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Systems approaches in pest management: The role of production ecology

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INTRODUCTION

Mission statement of production ecology

The population of the world in 1994 amounts to approximately 5,400 million people, and increases annually by about 100 million. Projections by the UN for the year 2050 show a population size between 8,000 and 12,000 million. Stabilisation of the population around 11,000 million is anticipated. The increase in the size of the population in combination with the demand for a more 'luxurious' food package, require growth of agricultural production. At the same time locally occurring over-exploitation of natural resources must be avoided and, where necessary, reversed. Hence, agriculture needs to meet a rising demand for marketable output, while satisfying ever tighter constraints with respect to toxicological safety of the product and impact of production techniques on nature, environment and landscape. These issues require a scientific analysis of socially relevant options for agricultural production activities at different levels of integration. Production ecology is an integrating scientific discipline which aims at exploring options for sustainable primary and secondary production systems (Rabbinge, 1986). Insight in the functioning of these agro-ecosystems is based on quantitative understanding of physical, chemical and eco-physiological processes that take place in such systems. Various ecological and socio-economic objectives and constraints determine the possibilities of these systems. Sustainability is used here in the sense that the possibilities for utilisation of the natural resources soil, water and air are not deteriorated irreversibly by current human activities.

Systems research and simulation models

Production ecology focuses on increasing insight in biological production processes at different hierarchical integration levels and expressing this insight in quantitative models. Relevant integration levels in production ecology are indicated in Figure 1. Each integration level is characterised by its temporal and spatial dimensions. In the production ecological systems approach, the central idea is that one must identify, delineate and understand a system in order to be able to influence it in a predictable manner (Spedding, 1990). Models are used as bridges between integration levels. They allow a better grasp of the behaviour of the system by using quantitative descriptions of processes or input-output relations at lower integration levels. In this way, knowledge at lower integration levels is scaled up to higher levels.

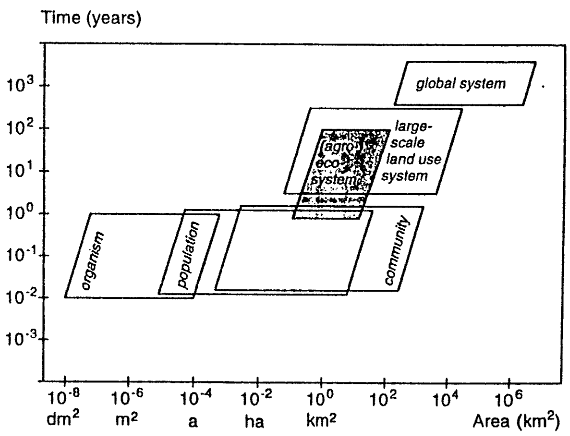

Figure 1. Time and spatial scales of integration levels, relevant in production ecology.

A simulation model is the product of an analytical phase, in which a system is decomposed into elements of which the behaviour is studied, and an integrative phase, in which models are used to synthesise the acquired knowledge. The analytical process leads to discoveries, new hypotheses and new insights at every lower level of integration. The synthesis-oriented approach leads into the opposite direction and results in understanding at every higher level of integration. The level of detail required in describing the underlying processes is determined by the objectives at the higher integration levels. Exploration of options for sustainable production requires thorough knowledge of elementary processes, useful models for integration of process knowledge and a continuous interaction between model and reality on experimental farms and in practice. Therefore, the analytical and the synthesising scientific approach in production ecology are complementary (Rabbinge and de Wit, 1989).

The systems approach is juxtaposed to the statistical approach in which a particular aspect of system behaviour is correlated to other aspects at the system level. The statistical approach results in descriptive models, which lack inherent causality.

Crop protection at different integration levels

Crop protection issues can be studied at different integration levels: pathosystem, crop system, cropping system, farm system, region and supra-regional level. Much disciplinary entomological and phytopathological research is conducted at the lower integration levels of cells, subcellular structures and biomolecules. Processes at adjacent integration levels have time coefficients (the reciprocal of the relative rates of change) that typically differ by one or two orders of magnitude, i.e. a factor 10 to 100. Simulation models are used to bridge two or maximally three levels of integration. Usually, lack of knowledge and large differences in temporal and spatial scales prohibit bridging of more than three integration levels. Moreover, the explanatory power and usefulness of a model may not increase substantially, or even decrease when there comes a large gap between the explanatory and explained level. Thus, plant-host interactions at the molecular level are seldom represented in epidemiological and crop growth models. Problems of aggregation are encountered when research results at the crop level need to be scaled up to the cropping system level. For example, at the cropping system level information is needed on population dynamics of the weed seed bank, which is of little concern for operational weed management during the growing season and has received little research attention for that reason.

The division of pest management issues into policy-oriented, strategic, tactical and operational (Conway, 1984) is based on differences in time and spatial scales. Policy-oriented issues concern the farm and higher integration levels, with time coefficients of at least several years. Examples are the governmental policy statements on crop protection in various countries, initially especially in South and South-East Asia. A recent culmination point is the declaration of 'Agenda 21' at the 'Earth Summit' in Rio de Janeiro, in which integrated pest management is embraced implicitly or explicitly (Table 2 in Zadoks, 1993). Strategic, tactical and operational questions may apply to the same spatial scale, e.g. a farmer's field, but they differ in temporal scale. Strategic questions at the field level address issues covering several growing seasons, while tactical questions concern effects within one growing season. Operational questions address 'how-to' problems and concern day to day implementation of decisions made at the tactical and strategic levels.

Irrespective of the integration level, crop protection issues comprise four elements, represented in the disease tetrahedron (Zadoks and Schein, 1979; Figure 2): the growth reducing factor or pest, the crop, weather or climate, and the human actor, be it a farmer or a policy maker. The pest interacts with the crop. The outcome of the interaction is determined by pest and crop attributes, which are influenced by weather and the human actor. Studies of such complex di- and tri-trophic systems easily lead to situations where 'everything affects everything' at the system level so that causes and effects cannot be disentangled. From a production ecological perspective, it is essential to

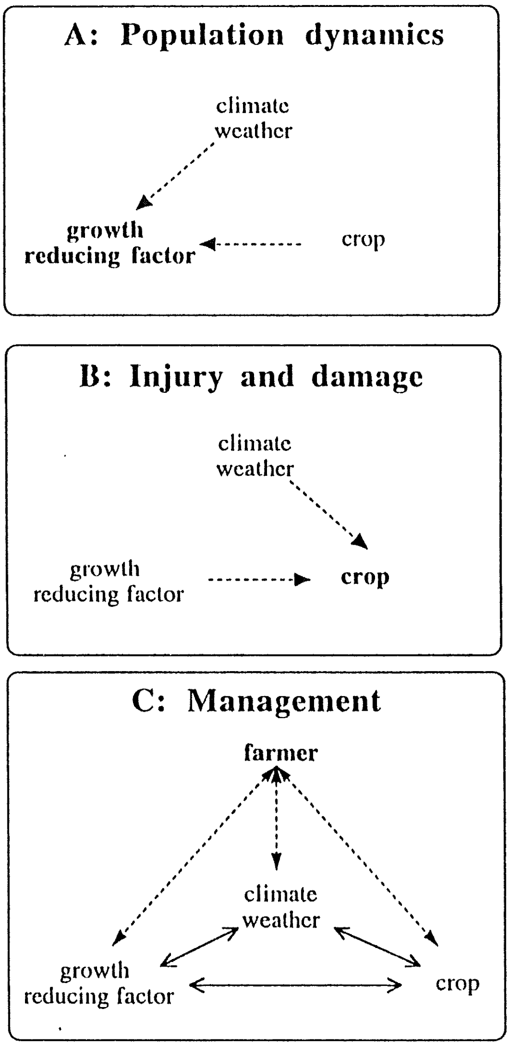

Figure 2. The disease triangle with emphasis on (A) population dynamics of the growth reducing factor, (B) injury and damage, and (C) crop protection.

distinguish population dynamics of the pest, crop damage, and management of the crop-pest system. Weather, nutritional state of the crop, and human interventions are input for models which explain temporal and spatial population dynamics (Figure 2a). In studies of damage, on the other hand, weather, population dynamics of the pest, and human interventions are input for crop growth models, which explain crop growth and production and the way these are affected by injury (Figure 2b). Such studies of population dynamics and damage provide the building blocks for pest management systems in which different strategies of human intervention are analysed with respect to the objectives of management (Figure 2c).

