedish archipelago. It offers a variety of shore types - from exposed rocky shores to more sheltered morainic shores (with shore-meadows) and strongly sheltered bays (with Phragmites communis Trin. stands).

During the last 300-400 years, relative land uplift at Hävero Prästäng amounted to ca. 5.6 mm/yr (Cramer, 1980, calculated according to Åse, 1964). Because of mineral and organogenic sedimentation (shore drift and plant necromass accumulation, respectively) in the Phragmites communis zone, the sheltered shores can have an even faster displacement than would follow from the summation of the factors slope and relative uplift. An estimate of the total horizontal shore displacement in the nature reserve has been obtained from comparison of maps from different times (Cramer, 1980).

Sampling methods

Three transects were laid out, running from water level up into older forest several meters above sea level. Along the transects (10x50m, 10x40m and 5x35m in size), we age-determined all woody species individuals by counting annual rings on cores or slices taken close to the stem base or by counting terminal bud scars. This method of tree age determination contains a source of error due to missing or badly developed rings, but the result can be taken as a minimum value for tree age.

We mapped all trees (in transect III the vast amounts of small plants were sampled in sub-plots and only the locations of these plots were mapped). Separated stems of clonally spreading species (e.g. Populus tremula) were treated as 'tree individuals' (Whitford, 1949). We then levelled the transects using grids of 1-2.5m width and interpolated the elevation of each tree above sea level.

The vascular plant vegetation was sampled in 22 relevés according to standard methods (Westhoff and van der Maarel, 1973), covering the whole area of the transects and 37 releves in the surroundings. Plant species nomenclature follows Lid (1974).

Water level data were obtained from the Swedish Meteorological Survey (SMHI) for the nearest tide-gauge, 'Forsmark', ca. 40 km north of the area. We transformed the observations from this station to take account of the difference in relative land uplift between Forsmark and the study area.

Data treatment

Woody species populations

We calculated site age at each tree's location by dividing elevation above sea-level 1984 (in mm) by relative land uplift (in mm/yr), assuming that sedimentation and erosion on these shores played a minor role in the displacement of the shore-line. Tree age data were converted to 'estimated year of establishment' by subtraction of the number of annual rings or terminal bud scars from 1984.

For reconstruction of the establishment history of the woody species populations, we applied regression analysis of tree/shrub age versus elevation (site age). This allowed us to test the hypothesis that establishment of tree individuals only takes place in a well-defined elevation range, as was demonstrated earlier for Alnus glutinosa (Cramer, 1985, 1986). We interpreted the slope of the significant age/elevation regressions as a measure of the populations' establishment (colonization) rate that can be compared to the speed of sea-shore displacement.

Transects I and II had their highest points at about 30 m distance from the shore. Therefore, we excluded all trees, that were not located between these highest points and the sea.

Vegetation

We first analyzed the vegetation data matrix (59 releves x 168 species, the latter counted separately for each stratum) with DCA (detrended correspondence analysis) ordination using the program DECORANA (Hill, 1979a, Hill and Gauch, 1980). We tested all attempts at classification of the data against the results of this ordination. For classification, TWINSPAN (two-way indicator species analysis - Hill, 1979b) was tried, but TABORD (van der Maarel et al., 1978) turned out to give a result closer to the ordination.

Results

Zonation of the woody species

The general zonation pattern of the woody species occurring close to the shores of the area is illustrated by Fig. 1 A-C for the three transects. Transects I and II were situated on relatively exposed shores, transect III in a sheltered bay. In the lower parts of the transects, tree species diversity increased with elevation. In general, only *Alnus glutinosa* and *Hippophaë rhamnoides* grew close to water level; a number of species grew higher up (*Fraxinus excelsior*, *Populus tremula*, *Acer platanoides*). In the highest parts, various forest types including *Picea abies* and/or *Pinus sylvestris* occurred.

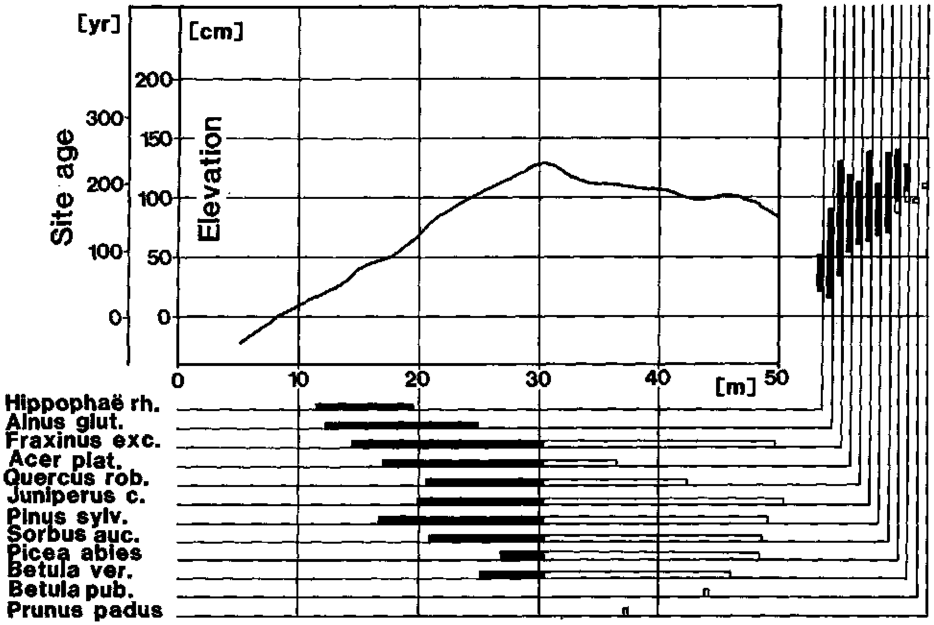

Fig. 1A. Horizontal and vertical distribution of woody species in the three transects. Vertical axes correspond to both elevation and (estimated) site age. Filled bars: sea-facing part of transect.

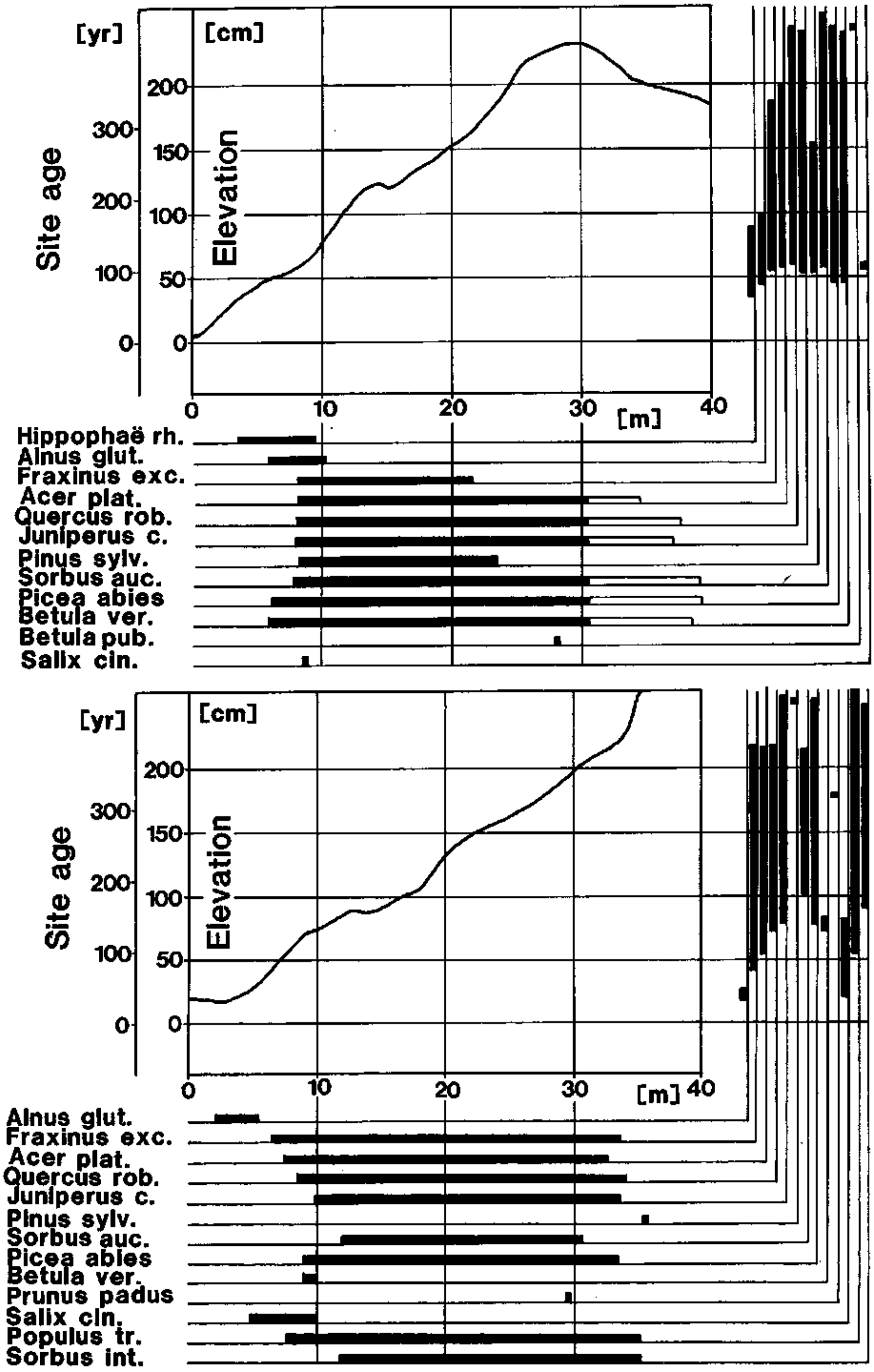

Fig. 1B (top) and 1C (bottom). For explanations, see Fig. 1A

Tab.1. Table of vegetation types ·

Cluster number	1	2	3	4	5	6	7	8	9	10	11
Scirpus tabernaemontani	4	-4-3-	22---	3---------	--------	--------	-----------	--	------	-	--
Scirpus uniglumis	-	-3-55	44243	46--------	--------	--------	-----------	--	------	-	--
Phragmites communis	-	68696	75454	---3---2--	112-22--	2--3----	2-----2----	--	------	-	--
Galium palustre	-	---1-	22423	----------	21--2---	--22-1--	222------2-	--	------	-	--
Caltha palustris	-	-----	--114	----------	--------	--------	-----------	3-	------	-	--
Mentha aquatica	-	---4-	73777	----------	----2222	2--2----	2----------	--	--1---	-	--
Triglochin maritimum	-	---23	33323	322232-221	-1-2----	-----1--	-----------	--	------	-	--
Juncus gerardii	-	----4	45747	54-3446433	64354334	32321---	-----------	--	------	-	--
Agrostis stolonifera	-	--22-	44453	3333326443	43234333	232-2232	2------2---	--	------	-	--
Aster tripolium	-	----2	---1-	222332-323	-------2	--------	-----------	--	------	-	--
Glaux maritima	-	----2	-3--4	3224435322	3323--22	--------	-----------	--	------	-	--
Plantago maritima	-	-----	--1--	---2222-2-	33423433	222-----	-----------	--	------	-	--
Centaurium littorale	-	-----	-----	----------	-213-133	--------	-----------	--	------	-	--
Odontites litoralis	-	-----	-----	----------	12443423	23------	-----------	--	------	-	--
Ophioglossum vulgatum	-	-----	-----	----------	244-44-2	2-------	-4---------	--	------	-	--
Leontodon autumnalis	-	-----	--1-2	------2--1	-2233233	2-2--233	-----------	--	------	-	--
Rhinanthus angustifolius	-	-----	----1	---------1	----5323	45342353	2----1-24--	--	------	-	--
Festuca rubra	-	-----	-----	--------2-	---55156	-43--545	3----------	--	------	4	--
Hippophae rhamnoides	-	-----	-----	-------1--	-----32-	8768-262	-----------	--	------	-	--
Alnus glutinosa	-	-----	-----	----------	----1---	--12--22	----1------	--	------	-	--
Festuca arundinacea	-	-----	---22	-----1-353	22133232	22342445	22233-2242-	1-	4-----	-	--
Valeriana salina	-	-----	--112	--------21	----2-22	32332322	3323-24233-	3-	32----	-	--
Filipendula ulmaria	-	-----	--113	----------	----2---	2-37-222	57872-76686	75	---3--	-	1-
Selinum carvifoliae	-	-----	----2	---------1	------22	-133-122	3-223-223--	2-	2--2--	-	--
Angelica arch.litoralis	-	-----	-----	----------	-------2	--3-2222	4323--32--2	--	------	-	--
Centaurea jacea	-	-----	-----	----------	--------	22232333	52232-33334	--	---2--	2	--
Inula salicina	-	-----	-----	----------	--------	32-33---	-3-4-2333-6	4-	3-----	-	--
Melampyrum nemorosum	-	-----	-----	----------	--------	-242-233	2-643726423	43	442332	2	3-
HIPPOPHAE rhamnoides	-	-----	-----	----------	--------	--------	88697376777	--	------	-	--
FRAXINUS excelsior	-	-----	-----	----------	--------	--------	----1623-25	--	6266--	5	--
ALNUS glutinosa	-	-----	-----	----------	--------	--------	------863--	43	------	-	--
SALIX aurita	-	-----	-----	----------	--------	--------	-----------	22	------	-	--
Crataegus monogyna	-	-----	-----	----------	--------	--------	-----------	12	------	-	--
Lychnis flos-cuculi	-	-----	---12	----------	--------	--------	-----------	3-	------	-	--
Geranium sanguineum	-	-----	-----	---------1	--------	-----2-2	----7---3--	1-	622---	-	--
Ranunculus acris	-	-----	-----	----------	--------	--2-----	----1----21	32	-2----	-	--
Populus tremula	-	-----	-----	----------	--------	---2----	-----------	22	----3-	-	--
Fraxinus excelsior	-	-----	-----	----------	--------	--------	-----1-----	26	5-343-	-	--
RHAMNUS frangula	-	-----	-----	----------	--------	--------	------2----	23	----2-	-	--
ALNUS GLUTINOSA	-	-----	-----	----------	--------	--------	-------6665	77	6566--	-	--
Anthriscus sylvestris	-	-----	-----	----------	--------	--------	---------2-	-1	2122--	-	--
Lysimachia vulgaris	-	-----	-----	----------	--------	--------	---------2-	4-	---2--	-	--
POPULUS TREMULA	-	-----	-----	----------	--------	--------	-----------	87	----75	-	--
Anemone nemorosa	-	-----	-----	----------	--------	--------	-----------	33	233-33	-	--
Ranunculus cassubicus	-	-----	-----	----------	--------	--------	-----------	34	2-2-42	-	--
Paris quadrifolia	-	-----	-----	----------	--------	--------	-----------	13	-2--32	-	--
POPULUS tremula	-	-----	-----	----------	--------	--------	-----------	36	--1-22	-	--
ACER platanoides	-	-----	-----	----------	--------	--------	-----------	-3	2-243-	-	--
SORBUS intermedia	-	-----	-----	----------	--------	--------	-----------	-2	1-2-2-	-	--
Lathyrus vernus	-	-----	-----	----------	--------	--------	-----------	-3	--2-3-	-	--
ROSA spec.	-	-----	-----	----------	--------	--------	-----2-----	-2	121-2-	2	--
Rubus saxatilis	-	-----	-----	----------	--------	--------	-------2---	-2	-----2	2	--
RIBES rubrum	-	-----	-----	----------	--------	--------	----------2	-2	-2---2	3	--
Galium boreale	-	-----	-----	----------	--------	--------	-----------	-2	22--2-	2	--
Platanthera chlorantha	-	-----	-----	----------	--------	--------	-----------	-2	-11-2-	2	--
Vicia cracca	-	-----	-----	----------	--------	----22--	-----------	3-	------	-	2-
Potentilla erecta	-	-----	-----	----------	--------	-------2	-------2---	-1	---2--	2	2-
Poa nemoralis	-	-----	-----	----------	--------	--------	---2------2	-2	242-2-	2	43
Melica nutans	-	-----	-----	----------	--------	--------	----4--2--2	32	44333-	3	62
Hepatica nobilis	-	-----	-----	----------	--------	--------	----2------	34	434254	3	4-
Dactylis glomerata	-	-----	-----	----------	--------	--------	----3-----3	22	33----	2	42
Acer platanoides	-	-----	-----	----------	--------	--------	-----1-----	-3	--134-	-	22
Roegneria canina	-	-----	-----	----------	--------	--------	-------2---	32	1--412	-	-2
Viola riviniana	-	-----	-----	----------	--------	--------	-------2---	-3	324242	-	32
Primula veris	-	-----	-----	----------	--------	--------	-------2---	12	233-3-	2	3-
Geum rivale	-	-----	-----	----------	--------	--------	--------3--	23	2-2--2	-	2-
BETULA VERRUCOSA	-	-----	-----	----------	--------	--------	--------7--	-5	-----6	-	87
Convallaria majalis	-	-----	-----	----------	--------	--------	-----------	44	346344	6	-3
Geranium sylvaticum	-	-----	-----	----------	--------	--------	-----------	22	223-32	-	32
PICEA ABIES	-	-----	-----	----------	--------	--------	-----------	11	--2636	5	77
Luzula pilosa	-	-----	-----	----------	--------	--------	-----------	2-	2----2	2	33
ACER PLATANOIDES	-	-----	-----	----------	--------	--------	-----------	-5	--657-	-	-4
Maianthemum bifolium	-	-----	-----	----------	--------	--------	-----------	-4	--2-2-	-	41
Dryopteris filix mas	-	-----	-----	----------	--------	--------	-----------	-1	----2-	-	22
LONICERA xylosteum	-	-----	-----	----------	--------	--------	-----------	-2	-22222	2	2-
Sorbus aucuparia	-	-----	-----	----------	--------	--------	-----------	-2	-2--2-	2	3-
Quercus robur	-	-----	-----	----------	--------	--------	-----------	-2	----22	2	32
SORBUS INTERMEDIA	-	-----	-----	----------	--------	--------	-----------	--	5-7-5-	-	--
Laserpitium latifolium	-	-----	-----	----------	--------	--------	-----------	--	--6-62	-	--
Polygonatum odoratum	-	-----	-----	----------	--------	--------	----2------	--	-32-34	3	--

Tab. 1. (continued)

FRAXINUS EXCELSIOR	-	-----	-----	----------	--------	--------	--------65	--	577575	5	--	
Ribes rubrum	-	-----	-----	----------	--------	--------	----------	--	2-2--2	3	--	
VIBURNUM opulus	-	-----	-----	----------	--------	--------	----------	--	-1-2--	2	--	
MALUS sylvestris	-	-----	-----	----------	--------	--------	---------2	--	225-2-	-	-2	
QUERCUS ROBUR	-	-----	-----	----------	--------	--------	----------	--	--2-37	-	3-	
Carex montana	-	-----	-----	----------	--------	--------	----------	--	2-----	-	23	
Ribes alpinum	-	-----	-----	----------	--------	--------	----------	--	---2--	-	23	
JUNIPERUS communis dead	-	-----	-----	----------	--------	--------	----------	--	----5-	-	56	
JUNIPERUS communis	-	-----	-----	----------	--------	--------	-2---2----	--	223---	7	-4	
Veronica officinalis	-	-----	-----	----------	--------	--------	----------	--	22----	2	4-	
SORBUS aucuparia	-	-----	-----	----------	--------	--------	----2-----	--	676-42	2	5-	
Fragaria vesca	-	-----	-----	----------	--------	--------	----------	--	2-2-52	3	42	
Polypodium vulgare	-	-----	-----	----------	--------	--------	----------	--	-22---	3	2-	
PINUS SYLVESTRIS	-	-----	-----	----------	--------	--------	----------	--	---6-2	5	-5	
Melampyrum sylvaticum	-	-----	-----	----------	--------	--------	----------	--	----2-	2	-2	
Rhamnus frangula	-	-----	-----	----------	--------	--------	----1-----	--	------	2	-2	
SORBUS AUCUPARIA	-	-----	-----	----------	--------	--------	----------	--	------	-	55	Species with >50% presence in at least one group
Lycopodium annotinum	-	-----	-----	----------	--------	--------	----------	--	------	-	32	
Phalaris arundinacea	-	-----	--1-3	--4-1--2-3	--------	-----3--	3----2--3-	--	------	-	--	Species with low presence
Sonchus arvensis	-	-----	--1--	--------2-	--------	--2--22-	-2--------	--	---2--	-	--	
Juncus spec.	-	-----	----2	----------	22------	--------	----------	--	------	-	--	
Carex extensa	-	-----	-----	----3----2	23-3----	--------	----------	--	------	-	--	
Sagina nodosa	-	-----	-----	----------	-2-----2	--------	----------	--	------	-	--	
Linum catharticum	-	-----	-----	----------	-1------	-2------	----------	--	1-----	-	--	
Stellaria palustris	-	-----	-----	----------	--------	--2-----	----------	--	-2----	-	--	
Lotus corniculatus	-	-----	-----	----------	--------	---3----	----------	--	------	-	-2	
Carex flacca	-	-----	-----	----------	--------	---2----	----------	--	----1-	-	--	
Taraxacum officinale	-	-----	-----	----------	--------	------2-	----------	-1	------	-	--	
Rumex acetosa	-	-----	-----	----------	--------	-------2	---------2	--	------	-	--	
HIPPOPHAE rhamn. dead	-	-----	-----	----------	--------	--------	--6-------	2-	------	-	--	
Poa trivialis	-	-----	-----	----------	--------	--------	--3--4---2	--	------	-	--	
Brachypodium pinnatum	-	-----	-----	----------	--------	--------	---2----2-	--	-2----	-	--	
Viola hirta	-	-----	-----	----------	--------	--------	----3-----	--	-23---	-	--	
Vincetoxicum hirundin.	-	-----	-----	----------	--------	--------	----2-----	--	---2--	-	--	
Juniperus communis	-	-----	-----	----------	--------	--------	-----1----	--	-21---	-	--	
Sedum maximum	-	-----	-----	----------	--------	--------	-----2---1	--	------	-	--	
ROSA canina	-	-----	-----	----------	--------	--------	------22--	--	---2--	-	--	
BETULA verrucosa	-	-----	-----	----------	--------	--------	-------3--	--	---2--	-	--	
PRUNUS padus	-	-----	-----	----------	--------	--------	---------2	--	-----2	-	--	
Milium effusum	-	-----	-----	----------	--------	--------	----------	-2	-3----	-	--	
Pyrola rotundifolia	-	-----	-----	----------	--------	--------	----------	-4	----4-	-	--	
RIBES uva-crispa	-	-----	-----	----------	--------	--------	----------	-2	----3-	-	--	
Ribes uva-crispa	-	-----	-----	----------	--------	--------	----------	-2	----2-	-	--	
Deschampsia caespitosa	-	-----	-----	----------	--------	--------	----------	-3	------	-	3-	
QUERCUS robur	-	-----	-----	----------	--------	--------	----------	--	5-----	2	--	
Anthoxanthum odoratum	-	-----	-----	----------	--------	--------	----------	--	2-----	2	--	
Campanula trachelium	-	-----	-----	----------	--------	--------	----------	--	2-----	-	2-	
Listera ovata	-	-----	-----	----------	--------	--------	----------	--	--2-2-	-	--	
Pimpinella saxifraga	-	-----	-----	----------	--------	--------	----------	--	---2--	2	--	
Picea abies	-	-----	-----	----------	--------	--------	----------	--	---2--	-	-1	
CORYLUS avellana	-	-----	-----	----------	--------	--------	----------	--	----32	-	--	
Vaccinium myrtillus	-	-----	-----	----------	--------	--------	----------	--	----1-	4	--	
Alchemilla spec.	-	-----	-----	----------	--------	--------	----------	--	------	1	2-	

Species with only single occurrences:

Group No.2: **Ranunculus baudotii**
No.3: **Potentilla anserina**
No.4: ***Juncus articulatus***
No.6: **Cirsium palustre, Sagina procumbens, Plantago major, Hieracium sp.**
No.7: **Galium verum, Satureja acinos, Prunus padus, Lythrum salicaria, RHAMNUS cathartica**
No.8: **Carex disticha, Iris pseudacorus, Lysimachia thyrsiflora, SALIX SPEC.**
No.9: **Glechoma hederacea, Achillea millefolium, Viburnum opulus, Ribes nigrum, Sorbus intermedia, MALUS SYLVESTRIS, Lonicera xylosteum, Angelica sylvestris, Epipactis helleborine. Daphne mezereum, PICEA abies, Hieracium sylvaticum,**
No.10: **Vaccinium vitis-idaea, Trifolium montanum, Stellaria graminea,**
No.11: **Trifolium medium, Huperzia selago, DAPHNE mezereum**

Notes: Species and genus names in capital letters: tree layer,
only genus name in capital letters: *shrub layer*
others: herb layer

'Agrostis stolonifera' includes also **Agrostis gigantea**,
'Angelica arch.litoralis' means **Angelica archangelica** ssp.litoralis

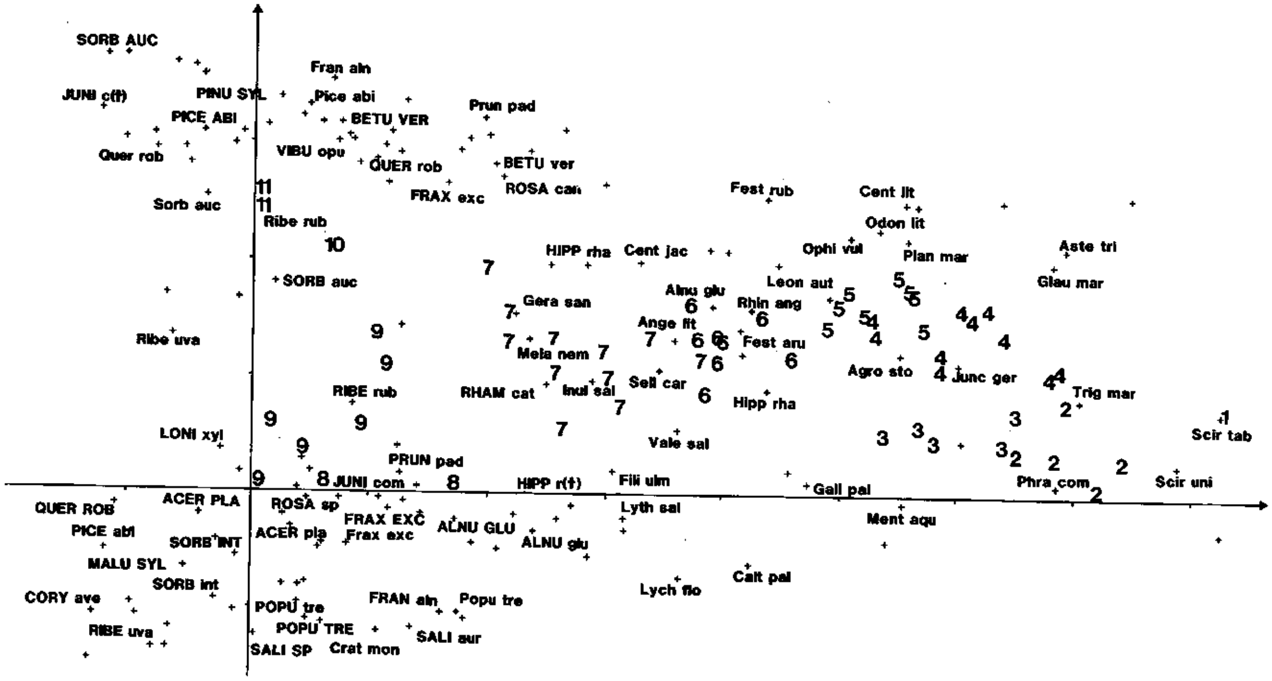

Fig. 2. DCA-ordination diagram of 59 relevés (first and second axis). Numbers are TABORD cluster codes and denote the location of samples, crosses denote species (some forest field layer species names omitted). Genus and species name in capitals: tree layer, genus in capitals: shrub layer, others: field layer species.

Floristic trends

DCA showed one major gradient of species composition along a first axis (eigenvalue: 0.863). Subsequent eigenvalues were much lower (0.314, 0.237, 0.164).

There is a strong (negative) correlation between altitudinal position of the samples and the first axis (Fig. 2). Field observations and the general requirements of many of the species suggest a good correlation between the second axis and the factor 'exposure'. The most sheltered transect in the dense *Phragmites communis*-reed is found close to the first axis while the others are situated at higher levels of the second axis.

We initialized the classification procedure TABORD with an arbitrary cluster array and set the program options at intermediate values. The resulting TABORD clusters were then plotted as an overlay on the DCA ordination diagram. When groups were very large, they were split into two or more sub-groups, and TABORD was run again with the cluster array obtained by this procedure. This iterative method of refining the cluster array (as suggested by van der Maarel et al., 1978) was repeated several times and resulted in a final table of vegetation types (Tab. 1).

Tab. 2 shows Wishart similarity ratios for the groups obtained with TABORD. On the lower parts of the shore, the average within-cluster similarities are clearly higher than the between-cluster similarities (groups 1 to 7: the open shore up into the *Hippophaë*-belt). In contrast, within-cluster similarities in the few remaining, much more species-rich woodland clusters are relatively lower. More samples would be necessary to establish a representative classification of these species-rich communities. Nevertheless, the location of these small groups 8 to 11 in the DCA-diagram shows that they are clearly separated (Fig. 2).

Tab.2 Sizes and Wishart similarity ratios for the final clusters in Tab.1

Cluster	Size	Average similarity ratio within the cluster	most similar cluster	between-cluster similarity ratio
1	1	1.0000	2	0.0783
2	5	0.6558	3	0.4299
3	5	0.8124	2	0.4299
4	10	0.6468	5	0.4553
5	8	0.6643	4	0.4553
6	8	0.5960	5	0.3784
7	11	0.5599	6	0.2979
8	2	0.4752	9	0.4090
9	6	0.4493	8	0.4090
10	1	1.0000	9	0.3928
11	2	0.4886	9	0.2989

Establishment history of the woody species populations

Tab. 3 lists the parameters of the regressions for tree age versus site age (elevation) separately for each species in each transect, the two exposed transects I and II together, and in all transects (see also Fig. 3 A-C). The following species showed establishment rates in agreement with the rate of sea-shore displacement, i.e. significant regressions of age versus elevation with slopes close to 0.56 cm/yr ($P<0.05$): *Alnus* glutinosa (transect II), Fraxinus excelsior (I, III), and Hippophaë rhamnoides (I, II). Others had significant correlations, but their slopes differed from the rate of sea-shore displacement: Alnus (transect I - steeper slope) and Picea (II - negative slope). The same tendencies were observed in regressions calculated on several transects lumped together.

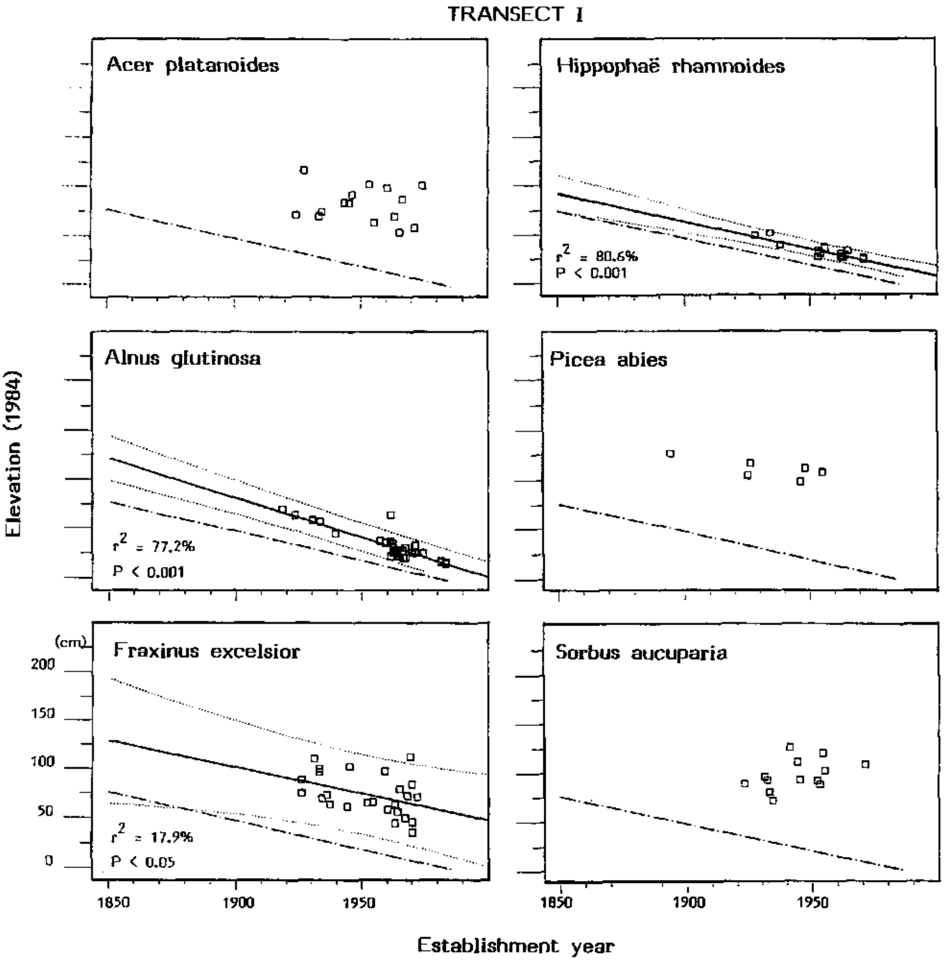

Fig. 3A. Diagrams of establishment year against elevation for each species in each transect (only shown, if more than 3 individuals could be age-determined. Significant regressions are plotted with 95%-confidence intervals. Dashed line denotes sea-shore displacement.

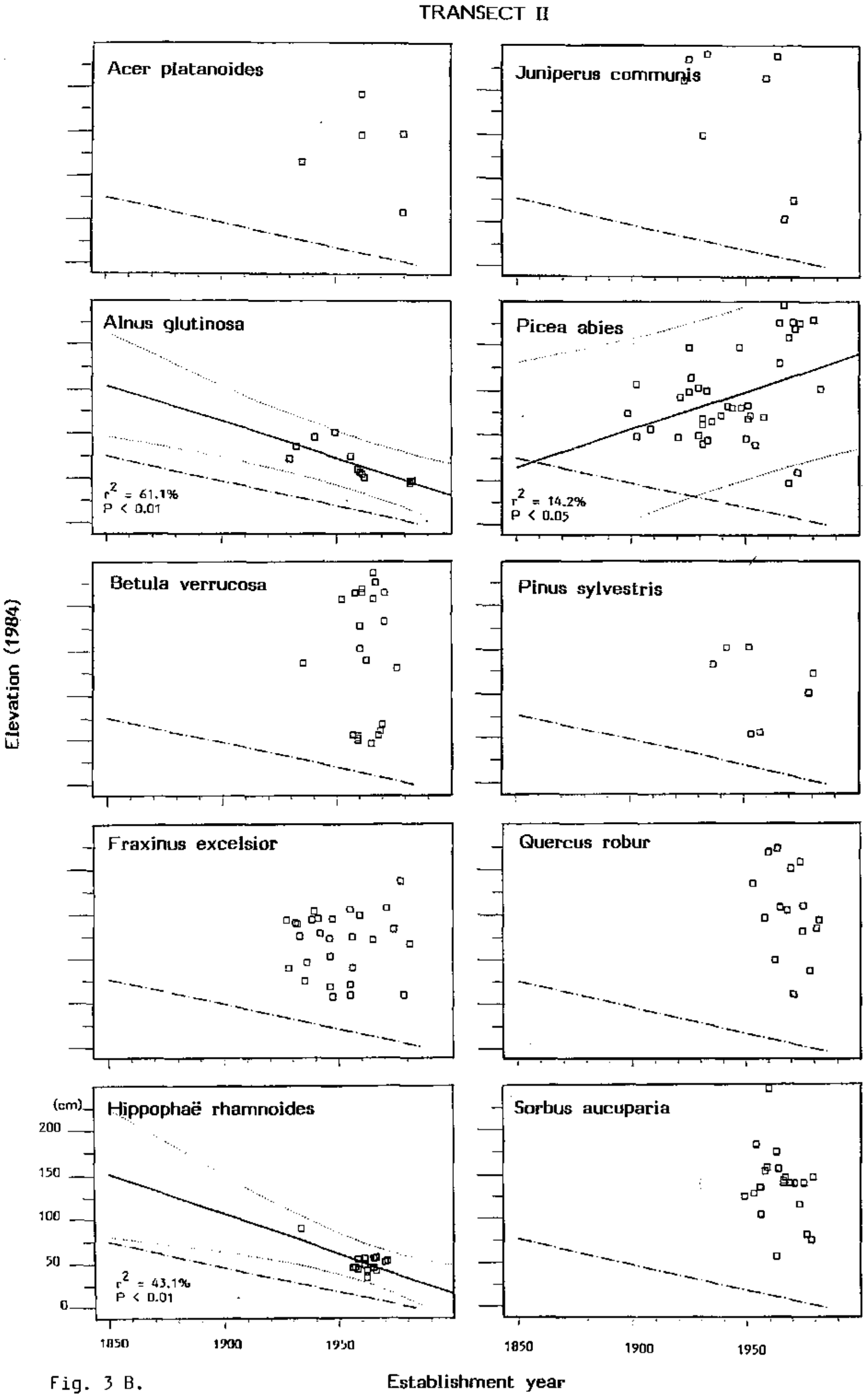
TRANSECT II
Acer platanoides
Juniperus communis
Alnus glutinosa
$r^2 = 61.1\%$
$P < 0.01$
Picea abies
$r^2 = 14.2\%$
$P < 0.05$
Betula verrucosa
Pinus sylvestris
Fraxinus excelsior
Quercus robur
Hippophaë rhamnoides
$r^2 = 43.1\%$
$P < 0.01$
Sorbus aucuparia
Elevation (1984)
(cm)
200
150
100
50
0
1850
1900
1950
1850
1900
1950
Establishment year

Fig. 3 B.

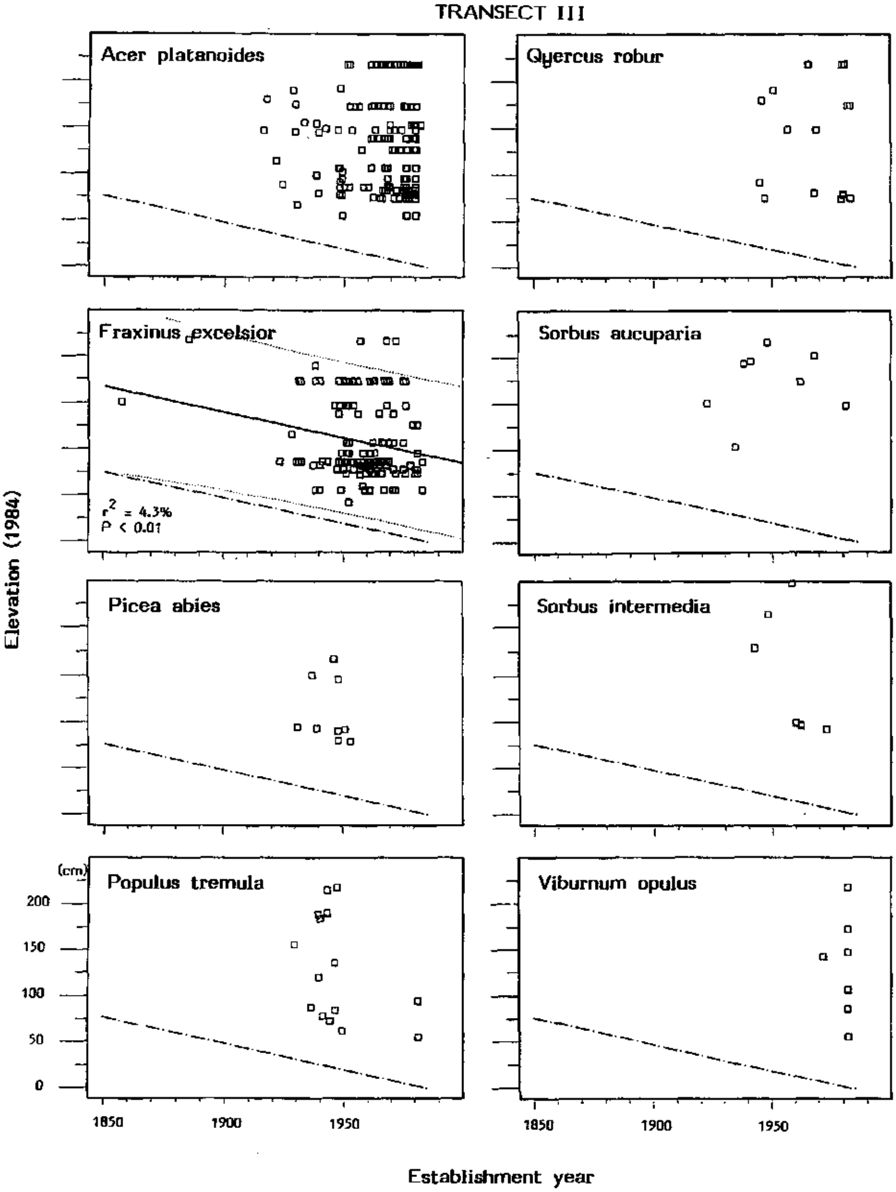

Fig. 3 C.(for explanations, see Fig. 3 A)

Tab.3. Regression analyses of tree age versus elevation (sea-facing slopes only)

	Transects														
Species	I			II			III			I+II			I+II+III		
	N +	r^2 S	b	N +	r^2 S	b	N +	r^2 S	b	N +	r^2 S	b	N +	r^2 S	b
Acer platanoides	15(--)	0.0	-	5(--)	3.1	-	205(1)	0.0	-	20(--)	0.8	-	225(1)	1.0	-
Alnus glutinosa	34(10)	77.2***	0.801	12(2)	61.1**	0.829	1(1)	-	-	46(12)	45.1***	0.892	48(13)	44.3***	0.887
Betula verrucosa	2(--)	0.0	-	22(1)	0.0	-	2(--)	-	-	24(1)	0.0	-	26(1)	2.1	-
Fraxinus excelsior	26(--)	17.9*	0.548	29(--)	0.0	-	178(--)	4.3**	0.491	55(--)	2.9	-	233(--)	3.1**	0.412
Hippophae rhamnoides	18(--)	80.6***	0.577	15(--)	43.1**	0.908	-(--)	-	-	33(--)	13.2*	0.482	33(--)	13.2*	0.482
Juniperus communis	3(2)	51.3	-	8(6)	30.4	-	2(18)	-	-	11(8)	4.9	-	13(26)	5.2	-
Malus sylvestris	2(--)	-	-	-(--)	-	-	-(--)	-	-	2(--)	-	-	2(--)	-	-
Picea abies	6(--)	57.9	-	39(2)	14.2*	-0.832	10(--)	15.6	-	45(2)	13.0*	-0.763	55(2)	8.1*	-0.676
Pinus sylvestris	2(--)	-	-	7(--)	5.7	-	1(--)	-	-	9(--)	1.2	-	10(--)	45.1*	1.721
Populus tremula	-(--)	-	-	-(--)	-	-	15(9)	15.6	-	-(--)	-	-	15(9)	15.6	-
Quercus robur	1(--)	-	-	15(--)	11.3	-	18(--)	3.2	-	16(--)	20.2	-	34(--)	4.6	-
Salix cinerea	-(--)	-	-	1(--)	-	-	2(--)	-	-	1(--)	-	-	3(--)	80.9	-
Sorbus aucuparia	13(--)	18.2	-	21(--)	8.1	-	8(--)	3.4	-	34(--)	10.4	-	42(--)	2.7	-
Sorbus intermedia	-(--)	-	-	-(--)	-	-	8(--)	19.9	-	-(--)	-	-	8(--)	19.9	-
Viburnum opulus	-(--)	-	-	-(--)	-	-	40(--)	0.3	-	-(--)	-	-	40(--)	0.3	-

Legend:
N number of trees with age datum
\+ " " " without age datum
r2 square of Pearson correlation coefficient
S Significance level for the correlation
* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$
b slope of the regression line

The establishment of Hippophaë rhamnoides followed the retreating shore-line with a speed similar to the speed of sea-shore displacement. Hippophaë is the pioneer woody species on more exposed shores in the region, spreading effectively by root suckers protruding between the stones in the coarse substrate. Its lower limit seems to be mainly determined by destruction from ice-movement in late winter.