In this contribution we will demonstrate the need for a production ecological approach in crop protection. First, crop ecological principles of primary production will be discussed. Next, attention will be focused on management of agricultural production systems and the role production ecology can play in improving systems management. Finally, we will discuss institutionalisation of the production ecological approach in crop protection research in Asia through a training and research project in rice production systems.

PRINCIPLES OF PRIMARY PRODUCTION

Production situations, production technologies and production levels

In the analysis of primary (and also secondary) production systems, distinction is made between production situations, production technologies and production levels (Rabbinge, 1993).

The production situation at a specific site is characterised by physical factors: climate, water availability and aspects of the soil such as compaction, stoniness, water holding capacity and steepness. Together, these factors determine the conditions for agricultural production. Soils characterised by high water holding capacity, high fertility and low stoniness in combination with high water availability allow higher yields than soils which have low water holding capacity, low fertility and high acidity or salinity in combination with poor water availability. Production technology is the total of production techniques and methods. This encompasses all cropping measures from before sowing till after harvest, such as ploughing, seed bed preparation, sowing, weed control, etc. The combination of production situation and production technology results in a production level. The production level represents the amount of product per hectare. In good production situations, a high production level can be realised with a given production technology. In poor production situations greater inputs are needed to reach the same production level, if possible at all. As a consequence, production in poor production situations is less efficient, both per unit area and per unit product than production in good production situations.

The production level is influenced by three categories of growth factors (Figure 3)

Growth defining factors

These determine the potential yield which is realised when crops grow with an ample supply of water and nutrients. Growth defining factors include site-specific environmental variables, such as temperature and incident radiation which depend on latitude and day of the year, and species-specific characteristics concerning physiology and geometry of the leaves and the roots, and phenology. Potential growth rates appear to be 2-3 μg (dry matter) J^{-1} (light) when expressed per unit of light, by definition the only limiting resource under optimal conditions. In temperate regions, potential growth rates range from 15 to 35 g dry matter per square meter per day. Situations where potential growth rates are reached are rare, and may occur only in protected cultivation.

Growth limiting factors

These comprise abiotic resources such as water and nutrients, which limit the growth rate of the crop to a value below the maximum when their supply is sub-optimal. The associated yield level is called 'attainable'. In conjunction with CO_2 uptake, water vapour is released through the stomata. The rate of transpiration depends on incoming radiation, vapour pressure deficit of the air, and stomatal aperture. About 150 to 300 g of water is transpired for each gram of dry matter assimilated. In other words, approximately 4 to 8 mm water are required per day to maintain a potential growth rate of 25 g (dry matter) m^{-2} (ground) day^{-1}. The nitrogen requirement for potential growth is in the order of 10 g m^{-2} (ground), assuming an LAI of 4 m^2 (leaf) m^{-2} (ground), a specific leaf area of 20 m^2 (leaf) kg^{-1} (leaf dry matter) and a leaf nitrogen

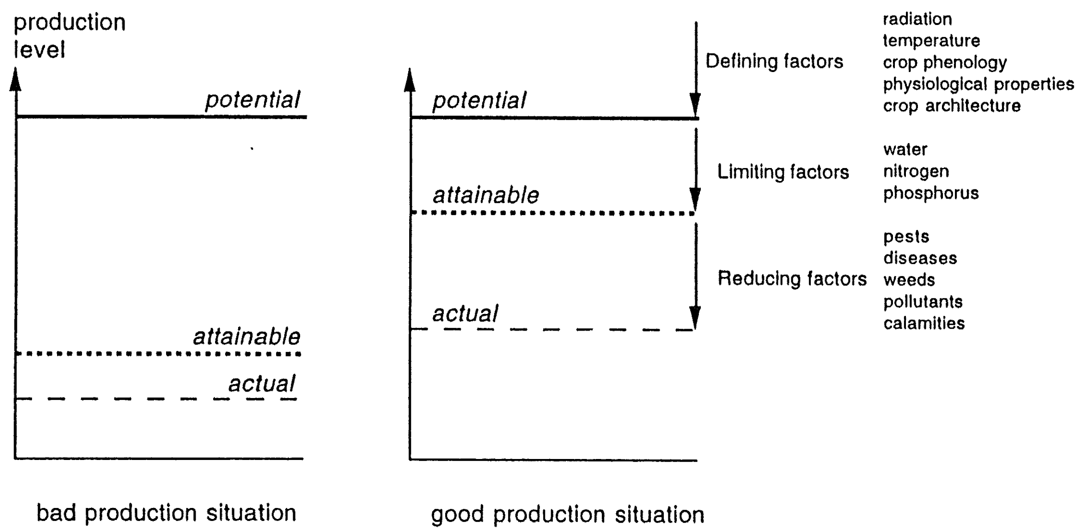

Figure 3. Production situation, production levels and associated principal growth factors.

content, necessary for maximum photosynthesis rates, of 5% on a dry matter basis. These values are only rules of thumb, and vary according to latitude, crop species and other factors. Van Keulen and Wolf (1986) present more accurate methods for estimating water- or nutrient limited growth rates.

Growth reducing factors

Pathogens, insects, weeds, pollutants of air, water and soil, and extreme weather conditions represent growth reducing factors. Due to these factors crop production is reduced from the attainable yield level to the 'actual' yield level. Especially with regard to pathogens, insects and weeds a wealth of information has been collected during the last 15 years concerning the way in which yield reduction is caused. Damage, i.e. the size of yield reduction, depends on the plant processes which are affected, i.e. the damage mechanisms, the growth rate of the healthy crop and the timing and intensity of growth reduction. Thus, damage by biotic growth reducing factors is the result of crop physiological, crop ecological and population dynamical processes.

Experimental results in the Sahel (West Africa; Figure 4) illustrate the interdependency of the effects of growth defining and growth limiting factors on crop growth. In the period June - July, directly after germination, water sets a maximum to the growth rate. From July till August, the low availability of phosphorus is the most limiting factor, while towards the end of the growing season the availability of nitrogen is the most limiting factor. Growth ends when the crop reaches physiological maturity, which is mainly a function of temperature. Because several limitations act simultaneously, human intervention aimed at alleviating the limitation by any one of the limiting factors would produce only modest increases in crop production. Pest management always operates within the constraints set by the growth defining and growth limiting factors. Damage due to, for example, early senescence caused by a disease will depend on the production level at which the crop is growing. Hence, crop protectionists need to have quantitative insight in crop growth processes as well as epidemiological processes, and their respective relations to external factors. Unfortunately, crop ecology is an underdeveloped aspect in training programs for crop protection students throughout the world.

Biotic growth reducing factors: Mechanisms of damage

The simplified example in the previous section shows that yield loss due to insects, pathogens and other growth reducing factors is a complex function of a large number of variables and depends on the production level. Experimental studies alone are inadequate to unravel the way in which complex systems with many interacting elements behave. Fortunately, explanatory simulation models provide powerful tools for identifying damage mechanisms and quantifying their relative and absolute contributions to yield loss.

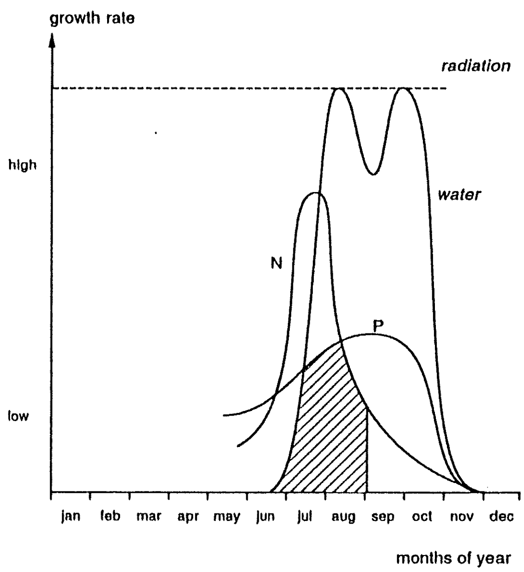

Figure 4. The effect of the relative availability of four principal growth factors - radiation, water, nitrogen and phosphorus - on plant growth in the Sahel. At any moment in time the uppermost line represents the potential growth rate, while the bottommost line represents the actual growth rate. The actual production is equal to the shaded area. After Penning de Vries and Van Keulen (1982).

Crop growth at the potential production level can be modelled at different levels of physiological detail (Spitters, 1990). A summary approach is based on empirical evidence that in many crops growing at the potential production level, the rate of growth is approximately proportional to the amount of light intercepted by green foliage (Monteith, 1977). A plot of total biomass against cumulative intercepted light (LI) results in a straight line. The slope of this line represents the average crop light-use efficiency (CLUE). Growth reducing factors may reduce LI, CLUE or both. When CLUE is unaffected by injury, the photosynthetic capacity of the green area is apparently unaltered. Injury then simply causes a reduction of the amount of energy available for crop growth and damage is proportional to the amount of energy foregone. When CLUE is decreased, the relation between damage and intercepted light is more complex. This warrants analysis of damage with a more comprehensive eco-physiological crop growth model.

In a comprehensive model of crop growth and development (e.g. SUCROS, Spitters *et al.*, 1989) daily rates of gross photosynthesis are simulated by combining the light profile in the crop with the light response of carbon assimilation by individual leaves. Gross carbon assimilation is conveniently described by a saturation curve, which is characterised by an initial light use efficiency and an asymptote at high light intensities (Figure 5). The rate of daily dry matter production is found by subtracting the rate of maintenance respiration from the calculated gross photosynthesis rate and accounting for the costs of conversion of assimilates into structural dry matter of the various organs. Integration over the days in the growing season results in total dry matter production. Damage mechanisms can be introduced into SUCROS at the level of whole plant processes (Figure 6).

Analysis of the effect of a growth reducing factor on crop growth and production proceeds along the steps shown in Figure 7. First, an inventory is made of the crop growth processes that are affected by the growth reducing factor (Rabbinge and Rijsdijk, 1981). Next, these (likely) damage mechanisms are ranked according to their relative importance. The most important ones are quantified using literature information and experiments. These damage mechanisms are then introduced into a crop growth model. Evaluation of the performance of the model shows to which extent the major causes of damage are understood, and whether additional damage mechanisms need be considered. When the model is in sufficient agreement with reality, it may be applied to situations for which no or limited experimental information exists. Such a model may, for instance, be used to study the effect of timing of disease on yield loss under different weather conditions. The level of detail in the crop model is dictated by the objectives of the study and the characteristics of the pathosystem. For instance, it may be necessary to distinguish different leaf layers to account for the vertical distribution of a pathogen. Technical details of the approach are described in Rabbinge *et al.* (1989).

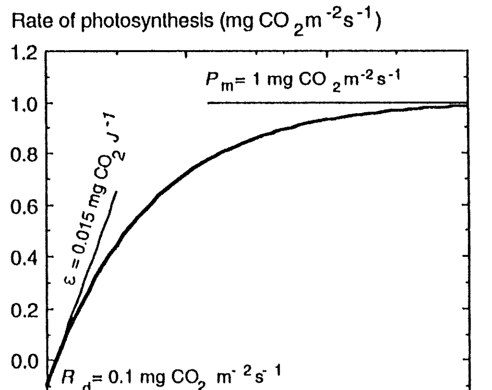

Figure 5. Illustration of a photosynthesis *versus* light response curve, characterised by the parameters P_m, ε and R_d. The curve is described by a negative exponential equation.

A typology of damage mechanisms can be drawn up which reflects the nature of the interaction between growth reducing factor and crop growth processes:

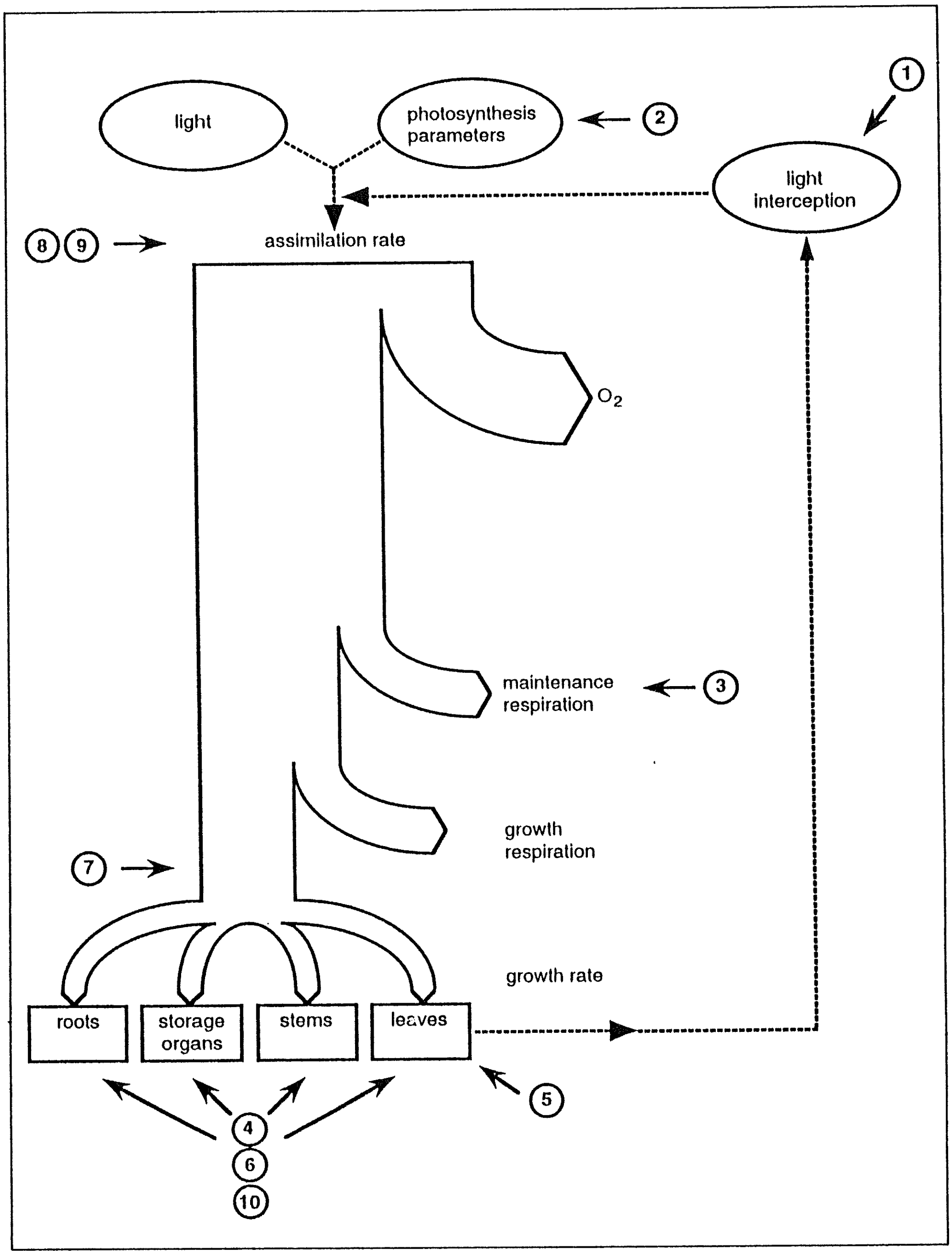

Figure 6. Schematic representation of an explanatory approach to modelling potential crop growth and injury, utilising the light profile within the canopy, photosynthesis characteristics of individual leaves, respiration and dry-matter partitioning. Arrows indicate potential damage mechanisms: (1) competition for light, (2) decrease of the rate of photosynthesis, (3) effects on respiration, (4) plant killing, (5) tissue necrosis and interception of light, (6) tissue consumption, (7) assimilate consumption, (8) hampering of water uptake, (9) induction of hormonal effects on stomatal regulation, and (10) deformations.

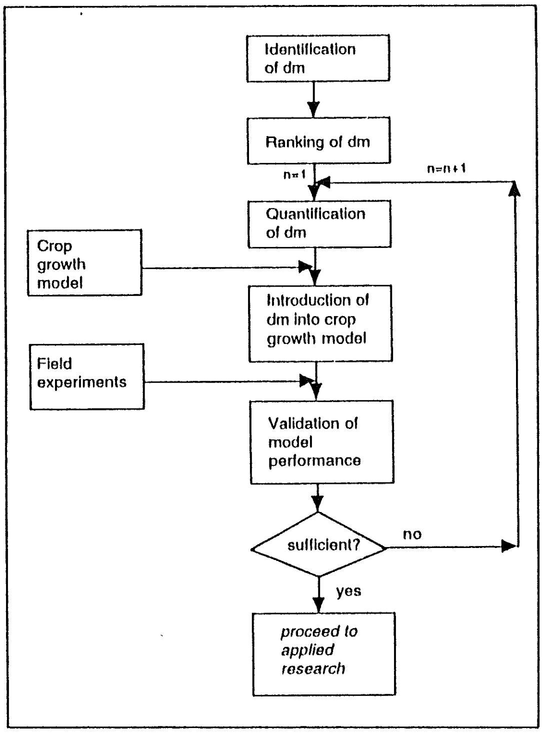

Figure 7. Schematised procedure for assessment of the effect of damage mechanisms (dm) on crop growth and production (Bastiaans and Kropff, 1991).