Alnus glutinosa is the pioneer species on slightly more sheltered shores. In transect I, the establishment rate of Alnus exceeded the rate of sea-shore displacement. This discrepancy can be explained by the substantial aggregation of shore drift material and litter in the alder woods, giving a higher level of the soil surface (Ugolini, 1968) for our measurements than existed when the seedlings established. In this respect, Alnus differed from Hippophaë, which showed an establishment rate more directly connected to the rate of sea-shore displacement. Disturbance (such as destruction by ice-movements and storm waves) is less intensive at the Alnus-sites, allowing greater accumulation of litter and drift material.

Fraxinus excelsior established in step with sea shore displacement in transects I and III, but the 29 individuals in transect II appeared irregularly at all elevations. The tree-age/site-age correlation in transect I results from a pattern similar to that of Alnus and Hippophaë (trees establishing only in a certain zone following the retreating shore line), but transect III deviated because of the vast numbers of small plants of varying age. These began to invade the transect around 1950 at a wide range of elevations. The weak, but significant correlation ($R2 = 4.3\%$) depends entirely on the three oldest Fraxinus individuals in the transect and disappears when they are removed from the analysis.

Acer platanoides, Quercus robur, Sorbus aucuparia and Betula verrucosa (like Fraxinus) invaded transect II and/or III rather suddenly around 1950 in a wide elevation range. No correlation between site age and tree age could be detected.

Many junipers (Juniperus communis) were found dead in all transects, especially in transect III. It was not possible to establish a significant correlation between age and elevation for the surviving junipers in any transect. All the dead juniper bushes were under a rather dense canopy of other trees, while the survivors grew near rocky outcrops at higher light intensities.

Populus tremula occurred only in the sheltered transect III. All but two individuals appeared between 1930 and 1950. Many trees were rotten inside and could not be age-determined. No regularity could be found in their establishment.

Discussion

Successional trends in the woody species

From these results, we infer a simple generalized scheme for the successional role of each woody species.

Establishment of the pioneers on the shores of the study area (mainly Alnus glutinosa and Hippophaë rhamnoides) is governed by the availability of open surfaces emerging from the sea. Alnus and Hippophaë do not establish elsewhere in the woodland communities studied, and both the beginning and the end of their life-cycle appear to be dependent on sea-shore displacement (Fig. 3).

The method of reconstructing the establishment history of these populations allows determination of their establishment rates. Where these rates are similar to the rate of sea-shore displacement, we infer that sea-shore displacement directly drives succession. Where establishment rates differ from sea-shore displacement, we can only make qualitative suggestions about the causes of succession.

Alnus glutinosa and Hippophaë rhamnoides show the effect of sea-shore displacement most clearly. We can make a distinction between the two species: sites with older Alnus-trees have a higher elevation than those of equally old Hippophaë-bushes. This difference agrees with the field observation that more litter and drift material is accumulated at the Alnus-site than at the Hippophaë-sites, leading to a local upheaval of the soil surface that is faster than relative land uplift (Ugolini, 1968). We suggest two main reasons for the difference in distribution of these two species: (1) a greater tolerance of Hippophaë towards mechanical disturbance (ice-movements and heavy wave action), removing most of the material accumulated on top of the substrate and (2) an important difference in substrate (much higher humus-content in the Alnus woodland). Here is a key to understanding the successional consequences of the different establishment strategies of these two species: intensive production of root suckers (Hippophaë - Pearson and Rogers, 1962, Ranwell, 1972) and relatively more intensive production of seedlings (Alnus - McVean, 1953, 1956). Vegetative propagation seems to be favoured by unstable, loose substrate; sexual propagation benefits from a lower degree of disturbance and availability of organic deposits (litter).

Fraxinus excelsior was shown to establish in step with sea-shore displacement in two of three transects, but with a much wider range of establishment elevation. Fraxinus germinates much more profusely than Alnus and seems to be able to make use of more 'safe sites' occasionally becoming available. We therefore regard Fraxinus as a transitional species, establishing where sea-shore displacement offers new sites but also favoured by other important changes in environment.

Such a change took place around the year 1950, when grazing in the area (mostly by sheep) ceased and no important human influence occured any more (E. Jansson, Trästa, pers. comm.). Today, there is still grazing of moose (Alces alces) and roedeer (Capreolus capreolus). The effects of cessation of sheep grazing can be seen in transects II and III illustrated by a sudden colonization of Acer platanoides (III), Betula verrucosa (II), Fraxinus excelsior (III), Quercus robur (II + III), and Sorbus aucuparia (II) into (presumably) open, park-line pastures with scattered trees. Evidence for this is also given by a series of air photographs, the oldest one from 1943, showing the rapid closing of the canopy. Note also that colonizing Betula verrucosa, both under primary successsion (close to the sea in transect II) as well as under secondary succession, was always closely followed by Picea abies (Fig. 1. A-C).

The increase of the species we found on former grazing areas is contrasted by the large number of dead Juniperus communis still standing in the shade of the dense canopy. In transect III, several of these dead junipers were now surrounded by Quercus indiviudals growing in circles of less than 1 m in diameter that seem to have been the first new trees appearing after sheep grazing had ceased. Similarly rapid secondary succession is known from both pastures and meadows in the same kind of woodland elsewhere in the region (Haeggström, 1983).

Age structure analysis of the woody species populations thus allowed for a distinction between secondary succession after release from grazing and the primary succession of the pioneers, Alnus and Hippophaë, that had been taking place already during the grazing period. But Alnus and

Hippophaë may still have been affected by grazing. The age/elevation graphs (Fig. 3.) indicate that both species established more profusely after grazing had ceased. For Hippophaë, this observation agrees with Ledwood and Shimwell (1971) and Ranwell (1972). Vinther (1983) showed that Alnus glutinosa can be favoured by (moderate) grazing, but Fremstad (1983) described the species as a common colonizer of completely abandoned grazing land in W-Norway.

Successional trends in the vascular plant vegetation

The generalizations made for the three transects imply a strong simplification regarding different successional pathways on varying substrates and/or degrees of exposure. These dimensions can be illustrated by the vascular plant vegetation analysis. The results of this analysis (Tab. 1., Fig. 2.) can be interpreted as chronosequences, because the evidence for the overall successional trend from open sea-shore communities to woodlands and forests is provided by both previous studies and by our demographic results.

Exposure to heavy wind and wave action is reflected both by the DCA-ordination (Fig. 2. separates wave-wash tolerating species like Aster tripolium and Glaux maritima from those more adapted to sheltered conditions, like Phragmites communis and Scirpus uniglumis) and by the TABORD-classification (Tab. 1. separates groups 2 + 3, sheltered, clearly from 4 + 5, exposed). Following the main successional trend through the ordination diagram (Fig. 2. right to left), we see a separation in at least two different site groups also at higher elevations. The species composition of the two main woodland groups shown on the left hand side of the diagram (group 10/11 versus group 8/9) reflects differences in soil characteristics resulting from topography and exposure:

- the 'sheltered group' (8/9) with species demanding relatively high levels of both moisture and nutrients (Populus tremula, Laserpitium latifolium, Lysimachia vulgaris, Anemone nemorosa). Due to a concave topography, these sites have been more subjected to accumulation of drift material than to wave erosion, when they passed through the water level. A rather fine substrate with high water capacity and high humus content is the result.
- the 'exposed group' (10/11) with species more adapted to drier conditions with lower nutrient levels (Pinus sylvestris, Lycopodium annotium, Melampyrum sylvaticum). The sites are located on convex features of the topography, such as highest areas of low former islands or outer parts of peninsulas. The soil is coarse with rocky outcrops in between and a thin humus layer.

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PRIMARY FOREST SUCCESSION ON BLOWN - OUT AREAS IN THE DUTCH DRIFT SANDS

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Summary

Blown-out areas in both former and recent drift sands of the Veluwe hills, central Netherlands, were chosen for research on primary succession. On 13 sample plots situated in open drift-sand areas or in Scots pine stands of different ages (the oldest approx. 130 years old) detailed analyses of the herbaceous and tree layers were carried out and the total amount of the dead organic matter (litter) incl. humus on and in the soil was determined. This enabled the succession of the plant and tree species as related to the age of the Scots pine stands and the litter/humus layer development to be ascertained.

Keywords: Blown-out areas, primary succession, initial litter and humus formation.

Introduction

This research took place in the area of Hulshorst drift sands, Leuvenhorst and Leuvenum Forest, NW Veluwe, central Netherlands. Much information is available about past forest developments in this area (old topographic and forest maps, forest administration records, etc.) and this can be used as the basis for research on forest succession. Using this material I was able to reconstruct the general forest development in this area over the past 130 years.

The research was concentrated on the blown-out areas, both former and recent. These blown-out areas provide good conditions for research in primary succession because of their uniformity. The substratum is a gravel-rich, coarse fluvio-glacial sand, often covered with a thin layer of fine drift sand. The only factor that can cause variation between sites is the layering of the substratum. Generally,the substratum is easily permeable to precipitation. Locally, however, a thickened substratum layer is present, resulting in a water supply different to that on "normal sites". These places are moist and can be recognized in the field by their vegetation (e.g. Calluna vulgaris and Juncus squarrosus in the initial successional stages; Molinia caerulea in later stages). These places were not involved in the research.

In the recent, unforested blown-out areas, no soil profile has developed. In the forested areas, shallow, micropodzol soils in initial stages of soil profile differentiation are developing.

Thirteen sample plots were chosen in the open sand area and in Pinus stands of different ages (the oldest being approximately 130 years old). On these plots the herbaceous and tree layers were analysed in detail and the total dead organic matter (litter) including humus, both aboveground and in the 25 cm mineral layer, was determined. This revealed the succession of plant and tree species as related to the age of Pinus stands and litter/humus layer development.

Succession

The succession starts when the coversand layer has been blown off and the level of the fluvio-glacial deposit has been reached. The course of the primary succession with its particular stages (phytosociologically defined) is given in figure 1. The initial stage is formed by *Corynephorus canescens,* later accompanied by *Festuca ovina* subsp. *ovina* and *Spergula morisonii*. It can be described as the *Spergulo-Corynephoretum* association. The following stage is dominated by *Polytrichum piliferum* and *Algae*. According to Stafleu & Westhoff (1940) it is the *Politrichum piliferum* facies of *Spergulo-Corynephoretum*.

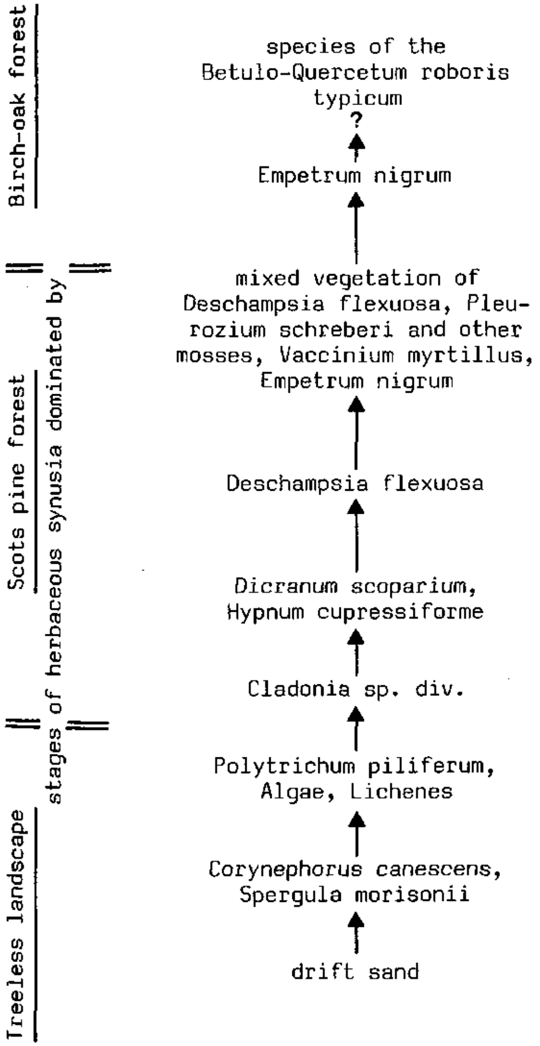

Fig. 1. Primary succession on blown-out areas in Hulshorsterzand and Leuvenum Forest

The initial stage of the forest is formed by Pinus sylvestris with lichens, which can be seen as some kind of Cladonio-Pinetum, later followed by Pinus forest with mosses, which refers to the association Leucobryo-Pinetum. In the next stage Deschampsia flexuosa becomes dominant for a long time. Progressive decay of its cover allows characteristic forest plants and mosses such as Vaccinium myrtillus, Empetrum nigrum, Pleurozium schreberi, Leucobryum glaucum etc. to infiltrate. The preliminary terminal stage, which is reached after approximately 100 years of development, is a Pinus forest with Empetrum nigrum, which is analogous to the Empetro-Pinetum association.

The successive development of vegetation on this site is given in table 1.

Table 1. Primary succession on blown-out areas in Hulshorst drift sands and Leuvenum forest.

Relevé no.	1	2	3	4	5	6	7	8	9	10	11	12	13
General characteristics													
E5 tree layer													
Total cover-%							50	70	60	60	50	40	30
Age (Pinus)							30	45	60	80	100	110	130
Pinus sylvestris							7	8	8	8	7	7	6
E4 tree layer													
Total cover-%												40	70
Age (Pinus)													40
Betula pendula												3	3
Pinus sylvestris													8
E3 shrub layer													
Total cover-%						5	4	2	-	5	10	30	5
Age (Pinus)						15						15	15
Pinus sylvestris						5	3	2	-	-	2	7	1
Betula pendula										4	5	1	1
E2 herb layer													
Total cover-%		10	40	10	10	20	30	10	40	50	50	65	70
Corynephorus canescens	1	5	7	5	4	6	6	-	-	-	-	-	-
Festuca ovina ssp.ovina			1	2	1	1	3	5	-	-	-	-	-
Spergula morisonii			1	2	3	1	1	3					
Pinus sylvestris					1	4	2	3	3	2	-	2	-
Calluna vulgaris							1	-	-	-	3	-	3
Agrostis vinealis								2	-	-	-	-	-
Deschampsia flexuosa								3	7	9	6	5	4
Betula pendula									1	2	1	1	2
Betula pubescens									1	2	-	-	1
Sorbus aucuparia									1	1	-	-	1
Quercus robur									1	1	1	1	1
Vaccinium myrtillus											4	1	3
Vaccinium vitis-idaea											1	-	3
Empetrum nigrum											3	7	7
Frangula alnus												1	-
Salix caprea													1
Erica tetralix													2
Carex arenaria													1
Galium saxatile													1
E1 moss layer													
Total cover-%				40	70	70	30	1	50	20	30	60	80
Polytrichum piliferum			1	7	8	8	6	-	-	-	-	-	-
Algae			1	5	5	3	5	-	-	-	-	-	-
Coenocaulon aculeatum				3	3	1	1	-	-	-	-	-	-
Cladonia sp. div.						3	1	2	1	1	1	2	-
Dicranum scoparium								2	5	6	3	6	2
Hypnum cupressiforme								2	7	3	4	4	5
Leucobryum glaucum									3	2	4	2	-
Dicranum polysetum									1	1	2	2	3
Campylopus fragilis									1	1	2	1	-
Polytrichum formosum										2	4	3	-
Pleurozium schreberi											2	7	7
Lophocolea bidentata												1	-

Note: Cover-abundance estimation according to the Braun-Blanquet ordinal transformation scale (Westhoff & Van der Maarel, 1973)

Spontaneous regeneration of *Pinus* in gaps or under a light canopy of the old stands leads to the repeating of the terminal stage. It can be designated as a progressive succession and iterative strategy. Possible retrogressive development, decay of the forest community without any tree regeneration, could lead to some kind of poor heathland becoming "Ersatzgesellschaft" of the forest (deflective strategy; Fanta, this volume). Alternative strategy (replacing of *Pinus* with an "earlier" succession tree species) cannot take place under these simplified circumstances because only one - pioneer - tree species is present.

In the transient and terminal stage of *Pinus* forests seedlings of broadleaved tree and shrub species appear regularly (*Betula pendula, Quercus robur, Frangula alnus; Betula pubescens* and *Fagus sylvatica* can also be present). They are, however, browsed by red and roe deer and rabbit, and therefore the broadleaved tree species cannot regenerate successfully on these poor sites. The only tree species that can survive under these circumstances is *Pinus*. If game browsing did not occur, succession might continue and reach some poor variant of birch-oak forest (*Betulo-Quercetum*) at least.

Relation "Vegetation succession-litter and humus formation"

The ecesis of plant and tree species is closely related to forest litter accumulation and humus formation (fig. 2). The first humus-producers are *Polytrichum piliferum* and *Algae*. Litter production depends on *Pinus*. The ecesis, dominance and decay of *Dechampsia flexuosa* cover is obviously closely related to the phase of maximum litter production in *Pinus* stands. The first forest plants (such as *Vaccinium myrtillus, Empetrum nigrum* and *Pleurozium schreberi*) appear when a humus layer (moder humus) is being formed as the result of slowly advancing fermentation. *Pinus* regenerates in gaps or under a light canopy cover of old stands, where little litter supply and more intensive decomposition take place.

Humus plays a very important part of this site, supplying the ecosystem with nutrients and water. It is possible that an increase of humus content in the ecosystem in the course of a few forest generations will automatically lead to a different type of terminal stage of succession, some poor variant of a birch-oak forest (such as if game browsing were excluded); the *Empetro-Pinetum* would then only be one of the pre-climax succession stages of the birch-oak climax community. The present *Empetro-Pinetum* should therefore be seen as a kind of disclimax dependent on the present impact of animals.

Scots pine forests planted on this site develop along the same lines as the spontaneous succession, but more rapidly. This is undoubtedly because litter production is greater in planted stands, which, compared with the spontaneous forests, are regularly kept in a dense canopy and produce more litter.

Conclusions

The analyses described provide much ecological information about plant and tree species strategies during succession. Using this information, development trends of the potential natural vegetations as related to this site can be predicted with great accuracy. Forest plant ecesis, cover culmination and decline, natural regeneration of forest trees, seedling survival, humus layer development and other dynamic phenomena can be better understood in terms of their interrelations within the framework of the entire ecosystem: they do not take place occasionally and in isolation, but have their logical place in the course of ecosystem development.

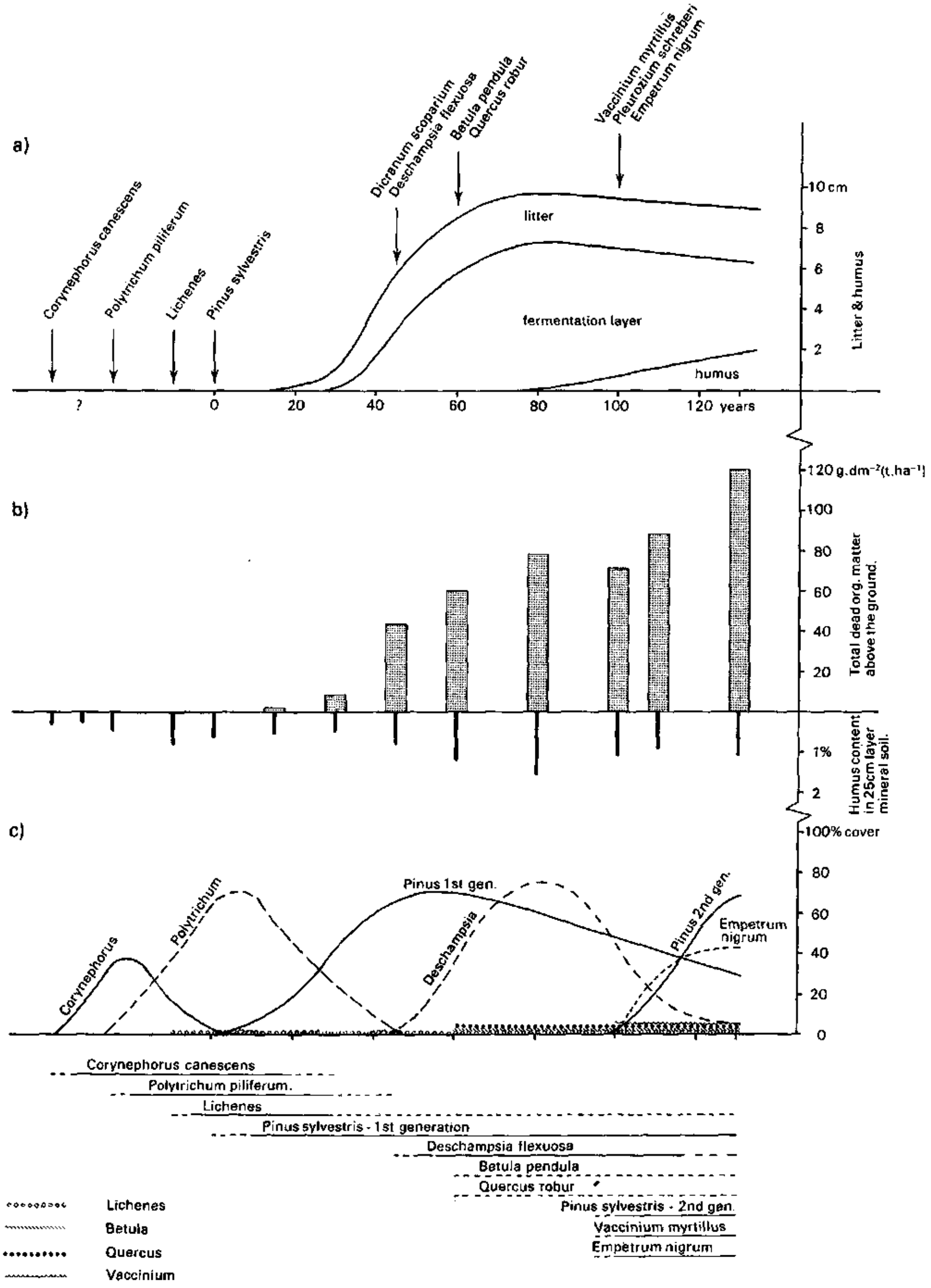

Fig. 2. Vegetation and forest succession as related to litter and humus formation in blown-out areas.

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DYNAMIQUE DE CICATRISATION DES OUVERTURES NATURELLES DANS DES RESERVES BIOLOGIQUES DE LA FORET DE FONTAINEBLEAU (Environs de Paris)

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Summary

The biological reserves of "La Tillaie" and "Le Gros Fouteau" in the Fontainebleau forest consist of a beech stand mixed with some hornbeams and oaks. In the middle ages, oak was dominant.

Openings caused by death of trees show three closing strategies:

1. Obstruction by enlargement of marginal crowns, major process in small gaps.
2. Growth recovery of shade tolerant species (beech and holly tree) with global growth increases.
3. Natural regeneration subsequent to the gaps, beech is now present nearly everywhere, alone.

Beech regeneration and development must be related to success and abundance of beechnut falls, gaps size, soil types and presence of herbaceous canopy.

Three stages were recognized; a rest one, before the first regeneration, an establishment one, when populations are setting up, a competition one, when mortality of youngest trees is appearing, due to crowns junction.

If some favourable factors appear simultaneously, old gaps, near the forest borders, may be colonized by shade intolerant species. These "opportunists" are Betula verrucosa, Pinus sylvestris, Quercus petraea or Fraxinus excelsior. Their populations are often colonized by hornbeam and mainly by beech which will replace them later because of his longer life (oak excepted).

The evolution of these reserves leads to a reduction of taxonomic diversity.

The global efficiency of those closing gaps strategies was determined by comparison of two clearing maps established in 1968-71 and 1980-82, lap without any important tree fall. Forest gaps, which occupied 11,5 % of both reserves area represent now less than 6 %. After the hurricanes of 1967, these reserves are now returning to a structural balance.

Keywords: Gaps, regeneration, forest succession, reserves, beech.

Introduction

Dans toute forêt non exploitée, les ouvertures provoquées dans le peuplement arborescent par la mort de grands arbres initient localement une phase de déstabilisation de plus ou moins longue durée. De nombreuses publications ont décrit ces perturbations dans leurs divers aspects mésologiques, floristiques et biologiques. La réorganisation structurale met en oeuvre différentes stratégies dont l'importance respective varie suivant la composition taxonomique du matériel végétal et les dimensions des ouvertures, et dont on trouve une description, pour la forêt tempérée, dans des publications telles que celles de MARKS (1974), CONNELL et SLATYER (1977), BORMANN et LIKENS (1979), OLIVER (1981).

Ces stratégies concernent soit la végétation antérieure à l'ouverture, soit l'établissement de nouveaux individus postérieurement à la perburbation. Les premières sont l'extension latérale des couronnes d'arbres périphériques, la formation par ceux-ci de branches basses dites épicormiques, la production de rejects de souche d'arbres endommagés, l'apparition de drageons sur les racines, la libération de tiges antérieurement réprimées par l'ombrage. Les individus qui s'établissent après l'ouverture proviennent de la germination de graines dormantes antérieurement enfouies dans le sol ou de celle de graines dont l'arrivée est postérieure. Les graines proviennent d'arbres du peuplement in situ ou extérieurs à celui-ci; les premières, qui appartiennent généralement à des espèces résistantes à l'ombrage, sont lourdes et dépourvues de moyens de dissémination; les secondes sont produites par des espèces intolérantes à l'ombrage et possèdent des moyens de dissémination par anémochorie ou ornithochorie.

Ces différentes modalités de fermeture des vides ont été reconnues et amplement décrites dans les forêts du nord-est des Etats-Unis auxquelles participent d'assez nombreuses espèces ligneuses. Dans les plaines d'Europe occidentale et centrale, on a également décrit des successions cycliques où les vides dans les peuplements d'espèces de stades terminaux sont colonisés par des espèces pionnières (WATT, 1925, KOOP, 1981, FALINSKI, 1978).

Les réserves biologiques intégrales de la Tillaie et du Gros Fouteau en forêt de Fontainebleau, dont les écosystèmes ont été décrits par ailleurs (LEMEE, 1978), constituent un cas original quant à leur peuplement ligneux qui est dominé fortement par une seule espèce, le hêtre, très tolérant à l'ombrage et qui assure actuellement pour l'essentiel la fermeture des vides.

Ces réserves sont situées à une cinquantaine de kilomètres au sud-est de Paris. D'une surface de 35 ha pour la Tillaie, de 25 ha pour le Gros Fouteau, elles sont localisées sur un plateau de 133 à 138 m d'altitude, presque entièrement constitué par le "calcaire de Beauce" recouvert d'un dépôt éolien de sable siliceux dont l'épaisseur varie de quelques décimètres à plus de deux mètres.

La température moyenne annuelle est de 10,15^{o}C et les précipitations de 70 cm avec une répartition mensuelle assez uniforme.

Les sols sont organisés selon une séquence en relation avec l'épaisseur du sable, depuis un sol brun lessivé jusqu'à un podzol humique en passant par des états intermédiaires de lessivage, puis de podzolisation (BOUCHON et al., 1973). Les groupements végétaux sont, sur le sol lessivé, le Melico-Fagetum (Ordre du Fagetalia), sur le sol podzolique et le podzol le Deschampsieto-Quercetum (Ordre du Quercetalia robori-petraeae), sur les sols à faible podzolisation superficielle un groupement intermédiaire.

L'arbre dominant est partout le hêtre (Fagus silvatica). Le chêne sessile (Quercus petraea) a été supplanté progressivement par le hêtre depuis l'abandon par l'homme de l'ancienne chênaie médiavale, comme le montrent les diagrammes polliniques de soils de la Tillaie (GUILLET et ROBIN, 1972) et du Gros Fouteau. Le charme (Carpinus betulus) et le houx (Ilex aquifolium), tolérants à l'ombrage, sont assez abondants, surtout au Gros Fouteau où ce dernier forme de nombreux fourrés.

Nous avons réuni ici nos principales observations sur la fermeture des clairières dont certaines ont fait l'objet de publications (FAILLE et al., 1984a et b, LEMEE, 1985) auxquelles nous joignons la description de la structure et de l'évolution des jeunes populations cicatricielles de hêtres.

Resultats

1. Origine des ouvertures actuelles

On distingue deux causes: l'une est continue dans le temps, c'est la mort sur pied des arbres âgés; l'autre est de fréquence aléatoire, il s'agit des déracinements et cassures par coups de vent, la dernière tempête dévastatrice étant passée en 1967. Au Gros Fouteau, les morts par sénescence et par coups de vent se répartissent de manière à peu près égale dans l'origine des clairières actuelles; par contre les forts coups de vent sont plus meurtriers à la Tillaie, qui, entourée partiellement de surfaces déboisées, est de plus surchargée en vieux arbres et renferme, dans sa partie nord, un podzol sur lequel l'enracinement est plus superficiel.

Les vides actuels ont été ouverts en une ou plusieurs fois et leur ancienneté est très variable.

2. Nombre et surface des ouvertures en 1980-81

La densité des ouvertures de surface supérieure à 5 m^2 à la verticale des bords de couronnes des parois est en moyenne de 7,5 par ha à la Tillaie, de 3,4 seulement au Gros Fouteau. Leur distribution par classes de surface montre dans les deux réserves une décroissance d'allure exponentielle jusqu'à 300 m^2 avec cependant quelques trouées beaucoup plus grandes à la Tillaie (Fig. 1).

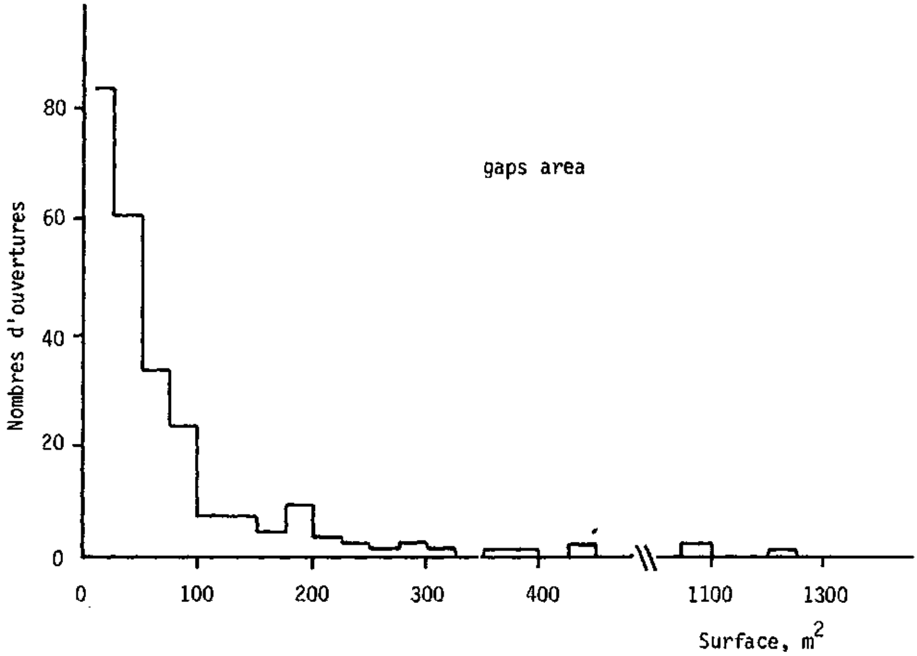

Fig. 1. Répartition de la surface des ouvertures de la Tillaie en 1980-81 (ouvertures de plus de 5 m^2).

3. Fermeture des clairières actuelles

a. Modalités: la résorption des vides est réalisée selon trois stratégies:
- croissance latérale des couronnes autour de l'ouverture; c'est le mode principal dans le cas d'ouverture par un seul arbre (Fig. 2);

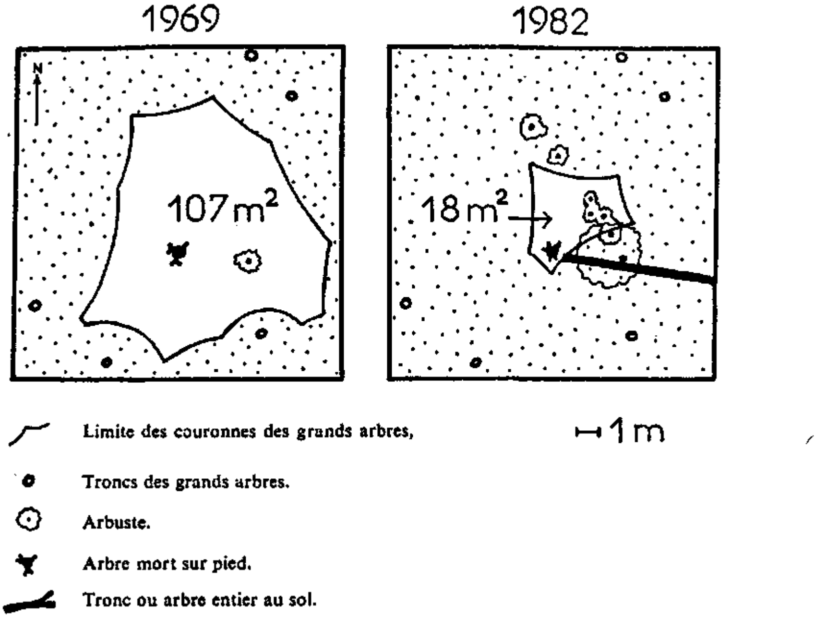

Fig. 2. Evolution d'une trouée ouverte entre 1965 et 1968 par mort sur pied d'un vieux hêtre. Malgré l'installation de quelques semis, la fermeture est assurée uniquement par accroissement latéral des arbres périphériques.

- libération d'un sous-étage arbustif constitué par le hêtre ou par le houx, essences résistantes à l'ombrage dont la croissance est accélérée après levée de la répression par la voûte (FAILLE et al., 1984; CLABAULT et LEMEE, 1980). Ce sous-étage est presque uniquement localisé sur les surfaces recevant le plus de rayonnement: sous les vieux chênes où l'arbre de remplacement est le hêtre et au voisinage des clairières où pénètre l'éclairement latéral; ces "éléments d'avenir" peuvent être assez denses pour que la mort d'un arbre ne dégage pas de surface vide;
- régénération par semis postérieurs aux ouvertures. A la différence des stratégies de cicatrisation par un matérial préexistant, celle-ci ne se met que progressivement en place (Fig. 3). La très forte prédominance du hêtre à la périphérie des clairières et son faible abroutissement par les cervidés font qui'il est de loin le mieux représenté dans les régénérations. Plusieurs conditions doivent être successivement réunies pour assurer son succès:

(1) abondance et réussite des faînées après l'ouverture (PONTAILLER, 1979);
(2) taux de survie suffisant des semis face à la prédation des herbivores et phytophages;
(3) absence de l'extension d'héliophytes sociales, fougère-aigle, ronce, _Calamagrostis epigeios_, _Brachypodium pinnatum_, qui entravent l'implan-

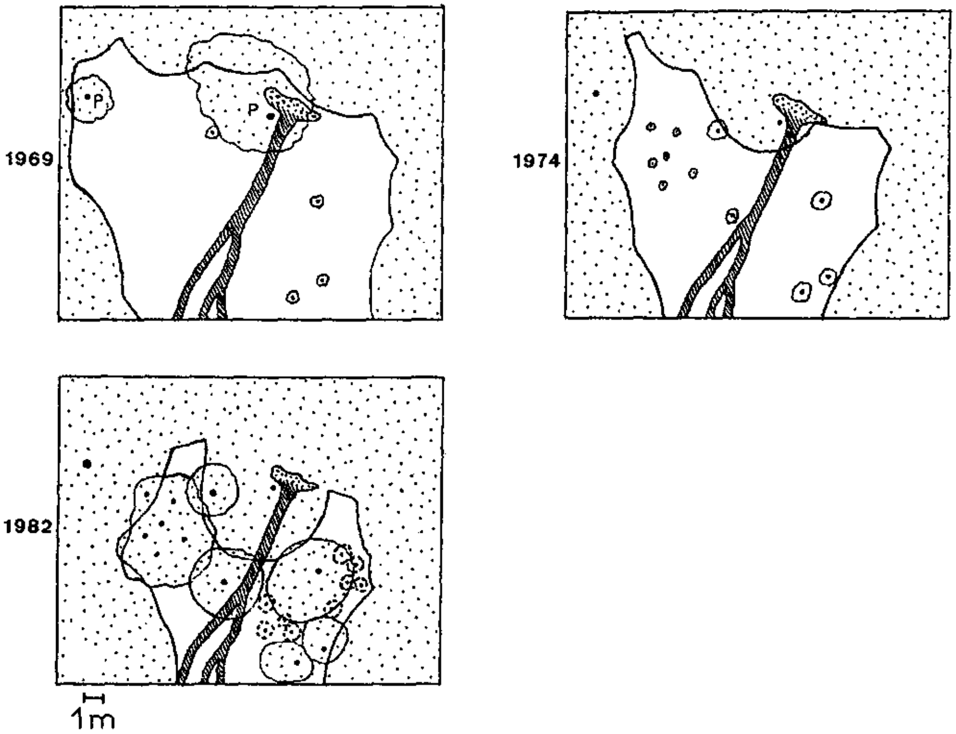

Fig. 3. Clairière ouverte par chablis en 1967. Fermeture par accroissement latéral des couronnes périphériques, développement de jeunes tiges préexistantes (P) et établissement de trois régénérations successives.

tation des semis; ce processus illustre le "modèle d'inhibition" des successions décrit par CONNELL et SLATYER (1977);

(4) extension modérée des fourrés de houx libérés par les ouvertures et sous lesquels aucune germination d'arbre ne peut s'implanter.

Outre ces facteurs de nature biologique, des caractères stationnels interviennent:

- la surface des ouvertures: la partie centrale des grandes ouvertures se referme plus lentement que leurs bords par suite de la plus faible quantité de semences qu'elle reçoit, observation déjà rapportée par WATT (1925) en Angleterre;
- la pédologie intervient dans la réussite des régénérations, les sols podzolisés étant défavorables par l'épaisseur de leur couverture organique biologiquement peu active (LE TACON, 1982) et l'extension rapide de la fougère-aigle dans leurs clairières.

b. Stades de la fermeture par régénération: nous avons distingué dans le processus de fermeture par régénération trois stades de durée differente d'une clairière à l'autre et à l'intérieur d'une même clairière:

(1) un stade d'attente jusqu'à ce que se produise une régénération; d'une durée parfois très longue lorsque s'installent des héliophites sociales. Le Calamagrostis epigeios, notamment, s'oppose aux régénérations jusqu'a ce que ses peuplements, viellis, commencent à dégenerer;

(2) un stade d'occupation où s'établissent des populations ouvertes à la suite de faînées non entièrement détruites;

(3) un stade de compétition lorsque, les couronnes étant dévenues confluentes, se constitue un fourré, puis un gaulis.

4. Evolution individuelle des hêtres: morphologie et croissance

Les modifications morphologiques du jeune hêtre après passage de l'état isolé aux conditions d'un peuplement fermé sont conformes aux descriptions classiques comparant la "forme spécifique" et la "forme forestière": élagage natural, obliquité plus accentuée des branches vers le haut, élévation du rapport de la hauteur de l'axe à son diamètre près de la base (Fig. 4), surface et volume de la couronne plus réduits par rapport au diamètre du tronc, répartition modifiée de la production au profit de l'axe (Tableau I). La relation entre la masse ligneuse aérienne, BL en kg, et le diamètre de l'axe à 15 cm, D en mm, répond pour les individus isolés à l'équation:

$$BL = 0{,}0293\ D^{2{,}64} \qquad (r = 0{,}995)$$

et pour les individus en populations fermées:

$$BL = 0{,}047\ D^{2{,}92} \qquad (r = 0{,}995)$$

Tableau I. Repartition de la biomasse aérienne du tronc, des branches et des feuilles en pour 100 du total, pour des hêtres isolés et en peuplements fermés (moyenne de 10 individus pour chaque populations).

	Tronc	Branches	Feuilles	Axe/Branches	Feuilles/Branches
Hêtres isolés	52,7	32,4	14,8	1,6	0,45
Hêtres en peuplements fermés	64,4	23,5	11,1	2,8	0,47

La figure 5 représente ces fonctions sous forme de régressions linéaires en coordonnées bi-logarithmiques. A diamètre basal égal, la biomasse est sensiblement plus grande pour les hêtres en populations fermées.

La masse surfacique foliaire, exprimée en g de matière sèche par cm^2, est de 0,42 pour les hêtres isolés, de 0,33 seulement lorsqu'ils sont en populations fermées.

Une autre modification importante qui intervient après la fermeture du peuplement est l'inégalité de la croissance, liée à la variabilité du microclimat lumineux. Les tiges dominantes gardent une élongation annuelle de l'axe et des rameaux médians ou supérieurs semblable à celle des individus isolés, avec des moyennes comprises entre 26 et 30 cm. Les tiges dominées ont des élongations réduites à une dizaine de cm.

La relation des caractères dimensionnels et pondéraux avec l'âge constitue une approche intégrée de la dynamique de croissance. Traduisible par des équations à probabilité très élevée pour les individus isolés, elle devient très médiocre pour les individus en populations denses, qui'il s'agisse de la hauteur, de diamètre de la tige ou de la couronne, de la biomasse ligneuse ou foliaire (Fig. 6).

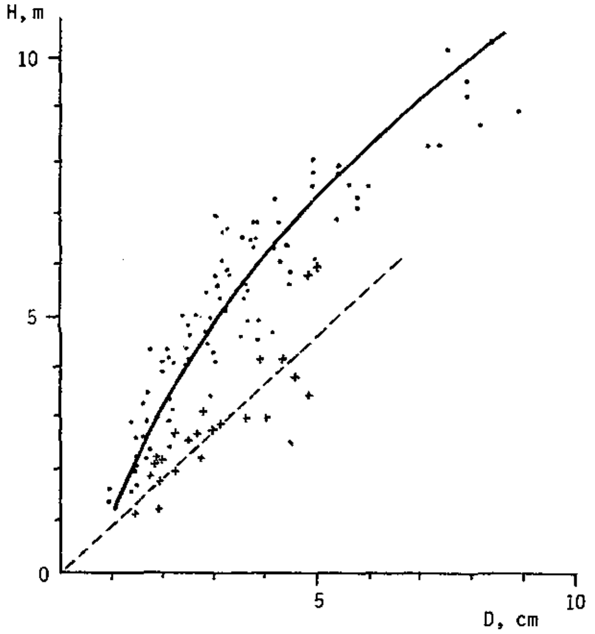

Fig. 4. Relation entre la hauteur H et le diamètre à 15 cm, D, dans de jeunes populations de hêtres ouvertes (+, ------) et fermées (., ———).

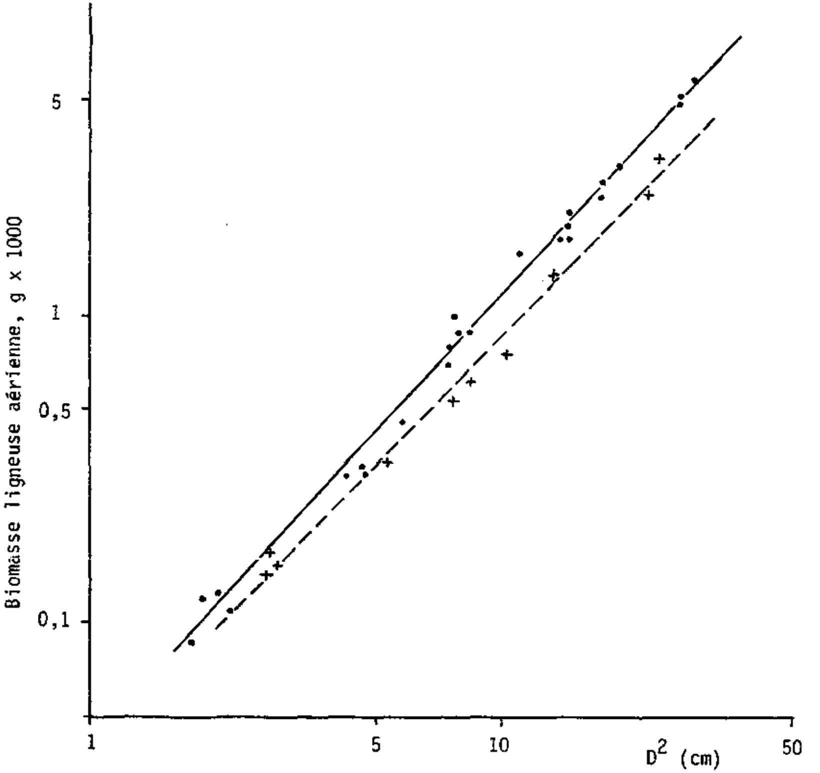

Fig. 5. Relation entre le diamètre du tronc à 15 cm, D, et la biomasse ligneuse aérienne pour les jeunes hêtres isolés (+, -----) et en populations fermées (., ———).