Competition

Weeds compete with crops for light, nutrients and water. The amount of damage depends strongly on the timing of attack. An example is found in field experiments by Kropff *et al.* (1984). Maize biomass was lower at high densities of *Echinochloa crus-galli* than at low densities. However, while a density of 100 *E. crus-galli* plants per m^2 caused a yield loss of 8% in 1982, it caused a yield reduction of 88% in 1983 (Figure 8). Analysis with a comprehensive simulation model for crop-weed interaction showed that the difference between the two years was explained by year to year variation in time of emergence of weed and maize plants: in 1982 the crop emerged 5 days earlier than the weed and did not suffer from competition for light. In 1983, weeds emerged at the same time as the crop, which resulted in intense competition for light (Spitters, 1984). A statistical approach based on the density-damage relationship of one year would not have predicted events in the other year.

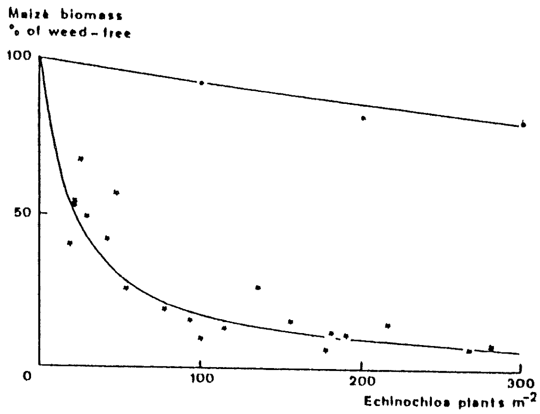

Figure 8. Final above-ground biomass of maize in 1982 (•) and 1983 (*), expressed as percentage of weed-free control, in dependence of initial density of *E. crus-galli* (Kropff *et al.*, 1984).

Decrease of the rate of photosynthesis

Many leaf pathogens and viruses decrease the photosynthetic capacity of the leaves they attack. Mites which cause minute injuries by sucking up epidermal cell contents, have a similar effect. The effect of different growth reducing factors on leaf photosynthesis can be described by a simple descriptive equation with one parameter (Bastiaans, 1991). The parameter in the equation, β, represents the ratio of a (real or imaginary) influence area of a lesion and its visible surface. The equation is valid when lesions are randomly distributed over the leaf. Application of this model to a number of growth reducing factors showed that for some leaf pathogens, such as *Phytophthora infestans* (Van Oijen, 1991), *Septoria nodorum* and *Puccinia recondita*, and for avocado brown mite, *Oligonychus punicae* (Van der Werf *et al.*, 1990) the decrease in leaf photosynthesis is proportional to the area covered with lesions, i.e. their β-values are not significantly different from 1. Similarly, for beet yellowing viruses the fractional decrease in crop photosynthesis is approximately equal to the fraction incident light which is intercepted by yellow leaves. For other growth reducing factors, for example powdery mildew, *Erisyphe graminis*, in wheat effects on photosynthesis are much larger than the fraction leaf area covered with lesions. These effects of mildew are thought to be caused by hormonal effects on stomatal regulation, since the initial light use efficiency of leaf photosynthesis is proportional with lesion cover, i.e. β equals 1, whereas for the maximum rate of photosynthesis the β-value is 6. In contrast to light utilisation at low light intensities, the maximum rate of photosynthesis is limited by the CO_2 supply and therefore by stomatal aperture. For leaf blast in rice, *Pyricularia oryzae*, β-values for both the maximum rate of photosynthesis and the initial light use efficiency exceed 1 (Bastiaans, 1991). Also for peanut leafspot (*Cercospora* sp.) β-values for leaf photosynthesis appear to exceed 1 (Van der Werf *et al.*, 1991).

Effects on respiration.

For many microscopic pathogens which multiply in leaves, an increase in leaf respiration has been described. It is often unresolved to which extent the increase is caused by processes related directly to the growth and reproduction of the pathogen, or by defense mechanisms of the plant.

Plant killing

Some pathogens, for example root fungi during seedling stages, kill entire plants. Such diseases cause substantial damage unless the crop is capable of compensating by increased tillering so that complete light interception is attained with a lower plant density. Killing of entire plants at later development stages causes damage which is approximately proportional to the number of plants lost. Using a well-tested comprehensive crop growth model, Rubia and Penning de Vries (1990) showed that killing of up to 20% of the tiller of rice cultivar IR64 at the vegetative stage, as may occur due to stem borer attack, had no important effect on grain yield, while yield loss almost equalled the proportional loss of tillers when injury occurred at the grain filling stage. Compensatory ability depends on cultivar, yield level and time of attack. At present experimental research is carried out to elucidate these relations further (Rossing *et al.*, 1993).

Tissue necrosis and interception of light.

Most leaf pathogens and some viruses cause local lesions. Eventually these lesions die off. Damage usually exceeds the loss of biomass because the dead spots continue to intercept light, and therefore, compete with other, productive tissues for this scarce resource. As a result the vertical position of the dead tissue in the canopy determines to a large extent the amount of damage. Van Roermund and Spitters (1990) analysed an experiment on yield reduction among seven winter wheat genotypes due to brown rust, *Puccinia recondita*, using a mechanistic crop growth model. Depending on the genotype, inoculation at pseudo-stem elongation resulted in epidemics of different intensity, the area under the curve ranging between 0.1×10^4 to 19×10^4 pustule-days $culm^{-1}$. Accelerated leaf and ear senescence due to brown rust accounted for 91% of total damage. Light interception due to leaf coverage by pustules accounted for less than 1%. The remainder of damage is due to assimilate uptake by the fungus (see below). Such analysis represents 'experiment-added-value' by yielding insights in the relative importance of damage mechanisms that could not have been obtained experimentally.

Tissue consumption

Many growth reducing factors consume plant organs, especially leaves. The amount of damage depends on the compensatory possibilities, which are a function of timing of attack, type of organ consumed and state of the crop. When the leaf area index is high, leaf consumption hardly reduces crop light interception and, photosynthesis and growth rate. At excessively high leaf area index values, leaf consumption can theoretically even increase growth, due to reduced maintenance respiration as a result of the reduction in biomass. Leaf consumption in the initial phase of exponential increase in leaf area can be extremely damaging because the resulting decrease in the relative growth rate leads to a delay in the moment of full light interception. As a result, potential growth rates are realised during a shorter period of time. Consumption of storage organs is very damaging, since plants usually lack compensatory potential. An indirect effect of leaf consumption is that the competitive position with respect to weeds deteriorates.

Assimilate consumption

Aphids suck up phloem sap and decrease the amount of assimilates available for respiration and growth. In addition, uptake of amino compounds may disrupt nutrient balances. During the exponential growth phase, assimilate tapping insects can delay the growth of leaf canopy as was shown in experiments (Hurej and Van der Werf, 1993) and through modelling (Groenendijk *et al.*, 1990). Assimilate tapping during the linear growth phase decreases the daily growth rate, especially due to uptake of sugars. A large part of the sugars consumed by aphids is excreted in the form of honeydew, because aphids regulate their rate of uptake of phloem sap such that they obtain sufficient amounts of amino acids, which occur only in low concentrations in phloem sap. The excreted honeydew seals off stomata, it can accelerate ageing of leaves and it enhances the pathogenicity of saprophytic and pathogenic fungi. Combined, these mechanisms can reduce the rate of photosynthesis. Detailed production ecological analysis showed that honeydew excreted by *Sitobion avenae* in winter wheat constitutes an important damage component, especially at very high production levels (Rossing, 1991).

Bastiaans and Teng (1994) showed that assimilate uptake by sporulating lesions of the fungus *Pyricularia oryzae* in rice under certain conditions accounts for about 20% of the damage. Assimilate uptake by *P. recondita* in winter wheat was found to account for 9% of total damage caused by brown rust (Van Roermund and Spitters, 1990; see above).

Hampering of water uptake

Root pathogens, such as *Verticillium* spp., and also nematodes, reduce crop growth by affecting the uptake of water. This may result in stomatal closure and reduced crop transpiration. Concomitantly, assimilation rate is reduced.