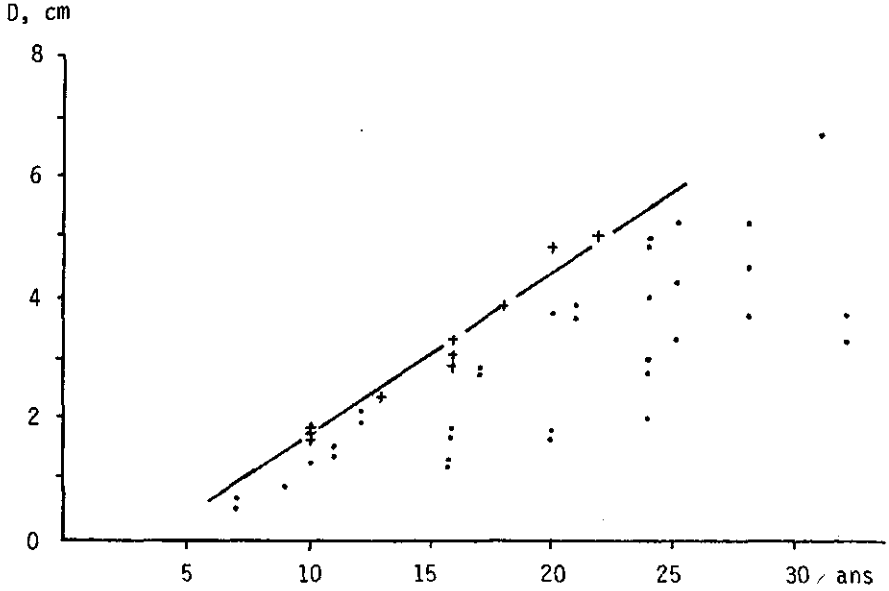

Fig. 6. Relation du diamètre du tronc à 15 cm avec l'âge de hêtres isolés (——,+) et en peuplements fermés (.).

5. Structure des populations fermées de hêtres

La densité des tiges vivantes atteint son maximum écologiquement tolérable dès la fermeture du peuplement, aucune nouvelle implantation ne pouvant plus réussir. Cette densité initiale, très variable, diminue ensuite par mortalité des tiges dominées. La densité de tiges vivantes établies sur 11 surfaces de 12 m^2 de gaulis était comprise entre 0,7 et 2,1 tiges par m^2 et leur âge s'étalait, dans une même surface, sur une quinzaine d'années pour un âge moyen de 14 à 27 ans (ex. fig. 7). La quantité de tiges mortes observables sur pied et au sol représentait en moyenne 25 % des tiges vivantes. Cette mortalité touche les individus les plus jeunes.

Les paramètres dimensionnels sont encore diversement répartis dans ces populations jeunes dont la fig. 6 donne un exemple. La projection horizontale des couronnes (ex. fig. 7) montre un indice de recouvrement compris entre 2,25 et 2,3; avec l'âge celui-ci diminue et dans un gaulis âgé il était seulement de 1,65.

L'indice de surface foliaire (LAI) augmente avec l'aire basale, s'élevant jusqu'à 8 dans le peuplement d'âge moyen le plus élevé. Au stade de futaie, il est ramené à 6 (LEMEE, 1978). Dans les hêtraies roumaines une semblable évolution a été observée (DECEI, 1983).

L'accumulation de biomass ligneuse aérienne varie de 0,9 kg/m^2 pour le peuplement d'âge moyen le plus bas (14 ans) à 5 kg/m^2 pour celui dont l'âge moyen est le plus élevé (27 ans), ce qui représente une accumulation moyenne de 315 g/m^2 par an entre 14 et 27 ans. Dans le même temps, la production foliaire est passée de 70 à 350 g/m^2.

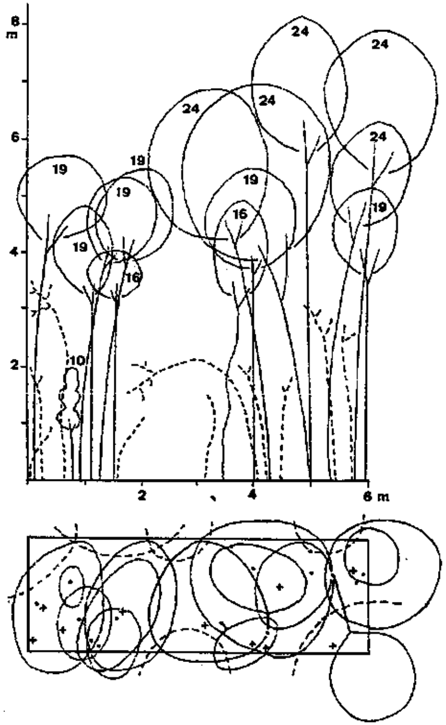

Fig. 7. Structure d'un jeune peuplement de hêtres en clairière refermée l'age des arbres fin 1984 est indiqué sur leurs couronnes.
---------- et + : Tiges mortes

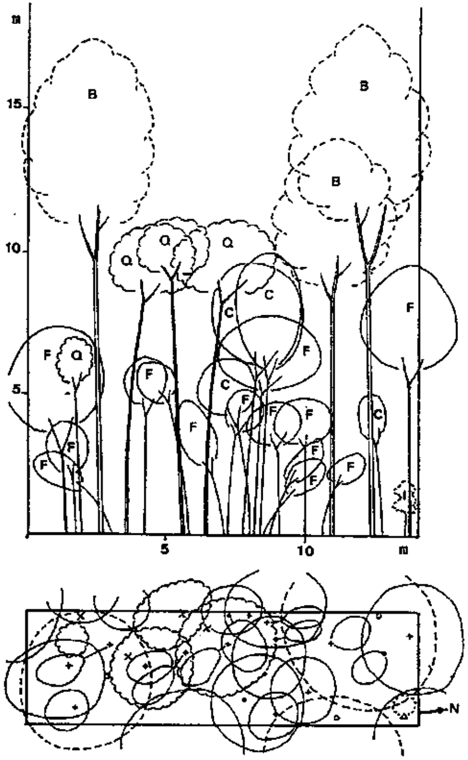

Fig. 8. Structure de peuplement arborescent d'une ancienne trouée colonisée par des espèces intolérantes à l'ombrage.
Bo Betula verrucosa F+ Fagus silvatica I△ Ilex aquifolium
Qx Quercus petraea C· Carpinus betulus

6. Ouvertures anciennes refermées par des espèces intolérantes à l'ombrage.

L'emplacement d'anciennes clairières est indiqué par des peuplements jeunes et approximativement équiennes de hêtres. Cependant, des essences peu ou non résistantes à l'ombrage ont l'opportunité de s'établir pendant la phase de clairière, d'où leur qualification fréquente d' "opportunistes". L'établissement de ces dernières en populations assez denses pour assurer la fermeture s'observe dans cinq anciennes trouées du Gros-Fouteau (ouvertes vers1930) qui ont été colonisées par le bouleau, le pin sylvestre (maintenant disparu) et le chêne, et dans deux clairières de la Tillaie colonisées par le frêne. Ces ouvertures sont toutes au contact des lisières ou à leur proximité.

Cette colonisation a été la résultante de la conjoction de facteurs favorables:
(1)une source de diaspores:
- proche des réserves pour les espèces anémochores, bouleau, pin, frêne;
- sur place pour le chêne, espèce à semences lourdes;
(2)l'ouverture de trouées assez grandes pour offrir des conditions microstationnelles favorables;
(3)des caractères biologiques propices tels que la production chaque année de nombreuses semences à moyens de dissémination efficaces, une croissance plus rapide et une fertilité plus précoce que celles des espèces résistantes à l'ombrage; cependant le chêne, qui ne présente pas ces caractères, est moins intolérant à l'ombrage;
(4)une faible pression biologique de la part des consommateurs, surtout Cervidès, ou des plantes à pouvoir compétitif élevé qui peuvent coloniser rapidement l'ouverture (fougère-aigle, Calamagrostis, Brachypodium pinnatum, ronce);
(5)l'absence de régénération importante du hêtre ou du charme antérieurement à l'apparition des opportunistes.

La stratification verticale des espèces préfigure la tendance évolutive. Le profil structural de la figure 8 montre un étage dominant discontinu de bouleau verruqueux et un étage intermédiaire de chênes. Ces derniers sont presque rejoints par quelques charmes et hêtres.Dans l'étage inférieur, le hêtre est fortement dominant; on y trouve quelques chênes dépérissants et de nombreux chênes morts. La tolérance de ces espèces à l'ombrage croît de haut en bas comme l'ombrage lui-même, en conformité avec le modèle de tolérance de CONNEL et SLATYER (1977) selon lequel "chaque espèce est capable de supporter une ombre plus forte que les précédentes". Dans la succession temporelle, le chêne, dont la longévité est supérieure à celle des autres essences présentes, est destiné à participer à la voûte après la mort des bouleaux.

Une clairière refermée par le frêne à la Tillaie comprend un individu isolé d'environ 50 ans et une population d'environ 30 ans qui, en compétition avec des charmes et des hêtres, commence à dépérir.

Discussions et conclusions

Dans la mosaîque des stades de succession cyclique d'une forêt inexploitée parvenue en état d'équilibre, les ouvertures créées dans la canopée par la mort d'arbres constituent une phase critique en provoquant un brusque changement des conditions écologiques et un renouvellement du matériel ligneux qui en fait, selon l'expression de OLDEMAN (1978), "le moteur de la sylvigenèse".

Ce renouvellement est assuré, dans les réserves étudiées ici, presque uniquement par le hêtre et selon les trois stratégies classiques: élargissement des couronnes (et de branches basses épicormiques), libération de tiges antérieurement réprimées, régénérations postérieures à l'ouverture. La première est constante, mais son importance diminue avec la dimension croissante des vides. La seconde est plus fréquente dans les cas d'agrandissement d'anciennes clairières qui ont facilité l'implantation de jeunes tiges à leur proximité par l'augmentation latérale d'éclairement. Mais de grandes surfaces vides demeurent ouvertes pour les régénérations par nouveaux semis.

La fermeture par régénération est contrôlée par de nombreux facteurs, soit stationnels (dimensions et forme des clairières, nature pédologique du sol), soit biologiques (irrégularité des faînées importantes, prédation des graines et des semis, concurrence d'espèces herbacées à recouvrement dense). Il en résulte un stade d'attente plus ou moins prolongée, surtout dans la partie centrale des grandes clairières. Le stade d'occupation, défini comme la durée nécessaire au recouvrement complet par les couronnes des colonisateurs, est lui-même de durée très variable et passe progressivement, dans une même ouverture, au stade de compétition où, les couronnes devenant jointives, aucun nouveau recrutement n'est possible. Le passage à ce nouveau stade est marqué par les changements suivants: modifications dans l'architecture et dans la répartition de la production individuelle; augmentation rapide de la biomasse vivante et de l'indice foliaire; mortalité élevée des tiges dominées, généralement les plus jeunes; conditions microclimatiques forestières reconstituées; retour au sol d'une matière organique plus abondante, où les branches élaguées ont une part importante.

La comparaison de la cartographie des surfaces aux stades d'attente et d'occupation à la Tillaie en 1968 et au Gros Fouteau en 1971 avec celle de ces stades en 1980-81 a permis d'établir leur évolution entre ces années. Cette évolution, qui est le bilan entre des ouvertures et agrandissements d'une part, des fermetures partielles ou totales d'autre part, passe de 14,9 à 6,3 % de la surface cartographiée à la Tillaie, de 6,16 et 3,34 % au Gros Fouteau. En 10 ans ces surfaces ont été réduites de moitié, 8,6 % et 3,85 % ayant été refermés respectivement à la Tillaie et au Gros Fouteau. En faisant l'hypothèse que la dynamique d'ouverture et de fermeture se poursuive identique à ce qu'elle a été lors de la décade 1970-80, un état d'équilibre représenté par une valeur minimale de surfaces ouvertes serait réalisé au cours de la dernière décennie de ce siècle, mais il s'agit d'une hypothèse optimiste, car de forts coups de vent peuvent ouvrir à nouveau comme en 1967 des vides importants et quelques clairières colonisées par des héliophytes sociales peuvent être retardées dans leur fermeture. Actuellement, la colonisation des vides est assurée par des essences d'ombre, hêtre et accessoirement charme et houx, car les conditions d'installation leur sont favorables. Cependant quelques anciennes trouées ont été colonisées par des espèces intolérantes à l'ombrage autour de 1930. Leur tendance évolutive est préfigurée par la stratification verticale des espèces: bouleau - chêne - charme - hêtre, ou frêne - hêtre. La longévité de ces espèces est déterminante dans cette évolution: la longévité du bouleau et du frêne est la plus faible, celle du chêne est la plus grande, de telle sorte que dans une cinquantaine d'années il subsistera seulement de ces anciennes trouées une voûte de chênes mêlés de hêtres avec quelques charmes. Une telle évolution se traduit par une diminution de la diversité taxonomique des ligneux que seules pourraient maintenir des perturbations assez importantes suivies de conditions favorables pour permette l'implantation d'opportunistes à intervalles plus courts que leur durée de vie. Tel n'est pas le cas: la localisation des populations d'opportunistes au voisinage des lisières est une indication de leur origine extérieure.

Les nombreuses études sur la dynamique des forêts feuillues nordaméricaines permettent une comparaison précise avec les réserves de Fontainebleau. Une

différence, exogène, est le passage d'ouragans ou de feux qui provoquent de larges ouvertures. L'autre, de nature endogène, est la plus grande richesse taxonomique et la plus grande diversité des caractères biologiques de peuplement ligneux. Les petites ouvertures dans les forêts âgées sont refermées essentiellement par les espèces du sous-étage tolérantes à l'ombrage, Fagus, Acer, Tsuga (OLIVER et STEPHENS, 1977, BREWER et MERRITT, 1978, HARCOMBE et MARKS, 1978, RUNKLE, 1981, etc.); cependant des espèces intolérantes, comme des bouleaux, peuvent s'y établir occasionnellement (BARDEN, 1980). Mais lorsque les vides sont de grandes clairières, trouées ou coupes, les espèces "opportunistes", des Prunus, Betula, Populus, s'établissent massivement (par ex. MARKS, 1974, BORMANN et LIKENS, 1977). Les conséquences sont:
(1)que le stade d'attente de notre hêtraie est très exceptionnel et que le stade d'occupation est très court; ce dernier correspond au "stade d'initiation" proposé par OLIVER (1981), notre stade de compétition qui lui succède correspondant à son "stade d'exclusion des tiges";
(2)que l'ouverture de nouvelles clairières entretient la permanence des opportunistes; des modèles successionnels appliquès à quelques localités suivant diverses méthodes confirment cette permanence (WAGGONER et STEPHENS, 1970, BOTKIN et al., 1972, BARDEN, 1980, 1981, RUNKLE, 1981).

Par contre, la hêtraie climacique à Fagus crenata du Japon montre une dynamique très proche de notre hêtraie par la prédominance absolue de cette espèce sur les espèces peu résistantes à l'ombrage, notamment un bouleau et un chêne (PETERS, 1985). Une autre analogie est l'existence de peuplements d'un bambou de genre Sasa qui peuvent y jouer temporairement le même rôle inhibiteur de la régénération que nos graminées (NAKASHIZUKA et NUMATA, 1982).

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PLANT SUCCESSION IN A MAN-MADE NORWAY SPRUCE ECOSYSTEM ON A CLEAR-CUT AREA AS RELATED TO SOIL PROCESSES AND NUTRIENT BALANCE

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Summary

Studies were made of changes in herb and juvenile woody vegetation under a mature Norway spruce stand and on a clear-cut area. Effects of logging and reforestation practices on the structure of surface humus and physical properties of surface soil layers on the clear-cut area were discussed. Changes were characterized of density and biomass under the influence of thinning in the mature spruce stand and during the progressive stage of secondary succession of the clear-cut vegetation. Succession stages are expressed by aboveground and underground biomass and areal dominance of prevailing species, concentration and supply of bioelements as well as relations to quality and quantity of humus and rate of decomposition.

Keywords: Norway spruce forest ecosystem, clear-cut area, biomass, humus, nutrients.

Introduction

The study of forest ecosystems using long-term integrated multi-disciplinary projects realized on stationary objects (long-term research areas) is carried out in many countries of the world. One of the research projects is conducted by the Institute of Forest Ecology, University of Agriculture, Brno, in the region of the Drahanská Uplands about 30 km north of Brno in Czechoslovakia. Problems of the dynamics of abiotic factors, populations of plants and animals, production and various biological processes are the most important questions in the study of relations and functions in the ecosystem.

The problem of plant succession in these studies is, however, studied as a minor one. Processes of changes in plant and animal populations as a result of competition and response of biota to the environment are in a close relation to problems of succession and, therefore, they should be investigated in the ecosystem studies.

The paper presents selected results of the ecosystem study dealing with the several years course of the first stages of secondary plant succession and their relation to soil processes and bioelement balance on a clear-cut area. Changes in the herb layer under a mature Norway spruce pure stand, a part of which was cut, are compared with conditions on the clear-cut area including impacts of management practices on soil and nutrients.

Material

The forest stand and site conditions of the area under study are characteristic of man-made Norway spruce pure stands in the region of Central Europe (49°26'31'' N, 16°41'30'' E): altitude 625 m, average annual precipitation 683 mm, average temperature 6.6°C, max. precipitation in the summer months, snow cover from November to March, relatively clear atmosphere (17 /mg m^{-3} SO_2). Soil: oligotrophic brown soil, loamy with gravel, pH of A horizon 3.7, layer of raw moder 6 cm. Forest type: beech forest with silver fir, sporadic occurrence of herb layer with Carex pilulifera as a characteristic species. Mature stand: 75-year-old Norway spruce monoculture, canopy density 0.9 - 1.0, throughfall 65 - 70% of precipitation, illumination of soil surface 1.5 - 3% of full light, standing volume of large timber (over 7 cm d.o.b.) 480 m^3 per ha).

Clear-cutting was carried out at the beginning of 1977, whole trees with crowns were skidded by wheel tractors along skidding trails. Reforestation of the felled area with Norway spruce was made using a rill planting machine in 1978.

Methods

Methods usual in production ecology (Evans 1972, Šesták et al. 1971) were used for estimating density and biomass of herb pupulations and juvenile woody species. In the undergrowth of the mature Norway spruce stand the number of plants was determined by direct counting and the parallel biomass sampling of individual species was done using destructive growth analysis. On the densely overgrown clear-cut area "types of dominance" (Whittaker 1973) easily distinguishable in the terrain according to the prevailing species and amount of aboveground biomass were differentiated every year. The areal proportion of these units was established every year using parallel transects covering the whole clear-cut area in constant intervals. Density and aboveground biomass were sampled according to the types of dominance by destructive sampling (Traczyk 1967) in the period of maximum values of biomass. Some growth analytical characteristics including the aboveground/underground ratio of phytomass were estimated using specially selected sets of samples of individual species. On 40 permanently fixed plots of 0.5 x 10 m, values of density and dominance of individual species were estimated to express successional changes in figures (Maarel et al. 1985) and spatial changes by means of isopleths (Numata 1982).

Analyses of soil and humus were carried out using standard methods usual in forest pedology. Chemical composition of organic matter was determined by atomic spectrophotometry. Soil respiration was determined by the absorption gravimetric method using soda lime on the soil surface under a metall bell inserted 8 cm deep into the soil.

Results and discussion

Mature stand

In the undergrowth of the mature Norway spruce stand 44 herb and naturally seeded juvenile woody species were presented in the period under study, viz 10 phanerophytes, 5 chamaephytes, 24 hemicryptophytes, 3 geophytes and 2 therophytes. The number of woody species in the undergrowth in the period 1977-1980 ranged from 62 to 365 individuals per ha. Populations of Picea abies and Sorbus aucuparia from self-seeding showed dominant position. In 1980, thinning was carried out in the spruce stand and a seed year also occurred. About 7.5 x 10^6 Norway spruce seedlings emerged in 1981. In 1982, their number decreased below 1.0 x 10^6 and in 1983 in the second half of the growing season, drought stress occurred in surface layers of the soil and the number of plants from self-seeding decreased to 0.46 x 10^6. In 1984, only 2100 spruce plants per ha were found.

The number of herbs in the undergrowth of the mature spruce stand did not exceed 1000 plants per ha in the period 1977-1979 (Vašíček 1979).

Their number approximately doubled in 1980-1981. In 1983, it increased to 13 000 and in 1984 ca. to 19 000 plants per ha. The effect of thinning became more evident only after 2 years, with the number of heliophilous species increased. The drought stress had no significant effect on the density of herb species. Response to thinning expressed in increased density was recorded mainly in <u>Galium scabrum</u>, <u>Chamaenerion angustifolium</u>, <u>Maianthemum bifolium</u>, <u>Mycelis muralis</u>, <u>Oxalis acetosella</u>, <u>Rubus idaeus</u>, <u>Vaccinium myrtillus</u> and <u>Viola sylvatica</u>.

Table 1. Values of aboveground biomass.

	Year							
	1977	1978	1979	1980	1981	1982	1983	1984
Juvenile woody species g ha^{-1}	3	7	3	4	31 463	4218	2094	85
Herb species g ha^{-1}	47	71	61	142	223	2798	2019	4026

Clear-cut area in conditions parallel to the mature Norway spruce stand

At the beginning of 1977 whole-tree logging was carried out in a part of the stand leaving only some small branches and foliage on the felled area. In the next year, the area was reforested with Norway spruce in 2 x 2 m spacing by means of a rill planting machine. This practice caused changes in soil surface layers creating specific conditions for secondary succession of plants:

(a) Changes in physical properties of the soil surface on skidding trails

Table 2. Bulk density and porosity of the soil on skidding trails compared with other areas.

	Year				
	1976 Before felling	1977	1979	1981	1981 Under herb roots
Bulk density					
skidding trails	1.27	1.79	1.68	1.72	1.50
other area	1.27	1.57	1.51	1.45	1.43
Porosity					
skidding trails	52.15	32.19	35.36	35.14	43.90
other area	52.15	40.65	41.69	45.70	46.80

Physical properties of the soil on skidding trails are affected mainly by the type of vehicle and the travelling frequency. In the loamy soil of the felled area it may be supposed that the initial values of soil bulk density and porosity on the skidding trails were restored within 10-15 years. The roots of the clear-cut area vegetation accelerate the process of improving physical properties of soil.

Parts of areas of the skidding trails were at the first stage occupied by the population of Juncus bufonius which decreased its density in 1978 and during 1979 it almost disappeared.

(b) Changes in the structure of surface humus appeared in the felled area. The total supply of organic matter in the soil surface increased from ca. 5.0 kg m^{-2} under the stand to 7.8 kg m^{-2} in the clear-cut area as a result of the fall of small and died branches and needles. Heterogeneity of humus distribution increased: the coefficient of variation (V) under the stand and in the clear-cut area amounted to 15 and 46 percent, respectively. Humus was accumulated in places around stumps and roots and soil wounding occurred as a result of skidding trees. The initial structure of the L, F and H layers was destructed and mixed. This resulted in the different quality of the surface humus in the clear-cut area.

(c) In the space of the rill planter local changes in the structure of soil surface layers appeared (mineral soil on the ground surface and changes in moisture conditions in the space of rills). Average moisture content in the soil 10 cm below the rill bottom amounted to 21.1% in the growing season 1978 and 21.8% in 1979 whereas in the depth of 10 cm below the soil surface outside the rill the moisture content amounted to 19.5% in 1978 and 18.1% in 1979 (Prax 1985).

(d) In the first 2 years after felling the stand microbial activity of humus decomposers considerably increased. This is illustrated by values of CO_2 production during soil respiration: average values for 1977-1978 in the old stand amounted to 1188 g m^{-2} $year^{-1}$ and in the clear-cut area free of vegetation 1306 g m^{-2} $year^{-1}$ (Grunda 1981). At the same time the decrease of pH and the increased shift of nitrates into lower horizons occurred.

This preparatory stage of plant succession lasting for about 2 years is characterized by the slight occurrence of remaining vegetation from the old stand and temporary occupation of skidding trails with Juncus bufonius. Uptake of nutrients was very low. This fact indicates occurrence of stress in the turnover of nutrients on the clear-cut area (see Ulrich 1981).

The third year after clear cutting is characterized by the stage of intensive occupation of the clear-cut area by vegetation. In the first half of the growing season 1979, the area was occupied by initial stages of clear-cut area vegetation, maximum density being in the vicinity of reforested rills. Juncus conglomeratus and Picea abies seedlings from natural regeneration, in particular, occupied the edges and sides of the rills more densely than the other area. The vicinity of the rills was occupied mainly with Senecio sylvaticus, Veronica officinalis and Acetosella vulgaris. This initial stage was characterized as follows: density 8.8 plants per m^2, aboveground biomass DM 5 g per m^2. Maximum proportion in phytomass showed juvenile plants of Rubus idaeus, Calamagrostis epigeios, Carex leporina and Juncus conglomeratus. Chamaenerion angustifolium showed the greatest number of plants but also the smallest phytomass. In the second half of the growing season very rapid growth and development of all clear-cut area vegetation species appeared supported by considerably high precipitation. Chamaenerion angustifolium occupied in the same year the larger part of the area with vigorous fertile plants. Biomass of the herb layer increased by the end of the growing season to several thousands of kg per ha, Chamaenerion angustifolium being a dominant plant.

In 1980, i.e. four years after establishment of the clear-cut area, the stage of full occupation of the area by herb vegetation and naturally regenerated trees and shrubs began as well as the stage of the optimum development of the clear-cut area vegetation. Changes of areas represented by main types of dominance of the herb layer and areas occupied by woody species as well as bare areas are represented for the period 1980-1984 in Tab. 3. During this period 98 plant species occurred in the clear-cut area, viz 10 phanerophytes 7 chamaephytes, 65 hemicrytophytes, 3 geophytes and 14 therophytes.

Out of the total number of species only 9 herb species and 5 naturally regenerated tree and shrub species showed dominant or subdominant position. Other species occurred only sporadicaly. Some species, e.g. Epilobium collinum, gradually disappeared from the area, other species disappeared and later appeared again. Of the most represented species the maximum of areal dominance was achieved in Juncus conglomeratus in 1981, Chamaenerion angustifolium in 1981 and Rubus idaeus in 1982. Calamagrostis epigeios as the major competitor of all other species increased the occupied area up to the end of the period studied. Other species mentioned in the table, particularly species of the genus Carex, gradually decreased their dominance.

The layer of naturally seeded woody species comprises mainly Betula verrucosa, Sambucus racemosa, Salix caprea and Populus tremula. In 1981, this layer, especially Sambucus racemosa and Salix caprea, was partly reduced by cutting off shoots adjacent to planted Norway spruce but the layer regenerated later again by sprouting. Some groups of naturally regenerated Norway spruce plants, mainly in the southern part of the felled area, grew vigorously and as soon as in 1983 and 1984 they occupied nearly the whole area of the naturally regenerated species. During these years, also planting of target species plays more important role in the occupation of the clear-cut area. Thus the area covered by herb vegetation becomes gradually reduced.

In 1980-1983, the aboveground biomass of the herb layer was approximately 8000 kg ha^{-1} (Tab. 4). This corresponded to the underground biomass of about 2000 kg ha^{-1} (Tab. 5). The aboveground and underground biomass of broadleaved woody species, the number of aboveground shoots and leaf area are given in Tab. 6. Data for the year 1981 are calculated from places occupied by this layer, and each year thereafter from the whole area. In 1981, a part of young trees was cut off, as mentioned above.

The whole biomass of naturally seeded herb and woody vegetation (except for Norway spruce) recorded in the period of a seasonal maximum ranged from 950 to 1167 g m^{-2} in 1980-1983, a peak being in 1981. Of the total amount, 200-276 g m^{-2} accounted for the underground biomass. The proportion of woody plants was 3-6%,

Density of the herb layer decreased in the order: 1226 (1980) >916 (1981) >747 (1982) >656 (1983) >355 (1984) plants per m^2. As for species growing in bunches, every shoot was considered an individual. Dynamics of Norway spruce in the felled area was not included in the calculation.

Analysis of the proportion of the total biomass of dominant species related to the total biomass of the herb layer in 1980-1984 showed that Chamaenerion angustifolium accounted for 41.4% in 1981 and 1982 but its proportion decreased to 22.2% in 1984. Juncus conglomeratus showed maximum proportion of 22.5% in 1980 but its proportion decreased to 4.9% in 1984. The proportion of Rubus idaeus increased from 19.9% in 1980 to 31.9% in 1984. The same applies to Calamagrostis epigeios, the proportion of which 6.2% in 1981 increased and reached 38.1% in 1984, thus becoming an absolute dominant species.

Table 3. Areas covered by herb and woody species in 1980-1984 on the clear-felled area Rájec.

(m^2)

Species	1980	1981	1982	1983	1984
Agrostis stolonifera	91	38	43	24	79
Calamagrostis epigeios	537	1 318	1 724	2 916	3 036
Carex leporina	862	475	282	190	64
Carex pallescens	113	70	67	78	54
Carex pilulifera	386	318	232	190	174
Chamaenerion angustifolium	3 315	3 333	3 130	2 316	1 583
Juncus conglomeratus	1 522	2 109	1 390	1 460	1 381
Rubus idaeus	1 305	1 770	2 356	1 843	1 776
Veronica officinalis	115	40	34	24	9
Other herb species	133	5	9	51	11
Herb layer total	8 379	9 476	9 267	9 092	8 156
Areas not covered by vegetation	1 180	254	42	48	73
Areas covered by naturally sown woody species	441	270	691	809	1 256
Areas covered by tree species from planting	-	-	-	51	515
Area total	10 000	10 000	10 000	10 000	10 000

Table 4. Aboveground biomass of the herb layer at the time of seasonal maximum in the clear-felled area Rájec in 1979-1984

(kg ha^{-1} DM)

Species	1979	1980	1981	1982	1983	1984
Agrostis stolonifera	-	42.6	17.5	26.9	56.0	37.8
Calamagrostis epigeios	18.3	796.1	622.2	1 339.8	1 743.3	1 506.5
Carex leporina	4.1	467.8	182.0	74.4	46.4	8.8
Carex pallescens	0.3	95.9	55.3	10.9	16.3	26.9
Carex pilulifera	1.1	353.7	251.6	89.5	53.6	11.7
Chamaenerion angustifolium	1.0	2 857.0	3 393.0	3 130.5	2 311.8	732.3
Juncus conglomeratus	3.2	1 813.4	1 748.3	980.1	936.3	161.7
Rubus *idaeus*	20.2	1 798.6	2 148.2	2 342.8	2 022.9	1 178.1
Veronica officinalis	-	68.7	42.7	7.0	4.8	1.2
Other herb species	1.7	54.7	58.8	13.6	7.9	1.1
Herb layer total	49.9	8 345.5	8 519.6	8 015.5	7 199.3	3 666.1

Table 5. Underground biomass of the herb layer at the time of seasonal maximum in the clear-felled area Rájec in 1979–1984

(kg ha^{-1} DM)

Species	1979	1980	1981	1982	1983	1984
Agrostis stolonifera	-	19.6	8.1	12.4	25.8	17.4
Calamagrostis epigeios	3.0	95.5	74.7	160.8	209.2	180.8
Carex leporina	1.9	191.8	74.6	30.5	19.0	3.6
Carex pallescens	0.1	52.8	30.4	6.0	9.0	14.8
Carex pilulifera	0.6	137.9	98.1	34.9	20.9	4.6
Chamaenerion angustifolium	0.2	971.5	1 153.6	1 064.4	786.0	249.0
Juncus conglomeratus	1.3	633.7	611.9	340.3	327.7	56.6
Rubus idaeus	5.1	359.8	373.2	468.6	404.6	235.6
Veronica officinalis	-	34.3	8.5	3.5	2.4	0.6
Others	0.3	18.8	20.3	4.9	2.8	0.4
Herb layer total	12.5	2 515.7	2 453.4	2 126.3	1 807.4	763.4

Table 6. Basic productional characteristics of the layer of naturally seeded woody species on the clear-felled area Rájec in 1981-1984

		Biomass in DM					
Year	Species	Aboveground biomass total	From it leaf biomass	Underground biomass	Biomass total	Leaf area	Number of shoots
		kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	m^2 ha^{-1}	Ind. ha^{-1}
1981	Betula verrucosa	5.7	1.6	1.7	7.4	18.0	15
	Salix caprea	67.9	14.4	23.9	91.8	202.5	425
	Sambucus racemosa	294.5	122.9	274.4	568.9	2 260.0	1 500
	Populus tremula	18.5	4.8	8.6	27.1	76.0	182
		Σ 386.6	143.7	308.6	695.2	2 556.5	2 122
1982	Betula verrucosa	44.9	10.8	9.6	54.5	140.2	147
	Salix caprea	20.6	4.2	8.2	28.8	57.7	225
	Sambucus racemosa	86.8	107.2	110.0	196.8	188.7	1 065
	Populus tremula	34.5	7.6	12.6	47.0	94.5	279
		Σ 186.8	129.8	140.4	327.1	481.1	1 716
1983	Betula verrucosa	75.7	15.7	9.4	85.1	224.8	124
	Salix caprea	22.5	4.3	10.2	32.7	57.3	306
	Sambucus racemosa	160.0	76.7	154.5	314.4	1 404.2	1 023
	Populus tremula	28.0	6.2	10.6	38.5	77.3	231
		Σ 286.2	102.9	184.7	470.7	1 763.6	1 684
1984	Betula verrucosa	93.3	21.8	14.5	107.8	283.0	153
	Salix caprea	37.5	7.9	12.2	49.7	108.0	150
	Sambucus racemosa	68.5	24.0	66.6	135.1	442.3	564
	Populus tremula	100.6	87.5	25.7	126.4	609.8	1 023
		Σ 299.9	141.2	119.0	419.0	1 443.1	1 890

From the viewpoint of clear-cut area vegetation and its development the period 1980-1983 can be regarded as the optimum stage. The values of the total biomass were relatively steady and preponderance of *Calamagrostis epigeios* over other herb species was evident. The proportion of naturally regenerated woody species was relatively uniform and had no marked effect on the growth of herbs.

In this optimum stage of development, soil processes and bioelement cycling acquire new qualities in the conditions of the clear-cut area. The distribution of populations of the dominant species is to some extent related to the state of humus layer on the soil surface. Bioelement fixation by the herb layer is very high compared with fixation by the mature stand.

Table 7. Bioelement content in mature Norway spruce stand and herb vegetation.

	Bioelement							
	N	P	K	Ca	Mg	S	Fe	Mn
Mature Norway spruce stand in 1981 kg ha^{-1}	58	11	42	66	7	12	6	19
Herb vegetation of the clear-cut area in 1981 kg ha^{-1}	221	28	176	28	28	12	5	17

According to the table, considerably higher values of bioelement uptake (N, P, K, Mg) were recorded in the felled area vegetation. Calcium is fixed more intensively by the mature stand. Bioelement concentration in herb tissues of various species is very different. Of the dominant herb species, the highest concentration in the aboveground biomass was recorded in N, viz *Chamaenerion angustifolium* 3.45%, *Rubus idaeus* 2.03%, *Calamagrostis epigeios* 1.47% and *Juncus conglomeratus* 0.77% DM. The total bioelement supply in the aboveground and underground biomass of the herb layer per ha in the period 1980-1984 is given in Tab. 8 which provides further information on the input of elements into the process of decomposition. Control analysis of N concentration in selected herb species was made in 1983 and 1984 to compare the results with those obtained in 1980 and 1981. For example, in *Chamaenerion angustifolium* N concentration decreased from 3.45% in 1981 to 1.23% in 1984, in *Rubus idaeus* the drop was from 2.03% in 1981 to 1.32% in 1984. N concentration in the aboveground biomass of *Calamagrostis epigeios* was in 1984 at the level of 1981. This indicates that changes in N concentration in the upper soil layers bring about changes in N concentration in some plant species.

At this optimum stage of the development of felled area vegetation, more intensive process of organic matter decomposition occurs owing to the input of herb dead matter into the decomposition chain. Comparisons of soil respiration in the *Calamagrostis epigeios* population in the clear-cut area and under the mature Norway spruce stand in 1981 and 1982 showed that the average production of CO_2 was 1826 and 1160 g m^{-2} $year^{-1}$, respectively. Cellulose decomposition under the spruce stand and in the felled area amounted to 3.18 and 6.54 mg per day per g, respectively. Rapid decrease of surface humus occurs in spite of increased contributions

Table 8. Supply of bioelements in DM of the herb layer phytomass in the period of seasonal maximum in 1980-1984 Clear-felled area Rájec.

(kg ha^{-1})

Year	N	P	K	Na	Ca	Mg	S	Mn	Fe	Zn	Cu 10^{-3}	Σ	Ash	Biomass DM
Aboveground														
1980	172.67	26.61	140.68	0,49	23.95	18.71	10.29	14.97	1.99	0.64	0.08	411.08	471.91	8,345.68
1981	194.21	23.35	143.37	0.50	27.29	20.97	10.28	15.51	1.99	0.66	0.09	438.12	473.99	8,519.64
1982	187.29	21.81	130.54	0.28	26.18	19.62	9.46	14.77	1,75	0.59	0.08	412.37	454.25	8,015.53
1983	103.71	18.16	111.47	0.26	21.12	15.80	8.43	13.15	1.62	0.51	0.07	294.30	407.29	7,199.28
1984	55.54	7.94	50.78	0.08	9.31	6.64	4.08	6.79	0.90	0.23	0.03	142.32	212.27	3,666.04
Underground														
1980	33.79	4.40	30.45	0.79	5.71	3.76	2.19	1.52	3.10	0.24	0.03	85.98	203.10	2,515.57
1981	26.90	4.75	32.72	0.67	6.45	3.82	2.06	1.36	2.72	0.21	0.02	81.68	191.73	2,509.84
1982	23.74	4.37	28.23	0.45	5.89	3.31	1.55	1.28	1.70	0.20	0.02	70.74	145.98	2,128.90
1983	19.91	3.41	22.62	0.40	4.53	2.68	1.36	1.18	1.66	0.20	0.02	57.97	129.69	1,807.41
1984	8.56	1.37	8.17	0.13	1.67	1.03	0.51	0.66	0.59	0.12	0.01	22.82	262.54	763.29

Table 9. Total supply of bioelements in A_0-horizon on the clear-felled area and in the stand in 1983 - Rájec.

(kg ha^{-1})

	N	P	K	Ca	Mn	Fe	S
Clear-felled area 1983	145	13	36	29	18	16	11
Norway spruce stand	756	47	66	66	?	263	65
Simulated area*	444	42	91	43	21	?	37

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* Area with the same A_0 horizon structure as under the stand but located on the clear-felled area (without vegetation influence)

of dead herb matter. In 1978, immediately after clear cutting, the average supply of surface humus was 78 027, in 1981 it decreased to 57 850 and in 1983 the supply was only 10 369 kg ha^{-1}. Bioelement supply in A_0-horizon in the clear-cut area in 1983 compared with the supply under the mature stand as well as supply simulated according to the state under the mature stand and subjected to felled-area conditions without herb input into the decomposition process is given in Tab. 9. Low supply of bioelements in the A_0-horizon in the felled area occupied by vegetation was induced by rapid decomposition, nutrient uptake by vegetation and their leaching to lower horizons. This promotes higher concentrations of some elements predominantly in F and H humus layers in the clear-cut area compared to the concentrations under Norway spruce stand, mainly in N and K.

Humus amount and quality and concentration of available nutrients in A_1-horizon increased under the influence of vegetation during the optimum stage of succession in the felled area.

Decline in phytomass production of herbs and decrease in N concentration in biomass of some herb species recorded in 1984 together with rapid growth of the retarding effect of the target species on production represents the beginning of the further stage in the development of the felled area vegetation in which the target woody species will become dominant.

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Posters

RELIEF DEVELOPMENT IN THE HULSHORSTERZAND DRIFT SAND AREA AND ITS IMPORTANCE FOR THE VEGETATIONAL SUCCESSION

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Drift sands are eolian deposits, originating by local redeposition of terrestrial Pleistocene deposits. Since the beginning of the Neolithic, local sand drifting occurred due to the clearance of vegetation by man. This proces continued in the course of time with increasingly serious consequences so that since the Late Middle Ages extensive spreading of drift sands occurred. Especially the well-sorted, well-rounded Late Pleistocene coversands were sensitive for wind erosion. Since the end of the last century the majority of drift sands have been reclaimed by afforestation with pine.

In The Netherlands drift sands occupy an area of approximately 800 km^2 of which 230 km^2 occurs on the Veluwe. At present only less than 5% of the drift sands are still active. The Hulshorsterzand forms part of an extensive drift sand area in the northern Veluwe but only 0.6 km^2 of this area is still active: 0.4 km^2 in the western part and 0.2 km^2 in the eastern part.

In the active drift sand areas extreme conditions prevail, determined by the exceptional microclimate, a low moisture content, a mineralogical poverty and an almost continuously mechanical erosion by drifting sand grains. Usually drift sands are also very poor in organic matter (<1.5%). The grain size distribution of the drift sands of the Northern Veluwe is characterized by a complete dominance of the fractions 105-150 μm and 150-210 μm. The mineralogical composition of the drift sands is very uniform. Weight percentages show that only <1% of the sands consists of heavy minerals (s.g.$\geq$ 2.89) and >99% of the grains has a lower specific gravity. This part mainly consists of feldspar (13-16%) and quartz (±85%). Due to the extreme conditions in the active drift sand areas a very characteristic vegetation exists. So marram (Ammophila arenaria) occurs as a pioneer on drift sand accumulations and grey-hair grass (Corynephorus canescens) in blown-out areas.

In general a great variety exists in the relief of the Hulshorsterzand drift sand area. For the greater part the original coversand relief has been eroded by the wind. Remains of the old relief are still indicated by the eroded podzol soil profile which is exposed in several places. In many parts the coversand has been removed completely and the underlying gravelly periglacial deposits are exposed in low lying flat, so called blown-out areas. In other parts the removed coversand has been redeposited again on these gravelly deposits and drift sand hills have been formed. Sometimes, especially in the originally low lying wet parts of the coversand relief, the wind could not desintegrate the podzol profile and drift sand accumulated on the podzol profile, forming a "plateau-dune". In these places an inversion of the relief has taken place, since the original low lying wet parts of the coversand relief now are the high dunes in the drift sand relief. In general these dunes are bordered by relative steep slopes in which the old podzol profile is still visible occasionally. Another typical form-type of the Hulshorsterzand area is the "bordering dune ridge". These ridges have been formed by drift sand accumulation at the edges of forests, mainly at the NE-E border of the area, due to the prevailing SW-W winds. These ridges are characterized by an asymmetrical slope profile. Due to the forest vegetation at the east this lee slope can become very steep (max. ± 31°), while the angle of slope af the windward side usually does not exceed approximately 8°.

The importance of the relief development for the vegetational succession is not only expressed in different species in the first stages of the primary succession as mentioned above, but can also be seen in completely forested drift sand areas. When comparing the vegetation on a plateau-dune and on a blown-out area these differences will become very clear.

In the completely forested area of the Leuvenum forest, S-SW of the Hulshorsterzand, it was found that the coverage of the soil by vegetation in blown-out areas usually is less than 40%. Only few species are responsible for this, mainly Deschampsia flexuosa and some mosses (a.o. Pleurozium schreberi). However, locally also Empetrum nigrum constitutes an important part of the vegetation. Extreme differences in vegetation occur on various parts of a single plateau-dune due to the relation between microclimate and slope orientation. The SW-slopes of these dunes dessicate relatively fast which is reflected in a poor soil vegetation of almost only grasses and mosses, covering less than 20% of the surface. On the other hand the NE slopes are mostly completely covered by vegetation consisting of Deschampsia flexuosa, Empetrum nigrum, Vaccinium myrtillus and several species of mosses. This is due to more moist conditions on this side of the dunes. Because of this the plants can exploit the possibilities of the blown-over soil profile which provides them with nutrients. The compactness of the soil profile usually causes the water to stagnate and sometimes the excess of water flows out over this compact profile and on these spots even peat growth is possible. The more humid conditions and the greater amount of humus on this side is also responsible for a better development of the micropodzolic soil compared with other sides of the dune. Even under forests less than 100 years old distinctly leached horizons have developed.

SPONTANE GEHÖLZBESIEDLUNG EINES KIESIG-SANDIGEN ROHBODENS IM RHEINISCHEN BRAUNKOHLENREVIER

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Summary

Spontaneous establishment of woody plants on gravely-sandy rough soils in the Rhenish lignite-mining area.

The establishment of woody plants has been observed on permanent plot (0,6 ha, fenced in) between 1966 and 1980. On the artificial deposit, gravely-sandy material, free of seed-banks, the settlement and also the distribution of woody plants was not continuous respectively uniform but depending on species and time. The stages of primary succession are shortly described.

1.Standortbeschreibung

Auf einer Innenkippe, 100 m unter Geländeniveau, wurde1966 eine 0,6 ha grosse Dauerbeobachtungsfläche eingerichtet. Das im Herbst 1965 verkippte kiesig-sandige Material war frei von Pflanzenkeimen und bestand aus Ablagerungen der Hauptterrasse des Rheins, die zusammen mit tertiären Lockersedimenten die Braunkohle überdecken und als Abraum beim Kohleabbau abgetragen werden. Die geschüttete Rohbodenfläche wurde grob planiert und anschliessend wilddicht gezäunt. Kennzeichnende Eigenschaften des Rohbodenmaterials sind Grobkörnigkeit, geringer Tongehalt, Nährstoffarmut, Fehlen organischer Substanz, hoher Säuregrad und geringes Wasserspeichervermögen.

In den ersten Jahren nach der Verkippung kommt es durch Wassererosion nach Starkregen zur Materialsortierung und Verlagerung (kleine Rinnen, Schwemmfächer, kiesreiche Partien). Eine merkliche Vermehrung der organischen Substanz durch Abbau des Bestandesabfalles findet nur in der obersten Bodenschicht bis 2 cm Tiefe statt.

2. Gehölzansiedlung

Insgesamt haben sich auf der 0,6 ha grossen Dauerbeobachtungsfläche während des Zeitraumes von 1966 bis 1980 15 Baum- und Straucharten angesiedelt. An der Erstbesiedlung waren fast ausschliesslich windverbreitete Gattungen beteiligt (Anemochorie: Betula pendula, B. pubescens, Populus x canadensis, Populus tremula, Pinus sylvestris, Salix caprea, Salix alba). Erst nach 6 - 8 Jahren kommen die ersten schweren, durch Vögel eingeschleppten Samen (Zoochorie u. Anthropochorie: Sambucus nigra, Padus serotina, Quercus robur, Q. petraea, Q. rubra, Robinia Pseudoacacia, Cytisus striatus, Sorbus aucuparia) auf und keimen, nachdem das Umfeld der Versuchsfläche mit Erlen und Pappeln aufgeforstet wurde. Zu den ausschliesslich auf offenem Rohboden keimenden Pionierarten gehören Weiden- und Pappelarten. Auch Birken sind Pionierbesiedler des offenen Rohbodens, doch erreichen sie nach 10 - 13 Jahren nochmals ein Maximum der Ansamung (Abb. 1).

Die Verteilung der Holzgewächse auf der Dauerbeobachtungsfläche nach 15 Jahren ist bei den einzelnen Arten unterschiedlich. Birken als Pioniere dominieren sowohl nach Anzahl (156 Exemplare) als auch Wuchshöhe (Abb. 2)

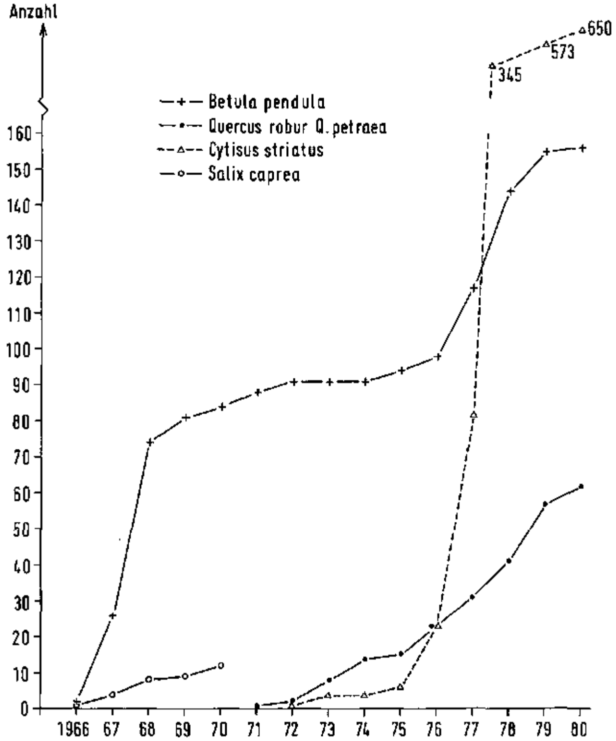

Abb. 1. Kumulative Häufigkeiten ausgewählter Baumsämlinge im Zeitraum von 1966-1980 auf der Untersuchungsfläche (0,6 ha). Ginster (Cytisus striatus) wurde nur auf 0,2 ha Fläche aufgenommen. Die übrigen Holzgewächse haben sich mit weniger als 10 Exemplaren angesiedelt bzw. breiten sich vegetativ aus.

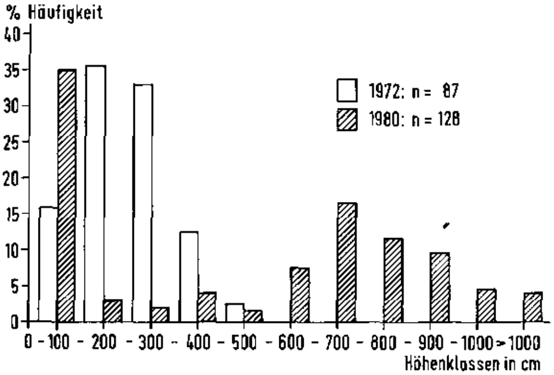

Abb. 2. Häufigkeitsverteilung der Birken nach Höhenklassen im Jahr 1972 und 1980. In der Verteilung der Höhenklassen von 1980 kommt ein frühes und spätes Ansiedlungsmaximum der Birken zum Ausdruck.

und weisen eine zufällige, ungleichmässig gehäufte Verteilung auf. Die später angesamten Eichen (77 Exemplare), nach den Birken am zweithäufigsten, haben sich meist unter dem Schirm älterer Birken angesamt ("Vogelsaat"). Die Sprosskolonien der Robinie und der Zitterpappel sind aufgrund ihrer vegetativen Ausbreitung insular verteilt. Ginster zeichnet sich durch einen Verbreitungstyp zwischen zufälliger und insularer Dispersion aus. Offenbar sind hier Selbstverbreitung (Autochorie) und Verschleppung der Samen durch Tiere wirksam.

3. Entwicklung der Holzgewächse

Im Verlauf der primären Sukzession erobern nichteinheimische Arten (Neophyten) beträchtliche Flächen und besetzen den Wuchsraum anstelle heimischer Arten für kürzere oder längere Zeit. Er sind hauptsächlich bei Rekultivierungsmassnahmen eingebrachte oder sekundär verbreitete Pflanzenarten (Cytisus striatus aus Portugal, Robinia pseudoacacia).

Die radiale Ausbreitung der Sprosskolonien erfolgt innerhalb von 10 Beobachtungsjahren bei der Robinie durchschnittlich 180 cm, bei der Zitterpappel 80 cm pro Jahr. Die Robinie erreicht 5 m, die Zitterpappel nur 2,5 m Sprosslänge. In ihrem Höhenwachstum sind beide Arten der Birke weit unterlegen (Abb. 2). Durch Probegrabungen wurde ermittelt, dass die Wurzelfläge der Birke 28 mal grösser als ihre Kronenfläche und somit in hohem Masse den örtlichen Standortbedingungen angepasst ist.

Die Ergebnisse der Wurzelgrabungen an Gehözen zeigen ein deutlich ausgeprägtes Horizontalwurzelsystem. Besonders die flache (5 - 15(20) cm), weit streichende Wurzeltracht von Birke und Kiefer weist darauf hin, dass zur Wasser- und Nährstoffaufnahme nur die oberste Bodenschicht ausgenutzt wird (Tab. 1).

Tab. 1. Grössenvergleich der Spross- und Wurzelsysteme ausgegrabener Gehölze.

	Alter Jahre	Sprosshöhe m	Kronenfläche m^2	Wurzelfläche m^2	max. Wurzelreichweite m
Waldkiefer	14	6,5	9	150	8,0
Hängebirke	13	8,7	7	200	10,0
Zitterpappel	11	2,5	(308)*	95*	9,0
Robinie	10	4,8	(290)*	170*	18,0
Traubeneiche	8	0,7	0,1	2,5	1,4

*Bei Zitterpappel und Robinie ist anstelle der Kronenfläche die Anzahl der Wurzelsprosse angegeben. Die Wurzelfläche ist die Zahl 1 m^2-Raster, die von mindestens einem Wurzelspross besetzt ist.

Nur der Ausschluss von Wild (Kaninchen, Rehe) durch Zäunung der Dauerbeobachtungsfläche ermöglichte das Aufkommen der Gehölze. Ausserhalb des Zaunes wurden die Holzgewächse und Kräuter durch Wildverbiss weitgehend vernichtet.

4. Sukzessionsstadien

Nach Merkmalen der Lebens- und Wuchsform (Raunkiaer) kann der zeitliche Ablauf der primären Sukzession in drei Abschnitte gegliedert werden:

1) Therophyten-Stadium (1. - 3.(4.) Vegetationsperiode).
   Bei gleichzeitiger Einwanderung kurzlebiger und ausdauernder Pflanzen dominieren Einjährige (Senecio viscosus, Poa annua, Senecio vulgaris, Vulpia myuros u.a.).

2) Geophyten-Hemikryptophyten-Stadium (3.(4.) - 12. Vegetationsperiode). Die Vorherrschaft der Therophyten wird durch Wurzelknospen- und Rhizom-Geophyten (Epilobium angustifolium, Calamagrostis epigejos u.a.) sowie Horst-Hemikryptophyten (Festuca trachyphylla u.a.) abgelöst. Bei zunehmender Konkurrenzwirkung der Birkenwurzeln und starker Ausbreitung der Moose und Flechten kommt es zu einem Arten- und Dichterückgang der krautigen Blütenpflanzen.
3) Moos- und flechtenreiches Phanerophyten-(Birken-)Stadium (10.(12.) bis über 15. Vegetationsperiode hinaus).
Birken bilden zusammen mit Gebüschen der Sprosskolonien von Zitterpappel, Robinie sowie Ginster und Salweide einen lichten Vorwald, in dem sich mit dem Aufkommen der Stiel- und Traubeneichen die natürliche Schlussgesellschaft, ein bodensaurer Laubmischwald, ankündigt.

SILVICULTURAL DESIGN, AN EXERCISE FOR STUDENTS

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The development of a forest stand subjected to silvicultural treatment is one example of a successional process, and the silvicultural system can only work well if this development indeed follows succession within the limits imposed by the site and potential forest types.

It is very difficult to plan and visualize the whole development of a forest stand from planting till harvest. This is partly due to the different reactions of forest tree species or even provenances to diverse environments (soil, climate), but mostly due to the long life cycle of trees and thus of forest stands. Hence, forestry students of the Agricultural University of Wageningen and other students can participate in a course of Silvicultural Design.

During this course, the participants (second year students) have to schedule the various silvicultural treatments, that guide a chosen forest stand (starting point) towards a desired type of forest stand and to visualize and design the projected growth and development of this forest.

The starting point, chosen by the participants, is a transect drawing of an existing forest drawn during the first week of the course by freshmen. The participants of the course Silvicultural Design have made such a transect one year earlier and assist the freshmen. As a consequence of the choice of a forest stand as starting point, the ecological conditions for the stand to be developed, are fixed too.

The desired forest stand, again chosen by the participants, should be in accordance with the ecological possibilities of the site and the policy of the forest owner.

After determining start and finish, the participants map out a rough treatment schedule on a given matrix, on which the points of time (decades) and the mode (heavy - light; heterogenous - homogenous) of the necessary treatments (regeneration, clearing, thinning and harvest) are depicted. To make this exercise more realistic, a calamity such as damage by diseases, pests or storm, forced heavy harvest, back log in thinning, is thrown in by the teacher. The participants now have to devise ways to guide the damaged stand still towards the desired aim and to draw a final treatment schedule.

The participants have to collect the necessary information themselves. Sources of information are 1) silvicultural diagrams, drawn by the participants during the first week of the course, based on data gathered in the neighbourhood of the freshmen transect; 2) yield tables; 3) monographs and other literature.

The participants present the results of this "exercise in thinking" in a small report containing 1) a preliminary rough treatment schedule and a final treatment schedule, the letter including ways to repair the damage done by the calamity; 2) a series of profile drawings and crown projection maps of crucial stadia in the development of the forest stand shortly before each major treatment; 3) a short type-written justification. It is clear, that emphasis is laid upon silvicultural aspects. Other aspects, e.g. economical, are only marginally included (many interferences are more expensive than a few), but attention for these aspects could be enlarged easily.

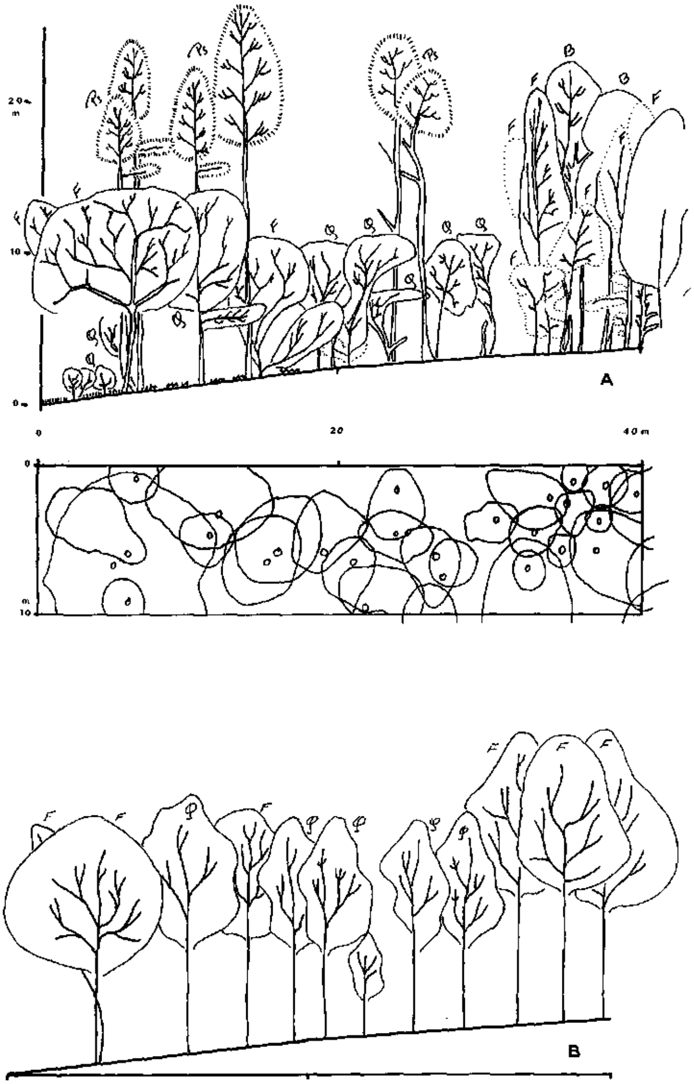
As an example, the definitive treatment schedule of one group of participants (Sj. Wartena; L. Reitsma; R. Wolf; M. de Lange) is shown in Fig. 1 and 2. This group chose to develop an old stand of Scots pine mixed with young beech and oak into a stand with a high nature value and possibilities for recreation. The devised calamity was a forced cutting of 50% of the stem volume at age ninety. Other examples (e.g. old beech forest into production stands; young stands of Douglas fir into recreational forest) could be given easily, indicating that this exercise can be used for forestry students interested in production forestry as well as for students more interested in nature conservancy.

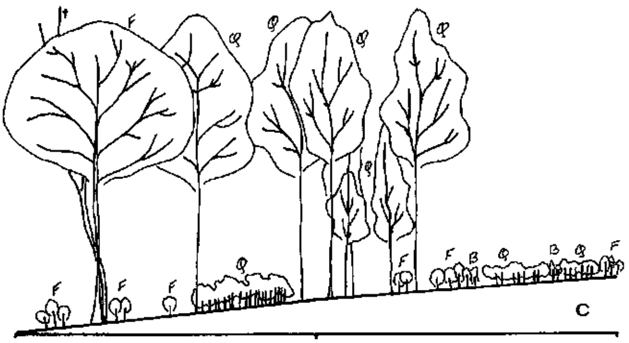
YEAR	CLEANING	THINNING AND CUTTING	REGENERATION
000	in natural regeneration	cut birch thin beech (70 y.)	natural regeneration
010		cut pine	
020		thin oak (50 y.)	
050		cut beech (120 y.)	plant oak
070		thin oak (20 y.) cut beech (120 y.)	plant maple plant douglas
090		calamity: cut 50% oak, no thinning douglas, maple, because damaged by harvest oak.	
100	damaged douglas		plant douglas regenerate oak
120	in natural regeneration	cut oak (150 y.), thin oak (20, 70 y.), douglas.	
140		cut beech (100 y.)	regenerate (plant) maple
150		cut maple and douglas (both 80 y.)	natural regeneration
160		thin maple (20 y.)	
170		cut oak (150 y.)	
180		cut douglas (80 y.)	
190		thin maple (50 y.)	
200		cut oak (150 y.)	

Fig. 1. Final treatment schedule. For explanation, see text.

Fig. 2. Profile drawings and crown projection maps of the starting point (A) and of the projected development of a stand at various ages (B: 30 year; C: 60 year; D: 80 year; E: 100 year: F: 130 year; G: 150 year; H: 180 year) towards the desired stand (I: 200 year). For treatment schedule see fig. 1; for further explanation see text.

Abbreviations: Ps = Pinus sylvestris; Pm = Pseudotsuga menziesii; F = Fagus sylvatica; B = Betula spec.; Q = Quercus robur; A = Acer pseudoplatanus.

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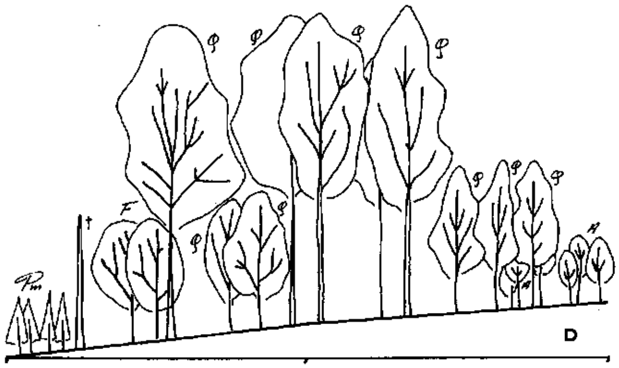
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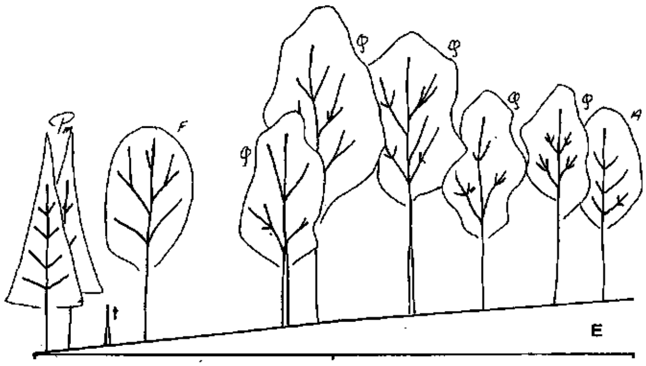
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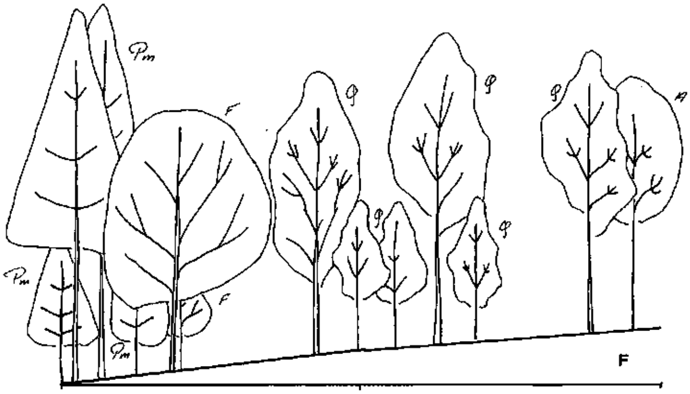
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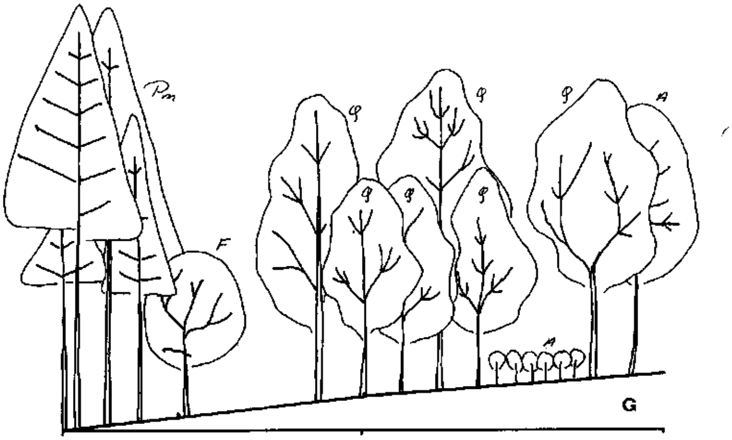
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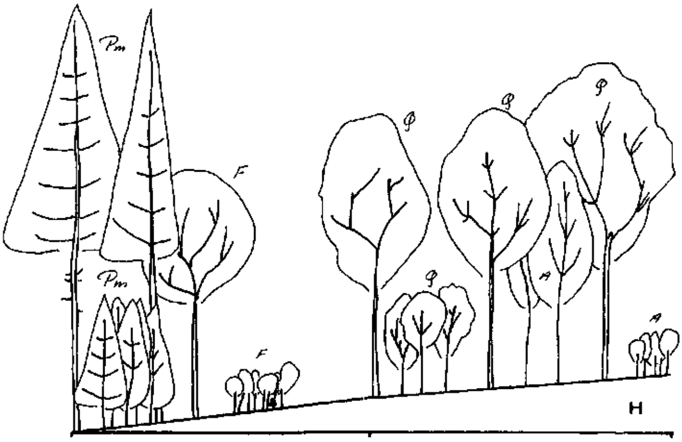
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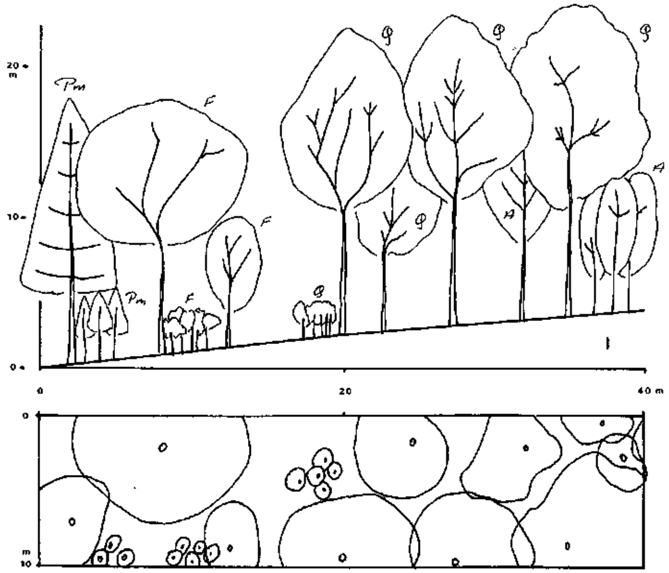
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NATURAL REGENERATION OF BEECH FOREST IN JAPAN

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In 1983, Japan was visited in order to study Japanese beech forest. In the preliminary survey, the first objective was to study certain aspects of Japanese Fagus crenata Blume (Fagus japonica Masein) forest, and compare these with European Fagus sylvatica L. and American Fagus grandifolia Ehrh. forest.

The second objective was to examine the possibilities of an integrated study of phytosociological, structural and ecophysiological characteristics of the regeneration unit level. The purpose was to find a mondial basis for comparison on the levels of the regeneration unit and the forest mosaic. The regeneration unit is regarded as a basic unit of development in a forest mosaic.

By means of literature the aspects of plant sociology, structure and ecophysiology of these forests were studied. A field study with belt transect, including soil analysis, was carried out to obtain á more detailed insight in beech forest structures and their relation to species composition and ecophysiology. The field study was carried out on the regeneration unit level.

The natural regeneration of beech was studied. Being the climatical climax forest ecosystem in the cool temperate zone of Japan, beech forest is maintained by natural regeneration of beech. This is perceived in the field, thus called the "Reality".

This reality consists of the regeneration unit and its environment (light, temperature, precipitation and soil), which are recorded separately. The regeneration unit is recorded by measuring and drawing structural aspects, counting plant species and measuring ecophysiological aspects, e.g. by means of belt transect analysis. Belt transects were made of regeneration units in different phases of development.

After recording, data were processed into models which describe different possible natural regeneration processes of beech forest (fig. 1). In a natural beech forest usually a canopy gap is caused by single tree fall. Hence the size is small. This gap may be filled by beech trees, other canopy tree species or a subcanopy tree species through natural regeneration.

In the analyzed beech forests other canopy tree species occurred with low frequency, while they could hardly compete with beech. The subcanopy tree species may be profit from advanced growth, but as it never reaches the upper structure layer it will be overgrown again by surrounding beech trees or a successor beech tree.

Subcanopy tree species, e.g. Acer mono and Acer sieboldianum, sometimes reacted in gap formation by restarting height growth. Maybe the age of the restricted subcanopy tree at the time of release determines the ability to restart height growth.

When a whole forest stand is removed by a natural disaster or by clearcut, then again natural regeneration will take place. First, pioneer trees may germinate, but beech seedlings may also be found. In the course of time beech will prove to be the strongest competitor.

However this model is not based on a set of carefully selected regeneration units, representative for all the sequential phases of development.

In a follow up research data will be collected from more selected representative regeneration units. Then a model for the development of an individual regeneration unit may be designed. Site conditions should be taken into account. A forest mosaic is composed of regeneration units in different phases of development. Hence, after studying presence and distribution of these units, the step to the higher level of forest mosaic can be made.

In this way the beech forest in the cool temperate zone of the Northern Hemisphere will be studied. The object of this study is to understand the general and local features of the ecology and the silviculture of the beech trees and forests.

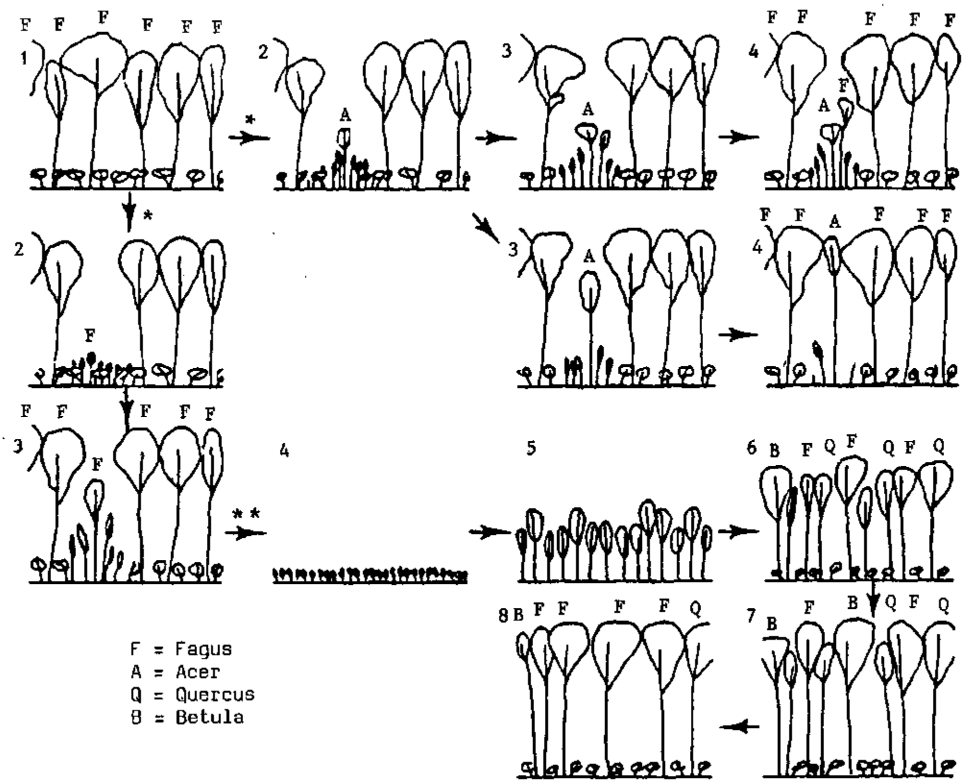

Fig. 1. Some hypothetical regeneration processes on optimal beech forest sites. The regeneration processes originated after single tree fall (*) or after clear-cut (**). Based on forest structures found in the different belt transects. (Peters, 1985).

This hand-out is based on:

Peters, R., 1985. Japanese beech forest. M.sc. thesis. Dept. Silviculture, Wageningen Agricultural University, The Netherlands.

THE DEVELOPMENT OF YOUNG DOUGLAS FIR STANDS ESTABLISHED AT VARIOUS SPACINGS

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The objective of this study was to examine the influence of initial spacing on the development of young Douglas fir stands in the Netherlands. Stand characteristics such as tree height, diameter, crown dimensions, diameter increment, stand volume etc. were examined. This was done both on a stand level and for the biggest trees per stand. These biggest trees are the potential crop trees, ± 200 per hectare.

From the total of nine stands studied, three examples of 16 year old stands on the same relatively good soil type, will be discussed here.

Stand A: spacing 3.0x3.0 meters, stand B: spacing 2.5x2.5 meters, stand C: spacing 2.0x2.5 m. Stand A was established on a clearcut area but the other stands on an area on which strip-cutting had been used.

To reconstruct both heightgrowth and crown development one site tree per stand was cut and analysed (see figure 1 appendix). This figure is a scale drawing of the site trees, the crowns of these trees are drawn for age 16, 15, 12, and 9. Differences in height are not representative for the stands. The site trees were selected on diameter only (d(g)=d (mean)+ 0.5 cm.). d(g) for: stand A=13.53 cm. , average height=8.77m.
stand B=11.55 cm. , average height=7.87m.
stand C=11.38 cm. , average height=8.93m.

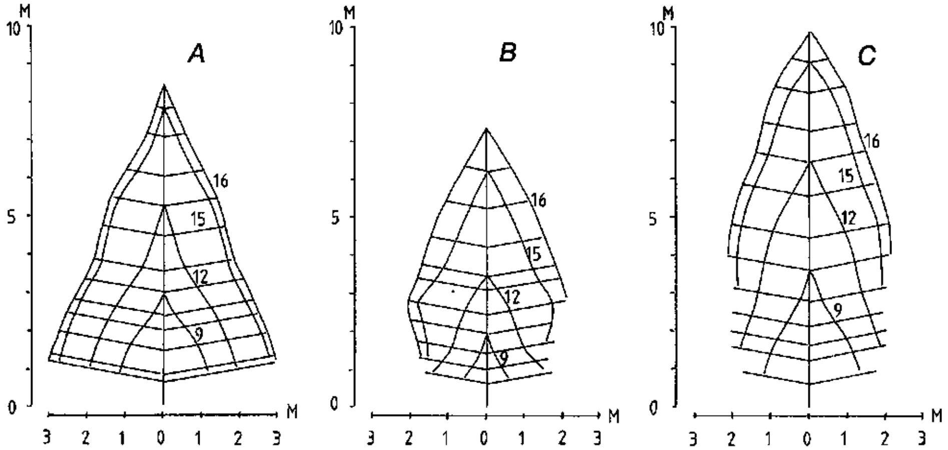

Fig. 1. The (schematic) development of the crowndimensions of the site tree in four steps, at age 9, 12, 15, and 16.

Stand development reconstruction

The transects in the appendix (figure 2) give an impression of the development of these three stands. The reconstruction is based on the crown development as indicated by the site tree, data from diameter increment borings and the present situation.

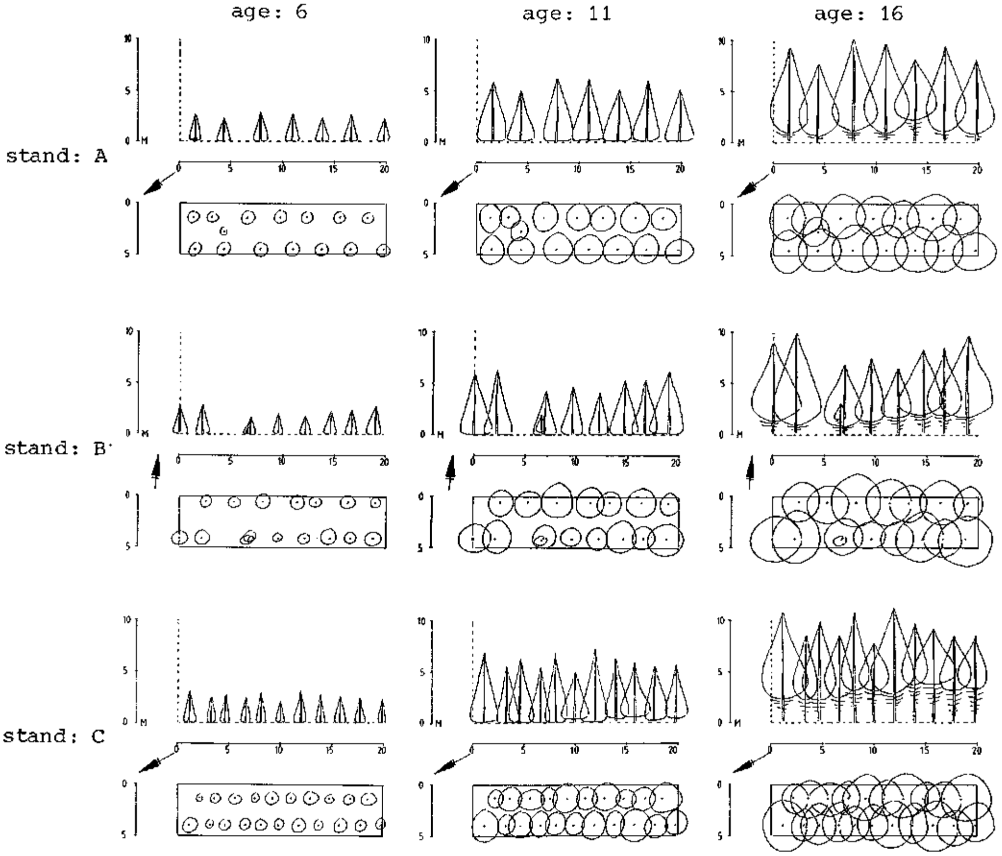

Fig. 2. Schematic transects, in a representative part of the stands, at three year intervals (at age 6, 11, and 16).

Results

The following is a summary of the results of all 9 stands studied. Possible trends were analysed statistically with the Spearman rank correlation test (a two-sided test with a reliability of 90% was used).

* Average crown width, crown length, crown projectionarea, crown cicumference, crown ratio, diameter, diameter increment, and treevolume increase significantly with increasing spacing.

* The dispersion of the diameter distribution, the total volume present, and the slenderness of the trees (h/d-ratio) decrease with increasing spacings.

* Height, topheight and basal area showed no significant change with changing spacings.

For the biggest trees per stand only crown dimensions and diameter increment were found to change significantly with varying spacings, the other parameters did not change significantly. This indicates that the development of the final crop trees is less influenced by initial spacing than the average tree.

References

Raffe, J.K., van and M. Roelvink. "De ontwikkeling van jonge douglasopstanden aangelegd met verschillende plantafstanden." (unpublished master thesis), Department of Silviculture, L.H. Wageningen, The Netherlands.

HIGH, LOW AND NO THINNING EXPERIMENT WITH DOUGLAS FIR IN THE NETHERLANDS

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Introduction

A significant increase of the total area of Douglas fir plantations in the Netherlands is to be expected within the next decades (Meerjarenplan bosbouw, 1985). In the governmental plans it is assumed that a high thinning regime is the optimal way to manage Douglas fir stands under Dutch growth conditions. However, in the literature there are some indications that high thinning methods are not ideal for all situations (Hall and Quenet, 1980, Cole, 1984, Schoenmakers and Emmingham, 1984). Therefore some supplementary studies on thinning in Douglas fir could be useful

Fortunately a demonstration experiment of high, low and no thinning was established 10 years ago in a 37-year old stand at the Veluwe near Oud-Millingen, which previously had been untreated. Data collection until now was merely on stand level. For a better understanding of the influence of thinning on stand development, single tree data as collected in this study should be more informative. One of the aims of this experiment was to analyse the structure and the diameter and social position distribution.

Methods

DBH, crown, projection area and coordinates of all trees in 6 different 0.1 ha plots were measured, supplemented by the measurement of tree height and crown height in a 5 m wide strip. Increment cores were also taken. A vertical diagram for each plot was made. For the analysis of the data the growth model of Faber (1983) was used.

Results

An example of a vertical diagram and a growing space map for the unthinned plot are given in figure 1 and figure 2. Vertical diagrams give a good idea of the structure and the social positions of a stand. The growing spaces give an indication of the within stand competition. Note the large amount of small trees and the narrow crowns. Figure 3 shows some of the plot data. The low thinning has the largest BA and volume followed by the unthinned plot. The social positions in figure 4 were taken from Faber's growth model. Note that the diameter distribution differs from the social position distribution.

Conclusions

- The dominant height of all plots is about the same ($h_{dom} = 20.8$). This is site class 4. Site differences between plots are therefore neglectable.
- The diameter distribution differs from the social position distribution. Selection on diameter only is not reliable for these plots.
- In this experiment the high thinning yielded the worst results. This could have important implications for future management. Therefore more detailed studies on thinning in Douglas fir are needed.

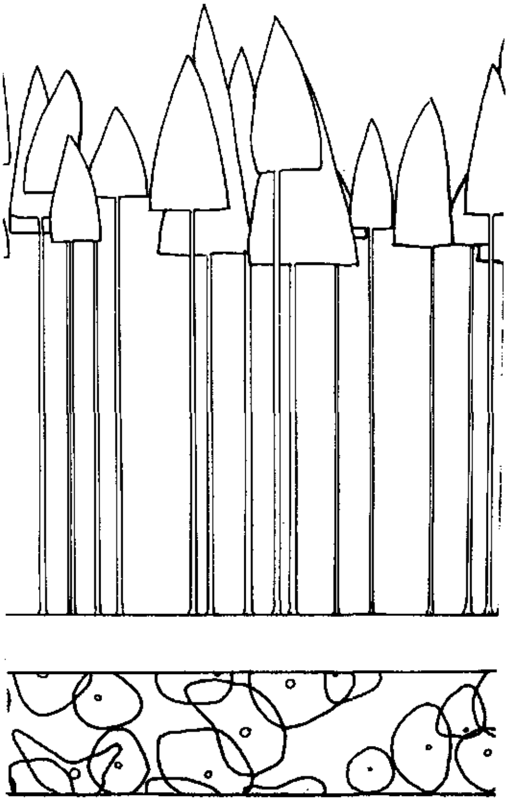

FIGURE 1

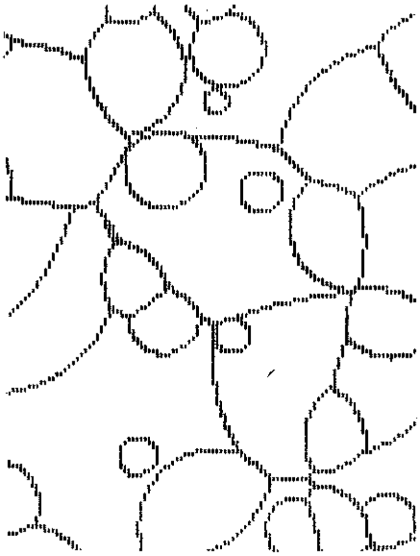

FIGURE 2

	replications	trees/ha	basal area /ha	volume /ha
HIGH	1	1600	25.7	259
	2	1000	25.5	222
LOW	1	1400	34.6	260
	2	1260	44.4	403
NO	1	1360	28.2	254
	2	1475	34.7	312

FIGURE 3

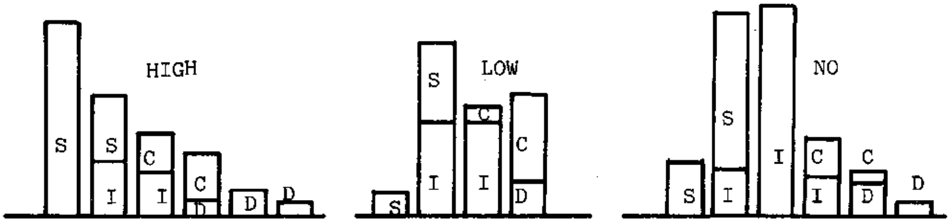

FIGURE 4

References

Cole, D.M., 1984. Crop-tree thinning in a 50-year old western larch stand: 25 year results. USDA forest service, Ogden.

Hall, T.H. and R.V. Quenet, 1980. Fertilization and thinning effects on Douglas fir ecosystem at Shawnigan Lake: 6 year growth response. Canadian Forest Service, Victoria.

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Section 3: Structure and Succession Research in Primaeval Forests and Forest Reserves

STRUCTURE OF THE PRIMAEVAL FOREST OF FIBY

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Institute of Ecological Botany, University of Uppsala, Uppsala, Sweden

Summary

The above-ground structure of the tree and shrub layer of three sites within the natural coniferous forest of Fiby is described. During the summer of 1984 three plots of 0.5 ha were established within different natural spruce forest communities. Each individual tree was mapped, several structural characteristics were measured, and overall stand characteristics were obtained. Major differences in structure among the three plots are related to the known history of the plots and probably to differences in the availability of nutrients and moisture.

Keywords: Above-ground structure, primaeval boreal forest.

Introduction

Descriptions of forest stand structure have long been used to give basic information for silvicultural, successional and regeneration studies and as input material for modelling and simulation of forest processes. Most of the commonly used descriptors of above-ground forest stand structure were developed in the late nineteenth century for forestry purposes. They were used to get a quick estimator for the amount of available and useable timber in a stand. Nowadays, main attention is still given to these tree size distributions and stand characteristics. Stand structure is often correlated with site conditions (e.g. Werger et al., 1984), with demographic properties of the stand to study dynamical processes within forest stands (e.g. Knowless and Grant, 1983) and the history of stand development (e.g. Henry and Swan, 1974; Oliver and Stephens, 1977).

The purpose of this paper is to give a complete description of the above-ground structure of three spruce forest communities in a primaeval forest reserve, and to assess and interpret the differences between the communities. This research is part of a larger research project at the Institute of Ecological Botany, Uppsala, started in the summer of 1984.

Material and methods

Research Area

The nature reserve 'Fiby Urskog' (the primaeval forest of Fiby) is located 20 km west of Uppsala, central Sweden. It is one of the best preserved examples of a natural boreo-nemoral coniferous forest in Sweden. The reserve is surrounded to the south and west by other forests, which act as a buffer to protect the reserve; in the east by agricultural land; and in the north by Lake Fiby (Fibsjön). The vegetation within the reserve consists mainly of two different forest types. On higher granite ridges an extremely slow-growing and open Scots pine (Pinus sylvestris L.) forest dominates. If not disturbed by trampling, the tops of these massive granite ridges are covered with a mosaic of cryptogams, especially lichens. Depressions between these ridges are occupied by patches of *Ledum palustre* L. and *Sphagnum* mire.

The major part of the forest consist of a Norway spruce (*Picea abies* L.) forest with some scattered pine and broad-leaved trees. The field layer vegetation varies from species poor dwarf-shrub dominated types to more species rich types. The spruce forest occurs on lower parts around the granite ridges on boulder moraines, glacial till and later sedimentary deposits. The spruce forest has a natural character, with an uneven age structure, standing dead trunks and many fallen logs in different stages of decomposition. A brief description of the forest, its history and its importance for nature conservation is given by Hytteborn and Packham (1985).

Sample plots

During the summer of 1984 I placed three permanent plots of 0.5 ha (50m by 100m) within the spruce forest communities of Fiby.

Plot 1 is situated in the most northern part of the reserve on a slope towards lake Fiby. It is a spruce forest with some pine, aspen (*Populus tremula* L.) and birch (*Betula pubescens* Ehrh. and *B.pendula* Roth.). At the top of the slope pine becomes more abundant, due to proximity to one of the ridge systems. The shrub layer is poorly developed and consists mainly of single saplings of spruce and a few scattered mountain ash (*Sorbus aucuparia* L.) and birch saplings. The herb layer is species-poor and consists mostly of bilberry (*Vaccinium myrtillus* L.), cowberry (*Vaccinium vitis-idaea* L.) and wavy hair-grass (*Deschampsia flexuosa* (L.) Trin.). Several moss species are abundant in the well developed moss-layer. The soil is mostly a moraine of coarse material, rich in boulders. There are only a few patches with finer sediments. Nutrient and water availability is poor.