Induction of hormonal effects on stomatal regulation.

Cyst nematodes appear to change stomatal behaviour of injured plants, even before water uptake is substantially decreased. The hypothesis has been put forward that release of abscissic acid by the roots in response to nematode colonisation induces these stomatal effects (Schans, 1992).

Deformations

Sucking insects often cause deformations. Sometimes, components with hormonal activity in the saliva of the insects play a role. Organ deformation itself can be a damage component if it concerns the harvestable parts. Leaf deformations such as aphid-induced curling can cause damage indirectly by decreasing light interception.

The typology of damage mechanisms is not exhaustive and may change as knowledge accumulates about the ways in which biotic and abiotic factors reduce crop growth. The examples illustrate the major damage mechanisms and underscore the importance of a systems approach in which models are used to increase understanding of the relative importance of various interacting processes for damage. Those same models are practically valuable because they may be used to explore how damage is affected by environmental conditions, the timing of attack and by control measures at different times.

Biotic growth reducing factors: Population dynamics

The size of yield reduction caused by biotic growth reducing factors is a result of their effect on crop growth processes and their population dynamics. Broadly, in population dynamical analyses emphasis may be on phenology, the development of individuals through various life stages, or on intensity, the time course of the density of the growth reducing factor in time and space. Understanding of the processes which determine development is still rudimentary.

However, for many growth reducing factors adequate models have been developed which describe the relation between phenology and external factors. Usually, temperature is the dominant factor governing developmental processes once a growth reducing factor has established a feeding relationship with the host. To allow infection, special environmental conditions may be required, for example with regard to relative humidity, leaf wetness period and photoperiod. In many crop systems descriptive phenological models have found a place in predicting the timing of critical events for crop protection at the field level. A recent overview of approaches and applications in western Europe is given by Secher *et al.* (1993).

The current understanding of the dynamics of the intensity of many growth reducing factors is still poor, mainly due to lack of insight in the biotic mortality factors that operate at the field level. From the progress made in entomological research on biological control it is evident that even in systems involving only one pest and one predator or parasitoid a large number of variables determines pest mortality. Simple approaches such as the classical Lotka-Volterra models are of some value in exploring general properties of biological control systems (Janssen and Sabelis, 1992; Van der Werf *et al.*, 1994), but they fall short in analysing the behaviour of specific systems because they disregard environmental influences, such as temperature, and important behavioural components at the individual level. Mechanistic models, that include descriptions of behaviour at the individual level are better suited fo. analysing behaviour of specific systems. The behaviour of predators and parasites is governed by their 'motivational state', which is strongly related to and can be modelled as the contents of a predator's gut (Fransz, 1974; Rabbinge, 1976; Sabelis, 1981; Mols, 1993) and a parasite's ovarioles (Van Roermund and Van Lenteren, 1994). Pest mortality due to predation or parasitisation is simulated depending on abiotic environmental conditions and pest distribution. Sensitivity analyses show how the likelihood of biological control is affected by traits of the plant host, pest or natural enemy. Simulations with a mechanistic model of the epidemiology of the insect baculovirus SeNPV in a population of beet army worm, *Spodoptera exigua,* in chrysanthemums show at which time virus sprays can be best applied to obtain highest pest mortality (Van der Werf *et al.*, 1991). Also for pathogens, mechanistic approaches lead to better understanding of system behaviour. Van der Werf modelled spatial spread of virus yellows in sugarbeet by simulating walking behaviour and virus transmission of individual *Myzus persicae,* the vector (Van der Werf *et al.*, 1989). The results of the preliminary model show a striking asynchrony between the presence of aphids and the appearance of yellowing symptoms (Figure 9), and indicate that there is scope for reducing the rate of virus spread by biological control of the aphid vector. In another example of a production ecological study Van Oijen (1991) set out to identify the major characteristics of potato cultivars which affect yield reduction by *Phytophthora infestans.* Sensitivity analyses showed that relative growth rate of a *Phytophtora* epidemic is determined to a large extent by the radial growth rate of the lesions. Since radial lesion growth is a process for which genotypic variation exists in *Solanum* spp., such production ecological studies are now used to guide breeding programmes.

So far, only approaches and applications at the field level were discussed. At the regional and supra-regional levels equally promising advances have been made. Combination of phenological models and climatic data using Geographical Information Systems provide insight into the risk of establishment of exotic pests (Sutherst, 1991). Such quantitative approaches can be used to focus quarantine efforts. When used in combination with different climatic change scenario's, changes in risk can be explored. An example is the assessment of the risk of re-establishment of malaria and malaria vectors in southern Europe, as a result of anticipated global warming (Jetten and Takken, 1994).

Understanding of epidemics at field-regional and supra-regional scale has benefited greatly from relatively simple and mathematically tractable models for the rate of advance of the epidemic wave fronts and the shape of those fronts (Van den Bosch *et al.*, 1988a,b, 1989). However, because these analytical models assume constant dispersal properties of disease and constant spore production rate and infectivity they are not very practical. For more practical types of analysis in spatial epidemiology, simulation approaches are needed. For instance, Zawolek (1989) uses simulation to investigate the consequences of stochasticity and dual spore dispersal mechanisms on formation of plant disease foci. Earlier on, enlightening simulation studies with a spatial model were conducted by Zadoks and Kampmeijer (1977). These simulation approaches which were developed at the field level, were in a very preliminary sense also applied at the (supra-)regional level.

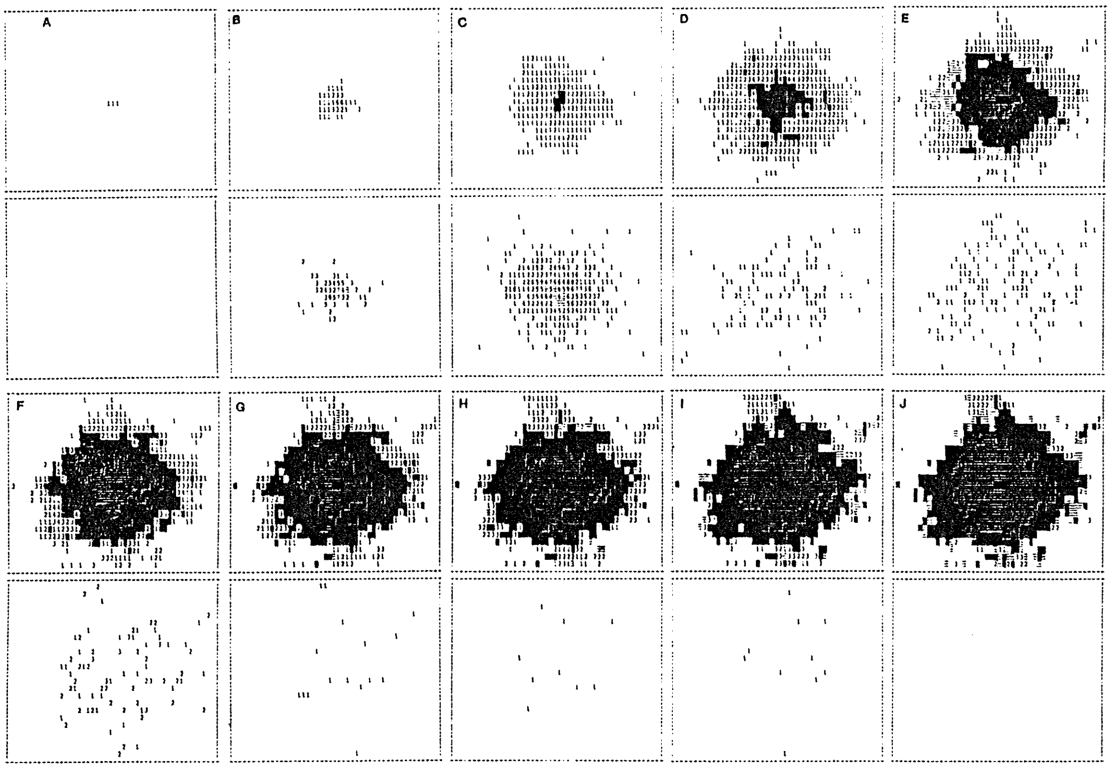

Figure 9. Simulated spatial spread of beet yellows virus in sugar beet by dispersing vector aphids, *Myzus persicae*. The simulation shown here represents an experiment in which three plants in the centre of a 12 x 12 m^2 field plot were inoculated with BYV on 23 June and after two days infested with 9 *M. persicae*. Duplicate graphs indicated by the letters A, B, C... show the simulated state of a plot at two week intervals. The upper graph of each 'duo' represents the spatial distribution of virus-infected plants, while the lower graph gives the spatial distribution of the aphids. In the upper figure, numbers indicate the proportion of leaf area infected with virus: (0): 0-0.1; (1): 0.1-0.2; etc. A shaded block indicates that the plant has symptoms. The type of shading indicates the proportion of infected leaf area: (⁝⁝⁝): 0-0.3; (▒): 0.3-0.6; (▦): 0.6-0.9; (■): >0.9. In the lower figure, numbers indicate the density of aphids per plant. Densities higher than 9 per plant are indicated with a shaded block (⁝⁝⁝).