Plot 2 is situated at the southern border of the reserve. This part of the forest was once used for forestry, but is now part of the buffer area around the nature reserve and is not used for forestry any longer. The age distribution is more even than within the most primaeval parts of the reserve. The oldest trees are about 150 years old (Claessen & Leemans, 1981). The forest is pure spruce, with few individuals of other tree species. The shrub layer is better developed than in the other plots and consists mostly of low shrubs of species such as mountain currant (*Ribes alpinum* L.), raspberry (*Rubus idaeus* L.) and honeysuckle (*Lonicera periclymenum* L.), some scattered mountain ash and hazel (*Corylus avellana* L.), and groups of saplings of spruce. The species-rich herb layer is a mosaic with patches dominated by wood sorrel (*Oxalis acetosella* L.), hepatica (*Hepatica nobilis* L.) and may lily (*Maianthemum bifolium* (L.) F.W. Schmidt); of bushgrass (*Calamagrostis arundinacaea* L.); and of bilberry, cowberry and cowwheat (*Melampyrum sylvaticum* L. and *M.pratense* L.). The soil consists of fine sediments and moraine with some scattered boulders and is more nutrient rich than in the older plots.

Plot 3 is situated in the western part of the reserve. It is a spruce forest with several big aspens and birches and some old pines. The shrub-layer is poorly developed and consists mainly of groups of or single saplings of spruce. The herb layer is species-poor, with dominant species of bilberry, cowberry and hair-grass. The moss-layer is well developed. The nutrient-poor soil consists of coarse and fine material with some big boulders.

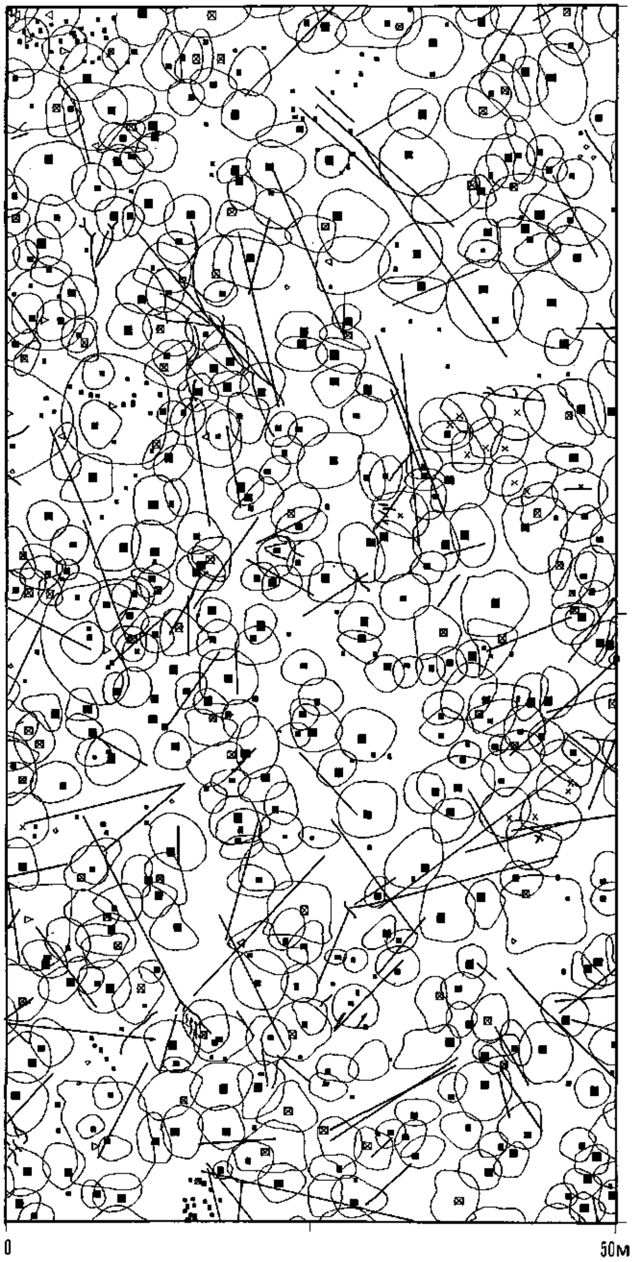

Fig. 1. Positions of the trees in plot 1. The dots represent the base of each individual tree. The different dot sizes represents the three size groups mentioned in the text. Only the crown projections of the two largest size classes are drawn. (■ = *Picea*, ⊠ = *Pinus*, ◁ = *Populus*, ▷ = *Betula*, ◇ = other species, × = dead standing trunc, — = fallen log)

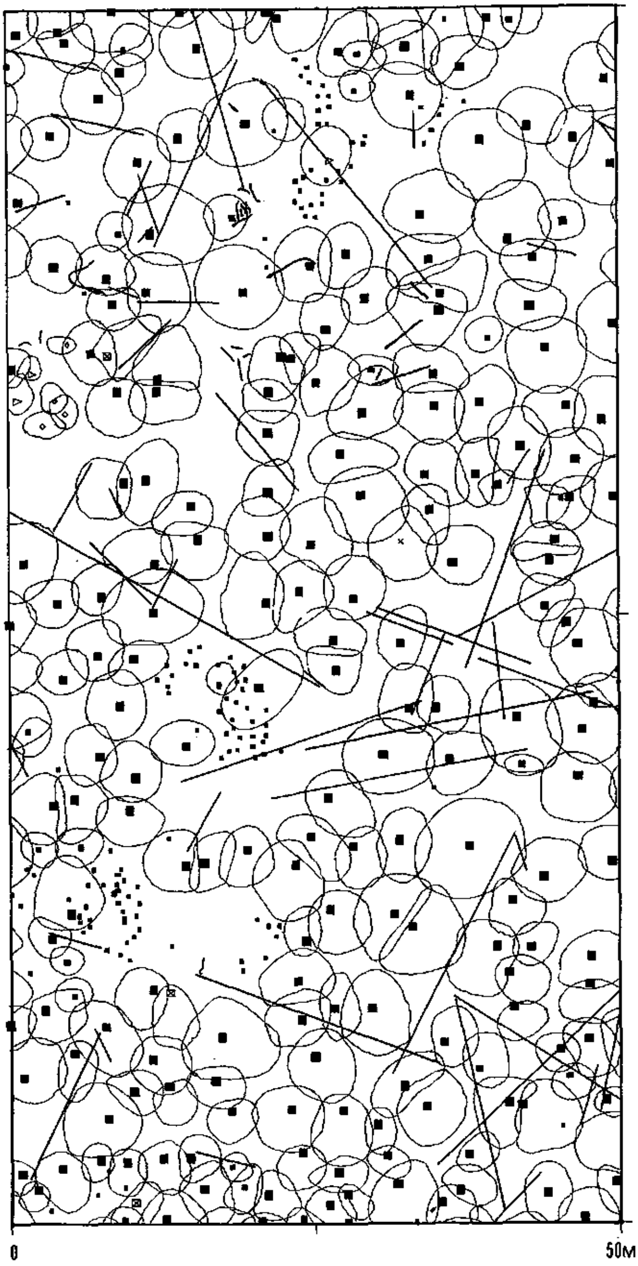

Fig. 2. Positions of the trees in plot 2. The dots represent the base of each individual tree. The different dot sizes represents the three size groups mentioned in the text. Only the crown projections of the two largest size classes are drawn. (■ = *Picea*, ☒ = *Pinus*, ◁ = *Populus*, ▷ = *Betula*, ◇ = other species, × = dead standing trunc, — = fallen log)

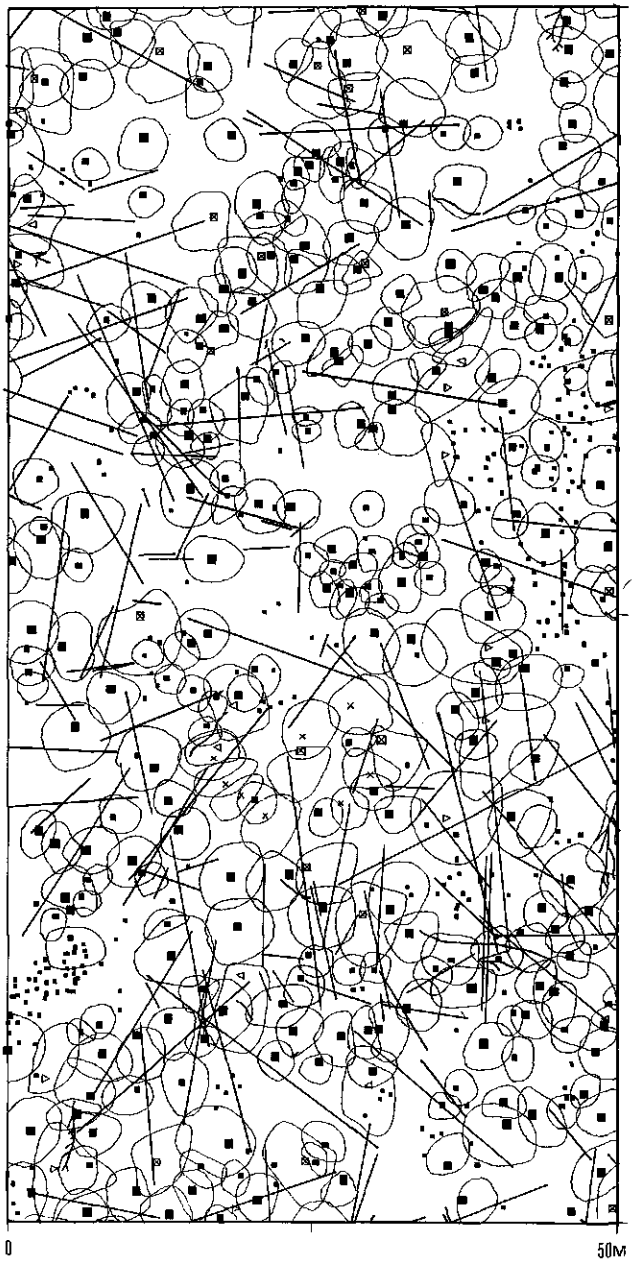

Fig. 3. Positions of the trees in plot 3. The dots represent the base of each individual tree. The different dot sizes represents the three size groups mentioned in the text. Only the crown projections of the two largest size classes are drawn. (■ = Picea, ⊠ = Pinus, ◁ = Populus, ▷ = Betula, ◇ = other species, × = dead standing trunc, — = fallen log)

Sample methods

Every individual of the tree species above 0.5 m height within these plots were mapped together with fallen logs, standing dead trunks and crown projections. Each individual was numbered and the species were noted. The following structural characteristics were measured: diameter at breast height (DBH), total tree height (Ht), crown length (Hc), bole height (Hb) and crown diameter (Dc). DBH was measured with a special tape, which while measuring the "circumference" outside bark, permits direct reading of the diameter. Heights were measured with a Suunto clinometer. This light and handy device is easy and accurate in use for the two most common species spruce and pine, but gives difficulties in the height measurement for the flat-crowned birches and aspens. For these two species there is a tendency to overestimate the total height, but because of the few individuals of these species, the measurement was not repeated with more acurate devices. Crown diameter was measured in two different directions (minimal diameter and maximum diameter); the mean between these two values is presented as the crown diameter. From these data, the following overall stand characteristics were computed: number of trees (N), maximum total treeheight (Htmax), and maximum basal area (BA). The ratios of bole height and crown length (Hb/Hc), crown length and crown diameter (Hc/Dc), total tree height and crown diameter (Ht/Dc), diameter at breast height and total tree height (DBH/Ht), and diameter at breast height and crown diameter (DBH/Dc) were also computed for each tree. The maps were used to measure gapsize.

Table 1. Number of individuals of each taxon (per 0.5 ha.)

	Picea	Pinus	Betula	Populus	Tilia	Alnus	Sorbus	total
plot 1	558	84	12	9	-	1	12	664
plot 2	396	6	-	6	3	-	4	415
plot 3	582	26	8	12	-	-	-	628

Table 2. Basal area of each taxon (m^2 per ha.)

	Picea	Pinus	Betula	Populus	Tilia	Alnus	Sorbus	total
plot 1	24.6	13.2	1.7	2.5	-	0.4	0.1	42.5
plot 2	43.0	1.3	-	0.5	0.2	-	0.1	45.1
plot 3	27.7	5.6	1.2	2.5	-	-	-	37.0

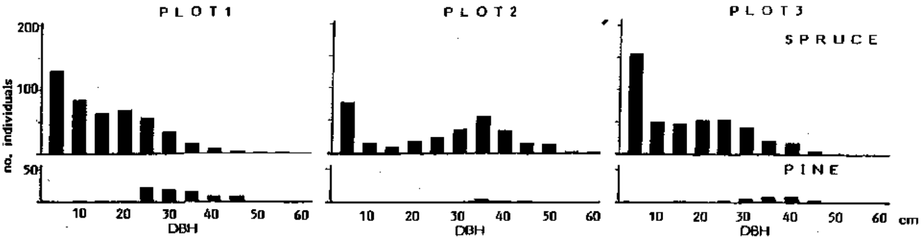

Fig. 4. DBH class distribution for the major tree taxa (spruce and pine) for plot 1-3. Figures are given in cm.

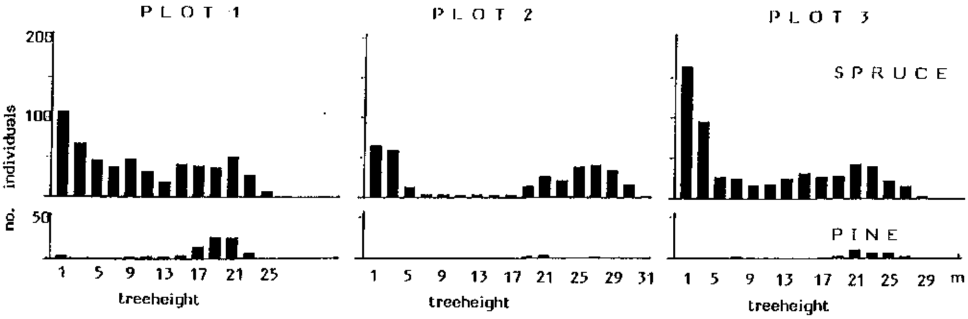

Figure 5. Total height class distribution for the major tree taxa (spruce and pine) for plot 1-3. Figures are given in m.

Results and discussion

The maps over plot 1 to 3 (Fig. 1-3) give a good impression of the above-ground structure of the plots and the differences between the plots. Plot 2 has an almost closed canopy, with only five distinct gaps; plots 1 and 3 have a more clumped canopy with many gaps of different sizes. In plots 1 and 3 it is difficult to distinguish all gaps from the many small openings in the canopy. The range of gapsize is different for the three plots: 50 to 450 m^2 in plot 1 (mean crown area is 11.8 ± 5.3 m^2 for mature spruce); 120 to 200 m^2 in plot 2 (mean crown area is 20.5 ± 8.8 m^2 for mature spruce); and 50 to 300 m^2 in plot 3 (mean crown area is 12.5 ± 5.2 m^2 for mature spruce). Clumped groups of seedlings and small saplings can be found in many of the bigger gaps, most obviously in plot 2.

Plot 2 differs also in the rather low number of windthrows, broken trunks and dead standing trees. Most of them died or were overthrown recently. The total number of fallen trunks for the two other plots are in the same order (80 per ha) as the figures given by Falinski, 1978, for a natural mixed coniferous forest stand in the Bialowieza reserve in Poland. Tree height distributions and DBH distributions for the most common tree taxa (spruce and pine) are drawn in fig. 4 and 5. For spruce all the distributions are bimodal; three different groups can easily be distinguished. The first group consists of small saplings (Ht < 5m and DBH < 0.10m). The second is an intermediate group of bigger saplings and young mature trees (Ht < 15.0m and DBH <0.20m), who have not yet reached the canopy. This group is poorly developed in plot 2, but abundant in the other two plots. The last group consist of all the mature trees (Ht >15.0m and DBH >0.20m), which form the canopy. A similar distribution is given by Nahashizuka and Numata, 1982, for a Japanese beech (Fagus crenata) forest. The height and DBH distributions for pine are unimodal. Small saplings of pine are seldomly found. Most individuals reach the canopy. Differences in shape of the size distributions of different taxa can easily be explained by competition for light under a closed canopy. Only spruce is capable of regenerating under a closed canopy.

The number of individuals (Table 1) within the tree plots are comparable with some natural mixed coniferous forest from the Alps in Austria (Mayer et al., 1972). The basal areas from the plots (Table 2) are low compared with a climax coniferous forest in Japan (BA= 85.8 m^2/ha, Suzuki, 1980), and very low if compared with old growth coniferous forests in the western United States (BA= 120 m^2/ha, Waring and Franklin, 1979), but comparable to figures given by Mayer et al. (1972) for the Austrian forests. Table 3 and 4 show that the trees grow bigger in all directions in plot 2. This tendency is also reflected in the different ratios (Table 5). Only the ratio DBH/Ht is not influenced and gives

Table 3. Some structural characteristics for the tallest trees (Ht< 15.0m). The mean values are given for all figures in meters and per 0.5 ha.

Picea

	N	Ht(max)	Ht	Hb	DBH	Hc	Dc
plot 1	175	24.9	19.2 ± 2.5	6.0 ± 2.3	0.26 ± 0.07	13.3 ± 3.0	3.8 ± 0.8
plot 2	204	32.1	24.9 ± 3.8	8.5 ± 3.2	0.35 ± 0.09	16.3 ± 3.9	5.0 ± 1.1
plot 3	188	28.7	20.9 ± 3.3	7.1 ± 2.8	0.28 ± 0.08	13.8 ± 3.8	3.9 ± 0.8

Pinus

	N	Ht(max)	Ht	Hb	DBH	Hc	Dc
plot 1	73	23.1	19.0 ± 1.9	13.0 ± 2.3	0.33 ± 0.07	6.0 ± 2.3	4.1 ± 1.0
plot 2	6	27.3	21.1 ± 3.2	13.7 ± 3.7	0.37 ± 0.04	7.4 ± 3.2	4.8 ± 0.6
plot 3	26	26.3	22.2 ± 2.3	15.3 ± 2.2	0.37 ± 0.06	6.9 ± 2.1	5.5 ± 1.1

Betula

	N	Ht(max)	Ht	Hb	DBH	Hc	Dc
plot 1	8	18.6	17.7 ± 0.7	9.1 ± 1.6	0.29 ± 0.11	8.5 ± 1.4	4.7 ± 1.0
plot 2	-	-	-	-	-	-	-
plot 3	8	23.5	21.5 ± 2.2	12.3 ± 3.5	0.31 ± 0.06	6.9 ± 2.1	5.5 ± 1.1

Populus

	N	Ht(max)	Ht	Hb	DBH	Hc	Dc
plot 1	7	23.4	21.9 ± 1.3	12.1 ± 1.6	0.44 ± 0.13	9.8 ± 1.9	8.0 ± 1.5
plot 2	2	21.0	18.7 ± 3.3	6.2 ± 0.0	0.31 ± 0.02	12.4 ± 3.3	6.0 ± 2.1
plot 3	11	26.4	23.9 ± 1.7	13.8 ± 2.3	0.37 ± 0.05	8.0 ± 1.9	6.9 ± 1.5

Table 4. Some structural characteristics for the trees (Ht > 5.0 m) for the two most common species. The mean values are given for all figures in meters and per 0.5 ha.

Picea	N	Ht	Hb	DBH	Hc	Dc
plot 1	350	14.4 ± 5.5	4.8 ± 2.7	0.19 ± 0.09	9.3 ± 4.6	3.4 ± 0.8
plot 2	229	23.3 ± 5.9	8.0 ± 3.4	0.32 ± 0.11	15.2 ± 4.8	4.8 ± 1.2
plot 3	302	16.8 ± 6.1	5.9 ± 2.8	0.22 ± 0.10	10.8 ± 5.0	3.5 ± 0.9
Pinus	**N**	**Ht**	**Hb**	**DBH**	**Hc**	**Dc**
plot 1	79	18.4 ± 2.8	12.6 ± 2.6	0.32 ± 0.08	5.8 ± 2.3	4.0 ± 1.0
plot 2	6	21.1 ± 3.2	13.7 ± 3.7	0.37 ± 0.04	7.4 ± 3.2	4.7 ± 0.6
plot 3	27	21.6 ± 3.7	14.8 ± 3.2	0.36 ± 0.08	6.8 ± 2.1	5.4 ± 1.1

Table 5. Means of the computed ratios for the trees (Ht > 5.0 m) for the two most common species.

Picea	N	Hb/Hc	Hc/Dc	Ht/Dc	DBH/Ht	DBH/Dc
plot 1	350	0.66 ± 0.54	2.7 ± 1.2	4.2 ± 1.5	0.013 ± 0.002	0.055 ± 0.021
plot 2	229	0.59 ± 0.38	3.2 ± 0.9	4.9 ± 1.1	0.014 ± 0.003	0.067 ± 0.017
plot 3	302	0.67 ± 0.48	3.1 ± 1.1	4.8 ± 1.5	0.013 ± 0.002	0.061 ± 0.021
Pinus	**N**	**Hb/Hc**	**Hc/Dc**	**Ht/Dc**	**DBH/Ht**	**DBH/Dc**
plot 1	79	2.66 ± 1.63	1.4 ± 0.6	4.8 ± 1.2	0.017 ± 0.004	0.081 ± 0.018
plot 2	6	2.26 ± 1.21	1.5 ± 0.6	4.5 ± 1.0	0.018 ± 0.003	0.079 ± 0.010
plot 3	27	2.41 ± 1.02	1.3 ± 0.3	4.1 ± 0.9	0.017 ± 0.002	0.067 ± 0.013

similar values for all the plots. There is a fixed relationship between height and diameter, regardless to differences in site conditions. The tree species do not reach their absolute maximum dimensions in the plots (compare Mayer et al., 1972, Falinski, 1978, and Mayer et al., 1979), due to poor site conditions and the specific 'storm gap' regeneration structure of these spruce forests. Spruce is, especially on boulder moraine, susceptible for windthrow (Sernander, 1936).

Major differences in structure among the three plots are related to the known history of the plots and probably to differences in the availability of nutrients and moisture.

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STUDY OF VEGETATION CHANGES IN NATURAL FOREST RESERVES IN SOUTH-WEST GERMANY

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Summary

Some permanent plots in the natural forest reserve (Bannwald) "Untereck" (Baden-Württemberg, FRG) have been monitored for 50 years; the results for two instable areas free from permanent vegetation cover (fig. 3) or covered only preforest stages rich in spruce (fig. 4) are described. The third example deals with an deteriorating older beech - silver fir stand (fig. 5, 6). Since 1970 the scale of the monitoring has been larger: today 1650 ha natural forest reserves (fig. 1) that are intended to become the virgin forests of tomorrow, and from which human interference is excluded and which are used as "open air laboratories" are being monitored.

Keywords: Vegetation succession, establishment of forests, natural forest reserves.

Introduction

Interest in the basic problems of succession and the thorough documentation of vegetation changes in areas of Central Europe with extensive forests, was expressed early in the century. One of the locations where this work has been pursued is in the natural forest reservation (Banngebiet, Bannwald) "Untereck". This reserve was established about 1935. In 1970 40 reserves were excluded from any direct human interference and designated for the study of natural vegetation development (Dieterich et al. 1970). Today there are about 1650 ha of forest reserves, sited in 43 different forests in Baden-Württemberg (fig. 1).

50 years of vegetation studies in the Bannwald 'Untereck'

Development of sites liable to erosion

Long-term observations are so far only available from the montane beech-silver fir region of the Swabian Jura (Bannwald "Untereck", figs. 1, 2, table 1). Vegetation scientists (Koch & v.Gaisberg, 1938, 1939) were originally especially interested in sample areas that were free from woody vegetation. There the question to be examined was whether such sites are always free from forest vegetation (and in that case can serve as a refuge for botanical species that could not survive under a tree cover), or whether these sites develop into a forest. The sites in question are very liable to erosion because they include extremely steep slopes with bedrock changing from marl to limestone.

The sample areas show a high degree of instability during the monitoring period (fig. 3). Only early stages of pioneer vegetation (composed of grasses, herbs, seedlings and small individuals of broadleaves woody species) have developed, but they are regularly destroyed

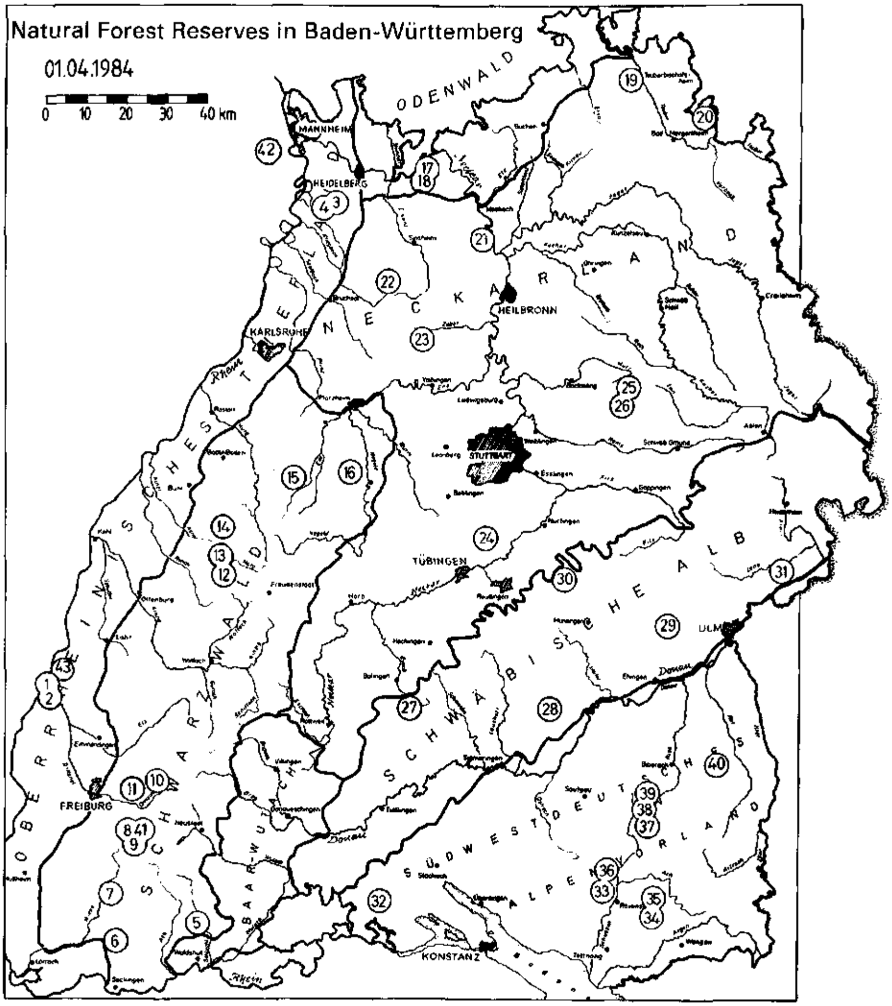
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Figure 1

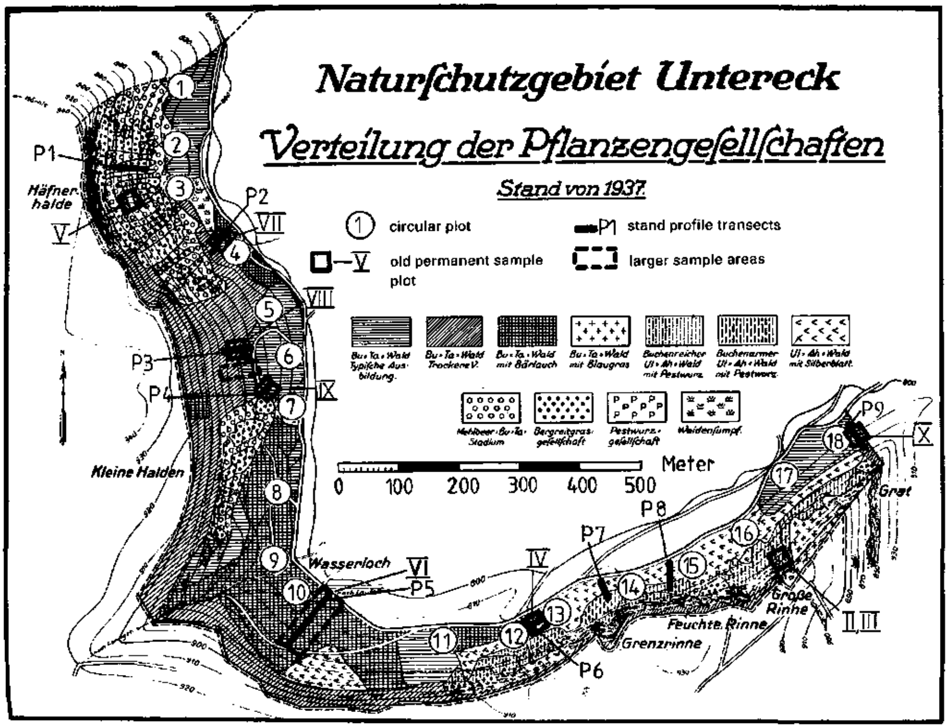

Fig. 2. Vegetation map of "Untereck" natural forest reserve (from Koch & v. Gaisberg, 1938). Position of old permanent sample areas II - X, circular plots 1 - 18, stand profile transects P 1 - P 9, and larger sample areas. Mapped vegetation communities: Bu-Ta-Wald: beech-white fir forest (typically dry, with Allium ursinum, and Sesleria caerulea). Ul-Ah-Wald: elm-maple forest (with Petasites albus, and Lunaria rediviva). Mehlbeer-Bu-Ta-Stadium: rowan-beech-white fir stage. Bergreitgrasgesellschaft: association of Calamagrostis varia. Pestwurzgesellschaft: association of Petasites albus. Weidensumpf: willow swamp.

Table 1. Forest reserves (Bannwälder) in Baden-Württemberg

No.* (Fig.1)	Name of forest	Short description	Size (ha)
1. Growth area "Oberrheinisches Tiefland" (Upper Rhine Basin)			
1.	Hechtsgraben	Riparian forest (Rhine valley)	15
2.	Bechtaler Wald	Oak-hornbeam forest	13
3.	Franzosenbusch	Scots pine forest on sandy soils (not natural)	17
4.	Kartoffelacker	Scots pine forest on sandy soil (n.nat.)	15
42.	Reissinsel	Riparian forest (Rhine valley)	15
43.	Taubergiessen	Riparian forest (Rhine valley)	170
2. Growth area "Odenwald" (Oden Forest)			
17.	Sautrieb	Beech-oak forest	12
18.	Schnapsried	Beech-oak forest with Scots pine	16
3. Growth area "Schwarzwald "(Black Forest)			
5.	Schwarzhalden	Beech-white fir forest	147
6.	Wehrstal	Beech-white fir forest	105
7.	Flüh	Beech-white fir forest	37
8.	Faulbach	Beech-white fir forest	20
9.	Napf	Mixed forest (high montaneous)	108
10.	Zweribach	Beech-white fir forest	97
11.	Conventwald	Beech-white fir forest	17
12.	Schliffkopf	Beech-white fir forest	15
13.	Wilder See-Hornisgrinde	Beech-white fir-spruce forest, forest bordering high bog	84
14.	Hoher Ochsenkopf	Spruce forest	41
15.	Wilseemoor	Forests bordering raised bog	181
16.	Waldmoor-Torfstich	Forest bordering raised bog	11
41.	Hirschfelsen	Mixed forest (montane)	20
4. Growth area "Neckarland" (Neckar Region)			
19.	Stammberg	Beech-oak and oak-wild service tree forests	23
20.	Lindach	Beech-oak forest	16
21.	Schlierbach	Beech-oak forest	27
22.	Greifenberg	Beech-oak forest	13
23.	Sommerberg	Beech-oak forest	12
24.	Eisenbachhain	Beech-oak forest	8
25.	Steinhäusle	Beech-white fir forest	22
26.	Wieslaufschlucht	Beech-white fir forest	53
5. Growth area "Schwäbische Alb" (Swabian Alb)			
27.	Untereck	Beech-white fir forest	33
28.	Kohltal	Maple-elm-lime forest	33
29.	Rabensteig	Steppenheide-forest	28
30.	Nägelesfelsen	Steppenheide-forest	12
31.	Grubenhaus	Beech forest with oak	16
6. Growth area "Südwestdeutsches Alpenvorland" (Foothills of the Alps)			
32.	Hohentwiel	Steppenheide-forest	20
33.	Glastobel	Maple-elm forest	32
34.	Edensbacher Mösle	Forests bordering raised bog	4
35.	Füremoos	Forests bordering raised bog	5
36.	Dornachried	Forests bordering raised bog	47
37.	Brunnenholzried	Forests bordering raised bog	75
38.	Allgaier Riedle	Swamp forest (common alder)	3
39.	Riedschachen	Forest bordering raised bog	11
40.	Freibergmisse	Anthropogenic spruce forest	1

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* No. on map

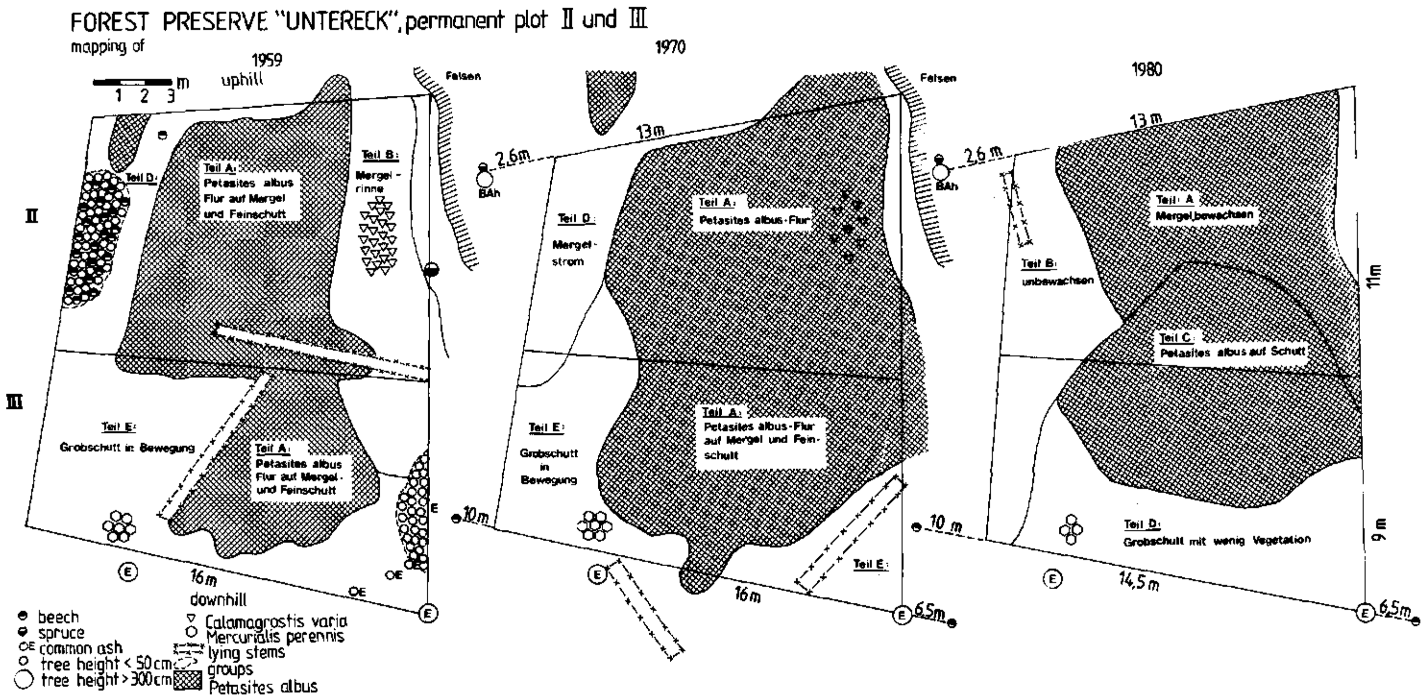

Fig. 3. Sequence of succession stages in "Untereck" natural forest reserve, permanent plots II and III, from 1959 to 1980. Dominant vegetation cover is shown in relation to the main substrate types (marl and limestone talus).

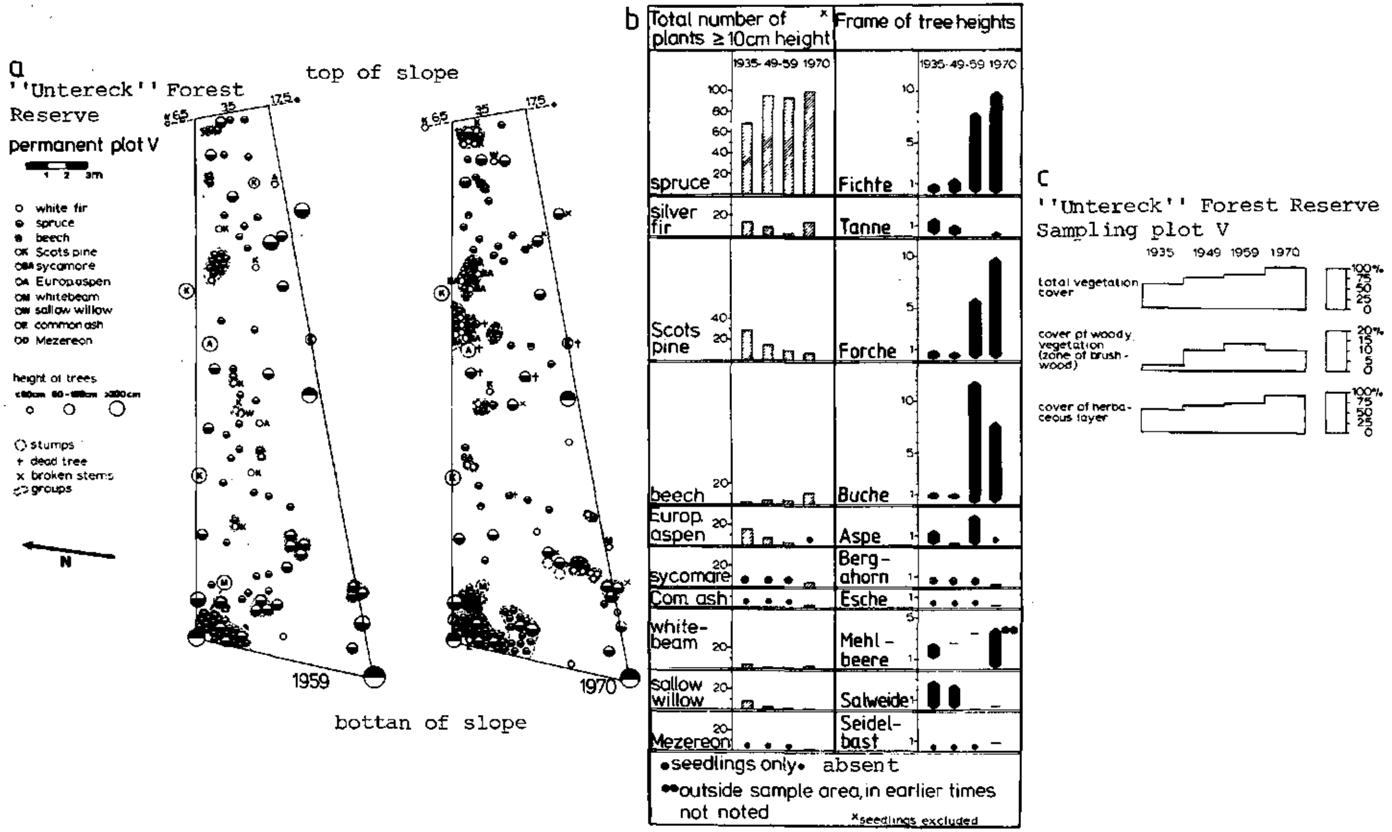

Fig. 4. Vegetation development of permanent sampling plot V in "Untereck" natural forest reserve, from 1935 to 1970. a: Two maps showing the distribution of ligneous plants in 1959 and 1970. b: Development of ligneous plants. c: Changes in total vegetation cover, of woody vegetation cover (scale enlarged) and of herbaceous vegetation cover.

by new landslides.

Therefore a durable vegetation cover cannot be attained. Site mosaic is small and inhomogeneous within short distances. Strips of woody patches on less eroded rocks are interspersed with open areas that occasionally suffer landslides that destroy even the preforest stages (see figure 4). Mass transports on an even greater scale occur occasionally in the slope region of the "Swabian Alb" (Bibus, 1985).

The vegetation of permanent plot V (fig. 4) has evolved from pioneer vegetation to a preforest plant association "Tofieldia - Picea - community" (Müller, 1975), which was covered by brushwood only to a small extent, even in 1970. In 1980 the total sample area was lost because of a landslip. Of the woody species, spruce had the most established individuals. The tallest trees were spruce, pine, and beech, whereas typical broadleaved pioneer trees were rare. The dominance of spruce is surprising, given figure 3 and the presumed final forest association which, according to Koch & v.Gaisberg (1938; see also Müller & Oberdorfer (1974) is thought to be a complex of Calamagrostio-Pinetum (on marly soils), Cytiso-Pinetum (on very shallow rocky sites), Tilio-Acerion communities (on loose rocks) and Carici-Fagetum (on deeper calcareous soils).

The reasons for the establishment of different tree species seedlings in the two plots can be found to a certain degree in local factors: the very small gap in figure 3 for example, is formed in beech - maple - ash stands, whereas the open slopes surrounding plot V are evidently strongly influenced by nearby stands rich in spruce.

Development of an established forest

Research plots on less steep and therefore more stable slopes with deeper (evolved) soils comprise beech forest communities with white fir (Lathyro-Fagetum with natural admixture of Abies alba; Müller & Oberdorfer, 1974). In the case of plot VI (fig. 5) the long-term development

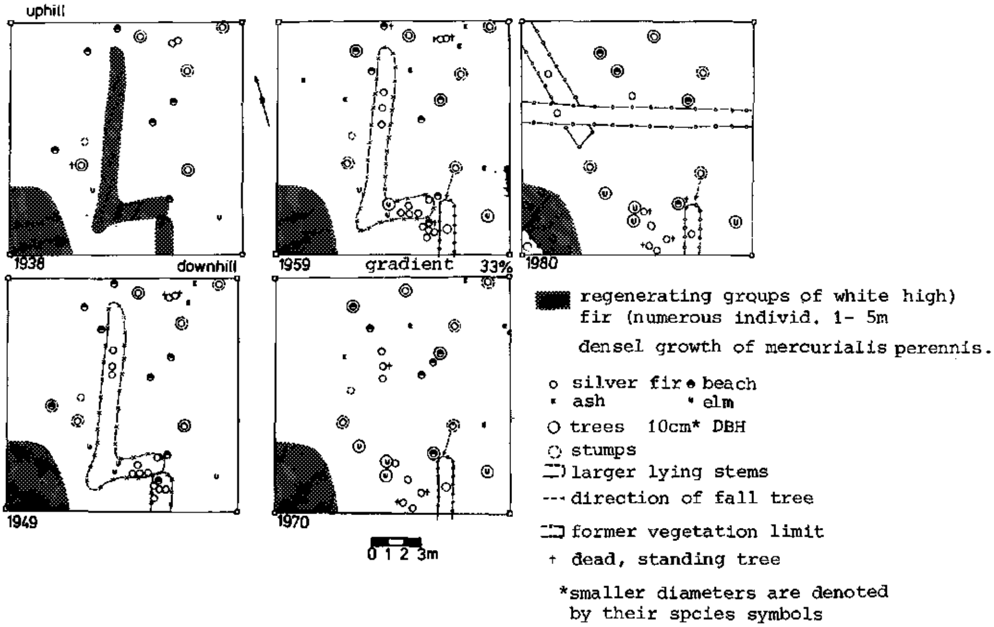

Fig. 5. "Untereck" natural forest reserve; vegetation development of permanent plot VI (200 m^2), 1938 - 1980.

of an old and relatively natural beech - silver fir stand is shown. The stand deterioration that began as early as 1938 (at that time the falling trees were up to 180 years old) accelerated between 1970 and 1980.

Individuals of Abies alba from an earlier regeneration period mostly die off under the developing canopy of Fagus sylvatica and Ulmus scabra.

The present-day structure of this plot is shown in stand profile transect fig.6). The permanent plot is located on the left side of the profile. Vitality and cover of the herbaceous vegetation diminish in relation to the lack of light, but all the floristic elements persist almost entirely. Some individuals - especially fern species such as Phyllitis scolopendrium or Polystichum aculeatum - seem to be very longliving and their presence in one spot can be traced back over several decades.

Soil development stages cover a very great scale from calcareous rocky or marly raw soils to brown rendzinas or terra fusca; some global parameters of decalcification and organic carbon accumulation are shown in tabel 2, together with carbon-related ratios of the major nutrient elements nitrogen, phosphorus, potassium,and KCl extracted calcium. As all soils of the sites studied are still in the buffer range of calcium carbonate, no major soil changes in the chemistry are anticipated in the immediate future. Changes in the more distant future can only be anticipated by more sensitive methods of analysing soil samples from "Untereck".

New aspects of succession research in natural forest reserves

The older research plots described above deal with special sites and special succession problems. The new research programme initiated in 1970 (Bücking et al. in this volume) is still in the phase of first inventories that as yet can seldom be interpreted in terms of succession processes. The central aim of this long-term research is to elucidate the competitive role of the different main tree species (beech, white fir, fir, oak, pine and others) on a greater number of normal site types in Germany. Successional stages should be documented as exactly as possible, because the long-term development of stands has to be ascertained. In contrast to other succession research programmes that try to evaluate succession processes by comparing results from neighbouring states, we think it important to follow as closely as possible the development in time of a special plot or a definite individual. Very many plots have to be studied, because starting the points of succession vary greatly, depending ~~on~~ on earlier human influence on forests and in site factors. The general rules of the competitive ability of main tree species that we are trying to identify in these "open air laboratories" cannot be ascertained without reference to local site factors and historical components.

In addition, natural forest reserves have been established in order to allow virgin forest to stabilize. These "Bannwälder" habe been called the "virgin forests of tommorow" (Dieterich et al. 1970). There are very few true virgin forests from which such forests could develop, although the genetic continuity is still maintained in the trees present in stands that have been allowed to regenerate naturally. But the small protected areas are surrounded by commercial forests or even by agricultural areas, from which they cannot be isolated. Therefore important changes of site factors interfere. Foresters have changed the conditions of competition and succession in the productive forests and created new dominants in

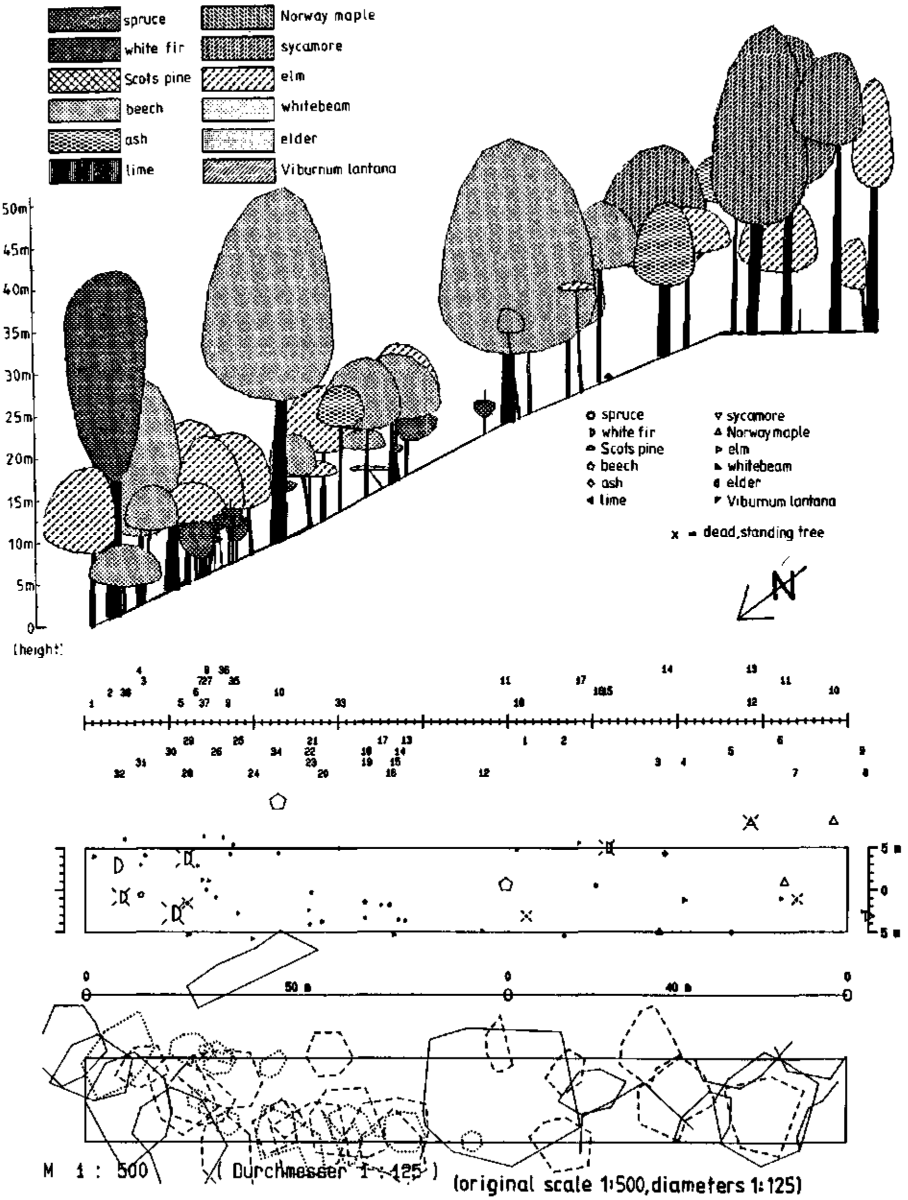

Fig. 6. 90 m stand profile transect from the centre of Bannwald "Untereck" showing a less steep section from 800 to 840 m. The permanent plot VI described in the text corresponds to the part of the profile between 2 to 15 m. Stand is dominated by broadleaved trees; it is a beech-white fir forest with some spruce (not present in profile transect), elm and ash in the lower parts and an ash-maple-elm forest in the upper parts of the profile.

Table 2. Soil chemical parameters of sampling areas in the "Untereck" natural forest reserve

Description of sampling area	pH		$CaCO_3$ (fine material) %	C_{org} %	C/N	C/P	C/K	C/Ca
	H_2O	KCl						
raw marl (vegetation-free)	8.05	7.90	82.5	1.1	18	24	2	8
raw marl (grass cover)	7.85	7.80	88.3	0.9	18	20	2	6
grass facies	7.70	7.70	75.0	3.7	66	80	9	14
beech, pine, spruce maple stand on stony marl raw soil	7.30	7.10	61.6	12.0	22	19	2	2
beech-silver fir stand (sampling area VI), Ah* (4 cm)	7.20	6.85	0.8	13.7	15	97	16	17
spruce small-pole wood (anthropogenic on a beech, silver fir forest site; sampling area IX)								
Ah (4 cm)	7.15	7.10	5.8	15.1	22	232	21	14

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*) Symbols according to Forstl. Standortsaufnahme (1978)

the landscape by introducing new commercially relevant species; the new forest diseases are going to be a very great problem to natural forest reserves, and modern game browsing continues former animal grazing, one of the most important impacts on forest tree composition (Wilmanns, 1977). The virgin forests of tomorrow will be natural only in the sense that direct human influence is excluded; indirect influences, however, cannot be avoided. They will therefore not be comparable with former primary forests but only correspond to natural potential vegetation of tomorrow in an ecosphere transformed by humans.

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Posters

THE STRUCTURE OF A 1000 YR OLD DOUGLAS FIR STAND IN WESTERN WASHINGTON

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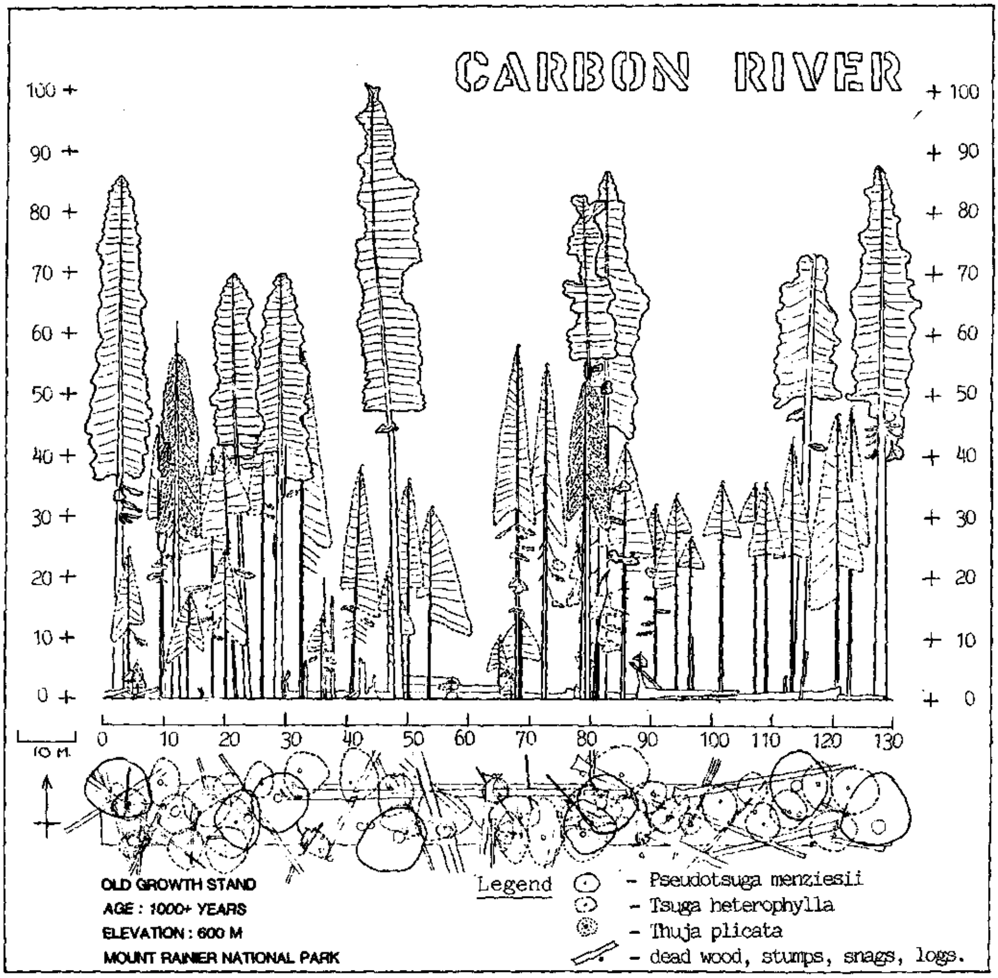
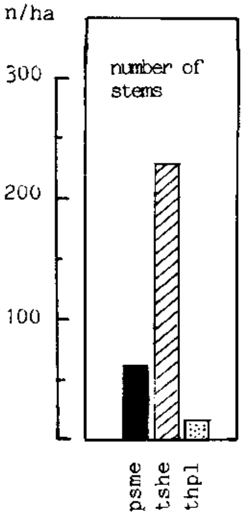
In 1984 the structure and dynamics of a series of natural Douglas fir stands in the Pacific Northwest was studied, forming a chronosequence of ages rangeing from 50 yr to 1000 yr old (Kuiper et al., in prep.). Vertical diagrams were made in 15 different Douglas fir stands on more or less comparable sites within the *Tsuga heterophylla* zone.

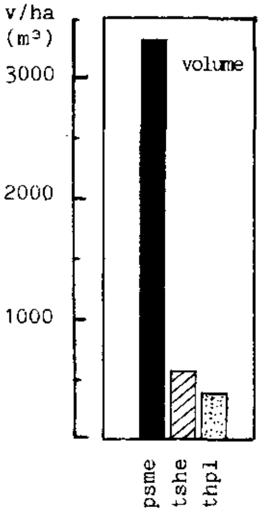
. In this paper an example of such a diagram of the structure of a 1000 yr old Douglas fir stand is presented. The stand is located in the Carbon River valley of Mount Rainier National Park, at an elevation of about 600 m.

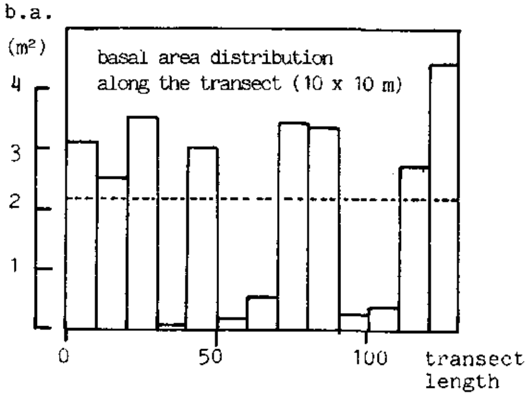


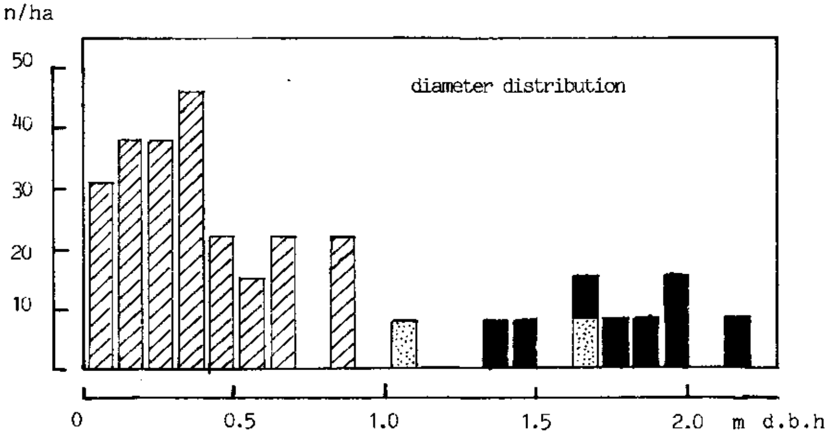
The large amounts of coarse woody debris is covered by mosses, an abundance of Tsuga heterophylla saplings and by sword ferns (Polystichum munitum).

The distribution of the number of stems, volume, basal area along the transect and the diameter at breast height is presented in the next figures. Since the location of the transect plot was selected in such a way that a maximum number of large Douglas fir trees were present in the 130 x 10 m strip, these data represent the upper limit of what actually can be found in such a forest community. Which is quite impressive: tree heights of 85-100 m; d.b.h. of 1.5 - 2.0 m; an average basal area of 220 m^2/ha and a total standing volume of 4320 m^3/ha.









This particular stand has the largest accumulation of down wood recorded for a stand thus far in the Pacific Northwest: a hectar plot contained 418 tons of logs/ha that covered 23% of the plot area (Franklin et al., 1981).

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THE REGENERATION OF COASTAL REDWOOD

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Aim and method

To analyse the structure and regeneration of coastal redwood (Sequoia sempervirens) in Northern California an architectural study was made. The study was made by constructing and interpreting vertical diagrams and maps of virgin old growth redwood stands on different sites, and by studying literature.

Results

Redwood has basically three regeneration strategies:

- by seed. Best seedling establishment is on mineral soil.
- by sprouts from buds at the base of the stem ("burl"). These buds are activated when a tree is damaged or deteriorating. The sprouts are reiterations.
- by crown-reiterations, to replace part of a damaged tree-crown.

The following disturbances belong to the natural dynamics of redwood forests and each have their special effect on the regeneration and survival of redwood.

- wind : uprooting of tree : in the resulting chablis seedlings can become established;
  : breaking of tree : vigorous sprouting or formation of crown-reiterations;
- flood : inundation : other species die, but redwood is tolerant of inundation;
  : deposition of silt: other species die, redwood seedlings can establish themselves;
- fire : redwood survives because of its thick bark;
  : other vegetation and the soil surface are removed, so that seedlings can establish themselves.

The size of the regeneration units caused by wind are small, only the size of one or a few trees. Flood and fire cause larger regeneration units, depending on the intensity of the disturbance.

Conclusions

Because of its three regeneration strategies and its vital reaction to disturbances, redwood is able to regenerate very successfully. Therefore, although it shows some characteristics of a pioneer species (e.g. fast growth), it is able to keep a dominant position in the old growth forests.

Unfortunately, the dynamics of redwood forests has recently been disturbed by fire control and a change in flooding regime. This seriously treatens the natural development of these forests.

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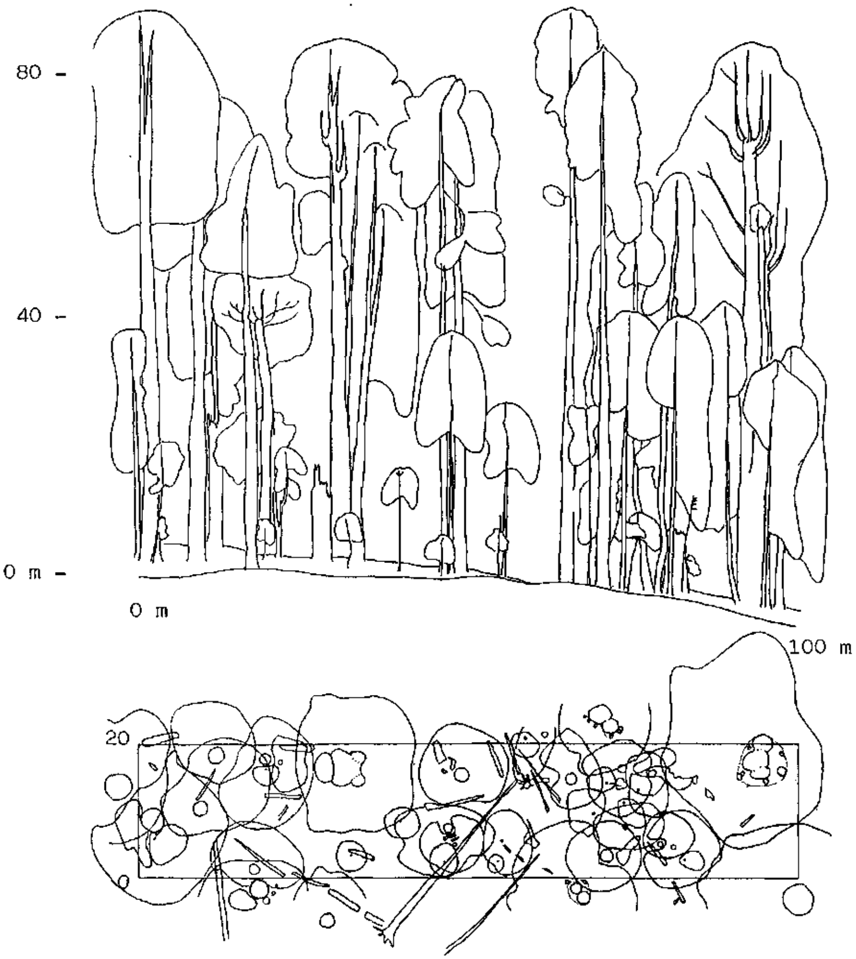
Mulder, A.J. and C.J.M. de Waart, 1984. Preliminary architectural study of coastal redwood (Sequoia sempervirens), LH Bosteelt, Wageningen.



Vertical diagram and crown projection map in Prairee Creek Redwoods State Park, showing reiterations and groups of sprouts (disturbances: wind and fire).

Section 4: Methods of Forest Succession Research Modelling Forest Succession

THE DESIGN OF A FOREST SUCCESSION MODEL

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Summary

A new general-purpose forest succession model has been developed using the basic design principles of "gap models" of the JABOWA type but with various processes differently formulated. In particular, tree growth and competition for light are modelled in a more realistic way while retaining previous models' simplicity and low data demands. The model is being used to simulate the composition and structure of natural forests in Sweden.

Keywords: Gap model, competition, tolerance, self-shading, succession.

Introduction

In 1972, Botkin, Janak and Wallis published an account of JABOWA, a computer simulation model of forest growth and succession for the northern hardwoods forests of the northeastern United States. JABOWA was shown to successfully reconstruct both time- and elevational trends in forest composition and diversity from a strictly mechanistic basis in autogenic and allogenic processes. Since then, a family of JABOWA-like models -- known collectively as "gap models" -- has been developed to simulate forest stand and forest ecosystem dynamics in environments ranging from subarctic-boreal to tropical. Many of these models and their applications are described by Shugart (1984). Shugart emphasizes that the processes included in gap models are common to all forests. He points out that gap models imply a theory of forest dynamics, with antecedents in the mosaic-dynamic view of plant communities associated with A.S. Watt's concept of "pattern and process".

This article is a short, preliminary outline of the principles of a forest succession model recently developed as part of a project to simulate compositional and structural dynamics in natural (primaeval or old-growth) forests. This new model is a gap model by Shugart's (1984) definition. It is similar to JABOWA and related models in its rationale and general structure, but differs in various ways, most importantly in the formulation of tree growth and competition for light. The design of the model was guided by the criteria of flexibility (to allow changes in parameters such as extinction coefficients, timestep or patch size, growth equations, or dimensional relationships to be made easily without causing inconsistencies); compatibility (with equations and units standardly used by plant physiologists, and with descriptions of forest composition, structure, biomass and production standardly made by foresters and forest ecologists); and realism in the formulation of processes, where this could be achieved without drastically increasing complexity, computation demands, or data requirements. This is strictly a preliminary account: mathematical and computational details are omitted. The model has been parametrized only for some north European tree species, but it could be adapted to other forest systems without major changes. It has been implemented as a FORTRAN 77 program.

General features of the model

Like other gap models, the present model is implicitly a spatial model. It depends on a discrete-space approximation, by which the forest stand is modelled as a collection of patches on the order of 0.1 ha in area. Resources (light and nutrients) are assumed to be averaged within patches, but resources levels on one patch are independent of resource levels on other patches. Thus interactions among individual trees occur within patches (irrespective of location) but not between patches.

The state description of the stand is stored in computer memory and updated at each timestep (normally one or two years). The state description of each patch consists of an array of trees, each characterized by three variables: taxonomic identity, diameter at breast height, and height to the base of the crown. The growth equations are deterministic, but establishment and mortality are stochastic and therefore the overall behaviour of the model is stochastic. It is not intended to simulate the actual state of any one patch, but rather a frequency distribution of states among patches.

Establishment occurs on each patch at the beginning of each timestep. Among the species included, any that can grow under the prevailing forest-floor conditions will become established. Establishment means the introduction of new trees with a small diameter at breast height. The expected number of new saplings established depends on the species.

Establishement of new saplings on a patch is followed by growth of all trees, and mortality of some trees. Individual tree death probabilities are determined from a reverse sigmoid function relating the (instantaneous) death rate to growth increments during the current timestep. The reasoning behind this function derives from the reasoning developed by Botkin et al. (1972) in terms of energy balance; the idea is that there is some threshold growth rate above which death may happen with low probability through various catastrophes, and below which death will happen with much higher probability through the tree's inability to repair damage. Mortality is one point in the model where the length of the timestep matters, because the probability depends on integrated assimilation during one timestep. Dead trees of species than can sprout are allowed to sprout if they were in the appropriate size range.

One consequence of the above formulation, which is simply a rationalization of the birth and death routines in all gap models, is that the demographic characteristics of the tree populations are controlled to a large extent by growth and competition; the number of individuals in a sapling cohort that will reach the canopy is strongly dependent on how fast those saplings can grow in height. Another consequence is the models ability to simulate gap-phase dynamics (the origin of the term "gap model"). Shade-intolerant species may be prevented from establishing for long periods, but may begin establishing again on a patch (and possibly out-compete shade-tolerant species) as soon as a large tree dies and lets sufficient light reach the forest floor.

Competition and tree growth

Competition for nutrients is handled in the present model in the same, implicit way as in JABOWA: growth rates of all trees are slowed as total patch biomass approaches a ceiling. This is a crude approximation and should ideally be replaced by a more explicit formulation of nutrient cycling. Models of the interaction between carbon and nitrogen dynamics of forests are an active research area (e.g. Ågren, 1985; Pastor and Post, 1985). Pastor and Post have implemented a decomposition-mineralization-litter production cycle with associated nitrogen availability response functions in a JABOWA-type gap model.

The finite patch size in all gap models stands for the horizontal averaging effects of root zone overlap and side shading (the geometry of light interception is not explicit in gap models). However, shading and net assimilation in response to light are modelled more explicitly in the present model than in previous gap models. Previous models from JABOWA onwards have assumed that all of a tree's leaves were concentrated at the top of a tree, thus exaggerating the asymmetry of light competition. The present model allows for vertical crown overlap and explicitly models self-shading, which becomes a principal factor slowing down the growth of trees in a closed canopy (cf. Ågren, 1982). This new formulation also avoids the need to specify the arbitrary maximum diameters required by previous gap models. In the present model, each tree's net assimilation is computed by summation in vertical steps from the top of the tree down to its basal crown height. Net assimilation per unit leaf area of a given tree at any given level depends on the available light, which in turn is computed as a function of leaf area index above that level (assuming a suitable growing-season average insolation and a overall value for the extinction coefficient). Light response curves of net assimilation are specified by three parameters: a maximum rate, a compensation point, and a "half-saturation" point. The maximum rate is absorbed into an overall growth scaling constant, which notionally includes allocation factors. The other two parameters determine different species aspects of shade tolerance. The compensation point together with the extinction coefficient determine the greatest leaf area index that a forest of a given species can support at a given latitude. The half-saturation point determines the growth efficiency of a species at low light intensities above the compensation point, relative to that species performance at higher light intensities. The compensation point also determines which species will establish in the understorey, while competition among species in the understorey is dependent on several factors including both these aspects of tolerance.

An interesting consequence of the formulation of growth rates in terms of asymptotic light response curves and negative exponential light attenuation through the canopy is that at least during the most productive phase of forest growth, the growth efficiency of the entire canopy of a singel-species stand declines almost linearly with increasing leaf area index. Intuitively, this is because at high light intensity where the attenuation curve is steep, the response curves are flat; the converse applies at low light intensities. This result can be demonstrated analytically (Ågren, 1983) and provides a link and a method of interconverting parameters between gap models written in terms of individual tree processes and ecosystem models simulating whole canopy processes.

The production of stemwood and leaves in gap models is computed at each timestep using simple equations relating various tree dimensions to one another. In the present model, tree height is modelled as an asymptotic function of diameter; leaf area per unit crown depth as an asymptotic rather than allometric function of basal area (since there is an upper limit to the crown diameter of an individual tree, however large its stem); and stemwood biomass as a factor times basal area times height. After diameter, height, and leaf area have been incremented for each tree on a patch, new compensation depths are calculated for each species; then any leaves which are below this depth are irreversibly dropped. This mechanism ensures that leaves that could not support themselves do not endure, and can cause the bases of the tree crowns -- especially of intolerant species in dense stands -- to gradually ascend.

Test and uses of the model

Leemans and Prentice (1985, and unpublished MS) tested the model's ability to simulate growth and competition in a mixed stand of Scots pine (intolerant) and Norway spruce (tolerant). We were able to reconstruct the vertical structure as well as the size class distributions and basal areas of the two species in an old-growth forest, Fiby Urskog (Leemans, this workshop). We are carrying out sensitivity analysis on this simple system. More extensive tests in various forest types in different parts of Sweden are planned, partly in collaboration with the Swedish environmental monitoring program (PMK). The model is intended to be used as an investigation tool in the study of succession and as a submodel for forest succession in large-scale simulations of the effects of environmental change.

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ECOLOGICAL MONITORING OF NATURAL AND SEMI-NATURAL FORESTS

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Summary

To start a multifunctional information system on forest development, an integrated method for forest monitoring has been developed. Data are collected at three different scale levels, i.e. one-tenth hectare blocks (50 adjacent vegetation plots and profile drawings), one-hectare blocks (chartings of tree foots and crowns) and ten-hectare blocks (vegetation and forest structure mappings). To overcome the limitations set by the two-dimensional images of plan and profile drawings, a three-dimensional computer model has been designed. Therefore, the coordinates of eight fixed points characterizing the tree foot, main stem fork and the extremities of the tree crown in positive and negative direction of the three dimensions are measured. By making use of the ellipsoid character of most deciduous trees, a best fitting wrapping can be constructed by connecting the eight points with quarters of ellipses. With help of the spatial model, profiles can be plotted automatically. By computing the hemisperical cover for fixed points at any desired position within the model, shading patterns can be simulated. A computed aerial view of the forest model can be used as a ground-truth for interpretation of remote sensing images.

Keywords: Forest structure model, hemispherical cover, remote sensing.

Introduction

A multifunctional information system on forest development for management purposes has been initiated. The system is to be used for quantitative and qualitative studies on patterns and processes in forest systems under semi-natural conditions. The methods to be used should meet the following requirements:

1. detect changes in forest vegetation structure and species composition on different scales in space and time;
2. quantify these differences to make them quickly comparable;
3. attain standardization in data collection for a longer time on many plots;
4. the collected data must demonstrate directly the patterns and processes to the manager in the field and they must provide a data base wide enough for modelling at different scale levels.

For objects to be included, preference should be given to forest areas where human interference has been excluded and that represent the potential natural vegetation types of The Netherlands as described by Van der Werf (in prep.). There are now some fifty permanent study areas in The Netherlands. For reference purposes, vegetation succession in some West European natural forests (Poland, Germany, France and England) is being studied with the same methods.

The project consists of three phases. In the first phase, the elaboration of appropriate techniques of data collection in the field has been completed for the vegetation component. As a basis for the

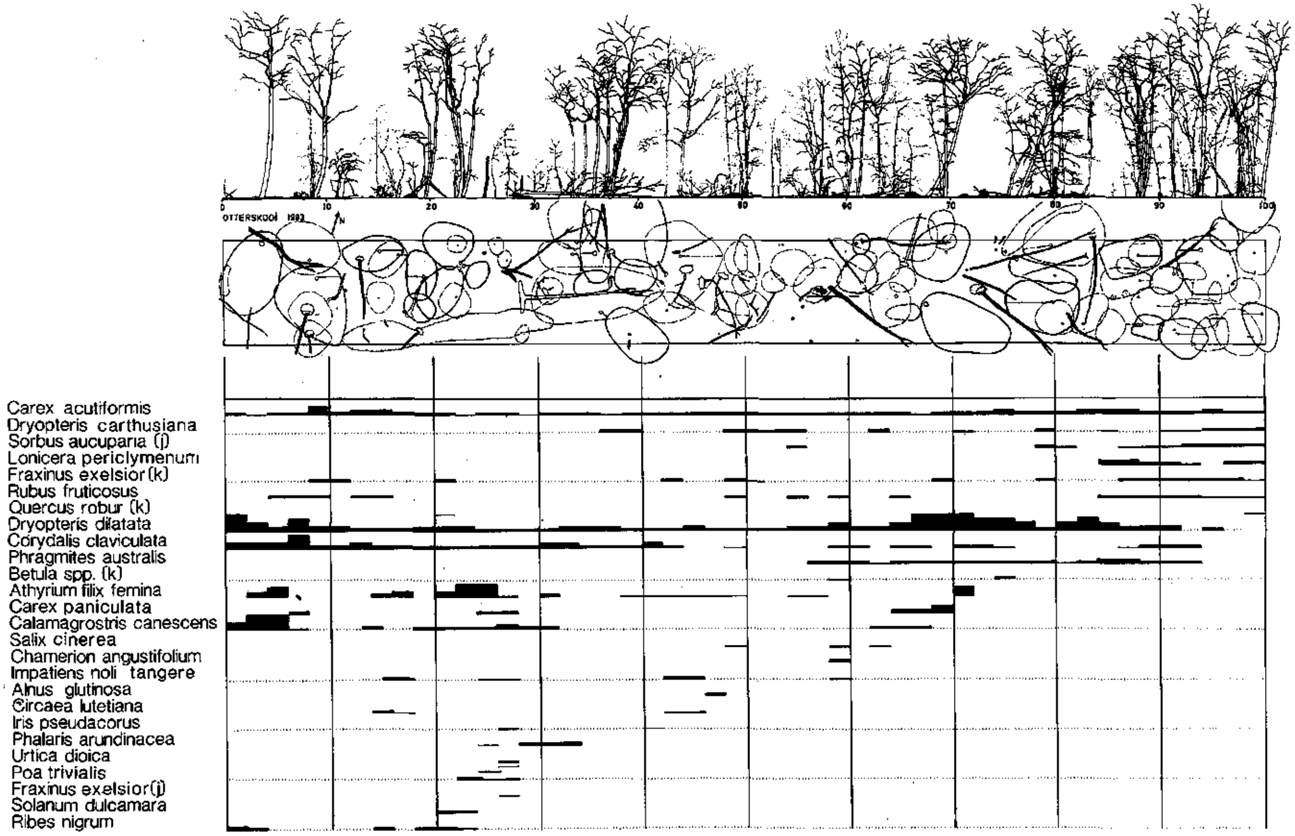

Fig. 1. One-tenth ha transect, blockdiagram indicates species cover in 50 adjacent 2 x 2 m quadrats along the centre line of the transect.

inclusion of fauna data in the system a review of the literature has been carried out (Van der Plaat, 1984). The second phase, i.e., the organization of data storage and retrieval, is making good progress. Data processing and interpretation, the third phase, have been started.

Data collection

A brief description of the data base for the vegetation component already available is given below. For the forest area to be included in the system, data are being collected on three scale levels:

1. One-tenth hectare strip transects
   The tree layer of the fixed transect measuring 10x100 m is characterized in great detail with profile drawings and crown projections. The herbaceous layer is described for fifty adjacent 2x2 m quadrats along the centre line of the transect, using a relevé technique (fig. 1).
2. One-hectare blocks
   To study the interactions between trees and between the tree layer and the herbaceous layer, information on a layer area in addition to the transect data is required. For instance the interception of diffuse light and changing oblique radiation can only be computed if data on all trees within a certain radius are incorporated.
   A larger area is also indispensable for a statistical approach to the risk distribution of toppling of trees due to their position in relation to surrounding trees. A zone with at least one maximum tree-length around the 10x100 m central strip transect in a block up to 70x140 m is therefore charted in the same way as the transect plan (fig. 2). Instead of profile sketches for each tree, height measurements are being made of the top of the crown, its largest width, the crown base, and the first living fork. In addition, a detailed vegetation map of this area on a scale 1:200 is made.

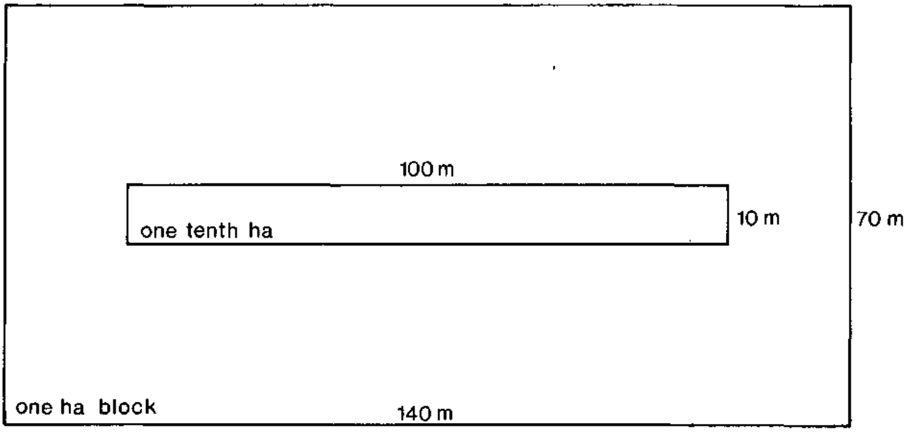

Fig. 2. Transect situated in the middle of the one hectare block.

For the strip transect and the hectare blocks, supplementary characteristics of the trees are noted in the field such as species, tree diameter at breast height, vitality and soundness (using the codes of the IUFRO), growth potential according to Hallé et al. (1978), and crown cover of the individual tree.

3. Ten-hectare blocks
   To monitor and quantify vegetation-pattern changes at the smallest scale level, an area of 10 to 40 ha around the one-hectare block is to be mapped from large scaled aerial photographs (1:1000-1:5000). The spatial patterns of vegetation composition and vegetation structure are drawn. The detailed ground-truth information collected in the strip transects and hectare blocks is used for reference.

The herb-layer analyses (1) will be repeated every two to three years. Major changes in the structure of the tree layer (1 and 2) will also be recorded. New profile and plan sketches may be required on average about every ten years.

Data storage and retrieval

To overcome the limitations set by the two-dimensional images of plan and profile drawings, a three-dimensional forest model has been developed. For computerized data processing all trees are described by coordinates for eight points characterizing tree foot, fork, top and bottom of the tree crown and the four extremities of the crown circumference in positive and negative x- and y-direction. The mentioned coordinates are partly derived from height measurements and further digitized from the hand-drawn plan. The indirect way proved to be better than direct field measurements of coordinates. The hand-drawn plan is the first control in precluding mistakes.

By making use of the ellipsoid character of most deciduous trees a best fitting wrapping can be constructed by connecting the four perifery points of the crown circumference with quarters of ellipses. So the top and the crown base are connected with the perifery points (fig.3).

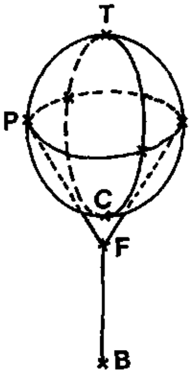

Fig. 3. Tree model consisting of quarters of ellipses on straight lines characterized by eight points: treefoot (B), fork (F), top (T), and bottom (C) of the tree crown and the four extremities of the crown circumference in positive and negative x- and y-direction (P).

In this way a model is constructed consisting of more or less asymmetric rugby balls on straight stems. Coniferous trees with a parabolic or cone like shape are described in the same way, only the perifery points are connected to the top with parabolas or straight lines.
At every height level, the circumscription of the crown is determined

by an other combination of quarters of ellipses that connect the four ellipsoid, parabolic or straight ribs between top or bottom of the crown and the four perifery points.

Data processing and interpretation

Plans and profiles at any place in the one-hectare blocks can be plotted by the computer. Integrated quantitative parameters have been developed and pilot studies are in progress to find relations between the various directly measured or derived parameter values, for example between crown surface and diameter at breast height. Work has begun on the design and testing of simulation models for prediction. For example, the model can be used to find correlation between species composition, occurrence and growth of young trees on the one hand and shading patterns determined by the forest structure on the other. The three-dimensional forest model allows computation of the hemispherical cover for fixed points as an indication of the interception of diffuse light and changing oblique radiation. A cumulative coverage value is computed from all tree crowns of the model that cover a certain angle of the hemisphere. To obtain radiation values the product can be processed in the same way as a fisheye or hemispherical photograph (Ducrey, 1975). These fisheye computations for radiation indication are made for the 50 adjacent relevées at the center of the strip transect or in a grid in the plan or profile to get an impression of horizontal and vertical light gradients. The forest model can be used as a ground-truth to verify charting of tree species and interpretation of vitality and structural characteristics from remote sensing images. An aerial view can be reconstructed from the data collected in the one-hectare blocks or the transects. In a grid for each pixel the height of the upper crown surface is computed and additional characteristics of the individual tree are stored. For the undulating crown surface a shading pattern can be simulated. Orientation and pixel size of the reconstructed aerial view can be chosen equally to that of a digital remote sensing image that covers the plot. The overlapping pixels of the remote sensing image and the reconstructed aerial view can be used for interpretation of pixels beyond the plot. The three-dimensional model contains information for detailed fauna habitat studies. Ornithologists can use the model for calculating relevant structural characteristics for breeding-bird populations. Furthermore the light climate simulation can be used to study the distribution patterns of animals, because radiation is closely related to other microclimatologic characteristics.

The model contains the information needed for simulation of forest dynamics, with the help of gap models of the JABOWA type. However, we hope that this information system will provide more sophisticated simulation models to be developed with detailed data on long-term forest dynamics for verification.

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Posters

METHODS FOR DOCUMENTING SUCCESSION IN FORESTS AS DEVELOPED AND APPLIED IN NATURAL FOREST RESERVES IN SOUTH-WEST GERMANY

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Older methods

Since 1938 the vegetation succession has been monitored in the "Untereck" natural forest reserve (Bannwald) in the Swabian Jura in the West German state of Baden-Württemberg (Bücking, this volume). The methods used are semiquantitative, combining vegetation mapping of small sample areas, plant association relevés after Braun-Blanquet, and maps of tree position; the fieldwork was not arduous.

Forstliche Grundaufnahme

Actual "Forest Survey" in the natural forest reserve (Forstliche Grundaufnahme; Kätzler et al. 1984; Bücking & Reinhardt, 1985) is preceded - as far as topographic conditions allow - by a survey of the reserve during which a one-hectare grid is measured and permanently marked out by boundary stones (fig. 1). The grid supplies an adequate orientation basis for the scientific research being done in the forest reserves, especially for mapping plant communities (Wilmanns, 1977) flora or fauna. Forest records are made in circular plots (radius normally 20 m) or on larger rectangular sample areas (up to one ha): the position of all standing trees, diameter breast height (minimum 4 cm), tree height (circular areas), lying dead trees and further criteria according to IUFRO classification for virgin forest research (Leibundgut, 1959) are recorded. Field data are computerized and the results are plotted and printed (figs. 2, 4; table 1). The circular plots normally lie on the grid intersections, but their position may be shifted in order to ensure sufficient representation of all stand or vegetation and site types and a detailed survey of about 5 - 10% of the reservation area (fig. 4). In each circular plot two small circles (radius 2 m; fig. 5) are designated for counting the regeneration of woody species (seedlings; older trees up to 10 cm, 11 - 50 cm, 51 - 100 cm, 1 m - 1,5 m, taller than 1,5 m; recorded areas amounting to 1 -20%). The plotter can process both site and vegetation characteristics (fig. 6). The actual aspect of each circular plot is shown by means of 360° photography: about 16 photographs are taken from the exact centre of the plot, beginning in the north and proceeding clockwise and overlapping (normal lens pictures, f = 50 mm). The most important vegetation and stand types are drawn by computer in stand profile transects directly from the field data (crown projections (greatest breadth of crown), projection of crown top, height of tree, diameter breast height, position of trees, slope of site). Trees are modelled by means of 4 quarters of ellipses (broadleaved trees, pine, white fir; fig. 8, from Weishaar) or triangular forms (spruce; fig. 9).

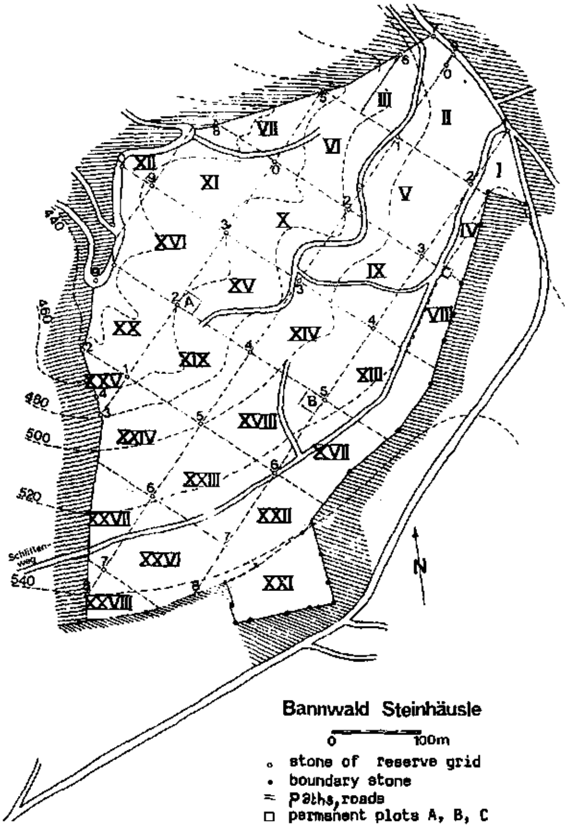


Fig. 1. Survey of a forest reserve. 1 ha grid, numbers of ha squaers.

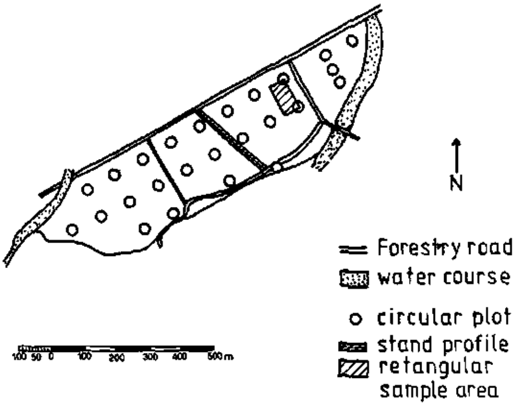
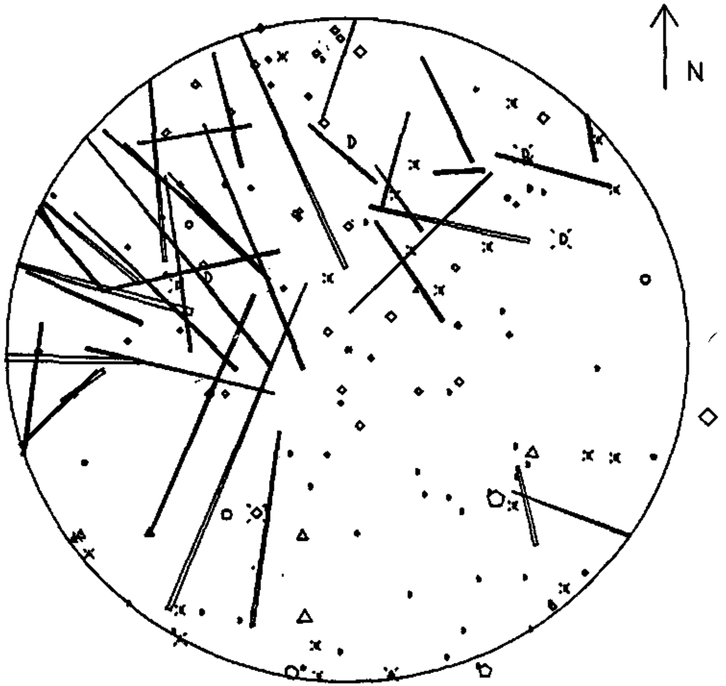


Fig. 2. Locations of circular plots, larger rectangular sample area and stand profile transect within a forest reserve, showing the relation between area studied and total area.