SYSTEMS MANAGEMENT

Farm management requires a major managerial effort at various levels of integration. We distinguish the levels of the farmer and the policy maker. At both levels the overall objectives are to ensure economically and ecologically sustainable agricultural production in the long term.

At the farm level a farmer's decisions include choice of crops to be grown, timing of selling, buying or storing products, and long-term investments in buildings, infrastructural changes and farming machinery. At this level, decisions are greatly affected by market situation and commodity prices. Ecological considerations have to be taken into account to guarantee the sustainability of the farm and to protect the environment. Constraints at this level comprise public regulations and private considerations on what is ecologically acceptable and sound. Decisions at the farm level set the constraints for decisions at the crop level.

At the crop level, the farmer must decide on crop variety, and on the timing and methods of seed-bed preparation, planting and harvesting, amount and frequency of fertiliser application and control of pests, diseases and weeds. The majority of these decisions are based on experience, perception and preference, and can be supplemented by insight supplied by agricultural research, education and extension.

At the policy level, various instruments are available for stimulating desired developments in crop protection at the (supra-)regional level. Product price regulations, land set-aside schemes, subsidies on inputs, and cultivar or pesticide registration procedures are but a few examples. Although discussions tend to focus on the instruments, first decisions on the objectives of crop protection policy as part of agricultural policy should be made. General objectives concerning sustainability should be made operational to enable evaluation of the effectiveness of the various instruments.

The current availability and use of external resources in agricultural production, such as artificial fertilisers, pesticides and machinery, is unprecedented in human history. As a consequence, historical experience is of little use for optimising management of current agricultural production systems. Since the 1950s quantitative knowledge of biological and agronomical consequences of a farmer's decisions increased dramatically, not only in industrialised agriculture but also in low input agriculture in many developing countries. An important part of these decisions concern crop protection. Pesticides have been the main instrument in crop protection since their large scale introduction, almost half a century ago. Decisions to apply pesticides usually occur at the end of a chain of decisions leading to a certain crop in a certain field. No feedback exists with decisions on, for instance, nitrogen fertiliser rates which may affect the occurrence of economically damaging levels of growth reducing factors. Thus, chemical pest control became the 'fudge factor' of crop production, and was used to correct previous agronomic decision errors. This role was made possible by the fact that costs of chemical control usually concern a small fraction of total production costs for a farmer. However, the use of pesticides causes major public costs, such as poisoning of non-target organisms, including man, pollution of soil, air and water, and occurrence of pesticide-resistant noxious organisms. Public concern about these issues has resulted in reconsideration of the objectives of crop protection, and the place of crop protection decisions in the hierarchy of agronomic decisions at field and farm levels. Increasingly, crop protection is considered as an integrated part of on-farm decision making which aims at optimising both economic and ecological sustainability criteria. To assist in improving decision making in crop protection, production ecological approaches have been developed.

Decision support at the farm level

Decision support at the farm level has been oriented predominantly towards solving tactical decision problems. Recently, the much broader goal of improving the general level of production ecological knowledge through training has attracted attention.

Production ecology and tactical decision support

Sound systems of tactical decision support comprise four building blocks: epidemiological relations, damage relations, sampling and monitoring methods and cost/benefit/risk analyses. An example of such system is the supervised control system EPIPRE, which provided recommendations on aphid and disease control in winter wheat in the Netherlands for over 15 years (Zadoks, 1989). We will use this system to illustrate the role of production ecology in farmer oriented decision support.

To develop epidemiological relations for forecasting, stage-structured simulation models were first used to investigate the extent to which the population dynamics of aphids and diseases were understood. For example, quantitative models of the diseases *Septoria tritici*, *Erysiphe graminis*, and *Puccinia recondita* showed that far fewer lesions developed in field experiments than was expected, using life-table data (Internal Reports, Department Theoretical Production Ecology). Moreover, the difference between simulated and observed disease progress appeared to vary per field. Sensitivity analyses of the epidemiological models showed that field specific factors affecting spore production, spore dispersal and host penetration were insufficiently understood or not quantified accurately enough. Therefore, for forecasts in EPIPRE, simple exponential models were used which were calibrated on field data using regression analysis.

Damage mechanisms of wheat diseases and aphids were studied in laboratory and field experiments, using mechanistic models of crop growth as a means of quantitative hypothesis testing. For *Puccinia recondita* and *Erysiphe graminis* these studies served to corroborate and extrapolate empirical damage relations used in forecasting. For aphids, damage relations derived from a wheat growth model into which uptake of assimilates by aphids and decreased leaf photosynthesis by honeydew were introduced, were as accurate as empirical damage relations derived from 15 years of field data obtained on more than 20 locations (Rossing, 1991). The mechanistic nature of the model and the inclusion of the effect of nitrogen shortage on growth and development, enabled assessments of damage at lower attainable levels of crop production. Similar studies have been carried out for other growth reducing factors, e.g. weeds (Kropff and Van Laar, 1993).

Key element in any supervised control system is an appropriate sampling and monitoring procedure to quantify the density of the damage causing organism. Sampling and monitoring approaches pragmatically utilise sample size and sampling frequency to compensate for the lack of understanding or predictability of system dynamics. Statistical theory and biological expertise are combined to derive sampling protocols which meet the requirements of simplicity, biological soundness, low labour requirement, compatibility with other crop management activities, and low costs relative to the value of the product (Rabbinge and Mantel, 1981). These requirements also apply to the monitoring protocol, the sequence of sampling protocols in the course of a growing season. In EPIPRE, forecasts of pest density and associated damage were updated using the sampling information on pest incidence collected by the farmer. In this way, field-specific prediction errors were kept in check. This updating procedure is known in operations research as decision-making with rolling planning horizon. Sample size, the number of tillers or leaves to be inspected, was chosen such that an acceptable coefficient of variation would be attained at densities close to the damage threshold. To minimise sampling effort absence/presence sampling methods were developed. Sampling intervals were adjusted to the actual situation so as to account for crop age, disease severity and its rate of change. Recently, further advances have been made in minimising not only the size of one sample, but also the number of sampling occasions needed during a growing season (Nyrop and Van der Werf, 1993). Basically, the smaller the estimated pest intensity during a sampling occasion relative to the damage threshold, the longer the interval before a next sampling need be taken. More uncertainty about future progress of the population and the concomitant damage results in shorter sampling intervals. The authors showed that such 'multipartite sequential classification' or 'adaptive frequency classification' can decrease the risk of erroneous (in)action which is caused by uncertainty in sampling estimates (Figure 10).

Analyses of costs, benefits and risks are needed to select the decision which best meets the objectives of the farmer. Recommendations are often implicitly tuned to reflect risk-averseness of the decision maker, but no explicit information is supplied on the uncertainty of the forecasts. An alternative approach is to present the riskiness of decision alternatives (Figure 11), and leave the choice of the best decision to the farmer (Rossing *et al.*, 1994).

Production ecology and training at the farm level

Evaluations of the EPIPRE system (e.g. Blokker, 1983) showed that farmers appreciated the educational aspects of EPIPRE even more than the (marginal) financial savings. Learning about the crop and its relations with the environment appears prominently in modern systems of farmer-oriented decision support. For instance, successful introduction of IPM in Indonesia was achieved through field schools of farmers at the village level, in which farmers exchanged experiences on level and regulation of pests and their natural enemies, and consequences for yield (Van de Fliert, 1993). Somers and Röling (1993) evaluated a number of projects in the Netherlands aimed at reducing the level of nutrient and pesticide inputs per unit area. They conclude that the adoption of such innovative production systems can only be achieved through a learning process which involves both farmers and extension agents, and during which there is a gradual change of

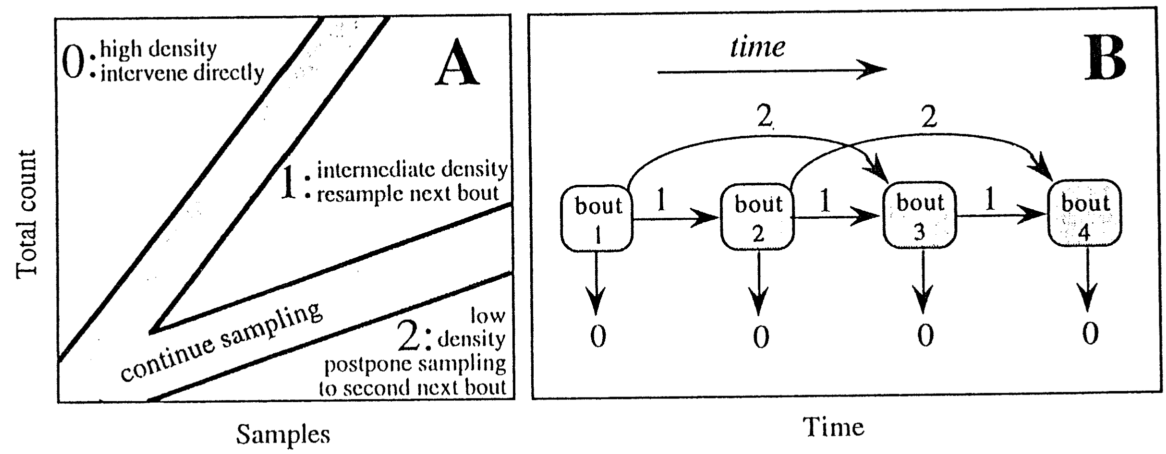

Figure 10. Example of a pest monitoring method that schedules sampling in time in a flexible way. Sampling is done sequentially and uses the double SPRT method (Figure 10A). (SPRT is the acronym for Sequential Probability Ratio test.) The double SPRT method has three alternative decisions: (0): density is currently high and requires an intervention; (2): density does not require immediate intervention, but sampling should be repeated soon to make sure that pest density still falls within acceptable limits; (3) pest density is quite low such that resampling can be postponed further into the future. Depending upon the outcome of sampling, the pest population will be monitored more or less frequently (Figure 10B). The performance of monitoring schemes using double SPRT or alternative sampling protocols can be simulated. The performance criteria are: 1. probability of intervention; 2. number of sampling bouts actually scheduled; 3. total number of samples in all bouts; 4. cumulative pest/disease density (average and percentiles); 4. density at intervention (average and percentiles). The outcomes of such simulations are similar to field tests of the monitoring protocol applied to European red mite, *Panonychus ulmi*, in apples.

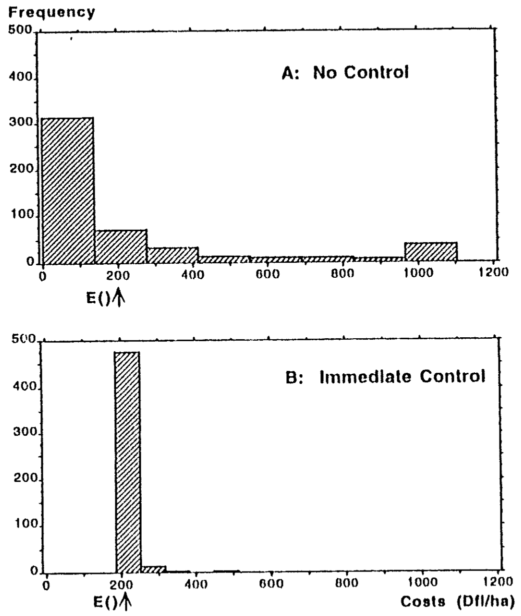

Figure 11. Simulated frequency distribution of costs of no chemical control (A) and immediate chemical control of aphids and brown rust jointly (B) in winter wheat, in 500 Monte Carlo runs. Initial state of the system: crop development stage 'full ear emergence', aphid incidence 5% of tillers, brown rust incidence 2% of leaves. Expected costs in (A) and (B) (indicated by arrows) are the same, implying that the initial state of the system represents a damage threshold.

objectives, targets and risk perception. This process differs from the adoption of single production techniques, such as mechanical weeding, in which the rate of adoption depends on the technical and entrepreneurial inclination of the farm community. Optimal adjustment of crop protection decisions in relation to other farm management decisions, represents a complex decision problem which requires highly skilled and trained farmers. As a consequence the role of extension changes from, traditionally, technology transfer and problem solving to facilitation and human development (Somers and Röling, 1993). In the examples from Indonesia and the Netherlands, the role of the extension service was to participate in and facilitate the learning process, rather than to provide prescriptive recommendations. Thus there is a shift from top-down to bottom-up approaches.

Production ecological knowledge can play an important role in these learning processes, since quantitative models provide a framework for evaluating 'what-if' questions about consequences of different levels of pest attack during various periods of the growing season. Well-tested models can be used to explore crop response under various environmental conditions. Such exploration helps to develop the intuition of decision makers with regard to ecological relations in a crop system. Similar applications of production ecological principles have been developed for formal teaching at the Wageningen Agricultural University (Rabbinge and Eveleens, 1993) and elsewhere. The explanatory nature of the models represents an essential requirement since it enables application under widely different environmental conditions. Development of a suitable interface between model and trainee calls for both production ecological knowledge and agricultural education expertise, and usually requires considerable intellectual and programming labour.

Decision support at the policy level

In the area of policy-oriented decision support explorative land use studies have shown much potential in demonstrating the consequences for land use of explicit objectives with respect to economic and ecological sustainability. Because ecological and short-term economic objectives are often conflicting, formulation of agricultural land use policy involves searching for acceptable compromises. Then, questions arise concerning the trade-off between, for instance, minimising pesticide input and maximising production levels in different production situations. To answer these questions, quantitative knowledge on production technical and production ecological relations in production systems is needed, in combination with information on the suitability of an area for different types of land use. The suitability of an area is assessed in a qualitative land evaluation. During this phase, information on climate, soil features such as texture, slope and drainage, and infrastructure is combined to arrive at an assessment of the production situation. In the next, quantitative phase, the production situation combined with predefined production technology results in a production level. For each production situation, production levels under irrigated, rain-fed and nutrient limited conditions can be distinguished. Production levels are formulated according to the concept of 'best technical means', implying that inputs are employed as efficiently as possible. For the definition of production technologies primary and secondary inputs are distinguished. For primary inputs such as water and nutrients substitution is scarcely possible. For secondary inputs, such as weeding technologies, substitution is possible. Depending on the time horizon of the study, current, experimental and theoretical production technologies are included. Finally, a linear programming model is used to find the mixture of production systems which provides the optimal compromise of objectives.

In a study of options for land use in the European Community the Netherlands Scientific Council for Government Policy (1992) analysed the scope for agricultural policy in the EC in the next 20 to 25 years. Four policy scenarios were formulated, based on main positions in the current political debate: (1) free trade and free market, (2) regional development, (3) nature and landscape and (4) environmental protection. The outcomes of the four scenarios showed that the continuing rise in productivity results in increasing land surpluses and further loss of jobs in agriculture, irrespective of policy. It also appeared that there exist good possibilities for more environmentally friendly agricultural production, which uses less than 25% of the current volume of active ingredients and fertiliser nitrogen. The concomitant production systems are characterised as highly productive with maximum use of eco-technological principles and biological purgatory tools, such as resistant and tolerant cultivars, high recovery of nutrients, biological control, sound crop rotations, 'catch crops' to minimise nutrient leaching, and combination of arable and animal husbandry with approximately closed nutrient cycles. Supra-regional land-use studies are envisaged for other regions, e.g. Tamil Nadu in India.

Land evaluation studies, whether at the supra-regional or at the regional and farm levels, have a bright future. They provide a framework for exploring management options at the farm and higher levels of integration, utilising production ecological knowledge at the crop and cropping system level. At the same time they provide an instrument for research prioritisation, by determining the relative importance of the lacks of information about various aspects of production systems for the outcome of the study.

In conclusion, the production ecological approach provides instruments for systems studies at different levels, which can be used to clarify the consequences of decision alternatives for the objectives of management, and thus provide a rational basis for decision making.