BANNWALD UNTERECK

circular plot No.3



radius : 20.00 m^2
area : 0.126 ha
(all data related to 1 ha)
basal area : 26.9 m (dead trees included)
number of stems : 1019 (" " ")
basel area : 32.2 m^2 (without dead trees)
number of stems : 812 (" " ")

* * * * * * * * * * *

lying trees : 39 (altogether)
lying trees : 38 (dead)

* * * * * * * * * * *

date of survey : 18.05.1983
surveyed by : Reinhardt/Gross/Deichner

Fig. 3. Plotter drawing of circular plot No. 3 from "Untereck" natural forest reserve.

Table 1. Computed data from circular plot No. 3 from "Untereck" forest reserve. Tree species: Bu beech, BAh sycamore, Es common ash, Fi spruce, Ta white fir, Ul mountain elm.

PROBEKREIS NR. 3

Oberschicht:

Baum	STAMMZAHL pro ha				GRUNDFLAECHE pro ha						BHD(Grdfl)		Hoehe
art	insgesamt		duerr		insgesamt		gruen		duerr		gruen	duerr	arith
	Stck	(%)	Stck	(%)	qm	(%)	qm	(%)	qm	(%)	cm	cm	m
Bu	8	2	0	0	1.6	8	1.6	100	0.0	0	51.0	0.0	30.0
BAh	56	17	8	14	5.0	26	4.8	96	0.2	4	35.9	19.0	25.5
ES	223	67	0	0	9.5	48	9.5	100	0.0	0	23.3	0.0	22.5
Fi	24	7	0	0	1.7	9	1.7	100	0.0	0	30.0	0.0	25.2
Ta	24	7	8	33	1.9	10	1.4	73	0.5	27	33.5	29.0	27.2
Sa.	334	100	16	5	19.8	100	19.0	96	0.8	4	27.6	24.5	23.6

Mittelschicht:

Baum	STAMMZAHL pro ha				GRUNDFLAECHE pro ha						BHD(Grdfl)		Hoehe
art	insgesamt		duerr		insgesamt		gruen		duerr		gruen	duerr	arith
	Stck	(%)	Stck	(%)	qm	(%)	qm	(%)	qm	(%)	cm	cm	m
Bu	24	9	0	0	0.1	2	0.1	100	0.0	0	6.8	0.0	11.0
BAh	24	9	24	100	0.5	11	0.0	0	0.5	100	0.0	15.9	
UL	8	3	0	0	0.1	1	0.1	100	0.0	0	9.0	0.0	9.3
ES	103	37	16	15	1.9	47	1.3	66	0.7	34	13.6	22.8	15.4
Fi	16	6	0	0	0.4	9	0.4	100	0.0	0	17.6	0.0	12.0
Ta	103	37	40	38	1.2	29	0.8	64	0.4	36	12.4	11.9	9.5
Sa.	279	100	80	29	4.1	100	2.6	62	1.6	38	12.8	15.8	12.1

Unterschicht:

Baum	STAMMZAHL pro ha				GRUNDFLAECHE pro ha						BHD(Grdfl)		Hoehe
art	insgesamt		duerr		insgesamt		gruen		duerr		gruen	duerr	arith
	Stck	(%)	Stck	(%)	qm	(%)	qm	(%)	qm	(%)	cm	cm	m
BAh	8	2	0	0	0.0	1	0.0	100	0.0	0	8.0	0.0	6.0
UL	8	2	0	0	0.0	0	0.0	100	0.0	0	5.0	0.0	
ES	80	20	0	0	1.1	31	1.1	100	0.0	0	13.3	0.0	5.8
Fi	16	4	0	0	0.0	1	0.0	100	0.0	0	4.0	0.0	2.0
Ta	294	73	111	38	2.4	67	0.8	35	1.5	65	7.6	13.2	5.7
Sa.	406	100	111	27	3.6	100	2.0	57	1.5	43	9.4	13.2	5.5

SUMME:

Baum	STAMMZAHL pro ha				GRUNDFLAECHE pro ha						BHD(Grdfl)		Hoehe
art	insgesamt		duerr		insgesamt		gruen		duerr		gruen	duerr	arith
	Stck	(%)	Stck	(%)	qm	(%)	qm	(%)	qm	(%)	cm	cm	m
Bu	32	3	0	0	1.7	6	1.7	100	0.0	0	26.2	0.0	15.8
BAh	88	9	32	36	5.6	20	4.9	87	0.7	13	33.3	16.7	22.7
UL	16	2	0	0	0.1	0	0.1	100	0.0	0	7.3	0.0	9.3
ES	406	40	16	4	12.5	46	11.9	95	0.7	5	19.7	22.8	19.7
Fi	56	5	0	0	2.1	8	2.1	100	0.0	0	21.9	0.0	14.8
Ta	422	41	159	38	5.5	20	3.0	55	2.5	45	12.1	14.1	8.1
Sa.	1019	100	207	20	27.5	100	23.6	86	3.8	14	19.3	15.4	15.1

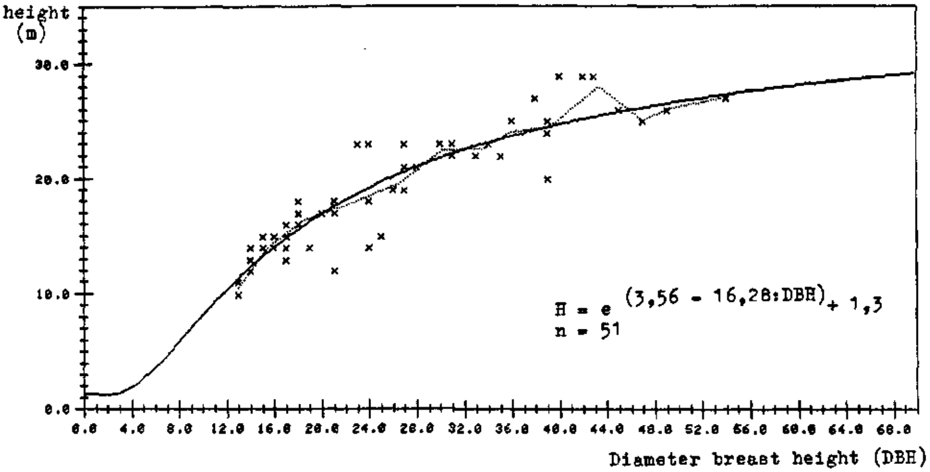


Fig. 4. Stand height curve of spruce (Picea abies) from the "Waldmoor-Torfstich" Black Forest reserve.

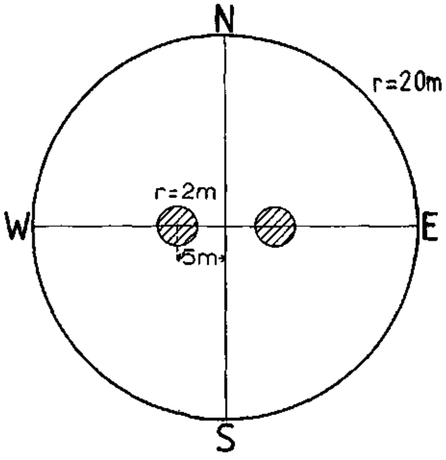


Fig. 5. Circular plot (r= 20 m), position of circular regeneration plots (r= 2 m) within the larger circular area.

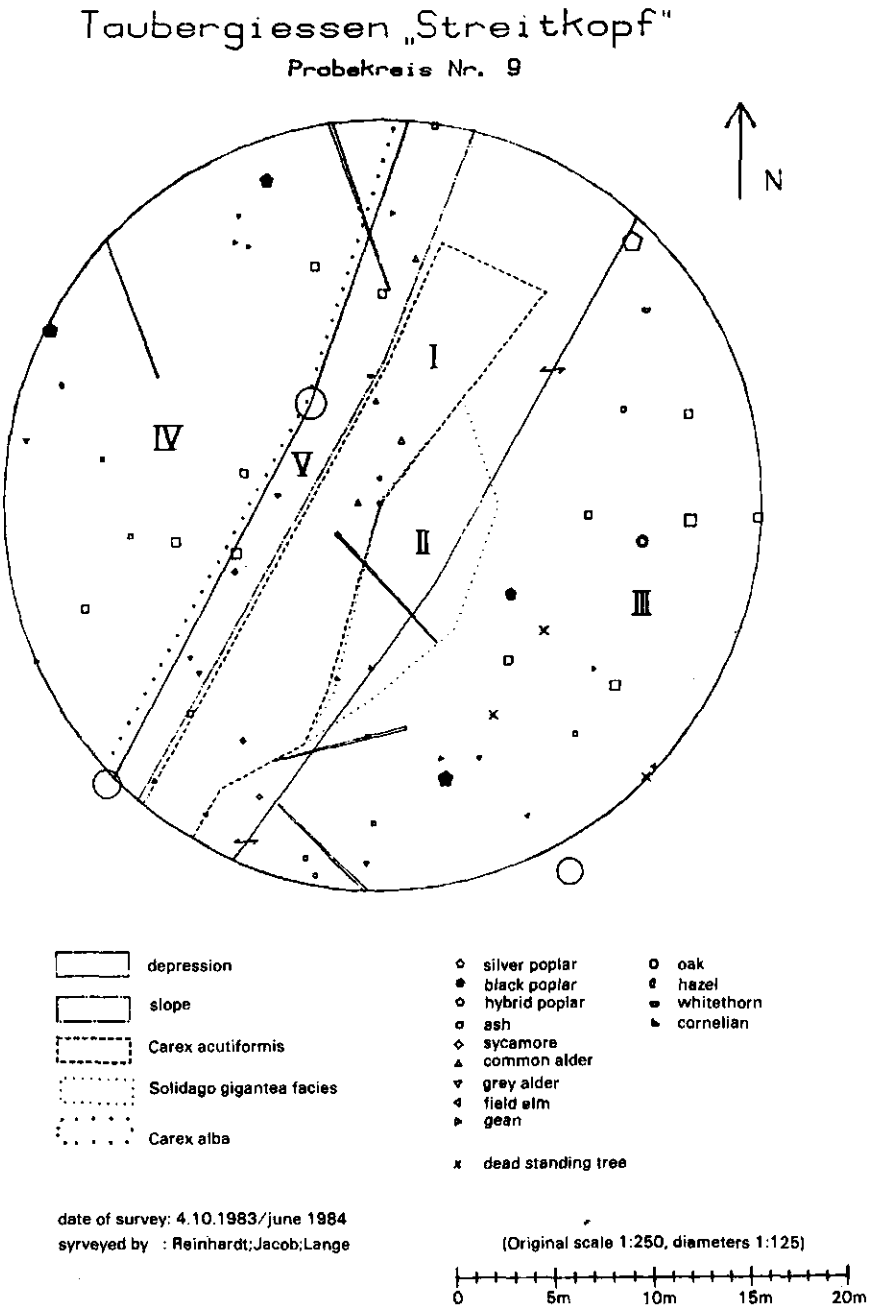


Fig. 6. Circular plot from "Taubergiessen" natural forest reserve, a Querco-Ulmetum stand in the ancient Rhine valley, in earlier times regularly inundated, showing position of trees according to figure 2, limites of vegetation and surface morphology (depression, slope). I Carex acutiformis, II Solidago gigantea facies, III dominant shrub layer, IV Carex alba facies, V Zone of transition (slight slope).

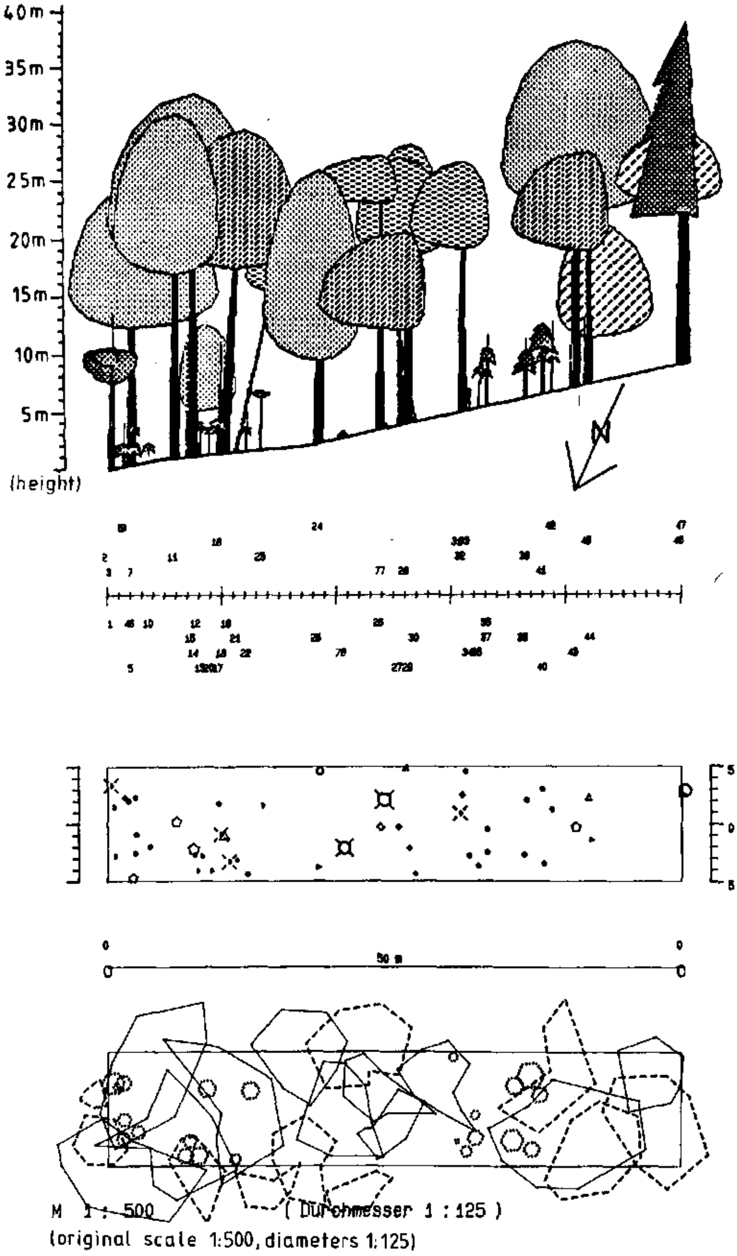


Fig. 7. Stand profile transect and crown projection from "Untereck" natural forest reserve. Above: stand profile; middle: numbers of trees; below: position of trees. Trees are indicated by their diameter breast height; in the lowest diagram: crown projection ---- upper story, - - - - middle story (>1/3 - <2/3 of stand height), ... lower story (<1/3 of stand height).

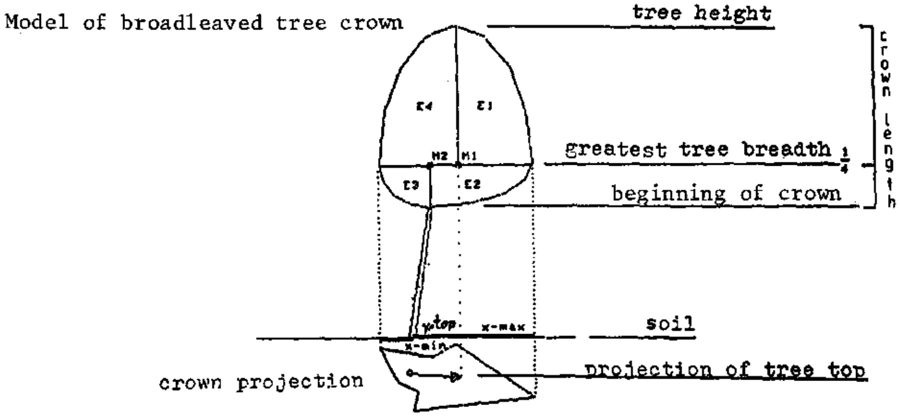


Fig. 8. Model of broadleaved tree crown. Broadleaved tree crown is modelled by means of 4 quarters of ellipses (E_1, E_2, E_3, E_4). E_1 and E_4 are centred in M_1, E_2 and E_3 in M_2. Line of greatest crown breadth is fixed at one-quarter of the crown length. The lowest green branch of crown diameter is represented as the greatest crown width to the East (x-max) and to the West (x-min); inclination of stem is derived from the projection of the tree top (x-top) and the tree position on the ground. White fir crowns are modelled in the same way, but with line of greatest crown breadth at 3/4 of crown length.

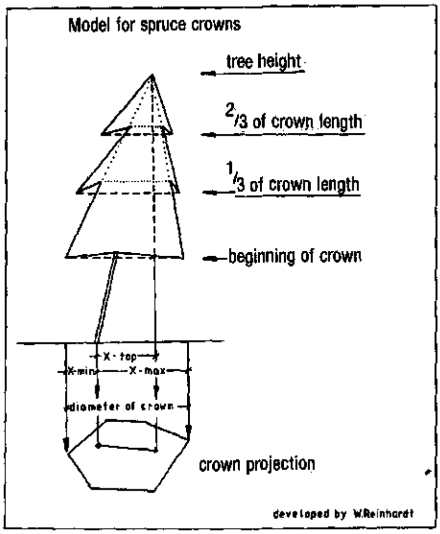


Fig. 9. Model of spruce crowns. Spruce crown is modelled by 6 overlapping triangles, corresponding to: the area from the tree top to the beginning of the crown; and from tree top to 1/3 and to 2/3 of crown height, respectively (black lines and hatched lines). In order to give a more realistic impression of spruce crown, the basal crown perimeter dips by 0.5 m, imitating the hanging down of spruce branches, and at 1/3 and 2/3 of crown small triangles, whose form is modelled from another set of triangles (dotted lines) are removed. All peripheral triangular points together form crown outline, which is finally filled in by the typical for spruce.

The method described will be applied to all 43 protected areas, which cover about 1650 ha; to date 17 reserves (about 900 ha) are already being studied or worked at. Surveys will be repeated every 10 to 20 years in order to ensure the continuity of succession research.

Acknowledgement: Some research presented here was financially supported by the German Research Community (DFG).

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SIMULATION OF GROWTH IN EVEN-AGED STAND OF DOUGLAS FIR

G.M.J. Mohren

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Wageningen, The Netherlands

Aim

Study of the influence of climate, hydrology, and species characteristics on forest stand growth, using a deterministic simulation model. Estimation of nitrogen and phosphorus demands of a forest stand in different production situations.

Method

- Simulation of canopy photosynthesis as determined by weather (temperature), radiation and ambient (CO_2 concentration), photosynthetic performance of the needles, and canopy structure (which determines interception of photosynthetic active radiation), using a simplified multilayer canopy model.
- Simulation of water availability in the root zone by keeping track of soil moisture. Transpiration is calculated using the Penman combination equation, with the canopy resistance determined by either canopy photosynthesis or by needle water potential. The effect that results in the highest canopy resistance determines the value for the resistance used in the transpiration model. Root uptake is determined by transpiration and available moisture in the root zone. If soil moisture approaches the wilting point, needle water potential drops, stomata close, and transpiration decreases. Stomatal closure induced by water shortage limits CO_2 uptake and decreases total canopy photosynthesis. Soil moisture is replenished by net precipitation reaching the forest floor, after canopy interception is accounted for. Canopy interception is calculated from storage capacity (determined by needle- and branch area index) and the magnitude and number of rainfall events.
- Estimation of net increment from gross canopy photosynthesis by taking into account maintenance and growth respiration. Maintenance respiration depends on the composition of the living tissue (notable protein content), growth respiration is related to the conversion of assimilates to structural dry matter and depends on the biomass formed. Net increment is distributed over needles, branches, stems and roots.
- Conversion of stem dry weight increment to volume increment, and distribution of volume increment over the individual trees, according to their competitive status in the stand.
- Estimation of nitrogen and phosphorus demand based on minimum and maximum tissue concentrations and by taking into account internal recycling.

Evaluation of the model performance is done by comparing simulation results with measurement series from permanent field plots.

For simulation of stand growth over a large period (50 - 100 yrs.), a thinning routine is applied which changes stand structure by removing a pre-set number of trees. Weather variables consist of daily values for temperature, radiation, vapour pressure, windspeed and precipitation. In case of long term simulations, daily input values are generated from monthly means.

Mohren, G.M.J., C.P. van Gerwen, C.J.T. Spitters, 1984. Simulation of primary production *in* even-aged stands of Douglas fir. Forest Ecology and Management, 9: 27-49.

Appendices

Appendix 1

PROPOSED DEFINITIONS FOR SOME TERMS IN FOREST DYNAMICS RESEARCH

Forest dynamics

Any change in time in vegetation (mainly in structure and in floristic composition), fauna, mycetes and/or soil in a forest stand. (All steady state processes are therefore excluded).

For theoretical and practical purposes, forest dynamics can be divided into four phenomena, which all take place simultaneously and at all spatial levels, but at different rates in time:

1. *Periodicity*
2. Fluctuations
3. Succession
4. Evolution

1. Periodicity

Regular, reversible quantitative changes, not affecting species composition, caused by the diurnal and annual rhythm of the weather, e.g. nocturnal flowering and folding of leaves, diurnal vertical migration of animals, seasonal aspects of tree and herb layer and of fungal synusiae.

2. Fluctuations

Irregular (stochastic), reversible, quantitative changes in the forest vegetation, fauna and soil e.g. shifts in dominance in the shrub, herb or moss layers owing to severe winters, very dry summers, spring flooding, insect plagues and diseases.

3. *Succession*

Directional changes in species composition of vegetation, mycetes and fauna can occur because of changes in environment (including climate and human factors). This is called allogenic (exodynamic, exogeneous) succession. Directional changes can also occur because of internal vegetation processes. This is called autogenic (endodynamic,endogeneous) succession.

Note: in every succession internal processes play a role, so there are no purely allogenic successions,only mixed and autogenic ones. The distinction between progressive, retrogressive(retrograde) and discessive succession is very important. The first leads to more complex, more stable communities with greather biomass, the retrograde successions have the opposite trend, and the discessive are neither progressive nor retrograde.

Successions may also be divided into primary and secondary, reversible and irreversible, linear and cyclic, natural and anthropogenic succession, or into "short-term" and secular successions. The latter are caused by geological processes, such as changes in macroclimate, or transgressions and regressions of the sea. Not to be confused with:

4. Evolution

A forest community evolves through the evolution or co-evolution of its component species and to other historical processes such as the immigration or extinction of species.

The time scale of periodicity is from one day to one year, that of fluctuations is from several years to decades, that of "short-term" successions is from decades to centuries, that of secular successions is from thousands to ten thousands of years, and that of evolution is millions of years.

The working group on Forest Dynamics proposes to concentrate on the middle part of the time scale i.e. on fluctuations and short-term successions.

Appendix 2

The workshop proposed to reprint the standard symbols used in forest mensuration to avoid possible confusions in mathematical modelling of forest succession.

On the next pages, the relevant letter of the IUFRO secretariat is reprinted, followed by the complete reprint of "The standardization of symbols in forest mensuration" published by IUFRO in 1959.

For more details in using statistical symbols see:

ISO Standards Handbook 3(1981) - Statistical Methods, 2nd ed. Int. Organization for Standardization, Geneve. ISBN 92 67 10054-8.

UNION INTERNATIONALE DES INSTITUTS
DE RECHERCHES FORESTIERES

INTERNATIONALER VERBAND FORSTLICHER
FORSCHUNGSANSTALTEN

IUFRO
Sekretariat
INTERNATIONAL UNION OF FORESTRY RESEARCH ORGANIZATIONS

Dr. J. Fanta
Research Institute for Forestry
and Landscape Planning "DeDorschkamp"
P.O. Box 23
NL-6700 AA Wageningen
Netherlands

Vienna/Vienne/Wien, February 27, 1986

Dear Dr. Fanta,

Referring to your letter of February 5, 1986, I am pleased to inform you that this letter is the permission to reprint mathematical and statistical symbols officially used by IUFRO in our publication 1959. This permission is exclusively for the proceedings of your workshop, September 1985 and connected with the request that the source (our publication from 1959) is mentioned in the proceedings.

There is no other IUFRO publication is this field.

Yours sincerely,

Otmar Bein

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INTERNATIONAL UNION OF FOREST RESEARCH ORGANIZATIONS

UNON INTERNATIONALE DES INSTITUTS DE RECHERCHES FORESTIERES

INTERNATIONALER VERBAND FORSTLICHER FORSCHUNGSANSTALTEN

The standardization of symbols in forest mensuration

Die Normung holzmesskundlicher Symbole

La Normalisation des Symboles dans les mesures forestières

1959

FOREWORD

The recommendations on the standardization of symbols in forest mensuration, which are given in this report, have been made by a small working group in Section 25 of the International Union of Forest Research Organizations which was appointed at the Congress of the Union held in Rome in 1953. Members of the group were asked to enquire into the possibility of standardizing the use of symbols (and the systems of measurement) in forest mensuration and to make recommendations. This they have now done and their report is being issued for the close consideration of Member Institutes and others interested in the subject.

The Union is indebted to the Section Leaders, Professor Dr. Y. Ilvessalo and his successor Professor Dr. Fehim Firat, for the encouragement they have given and particularly to the members of the working group, Ir. J. van Soest (Chairman), Monsieur P. Ayral, Professor Dr. R. Schober and Dr. F. C. Hummel (Secretary), for the efforts they have made to bring their study to a successful conclusion.

J. Macdonald, President.
H. van Vloten, Vice President.

A limited number of copies are available for sale to Non-Members of the Union at a price of two shillings per copy. Applications for them should be made to the President, International Union of Forest Research Organizations, c/o Forestry Commission, 25, Savile Row, London, W.1.

PREFACE

Les recommandations sur la normalisation des symboles dans les mesures forestières, qui sont données dans ce rapport, ont été faites par un petit groupe de travail de la Section 25 de l'Union Internationale des Instituts de Recherches Forestières, constitué lors du Congrès de l'Union tenu à Rome en 1953. On avait demandé aux Membres du Groupe d'examiner la possibilité de normaliser l'usage des symboles (et des systèmes de mesure) dans les mensurations forestières et de faire des recommandations. Leur travail est maintenant terminé et leur rapport est publié pour qu'il puisse être pris en considération par les Instituts-Membres et par les autres personnes qui s'intéressent à ce sujet. L'Union tient à remercier les Président de Section, M. le Prof. Dr. Y. Ilvessalo et son successeur M. le Prof. Dr. Fehim Firat, pour l'encouragement qu'ils ont donné, et tout spécialement les Membres du Groupe de Travail, M. l'Ingénieur J. van Soest (President), M. le Conservateur P. Ayral, M. le Prof. Dr. R. Schober et M. le Dr. F. C. Hummel (Secrétaire), pour les efforts qu'ils ont fait pour mener à bien leur étude.

J. Macdonald, Président
H. van Vloten, Vice-Président

Un nombre limité de copies peuvent être vendues aux non-Membres de l'Union au prix de deux shillings par exemplaire. Demande à adresser au Président de l'Union Internationale des Instituts de Recherches Forestières, c/o Forestry Commission, 25, Savile Row, London, W.1.

VORWORT

Die Vorschläge für die Normung holzmesskundlicher Symbole, welche in dieser Empfehlung gemacht werden, sind von einer kleinen Arbeitsgruppe der Sektion 25 des Internationalen Verbandes förstlicher Forschungsanstalten zusammengestellt worden. Die Arbeitsgruppe wurde während des I.U.F.R.O. Kongresses in Rom im Jahre 1953 gebildet. Die Arbeitsgruppe wurde gebeten, die Möglichkeit der Normung der Symbole und der Methoden der Holzvermessung zu untersuchen und Vorschläge dazu zu machen. Die Ausarbeitung solcher Vorschläge ist jetzt abgeschlossen und wird in Form eines Berichtes mitgeteilt. Dieser Bericht wird zur Anwendung durch die Mitgliederinstitute und andere hieran interessierte Forscher empfohlen.

Der Verband ist dem Sektionsvorstand, Herrn Professor Dr. Ilvessalo und seinem Nachfolger Herrn Professor Dr. Fehim Firat zu Dank verpflichtet für die Anregungen, die sie gegeben haben und insbesondere auch den Mitgliedern der Arbeitsgruppe, Herrn Ir J. van Soest (Vorsitzender), Herrn P. Ayral, Herrn Professor Dr. R. Schober und Herrn Dr. F. C. Hummel (Sekretär) für ihre Mühe, ihre Beratungen und Entwürfe erfolgreich zum Abschluss zu bringen.

J. Macdonald, Präsident
H. van Vloten, Vize-Präsident

Eine begrenzte Zahl Exemplare sind zu erwerben durch die Nichtmitglieder des Verbandes zum Preise von zwei brit. Schilling pro Exemplar. Anmeldungen hierzu erbeten an den Präsidenten des Internationalen Verbandes forstlicher Forschungsanstalten, c/o Forestry Commission, 25, Savile Row, London, W.1.

RECOMMENDATIONS ON THE STANDARDIZATION OF SYMBOLS IN FOREST MENSURATION

Prepared by

J. VAN SOEST, P. AYRAL, R. SCHOBER and F. C. HUMMEL

INTRODUCTION

The present proposals relate to the standardization of symbols, and were agreed at a meeting of the working group at Wageningen on October 26 and 27, 1954. These proposals were then circulated to all members of I.U.F.R.O. and not only to members of Section 25 who are most immediately concerned with forest mensuration, because mensurational symbols frequently occur in other forest literature as well. The proposals were submitted for discussion and approval at the I.U.F.R.O. congress at Oxford in July, 1956, and, after a few minor modifications, were accepted at a meeting of Section 25.

The working party considered that the main object of standardizing symbols is to make it as easy as possible for readers to understand what an author has to say, particularly when a paper is published in a language foreign to the reader.

GENERAL CONSIDERATIONS

In making these recommendations on the standardization of symbols, several conflicting interests had to be considered and reconciled, of which the most important ones were:

1. symbols should be easy to remember; they must be simple and there must *not* be too many;
2. they should be easy to reproduce on a typewriter and in print;
3. they should not conflict with mathematical or other symbols commonly found in forest literature;
4. symbols which have already become well-established internationally should not be altered if possible;
5. symbols should have precise meanings.

This last point is particularly difficult to reconcile with the others, and especially with the need to keep symbols simple and to restrict their number. The working group considered that the most satisfactory solution is to distinguish between three types of symbols and to prepare a separate list for each, i.e.:

1. a list of general forestry symbols in which very simple symbols are used, the precise definition of which in a particular context is left to the author to explain (preferably in a separate appendix, see recommendation number 4). The use of these general symbols is adequate in publications where a particular symbol, e.g. f for form factor, is used in exactly the same sense throughout, all form factors being based on the same methods of measurement and having been calculated in the same way;
2. a second list, offering suggestions on how the symbols given in the general list can be expanded, if necessary, e.g. when several types of form factor are being compared in a paper;

3. a third list giving mathematical and statistical symbols which are already used internationally among mathematicians and are commonly needed in forest literature. This list has been prepared by Mr. J. N. R. Jeffers of the British Forestry Commission. The working group wishes to acknowledge its indebtedness to Mr. Jeffers for his important contribution to the work.

A slight overlap between lists 1 and 3 could only have been avoided by changing symbols, which have become well-established internationally. In cases where the risk of confusion was considered small, the continued use of one symbol for two purposes was considered preferable to a change; for example, f is given as *form factor* in the first list and as *frequency* in the third.

General recommendations

In using symbols *the author should consider it his main object to make it as easy as possible for his readers to understand what he has to say.* The recommendations which follow are intended to assist authors to achieve this object.

There may, however, be exceptional cases *where the strict observance of these recommendations would be a hindrance rather than an aid to the achievement of this object; and in these cases a departure from the recommendations is not only justified, but even desirable.*

Specific recommandations

1. The general mensurational symbols given in appendix 1, should be used as far as possible.
2. When an elaboration of the symbols given in appendix 1 becomes necessary, this should be done in one of two ways:
   (a) either the symbols listed in appendix 2 should be used, for example $i_{d\ 21\text{-}40}$ to denote the total diameter increment of a tree between the ages of 21 and 40 years

   or

   (b) primes or numerical subscripts may be added to the symbols given in appendix 1, in the above example i' or i_1 instead of $i_{d\ 21\text{-}40}$. The more complicated but more descriptive symbols of alternative (a) will be preferable when the number of symbols is large, but each symbol occurs infrequently, while the use of primes and numerical subscripts (alternative (b)) is preferable when the number of symbols is small but each recurs many times. Elaborate symbols are a particular disadvantage in complicated mathematical formulae.
3. In mathematical and statistical calculations, the symbols given in appendix 3 should be used, in conjunction with, or instead of, the symbols given in appendices 1 and 2.
4. All publications in which more than a small number of symbols occur, should have a list of symbols giving precise definitions in a separate appendix, apart from any explanations that may be given in the text. In some instances the definition should also include a clear statement of how the

factor represented by a symbol was arrived at, e.g., in the case of a form factor it is necessary to state not only whether it is a natural or an artificial form factor, but also whether the volume from which it is calculated is over bark or under bark, whether the volume was measured to a specified diameter limit or not, whether it is stem-wood alone or whether branch-wood is included, and finally whether or not the volume was measured by sections.

RECOMMANDATION SUR LA NORMALISATION DES SYMBOLES DANS LES MESURES FORESTIERES

préparé par

J. VAN SOEST, P. AYRAL, R. SCHOBER et F. C. HUMMEL

INTRODUCTION.

Les présentes propositions sont relatives à la normalisation des symboles et résultent d'un accord réalisé entre les membres du groupe de travail lors d'une réunion à Wageningen les 26 et 27 octobre 1954. Ensuite, ces propositions ont été envoyées à tous les membres de l'I.U.F.R.O. et non pas seulement aux membres de la Section 25, qui utilisent le plus les mensurations dans les recherches forestières, car des symboles de mesures se trouvent fréquemment employés dans toute la littérature forestière. Les propositions ont été ensuite soumises pour discussion et approbation au dernier congrès de l'I.U.F.R.O. à Oxford en juillet 1956, et, avec quelques changements secondaires, ont été adoptées lors d'une réunion de la Section 25.

Le groupe de travail estime que l'objet principal de cette normalisation est de faciliter la compréhension des auteurs par les lecteurs et tout spécialement quand une oeuvre est publiée dans une langue étrangère au lecteur.

CONSIDERATIONS GENERALES.

La préparation de ces propositions pour la normalisation des symboles a fait apparaître qu'il était nécessaire de considérer et de concilier différents principes plus ou moins contradictoires, dont les plus importants sont :

1. *Les symboles doivent être faciles à retenir, c'est-à-dire qu'ils doivent être simples et qu'il ne doivent pas être trop nombreux.*
2. *Ils doivent être faciles à reproduire par une machine à écrire et à imprimer.*
3. *Ils ne doivent pas être en contradiction avec des symboles mathématiques ou avec d'autres symboles, couramment employés en littérature forestière.*
4. *Les symboles qui ont déjà un caractère international ne doivent pas être changés, quand celà est possible.*
5. *Les symboles doivent avoir des significations précises.*

Ce dernier point est particulièrement difficile à concilier avec les autres et spécialement avec la nécessité d'adopter des symboles simples et peu nombreux. Le groupe de travail a émis l'opinion que la solution la plus satisfaisante était de distinguer trois types de symboles et de préparer une liste pour chacun, à savoir :

1. *Une liste de symboles forestiers généraux, dans laquelle des symboles très simples sont employés et dont la signification exacte dans une communication particulière doit être expliquée par l'auteur (de préférence dans un appendice, voir recommandation numéro 4). L'usage de ces symboles généraux est tout indiqué dans des communications où un symbole particulier, par exemple f pour coefficient de forme, est employé continuellement dans le même sens, parce que tous les coefficients de forme sont basés sur les mêmes méthodes de mesurage et calculés de la même manière.*
2. *Une deuxième liste, proposant une méthode pour préciser les symboles donnés dans la liste générale, quand cela est nécessaire, par exemple quand des types différents de coefficients de forme sont comparés dans une communication.*
3. *Une troisième liste de symboles mathématiques et statistiques qui sont déjà d'un emploi international chez les mathématiciens et qui sont utilisés couramment dans la littérature forestière. Cette liste a été préparée par M. J. N. R. Jeffers de la British Forestry Commission. Le groupe de travail tient à remercier M. Jeffers pour son importante contribution à ce travail.*

Un certain chevauchement entre les listes 1 et 3 ne pourrait être évité qu'en changeant des symboles, qui ont déjà un usage international. Dans des cas où le risque d'erreur a été considéré comme minime, on a préféré continuer à employer un même symbole pour deux objets plutôt que de changer de symbole ; par exemple f a été adopté comme coefficient de forme *dans la première liste, et comme* fréquence *dans la troisième.*

RECOMMANDATIONS GENERALES.

En utilisant les symboles, l'auteur a pour but principal d'essayer de rendre aussi facile que possible à ses lecteurs la compréhension de ce qu'il veut dire. *Les recommandations suivantes doivent aider les auteurs à atteindre cet objet.*

Cependant, il y a peut-être des cas exceptionnels où l'observation stricte de ces recommandations serait plus une gêne qu'une aide pour arriver à cet objet; et dans ces cas une modification des propositions n'est pas seulement justifiée, mais elle est même désirable.

RECOMMANDATIONS PARTICULIERES.

1. *Les symboles généraux donnés dans l'annexe 1 doivent être utilisés autant qu'il est possible.*
2. *Quand une précision des symboles cités dans l'annexe 1 sera nécessaire, elle devra être apportée d'une des deux manières suivantes :*
    (a) ou bien les symboles indiqués dans l'annexe 2 doivent être employés, par exemple $d_{21\text{-}40}$ *pour indiquer l'accroissement total du diamètre d'un arbre entre les âges de 21 et 40 ans.*

(b) ou bien des accents ou des indices peuvent être ajoutés aux symboles donnés dans l'annexe 1 ; dans l'exemple cité ci-dessus on écrirait i' *ou* i_1*, au lieu de* $i_{d\,21\text{-}40}$. *Les symboles plus compliqués mais plus parlants de la solution (a) seront préférables quand le nombre de symboles utilisé est grand, mais chaque symbole étant employé peu souvent. Au contraire, l'usage des accents et indices de la solution (b) est préférable quand le nombre des symboles est petit mais chaque symbole revenant alors plusieurs fois. Les symboles complexes sont particulièrement désavantageux dans des formules mathématiques compliquées.*

3. *Dans les calculs mathématiques et statistiques, les symboles, donnés dans l'annexe 3 doivent être utilisés en combinaison avec ou à la place des symboles, cités dans les annexes 1 et 2.*
4. *Toutes les communications dans lesquelles se trouvent un nombre de symboles assez important, doivent être accompagnées d'une liste de symboles donnant leur définition précise, dans une annexe en plus des autres explications éventuellement données dans le texte. Dans certains cas, la définition doit également expliquer comment on a calculé le facteur, représenté par un symbole ; par exemple dans le cas d'un coefficient de forme, il est nécéssaire non seulement de préciser si c'est un coefficient de forme naturel ou artificiel, mais encore si le volume à partir duquel il est calculé est un volume sur ou sous écorce, si le volume a été mesuré jusqu'à une limite de diamètre donné ou non, s'il ne s'agit que de bois de tige ou si le bois de branches y est compris, et finalement si le volume a été mesuré par tronçons ou non.*

VORSCHLÄGE FÜR DIE NORMUNG HOLZMESSKUNDLICHER SYMBOLE

ausgearbeitet von

J. VAN SOEST, P. AYRAL, R. SCHOBER und F. C. HUMMEL

EINLEITUNG

Die gegenwärtigen Vorschläge behandeln die Normung von Symbolen ; sie wurden auf einer Tagung der Arbeitsgruppe in Wageningen am 26. und 27. Oktober 1954 vereinbart und anschliessend nicht nur den an der Holzmesskunde unmittelbar interessierten Mitgliedern der Sektion 25, sondern allen Verbandsmitgliedern zugesandt, da ja Messungssymbole häufig auch auf anderen Gebieten des forstlichen Schrifttums verwendet werden. Die Vorschläge wurden dem I.U.F.R.O.-Kongress in Oxford im Juli 1956 zur Diskussion und Beschlussfassung vorgelegt und mit einigen geringfügigen Änderungen auf einer Sitzung der Sektion 25 angenommen.

Die Arbeitsgruppe sah den Hauptzweck der Symbol-Normung darin, dem

Leserkreis die Ausführungen eines Verfassers so leicht verständlich wie möglich zu machen, besonders für Arbeiten, die in einer dem Leser fremden Sprache erscheinen.

ALLGEMEINE ERWÄGUNGEN

In der Ausarbeitung der gegenwärtigen Vorschläge mussten verschiedene einander widerstrebende Interessen berücksichtigt und gegenseitig abgestimmt werden ; die wichtigsten waren :

1. Die Symbole sollen sich dem Gedächtnis leicht einprägen, also einfach und nicht zu zahlreich sein ;
2. sie sollen auf der Schreibmaschine und im Druck leicht wiederzugeben sein ;
3. sie sollen nicht im Widerspruch stehen zu den in der forstlichen Literatur allgemein verwendeten mathematischen oder anderen Symbolen ;
4. Symbole, die sich schon im internationalen Gebrauch eingebürgert haben, sollen möglichst nicht geändert werden ;
5. Die Symbole sollen scharf umrissene Bedeutungen haben.

Besonders schwierig ist es, diesen letzten Punkt mit den vorangehenden in Einklang zu bringen, vor allem mit der Notwendigkeit einfacher und zahlenmässig beschränkter Symbole. Die Arbeitsgruppe hielt es für die zweckmässigste Lösung, drei verschiedene Symboltypen herauszuarbeiten und dementsprechend für jeden Typ eine Sonderliste zu erstellen, nämlich

1. eine Liste allgemeiner forstlicher Symbole unter Verwendung sehr einfacher Zeichen, deren genaue Umschreibung im speziellen Zusammenhang dem Verfasser überlassen wird (vorzugsweise in einem besonderen Anhang siehe Vorschlag Nr. 4). Diese allgemeinen Symbole genügen zum Gebrauch in Veröffentlichungen, in denen ein spezielles Symbol, z.B. *f* für Formzahl, durchlaufend in genau gleichem Sinne gebraucht wird, da alle erwähnten Formzahlen auf denselben Messungsmethoden und derselben Berechnungsweise beruhen.
2. eine zweite Liste mit Vorschlägen zu einer evtl. notwendigen Ergänzung der Symbole der allgemeinen Liste, z.B. in Fällen, in denen in einer Arbeit verschiedene Formzahl-Typen verglichen werden.
3. eine dritte Liste : Mathematische und statistische Symbole, die schon international von Mathematikern verwendet und in der forstlichen Literatur allgemein benötigt werden. Diese Liste wurde von Mr. J. N. R. Jeffers der britischen Forestry Commission ausgearbeitet. Die Arbeitsgruppe wünscht, Mr. Jeffers ihren Dank für seinen wichtigen Beitrag zu der Arbeit auszusprechen.

Eine geringe Überschneidung der Listen 1 und 3 hätte sich nur vermeiden lassen durch Änderung gewisser Symbole, die sich schon international eingebürgert haben. Wo die Gefahr einer Verwechslung für gering erachtet wurde, zog man daher einer Änderung die Beibehaltung eines Zeichens für zwei Zwecke vor, z.B. *f* steht in der ersten Liste für *Formzahl* und in der dritten Liste für *Frequenz.*

ALLGEMEINE VORSCHLÄGE

Beim Gebrauch von Symbolen *sollte der Verfasser sein Hauptziel darin sehen, den Lesern seine Ausführungen so leicht verständlich wie nur möglich zu machen.* Die nachfolgenden Vorschläge bezwecken, den Verfassern die Erreichung dieses Zieles zu erleichtern.

Es kann jedoch Ausnahmefälle geben, *in denen die strenge Einhaltung dieser Vorschläge dem erwähnten Hauptzweck eher hinderlich als förderlich wäre ; in solchen Fällen ist es natürlich nicht nur gerechtfertigt, sondern sogar wünschenswert, von den Vorschlägen abzuweichen.*

BESONDERE VORSCHLÄGE

1. Soweit als möglich sollen die allgemeinen holzmesskundlichen Symbole lt. Anhang 1 verwendet werden.
2. Wo eine Ergänzung der Symbole im Anhang 1 nötig wird, sollte einer der nachstehend beschriebenen zwei Wege begangen werden :

   Entweder

   (a) sollen die Symbole gemäss Liste 2 gebraucht werden, z.B. $i_{d\,21\text{-}40}$ für den Durchmesserzuwachs eines Stammes im Altersbereich von 21—40 Jahren

   oder

   (b) es können den Symbolen des Anhanges 1 Akzente oder Zusatzzahlen (Zahlensubskripte) beigefügt werden, im obigen Beispiel i' oder i_1 statt $i_{d\,21\text{-}40}$. Die komplizierteren, dafür aber anschaulicheren Symbole der Alternative (a) werden zu bevorzugen sein, wenn eine grosse Anzahl von Zeichen verwendet wird, aber jedes von ihnen nur selten vorkommt ; dagegen werden Akzente oder Zusatzzahlen (Zahlensubskripte) lt. Alternative (b) den Vorzug dort verdienen, wo eine kleine Anzahl häufig wiederkehrender Symbole in Frage kommt. Ergänzte Zeichen sind in verwickelten mathematischen Formeln besonders nachteilig.
3. In mathematischen und statistischen Berechnungen sollen die Symbole gemäss Anhang 3 benützt werden und zwar entweder im Verein mit denen der Anhänge 1 und 2 oder an ihrer Stelle.
4. Alle Veröffentlichungen mit einer mehr als geringfügigen Anzahl von Symbolen sollen abgesehen von irgendwelchen textlichen Erklärungen in einem besonderen Anhang die gebrauchten Symbole verzeichnen und ihre Bedeutung genau umschreiben. In gewissen Fällen sollte die Umschreibung auch deutlich darlegen, wie der durch ein Symbol repräsentierte Faktor erarbeitet wurde. Im Falle einer Formzahl ist z.B. nicht nur die Angabe notwendig, ob es eine echte oder unechte Formzahl ist, sondern auch, ob die zugrundegelegte Masse mit oder ohne Rinde vermessen wurde, ob die Masse bis zu einer bestimmten Durchmessergrenze gemessen wurde, ob es sich nur um Schaftholz handelt oder ob auch Astholz miteinbezogen wurde und schliesslich, ob die Masse sektionsweise vermessen wurde oder nicht.

Appendix 1
Annexe 1
Anhang 1

LIST OF GENERAL SYMBOLS IN FOREST MENSURATION
LISTE DES SYMBOLES GENERAUX DE MESURES FORESTIERES
ÜBERSICHT DER ALLGEMEINEN HOLZMESSKUNDLICHEN SYMBOLE

c	circumference or girth	*c*	*circonférence*	c	Umfang
d	diameter	*d*	*diamètre*	d	Durchmesser
f	form factor	*f*	*coefficient de forme*	f	Formzahl
g	basal area at 1.3 m (= 4 ft. 3 ins.)	*g*	*surface terrière à 1,30 mètre*	g	Grundfläche in 1.3 m Höhe
h	height	*h*	*hauteur*	h	Höhe
i	increment	*i*	*accroissement*	i	Zuwachs
k	form quotient	*k*	*coefficient de décroissance*	k	Formquotient
n	number (of stems, years, etc.)	*n*	*nombre (de tiges, d'années, etc.)*	n	Anzahl (Stammzahl, Anzahl der Jahre etc.)
p	increment per cent (volume, value, etc.)	*p*	*taux (volume, valeurs, etc.)*	p	Zuwachsprozent (Masse, Wert etc.)
t	age	*t*	*âge*	t	Alter
v	volume	*v*	*volume*	v	Masse

Capital letters should generally be reserved for one of two purposes: either to denote totals per unit area (e.g. V = volume per ha) or population totals in sampling schemes.

Les majuscules doivent, d'une manière générale, être réservées pour un des deux objets suivants : soit mesure totale à l'unité de surface (par exemple V = volume par ha), soit population totale dans un échantillonnage.

Grosse Buchstaben sollen in der Regel für einen von zwei Zwecken reserviert werden: entweder für Gesamtwerte pro Flächeneinheit (z.B. V = Masse pro ha) oder für Populationsgesamtwerte in Probeaufnahmen.

Appendix 2
Annexe 2
Anhang 2

ELABORATION OF THE MENSURATION SYMBOLS GIVEN IN APPENDIX 1

Note : 1. Sometimes the rigid adherence to the principles recommended for elaborating symbols would lead to several tiers of subscripts. These should, however, be avoided unless there is danger of confusion ; *e.g.* the suggested symbol for increment is i and that for volume of stem wood over 7 cm. diameter is v_7, but the increment relating to that volume should be written as i_{v7} and *not* as i_{v_7}.

2. Some of the symbols recommended involve the use of decimal points. In some countries these are normally shown by a comma (e.g. 0,1) in other countries by a point (e.g. 0.1). In this appendix decimals are shown as points, but there is no objection to commas being used instead.

3. Underbark measurements may be indicated by attaching u as a subscript to the corresponding symbol, for example, d_u to denote underbark diameter, V_u to denote total volume of stemwood underbark.

PRÉCISION DES SYMBOLES DE MESURES FORESTIÈRES, DONNÉS DANS L'ANNEXE 1

Note : 1. Parfois l'obéissance absolue aux principes reconnus nécessaires pour préciser les symboles, conduirait à une cascade d'indices. Cependant, ces indices doivent être évités, à moins qu'il y ait risque de confusion; par exemple: le symbole proposé pour "accroissement" est i et celui pour "bois fort de la tige" est v_7, *mais l'accroissement qui se rapporte à ce volume doit être écrit* i_{v7} *et* non i_{v_7}.

2. Quelques symboles recommandés exigent l'usage de décimales. Dans quelques Pays, il est d'usage de les indiquer par des virgules (par exemple 0,1) dans d'autres Pays par des points (par exemple 0.1). Dans cette annexe les décimales sont indiquées par des points, mais il n'y a pas d'inconvénient à utiliser des virgules à la place des points.

3. Pour indiquer les mesures sous écorce, la lettre u peut être ajoutée en indice aux symboles correspondants, par exemple d_u *indique le diamètre sous écorce,* V_u *indique le volume total sous écorce.*

ERGÄNZUNG DER HOLZMESSKUNDLICHEN SYMBOLE DES ANHANGES 1

Bemerkung : 1. Die strenge Einhaltung der vorgeschlagenen Grundsätze für die Symbolergänzung würde zuweilen zu mehreren Stufen von Zusatzzeichen (Subskripten) führen. Dies sollte jedoch vermieden werden, es sei denn, dass die Gefahr einer Verwechslung besteht; z.B. ist das vorgeschlagene Zeichen für den Zuwachs i und das fur die Schaftderbholzmasse v_7, aber der auf diese Masse bezogene Zuwachs soll mit i_{v7} und *nicht* mit i_{v_7} bezeichnet werden.

2. Verschiedene der in Vorschlag gebrachten Symbole schliessen den Gebrauch von Dezimalstellen ein. In einigen Ländern ist die dafür gebräuchliche Schreibweise ein Komma, (z.B. 0,1), in anderen ein Punkt (z.B. 0.1). In dem gegenwärtigen Anhang sind die Dezimalstellen durch vorangehenden Punkt angedeutet, jedoch besteht kein Einwand gegen die Verwendung von Kommas anstelle von Punkten.

3. Messungen ohne Rinde können durch das Zusatzzeichen u zum entsprechenden Symbol angezeigt werden. So bedeutet z.B. d_u Durchmesser ohne Rinde, V_u Gesamtmasse ohne Rinde.

SYMBOL SYMBOLE SYMBOL	DEFINITION DEFINITION BEGRIFF	EXPLANATION EXPLICATIONS ERLÄUTERUNG
c	I. Circumference or girth	Expand as in "Diameter" below.
	Circonférence	*Mêmes indices que ci-dessus pour "diamètres."*
	Umfang	Ergänzung wie unten für "Durchmesser" angegeben.
d	II. Diameter 1. Diameter at 1.3 m (4 ft. 3 ins.) diameter of a single tree	explain whether measured by tape or by caliper; and if by caliper whether by single measurement or by two measurements at right angles.
	Diamètre *1. Diamètre à hauteur d'homme (1,30 m) diamètre d'un seul arbre.*	*expliquer si le diamètre est mesuré au ruban ou au compas, et dans ce dernier cas, s'il s'agit d'une mesure unique ou de deux mesures suivant 2 diamètres perpendiculaires.*
	Durchmesser 1. Durchmesser in 1.3 m Höhe Durchmesser des Einzelstammes	Angabe, ob mit Messband oder Kluppe vermessen; falls gekluppt, ob es sich um einfache oder um kreuzweise Messungen handelt.
d_g	diameter corresponding to mean basal area of stand	the mean basal area $(\bar{g}) = \frac{\Sigma g}{n} = \frac{G}{N}$
	diamètre de la tige de surface terrière moyenne	*surface terrière moyenne* $(\bar{g}) = \frac{\Sigma g}{n} = \frac{G}{N}$
	Durchmesser des Grundflächen-Mittelstammes	mittlere Grundfläche $(\bar{g}) = \frac{\Sigma g}{n} = \frac{G}{N}$
$\bar{d}$	arithmetic mean diameter	
	diamètre moyen arithmétique	$\bar{d} = \frac{\Sigma d}{n}$
	arithmetischer Mitteldurchmesser	
d_M	diameter of median tree	if the trees are arranged in order of diameter, starting with either the largest or smallest diameter, the position of the median tree is found from $\frac{n+}{2}$
	diamètre de la tige médiane	*quand les arbres sont rangés par ordre de diamètre, croissant ou décroissant, la position de la tige médiane est celle du* $\left(\frac{n+1}{2}\right)^{\grave{e}me}$ *arbre*
	Durchmesser des Stammzahl-Zentralstammes	wenn die Bäume in steigender oder fallender Reihenfolge der Durchmesser geordnet sind, ergibt sich die Lage des Stammzahlzentralstammes aus $\frac{n+1}{2}$

SYMBOL SYMBOLE SYMBOL	DEFINITION DEFINITION BEGRIFF	EXPLANATION EXPLICATIONS ERLÄUTERUNG
d_{gM}	diameter of median basal area tree	is found in the same way as d_M, but now the numbers in each diameter class are weighted by basal area: $\frac{\Sigma g}{2}$
	diamètre de la tige de surface terrière médiane	*est trouvé de la même manière que* d_M, *mais maintenant les nombres de chaque classe de diamètre sont pondérées par les surfaces terrières:* $\frac{\Sigma g}{2}$
	Durchmesser des Grundflächen-Zentralstammes	wird auf analoge Weise gefunden wie d_M, jedoch werden die Stammzahlen jeder Durchmesserklasse nach ihren Grundflächen gewogen: $\frac{\Sigma g}{2}$
d_+ and d_-	diameters of Hohenadl's sample trees	$d_+ = d + \sigma_d$ and $d_- = d - \sigma_d$ where σ_d is the standard deviation of d
d_+ *et* d_-	*diamètre des tiges d'essai de Hohenadl*	$d_+ = d + \sigma_d$ *et* $d_- = d - \sigma_d$ *ici* σ_d *est l'écart type de* d
d_+ und d_-	Durchmesser der Hohenadl'schen Mittelstämme	$d_+ = d + \sigma_d$ und $d_- = d - \sigma_d$ wobei σ_d die mittlere Abweichung von d ist
	2. Other diameters Diameters at points other than breast height are indicated by subscripts e.g.	
$d_{0.5h}$	diameter at half of total height from ground	
	2. *Autres diamètres* *Les diamètres à des hauteurs autres que la hauteur d'homme sont indiqués par des indices* *par exemple*	
$d_{0.5h}$	*diamètre à mi-hauteur à partir du sol*	
	2. Andere Durchmesser Durchmesser in anderen Messhöhen als in Brusthöhe werden durch Zusatzzahlen (Subskripte) angegeben, z.B.	
$d_{0.5h}$	Durchmesser in halber Gesamthöhe vom Boden	
$d_{0.1h}$	diameter at 0.1 of total height from ground *diamètre à 1/10 de la hauteur, à partir du sol* Durchmesser in 0.1 der Gesamthöhe vom Boden	

SYMBOL SYMBOLE SYMBOL	DEFINITION DEFINITION BEGRIFF	EXPLANATION EXPLICATIONS ERLÄUTERUNG
$d_{0.2h}$	diameter at 0.2 of total height from ground *diamètre à ²/₁₀ de la hauteur, à partir du sol* Durchmesser in 0.2 der Gesamthöhe vom Boden aus	
d_6	diameter at six meters from ground *diamètre à 6 m, à partir du sol* Durchmesser in 6 m vom Boden aus	
g	III. Basal area *Surface terrière* Grundfläche basal area at 1.3 m (= 4 ft. 3 ins.) *surface terrière à 1,30 m* Grundfläche in 1.3 m Höhe	the symbol g is expanded in the same way as d *pour le symbole g on se sert des mêmes indices que pour d* die Ergänzung des Symbols g erfolgt in der gleichen Weise wie bei d angegeben
h	IV. Height *Hauteur* Höhe total height from ground to tip of tree *hauteur totale de l'arbre du sol jusqu'à l'extrémité* Scheitelhöhe	
h_L	mean height by Lorey's formula *hauteur moyenne d'après Lorey* Mittelhöhe nach Lorey	$h_L = \frac{g_1 \times h_1 + g_2 \times h_2 + \dots\dots}{g_1 + g_2 + \dots\dots}$
$\overline{h}$	arithmetic mean height *hauteur moyenne arithmétique* arithmetische Mittelhöhe	$\overline{h} = \frac{\Sigma h}{n}$
h_g	height corresponding to mean basal area *hauteur de la tige de surface terrière moyenne* Höhe des Grundflächen-Mittelstammes	as determined from the regression of height on diameter (or basal area) *déterminée par la régression de la hauteur sur le diamètre (ou la surface terrière)* über dem entsprechenden Durchmesser (oder Grundfläche) aus der Höhenkurve abgelesen
h_d	height corresponding to arithmetic mean diameter *hauteur de la tige de diamètre moyen arithmétique* Höhe des arithmetischen Mitteldurchmesserstammes	

SYMBOL SYMBOLE SYMBOL	DEFINITION DEFINITION BEGRIFF	EXPLANATION EXPLICATIONS ERLÄUTERUNG
h_{dM}	height corresponding to median diameter *hauteur de la tige de diamètre médian* Höhe des Stammzahl-Zentralstammes	as determined from the regression of height on diameter (or basal area) *déterminée par la régression de la hauteur sur le diamètre (ou la surface terrière)* über dem entsprechenden Durchmesser (oder Grundfläche) aus der Höhenkurve abgelesen
h_{gM}	height corresponding to median basal area *hauteur de la tige de surface terrière médiane* Höhe des Grundflächen Zentralstammes	
h_{dom}	average height of dominant trees, sometimes also referred to as "top height" *hauteur moyenne des arbres dominants, quelquefois appelée hauteur dominante* Durchschnittshöhe der herrschenden Stammklasse, gelegentlich auch als „Oberhöhe" bezeichnet	the exact definition must be given in text *il faut expliquer la définition exacte dans le texte* der genaue Begriff ist im Text zu definieren
k	V. Form quotients *Coefficient de décroissance* Formquotienten artificial form quotient based on diameters at half total height and at breast height *coefficient de décroissance artificiel, basé sur les diamètres à mi-hauteur et à hauteur d'homme* unechter Formquotient, basiert auf Durchmessern in halber Höhe und in Brusthöhe	$k = \frac{d_{0.5h}}{d}$
$k_{6/1.3}$	other form quotients as well as true form quotients are indicated by subscripts e.g. artificial form quotient based on diameters at 6 m and 1.3 m from ground	$k_{6/1.3} = \frac{d_6}{d}$
$k_{6/1.3}$	*les autres coefficients de décroissance sont expliqués par les indices par exemple* *coefficient de décroissance artificiel, basé sur les diamètres à 6 m et à 1,30 m à partir du sol*	
$k_{6/1.3}$	andere unechte Formquotienten und echte Formquotienten sind durch Zusatzzeichen (Subskripte anzuzeigen z.B. unechter Formquotient, errechnet aus Durchmessern 6 m und 1.3 m vom Boden	

SYMBOL SYMBOLE SYMBOL	DEFINITION DEFINITION BEGRIFF	EXPLANATION EXPLICATIONS ERLÄUTERUNG
$k_{0.5h/0.3h}$	natural form quotient based on diameters at 0.5 and 0.3 total height from ground *coefficient de décroissance naturel, basé sur les diamètres à* $^5/_{10}$ *et à* $^3/_{10}$ *de la hauteur, à partir du sol* echter Formquotient, basiert auf Durchmessern in 0.5 und 0.3 der Gesamthöhe vom Boden aus	$k_{0.5h/0.3h} = \frac{d_{0.5h}}{d_{0.3h}}$
k_a	absolute form quotient *coefficient de décroissance absolu* absoluter Formquotient	$k_a = \frac{d_{\frac{1}{2}(h + 1.3)}}{d}$
v	VI. Volume *Volume* Masse total stemwood from ground to tip of tree (without branchwood) *volume total de la tige, du sol jusqu'à l'extrémité de l'arbre (sans bois de branche)* Gesamtschaftholzmasse von Boden bis zum Scheitel ohne Astholz	1. all volumes are over bark unless otherwise stated. 2. mean volumes, unless otherwise stated, are always derived from the total volume per unit area divided by the number of trees e.g. $\bar{v}_7 = \frac{\Sigma v_7}{n}$ 3. method of volume measurement or determination should always be explained. *1. sans autre indication, tous les volumes s'entendent sur écorce.* *2. sans autre indication, les volumes moyens sont toujours dérivés du volume total à l'unité de surface divisé par le nombre d'arbres, par exemple :* $\bar{v}_7 = \frac{\Sigma v_7}{n}$ *3. il faut toujours expliquer la méthode de mesure ou de détermination du volume.* 1. falls nicht anders vermerkt, verstehen sich alle Massen mit Rinde. 2. falls nicht anders vermerkt, sind die mittleren Massen immer hergeleitet aus der Gesamtmasse pro Flächeneinheit dividiert durch die Anzahl der Bäume, z.B. $\bar{v}_7 = \frac{\Sigma v_7}{n}$ 3. die Methode der Holzmassenermittlung soll immer erklärt werden.
v_7	stem wood above 7 cm diameter *volume bois fort de la tige (au-dessus de 7 cm de diamètre)* Schaft-Derbholzmasse	
v_b	total tree volume (stem wood and branchwood) *volume total de l'arbre (tige et branches)* Baumholzmasse	
v_{7b}	tree volume above 7 cm diameter *volume bois fort de l'arbre* Baum-Derbholzmasse	
v_a	total branch wood *volume bois de branche total* Gesamtastholz	
v_{7a}	branchwood above 7 cm diameter *volume bois fort de branche* Astderbholz	
f	VII. *Form factors* *Coefficients de forme* Formzahl artificial stem wood form factor *coefficient de forme artificiel de la tige* unechte Schaftholz-Formzahl	$f = \frac{v}{gh}$

SYMBOL SYMBOLE SYMBOL	DEFINITION DEFINITION BEGRIFF	EXPLANATION EXPLICATIONS ERLÄUTERUNG
f_7 f_b f_{7b}	other artificial form factors *autres coefficients de forme artificiels* andere unechte Formzahlen	$f_7 = \frac{v_7}{gh}$ $f_b = \frac{v_b}{gh}$ $f_{7b} = \frac{v_{7b}}{gh}$
$f_{0.1h}$	true stem wood form factor *coefficient de forme naturel du bois de la tige* echte Schaftholz-Formzahl	$f_{0.1\,h} = \frac{v}{h_{g0.1h}}$
i	VIII. Increment *Accroissement* Zuwachs increment of a tree in one year *accroissement annuel d'un arbre* Zuwachs eines Baumes in einem Jahre	*i* and *I* always refer to the increment in one year unless otherwise stated *sans autre indication, i et I se réfèrent toujours à l'accroissement annuel* falls nicht anders vermerkt, beziehen sich i und I immer auf den Zuwachs in einem Jahre
I	increment of a unit area in one year *accroissement annuel à l'unité de surface* Jahreszuwachs pro Flächeneinheit	
$\bar{i}$	arithmetic mean increment of a number of trees in one year	the bar (—) should be used to denote the averaging of trees but *not* for averaging years. The averaging of years is simply indicated by the subscripts showing the ages or period to which the periodic annual increment refers.
$\bar{i}$	*accroissement moyen annuel arithmétique d'un certain nombre d'arbres*	*la barre (—) doit être utilisée pour indiquer qu'il s'agit d'une moyenne d'arbres et* non *d'une moyenne d'années. Il faut désigner simplement les moyennes d'années par des indices, qui indiquent l'âge ou la période auxquels l'accroissement annuel périodique se réfère.*
$\bar{i}$	arithmetischer Durchschnittszuwachs einer Anzahl Bäume in einem Jahre	der Strich (—) soll gebraucht werden um anzudeuten, dass der Baum und *nicht* der Jahresdurchschnitt zugrundegelegt wurde. Ein Jahresdurchschnitt wird einfach durch Zahlensubskripte angegeben, die das dem periodischen Jahreszuwachs zugrundegelegte Alter oder den Zeitraum angeben.

SYMBOL SYMBOLE SYMBOL	*DEFINITION* DEFINITION BEGRIFF	EXPLANATION EXPLICATIONS ERLÄUTERUNG
	the periodic annual increment of a tree is indicated by subscripts, e.g.	
i_{21-30}	the periodic annual increment of a tree between the ages of 21 and 30 years	
	il faut indiquer l'accroissement annuel périodique par des indices, *par exemple*	
i_{21-30}	*l'accroissement annuel périodique d'un arbre entre les âges de 21 et 30 ans*	
	der periodische Durchschnittszuwachs eines Baumes pro Jahr wird durch Zahlensubskripte angegeben, z.B.	
i_{21-30}	der periodische Durchschnittszuwachs eines Baumes im Altersbereich von 21—30 Jahren	
	the total increment over a period is indicated by adding the summation sign to the above i.e.	
Σi_{21-30}	the total increment of a tree between the ages 21 and 30 years	
	l'accroissement total dans une période est indiqué en ajoutant le signe sigma aux autres signes :	
Σi_{21-30}	*l'accroissement total d'un arbre entre les âges de 21 et 30 ans*	
	um den Gesamtzuwachs in einem Zeitraum anzugeben wird das Summierungszeichen dem obengenannten Zeichen vorangestellt:	
Σi_{21-30}	der Gesamtzuwachs eines Baumes im Altersbereich von 21—30 Jahren	
	subscripts are also used to denote the character to which the increment refers, e.g.	
i_d	diameter increment in a year	
	Les indices sont aussi employés pour indiquer le caractère auquel l'accroissement se réfère, *par exemple*	
i_d	*accroissement annuel du diamètre*	
	Zusatzzeichen (Subskripte) werden auch gebraucht, um den Zuwachs zu spezifizieren, z.B.	
i_d	Durchmesserzuwachs in einem Jahre	

SYMBOL SYMBOLE SYMBOL	DEFINITION DEFINITION BEGRIFF	EXPLANATION EXPLICATIONS ERLÄUTERUNG
i_g	basal area increment in a year *accroissement annuel de la surface terrière* Grundflächenzuwachs in einem Jahre	
i_v	volume increment in a year *accroissement annuel du volume* Massenzuwachs in einem Jahre	
i_{v7b}	increment of stem wood and branchwood over 7 cm. diameter in a year *accroissement annuel du bois fort total* Derbholzzuwachs in einem Jahre	NOT: $i_{v_{7_b}}$ *NON PAS:* $i_{v_{7_b}}$ NICHT : $i_{v_{7_b}}$
$I_{v7b\,31\text{-}50}$	the periodic annual increment per unit area of stem wood and branch wood over 7 cm diameter between the ages 31 and 50 years *accroissement annuel périodique par unité de surface du bois fort total entre les âges de 31 et 50 ans* der periodische Durchschnittszuwachs (pro Flächeneinheit) des Baumderbholzes im Altersbereich von 31—50 Jahren	NOT : $I_{v_{7_{b_{31\text{-}50}}}}$ *NON PAS:* $I_{v_{7_{b_{31\text{-}50}}}}$ NICHT : $I_{v_{7_{b_{31\text{-}50}}}}$
p	increment percent *taux d'accroissement* Zuwachsprozent	

Appendix 3
Annexe 3
Anhang 3

A LIST OF MATHEMATICAL AND STATISTICAL SYMBOLS WHICH ARE USED INTERNATIONALLY AMONG MATHEMATICIANS AND ARE COMMONLY NEEDED IN FOREST LITERATURE

In this list, only symbols which are generally accepted have been included. The list is divided into five sections :

(a) Letters of the alphabet :

Small Roman
Capital Roman
Greek

(b) Symbols of relation ;
(c) Symbols of operation ;
(d) Use of indices ;
(e) Use of subscripts, primes, etc.

LISTE DES SYMBOLES MATHÉMATIQUES ET STATISTIQUES D'UN EMPLOI INTERNATIONAL CHEZ LES MATHÉMATICIENS ET QUI SONT UTILISES COURAMMENT DANS LA LITTÉRATURE FORESTIÈRE

Dans cette liste on ne trouve que des symboles, qui sont acceptés généralement. La liste est divisée en cinq sections :

(a) Lettres de l'alphabet:

minuscules romaines
majuscules romaines
grecques

(b) Symboles de relation ;
(c) Symboles d'opération ;
(d) L'usage des exposants ;
(e) L'usage des indices, accents, etc.

VERZEICHNIS MATHEMATISCHER UND STATISTISCHER SYMBOLE, DIE IN DER INTERNATIONALEN FACHLITERATUR ANWENDUNG FINDEN UND AUCH IM FORSTSCHRIFTTUM ALLGEMEIN BENÖTIGT WERDEN

In dieser Übersicht sind nur Symbole erwähnt, die allgemein anerkannt sind. Die Übersicht zerfällt in fünf Abschnitte:

(a) Buchstaben des Alphabets:
Kleine lateinische
Grosse lateinische
Griechische
(b) Beziehungssymbole;
(c) Behandlungssymbole;
(d) Gebrauch von Indexwerten (Exponenten);
(e) Gebrauch von Zusatzzeichen (Subskripten), Akzenten usw.

(a) Letters of the alphabet

(a) Lettres de l'alphabet

(a) Buchstaben des Alphabets

Small Roman letters are used to indicate observed or calculated values. The following have special meanings :

Les minuscules romaines *sont utilisées pour indiquer les valeurs observées ou calculées. Les suivantes ont des significations spéciales :*

Kleine lateinische Buchstaben werden gebraucht, um beobachtete oder berechnete Werte anzugeben. Die folgenden haben besondere Bedeutungen.

LETTER LETTRE BUCHSTABE	GENERAL USE USAGE GENERAL ALLGEMEINE GEBRAUCH	SPECIAL USES AND EXAMPLES USAGES SPECIAUX ET EXEMPLES BESONDERE ANWENDUNGEN UND BEISPIELE
a b c	algebraic constants *constantes algébriques* algebraische Konstanten	a is also used as the intercept of a regression line on the dependent axis. b is also used as the coefficient of regression a *est également utilisé comme ordonnée à l'origine d'une droite de régression.* b *est également utilisé comme coefficient de régression* a wird auch gebraucht für das Interzept einer Regressionslinie auf der abhängigen Achse. b wird auch gebraucht für Regressionskoeffizient
e	the base of natural logarithms *base des logarithmes népériens* die Grundzahl natürlicher Logarithmen	$e \doteqdot 2.71828$
f	frequency in statistical distributions *fréquence dans les distributions statistiques* Frequenz in statistischen Verteilungen	
i	used in algebra for $\sqrt{-1}$ *employé en algèbre pour* $\sqrt{-1}$ wird in der Algebra gebraucht für $\sqrt{-1}$	also used to denote an interval in conjunction with other symbols *est aussi utilisé pour indiquer un intervalle conjointement avec d'autres symboles* ferner gebraucht, um in Verbindung mit anderen Symbolen ein Intervall anzudeuten
m	estimate of moments in statistical distributions *estimation des moments dans les distributions statistiques* Schätzung von Momenten in statistischen Verteilungen	
n	the number of items or values *nombre d'observations ou valeurs* Anzahl von Beobachtungen oder Werten	

LETTER LETTRE BUCHSTABE	GENERAL USE USAGE GENERAL ALLGEMEINE GEBRAUCH	SPECIAL USES AND EXAMPLES USAGES SPECIAUX ET EXEMPLES BESONDERE ANWENDUNGEN UND BEISPIELE
p	probability, or proportion, of successes *probabilité ou proportion de succès* Wahrscheinlichkeit oder Verhältnis von Erfolgen	used in statistical distributions *utilisé dans les distributions statistiques* in statistischen Verteilungen gebraucht
q	probability of failure ($q = 1 - p$) *probabilité d'insuccès* ($q = 1 - p$) Wahrscheinlichkeit oder Verhältnis von Misserfolgen ($q = 1 - p$)	
r	estimate of coefficient of correlation *estimation du coefficient de corrélation* Schätzwert des Korrelationskoeffizienten	
s	estimate of standard deviation, or standard error *estimation de l'écart-type ou de l'erreur type* Schätzwert der mittleren Abweichung oder des mittleren Fehlers	
t	STUDENT's *t*, a test of statistical significance t *d'après STUDENT, test de signification statistique* t nach STUDENT, ein Testwert für die statistische Signifikanz	
w	range of values, i.e. difference between maximum and minimum values in a sample *étendue d'une série, c'est-à-dire la différence entre les valeurs maximum et minimum dans un échantillon* Streuungsbereich, d.h. Differenz zwischen Maximal- und Minimalwerten in einer Stichprobe	
x y z	algebraic variables *variables algébriques* algebraische Variabeln	in regression analysis, x is used for the independent variable, and y for the dependent variable *dans les analyses de régression* x *est employé pour désigner la variable indépendante,* y *la variable dépendante* in Regressionsanalysen wird x gebraucht für die unabhängige Veränderliche, y für die abhängige Veränderliche

Capital Roman letters are commonly used in statistical work to denote individual values, in contrast to small Roman letters used to denote deviations from the mean, e.g.

$$X_1 - \overline{x} = x_1, \text{ and } X_2 - \overline{x} = x_2, \text{ etc.}$$

Les majuscules romaines *sont généralement utilisées dans des travaux statistiques, pour indiquer des valeurs observées individuelles, par opposition aux lettres minuscules romaines, qui indiquent les déviations par rapport à la moyenne, par exemple :*

$$X_1 - \bar{x} = x_1, \quad \text{et} \quad X_2 - \bar{x} = x_2, \text{etc.}$$

Grosse lateinische Buchstaben werden allgemein gebraucht in statistischen Arbeiten um individuelle Werte anzudeuten, im Gegensatz zu kleinen lateinischen Buchstaben, die Abweichungen vom Mittelwert angeben, z.B.

$$X_1 - \bar{x} = x_1, \text{ und } X_2 - \bar{x} = x_2, \text{usw.}$$

The following have special meanings :

Les lettres suivantes ont des significations particulières, à savoir:

Die Folgenden haben besondere Bedeutungen:

LETTER LETTRE BUCHSTABE	GENERAL USE USAGE GENERAL ALLGEMEINER GEBRAUCH	SPECIAL USES AND EXAMPLES USAGES SPECIAUX ET EXEMPLES BESONDERE ANWENDUNGEN UND BEISPIELE
F	Snedecor's F, the variance ratio used in tests of significance in analysis of variance *F d'après SNEDECOR, rapport de variance utilisé dans des tests de signification en analyse de variance* F nach Snedecor, das Variationsverhältnis, gebraucht in Signifikanzprüfungen in der Varianzanalyse	
N	a number of values (usually a total number) *nombre de valeurs (le plus souvent un nombre total)* eine Anzahl Werte (meistens eine Gesamtzahl)	$n_1 + n_2 + \dots\dots + n_r = N$
R	coefficient of multiple correlation *coefficient de corrélation multiple* vielfacher Korrelationskoeffizient	

Greek letters are commonly used to denote unknown population values, or parameters, of which values denoted by small Roman letters are estimates. The following have special meanings :

Les lettres grecques sont généralement utilisées pour désigner des valeurs ou des paramètres inconnus de la population, dont les estimations sont désignées par des lettres minuscules romaines. Les lettres suivantes ont des significations particulières, à savoir :

Griechische Buchstaben werden allgemein gebraucht um unbekannte Populationswerte oder Parameter anzudeuten, deren Schätzwerte mit kleinen lateinischen Buchstaben angegeben werden. Die Folgenden haben besondere Bedeutungen:

LETTER LETTRE BUCHSTABE	GENERAL USE USAGE GENERAL ALLGEMEINER GEBRAUCH	SPECIAL USES AND EXAMPLES USAGES SPECIAUX ET EXEMPLES BESONDERE ANWENDUNG UND BEISPIELE
β	population value of regression coefficients (of which b is an estimate) *vraie valeur du coefficient de régression de la population (dont* b *est une estimation)* Populationswert von Regressionskoeffizienten (b ist der entsprechende Schätzwert)	
η	correlation ratio *rapport de corrélation* Korrelationsverhältnis	
ϑ	any given angle measured from the horizontal *tout angle mesuré à partir de l'axe horizontal* irgendein Winkel, von der Horizontalachse gemessen	
μ	theoretical moments of statistical populations *moments théoriques des populations statistiques* Theoretische Momente statistischer Populationen	
π	a constant *une constante* eine Konstante	$\pi \doteqdot 3.14159$
ϱ	coefficient of correlation of a population *coefficient de corrélation d'une population* Korrelationskoeffizient einer Population	
σ	standard deviation of a population *Ecart-type d'une population* mittlere Abweichung einer Population	
χ^2	chi-square, a test of statistical "goodness of fit" *Un test servant à juger de la qualité d'un ajustement statistique* Chi-Quadrat, ein kritischer Wert für statistische Anpassung	

[For Σ, $\triangle$, δ etc., see symbols of operation].

(Pour Σ, $\triangle$, δ etc. . ., voir les symboles d'opération).

[Wegen Σ, $\triangle$, δ usw., siehe unter „Behandlungssymbole"].

(b) Symbols of relation

(b) Symboles de relation

(b) Beziehungssymbole

SYMBOL SYMBOLE SYMBOL	EXAMPLE OF USE EXEMPLE D'USAGE ANWENDUNGSBEISPIEL	MEANING SIGNIFICATION BEDEUTUNG
$=$	$a = b$	a equals b a *égale* b a ist gleich b
$\equiv$	$a \equiv b$	a is identical to b a *identique à* b a ist identisch mit b
$\doteqdot$ or $\simeq$	$a \doteqdot b$	a is approximately equal to b a *peu différent de* b a ist annähernd gleich b
$\neq$	$a \neq b$	a does not equal b a *différent de* b a ist nicht gleich b
$>$	$a > b$	a is greater than b a *supérieur à* b a ist grösser als b
$\geqq$	$a \geqq b$	a is greater than or equal to b a *supérieur ou égal à* b a ist grösser als oder gleich b
$<$	$a < b$	a is less than b a *inférieur à* b a ist kleiner als b
$\leqq$	$a \leqq b$	a is less than or equal to b a *inférieur ou égal à* b a ist kleiner als oder gleich b
$\pm$	$a \pm b$	the value a has a standard error b (Note : the ± should always be followed by a standard error of the mean, not a standard deviation of individual values). *la valeur a a un écart-type* b. *(Note : le signe ± doit toujours être suivi d'un écart-type de la moyenne, et non d'un écart-type des valeurs individuelles.)* der Wert a hat einen mittleren Fehler b (Bemerkung : Nach dem ± Zeichen soll immer der mittlere Fehler des Mittels folgen, nicht die Standardabweichung der individuellen Werte).

(c) Symbols of operation

(c) Symboles d'opération

(c) Behandlungssymbole

SYMBOL SYMBOLE SYMBOL	EXAMPLE OF USE EXEMPLE D'USAGE ANWENDUNGSBEISPIEL	MEANING SIGNIFICATION BEDEUTUNG
∞	$\frac{1}{0} = \infty$	infinity *l'infini* unendlich
Δ		differences *différences* Differenzen
Σ	$\sum_{i=1}^{n} x_i = y$	$x_1 + x_2 + x_3 + \dots + x_n = y$
Π	$\prod_{i=1}^{n} x_i = y$	$x_1 \cdot x_2 \cdot x_3 \dots x_n = y$
$\lim_{x \to \infty}$	$\lim_{x \to \infty} y = 0$	the limit of y as x tends to infinity is 0 (where y is assumed to be some function of x). *la limite de y est 0 quand x tend vers l'infini (il est supposé que y est une certaine fonction de x).* Der Grenzwert von y ist gleich 0, wenn x unendlich gross wird (vorausgesetzt, dass y eine Funktion von x ist)
	n !	factorial of n $n = n(n-1)(n-2) \dots 3.2.1.$ (also written as $\underline{\lfloor n}$) *factorielle n* *$n! = n(n-1(n-2) \dots 3.2.1.$* *(on peut aussi écrire $\underline{\lfloor n}$)* n faktoriell $n! = n(n-1)(n-2) \dots 3.2.1.$ (wird auch als $\underline{\lfloor n}$ geschrieben)
	6 !	6 ! = 6 × 5 × 4 × 3 × 2 × 1
$\binom{n}{r}$	$\binom{4}{2}$	number of possible combinations of 2 objects out of a total of 4 objects (also written as nC^r or nCr) *nombre de combinaisons possibles de 4 objets pris 2 à 2* *(on peut aussi écrire nC^r ou nCr)* Anzahl möglicher Kombinationen von 2 Objekten aus einer Gesamtzahl von 4 Objekten (wird auch nC^r oder nCr geschrieben)

SYMBOL SYMBOLE SYMBOL	EXAMPLE OF USE EXEMPLE D'USAGE ANWENDUNGSBEISPIEL	MEANING SIGNIFICATION BEDEUTUNG
$F(x)$	$y = F(x)$	y is some function of x *y est une fonction de* x y ist irgendeine Funktion von x
$\frac{\delta y}{\delta x}$		the ratio of a small increase in y to a corresponding small increase in x *rapport d'un accroissement infiniment petit de* y *à l'accroissement infiniment petit correspondant de* x das Verhältnis einer kleinen Zunahme in y zu einer entsprechenden kleinen Zunahme in x
$\frac{dy}{dx}$		the limit of $\frac{\delta y}{\delta x}$ as δx tends to zero *la limite de* $\frac{\delta y}{\delta x}$ *quand* δx *tend vers zéro* der Grenzwert von $\frac{\delta y}{\delta x}$, wenn δx Null zustrebt
$\int$		indicates indefinite integration *indique une intégrale indéfinie* gibt eine unbestimmte Integration an
	$\int_0^\infty x.\, dx$	integration of x between zero and infinity *intégrale de* x *entre zéro et l'infini* Integration von x zwischen Null und Unendlich
$\mid\ \mid$	$\lvert a \rvert$	the value of a without regard to its algebraic sign *valeur absolue de* a der Wert von a ohne Beachtung seines algebraischen Vorzeichens

(d) *Use of indices*

Indices may be used to indicate powers, roots, reciprocals.

(d) L'usage des exposants.

On peut utiliser les exposants pour indiquer les puissances, les racines, les inverses.

(d) *Gebrauch von Exponenten*

Exponenten können gebraucht werden, um Potenzen, Wurzeln, Reziprokwerte anzugeben.

GENERAL SYMBOL SYMBOLE GENERAL ALLGEMEINES SYMBOL	EXAMPLE OF USE EXEMPLE D'USAGE ANWENDUNGSBEISPIEL	MEANING SIGNIFICATION BEDEUTUNG
x^n		the nth power of x *la puissance $n^{ième}$ de* x die n-te Potenz von x
	x^2	the square of x *carré de* x x-Quadrat
	x^3	the cube of x *cube de* x die Kubikzahl von x
$x^{\frac{1}{n}}$		the nth root of x *racine $n^{ième}$ de* x die n-te Wurzel aus x $\sqrt[n]{x}$
	$x^{\frac{1}{2}}$	the square root of x *racine carrée de* x die Quadrat-Wurzel aus x $\sqrt{x}$
	$x^{\frac{1}{3}}$	the cube root of x *racine cubique de* x die Kubikwurzel aus x $\sqrt[3]{x}$
x^{-1}		the reciprocal of x, $\frac{1}{x}$ *l'inverse de* x, *c'est-à-dire* $\frac{1}{x}$ der Reziprokwert von x, $\frac{1}{x}$
	x^{-2}	$\frac{1}{x^2}$
	$x^{-\frac{1}{2}}$	$\frac{1}{\sqrt{x}}$ [but beware of $\tan^{-1}x$, $\sin^{-1}x$, $\cos^{-1}x$, which denotes the *angle* whose tangent *is* x etc., and *not* $\frac{1}{\tan x}$, $\frac{1}{\sin x}$, $\frac{1}{\cos x}$] $\frac{1}{\sqrt{x}}$ [*attention :* $tg^{-1}x$, $\sin^{-1}x$, $\cos^{-1}x$ *désigne* ar x, *etc* ... *et* non $\frac{1}{tg\ x}$, $\frac{1}{\sin x}$, $\frac{1}{\cos x}$]. $\frac{1}{\sqrt{x}}$ [Achtung: *tang* $^{-1}$ x, *sin* $^{-1}$ x, *cos* $^{-1}$ x bedeutet den *Winkel*, dessen Tangens usw. x ist, und *nicht* $\frac{1}{tang\ x}$, $\frac{1}{\sin x}$, $\frac{1}{\cos x}$].

(e) Use of subscripts, primes, etc.

Subscripts may be used to identify particular values,

e.g. $x_1 + x_2 + x_3 + x_4 = \Sigma x_i$

(where $i = 1, 2, 3, 4$)

Special subscripts may be used to indicate particular estimates or constants

e.g. $\sigma_{\overline{x}}$, the standard error of the mean.

In regression analysis, subscripts are used to denote dependence and independence,

e.g. $b_{12.345\ldots n}$ is the regression coefficient of x_1 on x_2 when $x_3, x_4, x_5 \ldots\ldots\ldots x_n$ are held constant.

Primes may be used to indicate particular values of a variable, e.g. x', x'' x'''.

Averages : The arithmetic mean should be indicated by a small bar placed over the variable,

e.g. $\frac{1}{n} \Sigma x = \overline{x}$

Best estimates. Estimates obtained by least-squares theory (e.g. by regression) are indicated by placing a circumflex over the variable.

e.g. $\hat{y}$

(e) L'usage des indices, accents, etc...

Des indices peuvent être utilisés pour indiquer des valeurs particulières.

Par exemple $x_1 + x_2 + x_3 + x_4 = \Sigma x_i$

(*où* $i = 1, 2, 3, 4$).

Des indices peuvent être utilisés pour indiquer des estimations ou des constantes particulières.

Par exemple $\sigma_{\overline{x}}$ *est l'écart-type de la moyenne.*

Dans les analyses de régression, on se sert d'indices pour indiquer la dépendance et l'independance.

Par exemple $b_{12.345\ldots.n}$ *est le coefficient de régression de* x_1 *sur* x_2, *quand* $x_3, x_4, x_5 \ldots\ldots\ldots x_n$ *sont tenus constants.*

Les accents peuvent être utilisés pour indiquer des valeurs particulières d'une variable. Par exemple x', x'', x'''.

Moyennes. Il faut indiquer la moyenne arithmétique au moyen d'une petite barre sur la variable.

Par exemple $\frac{1}{n} \Sigma X = \overline{X}$

Meilleures estimations. Les estimations obtenues par la méthode des moindres carrés (par exemple au moyen d'une régression) sont indiquées par un accent circonflexe sur la variable.

Par exemple: $\hat{y}$

(e) Gebrauch von Subskripten (Zusatzzeichen), Akzenten usw.

Subskripte (Zusatzzeichen) kann man verwenden, um besondere Werte zu identifizieren,

z.B. $x_1 + x_2 + x_3 + x_4 = \Sigma x_i$

(wobei $i = 1, 2, 3, 4$)

Besondere Zusatzzeichen können gebraucht werden, um besondere Schätzungen oder Konstante anzuzeigen,

z.B. $\sigma_{\overline{x}}$, der mittlere Fehler des Mittels.

In der Regressionsanalyse werden Zusatzzeichen gebraucht, um Abhängigheit und Unabhängigkeit anzudeuten,

z.B. $b_{12.345 \ldots . n}$ ist der Regressionskoeffizient von x_1, auf x_2, wenn x_3, x_4, x_5, ……… x_n konstant gehalten werden.

Akzente dürfen gebraucht werden um besondere Werte einer Variabel anzudeuten, z.B. x', x'', x'''.

Mittel. Das arithmetische Mittel wird angegeben mittels eines kleinen Striches über der Variabel,

z.B. $\frac{1}{n} \Sigma x = \overline{x}$

Beste Schätzungen, Schätzungen, die man erhält mit der Methode der kleinsten Quadrate (z.B. mittels Regression), werden angegeben durch einen Zirkonflex über der Variabel.

z.B. $\hat{y}$.

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