INSTITUTIONALISATION OF PRODUCTION ECOLOGICAL APPROACHES

The production ecological approach requires a new type of agronomists, and more specifically, also a new breed of crop protection scientists. Systems analysis comprises an analysis phase and a synthesis phase. The analysis phase is compatible with the traditional reductionist scientific method, which produced the disciplines entomology, phytopathology, nematology and virology. The synthesis phase, however, necessitates a generalistic approach with interdisciplinary work at different integration levels. This means that the traditional borders between, for example, entomology and phytopathology disappear, and organism-oriented approaches need to be replaced by system-oriented methods. The result may be crop protectionists who combine sufficient understanding of specific patho-systems with affinity for general unifying concepts and their application in practical crop protection. An example of capacity building in production ecology along these lines is the ongoing project SARP, short for Systems Analysis and simulation in Rice Production. We will discuss the approach in this project and outline its mid-term results.

Outline of the SARP project

SARP was started in 1984 by national agricultural research centers (NARCs) in south, east and south-east Asia, the Centre for Agrobiological Research in Wageningen (now: Research Institute for Agrobiology and Soil Fertility (AB-DLO)) and the Department of Theoretical Production Ecology of the Wageningen Agricultural University (WAU-TPE), in collaboration with the International Rice Research Institute (IRRI). Aim of the project was and is to build research capacity in the field of systems approaches at the NARCs and at IRRI with the help of modern systems research techniques. This goal is rooted in the proposition that research efficacy and efficiency can be much enhanced by a systems approach. The long-term goal is to further enhance sustainable productivity of rice-based systems. Staff time is contributed by participating institutes. Funds for training, exchange of scientists, and coordination are contributed by the Directorate General for International Cooperation (DGIS) of the Dutch Ministry of Foreign Affairs.

During the first two phases, before 1991, three training programs were held under SARP auspices. In total 91 researchers from 16 NARCs throughout south-east Asia and IRRI (Figure 12) were trained in the use of systems analysis and computer simulation modelling as a tool in their research activities. Some of these teams have later organised their own national training courses for sister institutes, the so-called second generation teams (Figure 12). Training was followed by case studies within the informal SARP network, to actively introduce the approach in the NARC's research programs. Case study topics were selected by the participants in accordance with ongoing research at their institutes. During the case studies the teams were visited by SARP staff for technical and scientific support.

Trainees were always part of a team with a critical mass of at least four researchers from the same NARC. At least one member was a crop physiologist. The other members came from various disciplines. Each team had the support of a senior scientist, the team supervisor who maintained close links with the NARC's research policies. One of the scientists in the team was selected to be team leader. Each team consisted of different disciplines to ensure a focus on the rice *system*, rather than carrying out research in the traditional *disciplines*, with a major risk of neglecting important system aspects. Various workshops and a closing conference in Bangkok were organised. A substantial number of publications show the results of the training period 1984-1991. A detailed review of the project is given by Ten Berge (1993).

SARP's third phase covers 1992 to 1995. Emphasis is placed on collaborative research. From the training programs four themes emerged as a framework for collaborative research:

- agro-ecosystems: agro-ecological zonation, timing of crops and crop sequences, optimisation of regional water use;
- potential production: crop responses to light and temperature, development and morphogenesis;
- crop and soil management: water and nitrogen management for different soils, rice varieties, plant spacing, plant establishment;
- crop protection: mechanisms of damage by pests and diseases.

The aims in the third phase of SARP are:

- to reinforce the teams and to support joint research programs within the informal network;
- to develop applications at the crop and agro-ecosystem level aimed at both policy makers (e.g. through studies on agro-ecological zonation), and extension workers and farmers (e.g. by directing research to development of tools for advice on nitrogen and pest and disease management);
- to support national training programs when they arise;
- to transfer coordination of the project to NARCs and IRRI.

Participants in the crop protection theme prioritised a few pathosystems for joint research: the insect pathosystem rice-stem borer (SB, five species are of economic importance), the

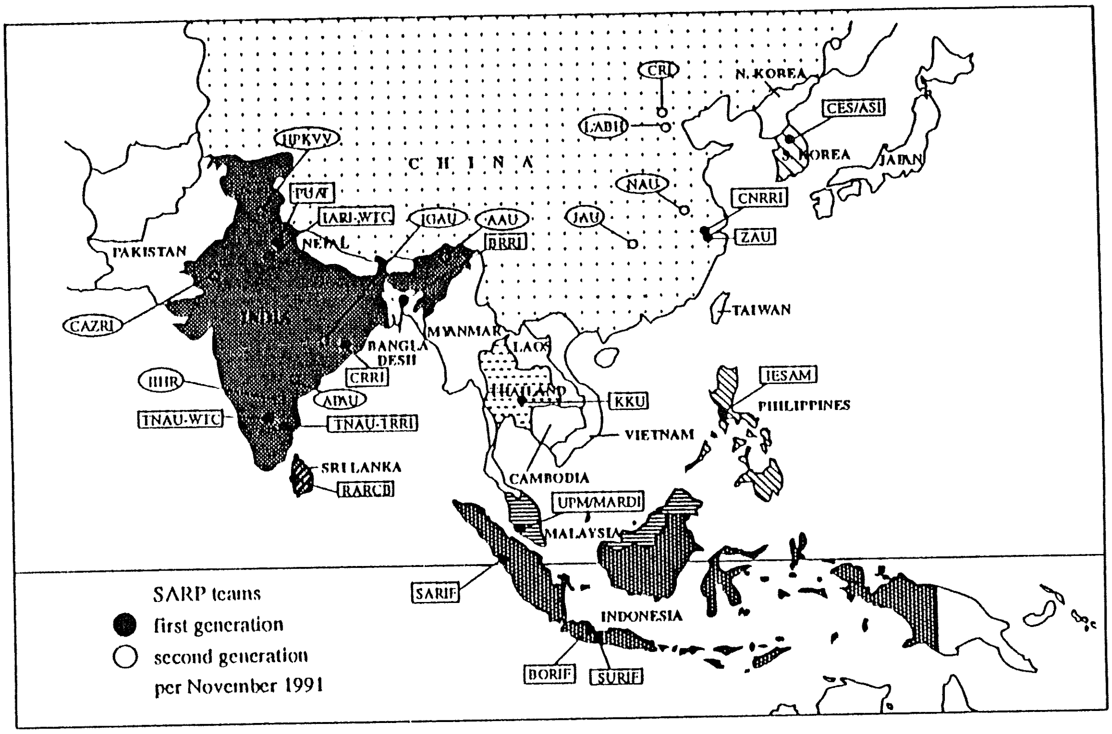

Figure 12. Geographic distribution of National Agricultural Research Centres (NARCs) that participated in training programs of SARP: Systems Analysis and simulation in Rice Production.

bacterial pathosystem rice-bacterial leaf blight (BLB, *Xanthomonas campestris* pv. *oryzae*), and the fungal pathosystem rice-sheath blight (ShBl, *Rhizoctonia solani*). Criteria used in the selection procedure included the number of teams that was already actively involved in research on the pathosystem (reflecting, among others, the economic importance of the pest and the disease), the current state of knowledge on damage mechanisms, and the scientific support available at IRRI and in Wageningen. A research agenda was developed during workshops and a priority was given to research into damage mechanisms and field experiments aimed at testing the crop models. Since quantification of damage mechanisms often requires specialised equipment, appropriately equipped institutes were identified. For the validation experiments a joint experimental procedure was agreed upon to optimally utilise the project's network character (Rossing *et al.*, 1993).

SARP's impact on NARCs

The mid-term results of SARP's approach for institution building were evaluated in a workshop organised in December 1993 by ISNAR under co-sponsorship of ICASA (International Consortium for the Application of Systems approaches in Agriculture) and the Dutch Ministry of Development Cooperation (Goldsworthy and Penning de Vries, 1994). The institutionalisation process and the collaboration between NARCs, IRRI, WAU-TPE and AB-DLO was characterised by ten features, that contributed substantially to the successful assimilation of systems approaches by the NARCs:

- training of teams, rather than individuals
- commitment of the NARCs to integrate systems analysis in their institutional approach
- intensive initial training during six weeks
- case studies by teams in their home institutes
- backstopping of the teams
- guaranteed availability of appropriate equipment and funding for experiments
- communication between NARCs, IARCs and advanced research organisations
- networking initialised by IRRI
- continuous involvement of the supervisors, representing the management of the institutes; and last but not least
- a very enthusiastic group of scientists convinced of the need for a systems approach and capable of creating a productive atmosphere.

The production ecological procedures and approaches that were implemented in many research centres in Asia will help to introduce economically competitive, environmentally friendly, agronomically advanced and ecologically sound integrated pest and disease management systems. The ultimate aims of agricultural research may thus be brought one or two steps nearer.

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