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The bridge function of crop ecology

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Introduction

In September 1985 the Agricultural University of Wageningen introduced crop ecology as the first common chair in academic education in the Netherlands.

The term 'crop ecology' comprises the terms crop — plants or fruit grown for specific anthropocentric purposes — and econology, the study of interactions between plants and their relations with the biotic and abiotic environment. Crop ecology, therefore, may be defined as the study of the relations between crops and their environment. It is an interdisciplinary field that combines information from various disciplines. It bridges gaps between basic sciences such as plant physiology, plant ecology, environmental physics and chemistry on the one hand and the applied agricultural sciences such as agronomy, crop protection, plant breeding, soil science and plant nutrition on the other.

This strengthening of the common basis of crop production in various fields started with the creation of the Department of Theoretical Production Ecology in 1968. The research covers not only the behaviour of a system as a whole but also the basic processes underlying this behaviour. Knowledge of these general principles provides considerable insight into the behaviour of whole systems. For example, the effects of changes in N fertilization are studied not only by means of measurements of the resulting changes in crop yield but also by examining details of plant physiology and ion transport in the soil. In crop ecology the emphasis is on analysis of the consequences of these processes in crop growth and development, and not simply on structured description.

The approach to be used depends on the subject of study. In the past simulation models have been valuable as integrative tools to provide insight into the behaviour of systems. It is thus an appropriate method in this interdisciplinary field, although other approaches are also possible. Crop ecology requires close cooperation between agronomists, crop protectionists and workers in the basic sciences such as physics, chemistry and biology. This is illustrated in the following examples.

Crop growth and production

Growth, the increase in the quantity dry matter, is expressed per plant in individual plants and per m^2 in crops. The most important above-ground factors influencing plant growth are temperature, radiation, humidity, wind speed and CO_2 concentration in the air. When factors such as nutrients and water are abundant and damaging factors such as pests, diseases and weeds are absent, the 'potential growth rate' is achieved. This is determined by the optical, geometrical, physiological and phenological characteristics of the crop and the prevailing weather conditions. Computations confirmed by experimental observations have shown that under these circumstances the growth rate in dry matter reaches values between 150-250 kg ha^{-1} day^{-1}. Thus, if the growing season has a length of about 100 days (as in the Netherlands), the potential biomass production reaches values between 15 and 25 tonnes dry matter per hectare. In such conditions, research is concentrated on the basic principles of energy absorption and CO_2 assimilation, and on crop morphogenesis. This knowledge can then be used to improve the manipulation of environmental factors, such as temperature, humidity and light intensity in glasshouses, to achieve maximum production without excessive energy costs. In glasshouse horticulture technical manipulation of environmental conditions is no longer in its infancy. However, lack of detailed knowledge of the processes determining the growth of these crops limits the fine-tuning which is technically possible. Various projects of the Department of Theoretical Production Ecology and the Centre of Agrobiological Research are intended to provide more insight into these processes under various constant and fluctuating abiotic conditions. CO_2 assimilation, respiration (for maintenance and growth) and transpiration are studied in detail for that reason. In some cases, studies at subcellular level are needed, such as those on maintenance respiration and carboxylation resistance. These studies, however, are limited in number and size; information currently available should suffice to provide the insight needed to manipulate the crops to achieve maximum returns at low cost. In protected crops potential yield levels may be reached. This, however, rarely or never occurs under field conditions. The difference between potential and actual yields is very large. More than 99 % of the world's agriculture is carried out in conditions in which at least one growth factor is limiting. Water or nutrients, or both, are not at optimal levels, so that growth during parts or all of the growing season does not reach its potential level. A considerable part of the crop production in the world takes place at the minimum yield levels of 800 kg grain equivalents per ha.

In Table 1 four production levels are distinguished and some characteristic values given. For these computations a typical transpiration coefficient of 300 kg transpired water per kg dry matter produced was used, and a minimum level for nitrogen of 1 % and for phosphorus of 0.05 % is assumed. The levels indicated in Table 1 seldom occur in this schematized form. Water may be so limiting that total dry matter production is lower than at level 4, so the indicated levels are merely rules of thumb. In practice many other sets of conditions may be encountered.

Level 1 occurs very rarely. Most agricultural research (in both the laboratory and the field) is concentrated on this production level. This is understandable, since many processes in agricultural production are affected by suboptimal conditions, so it is sometimes unclear whether real effects or 'noise' are being measured. Traditional agricultural research is based on the 'dose-effect' approach, i.e. factors are varied and the behaviour of the system as a whole is studied. By using sophisticated statistical methods and intelligent experimental layouts the effects of several fac-

Table 1. Four production levels (after: de Wit & Penning de Vries, 1982).

Production level (situation)	Limiting factor	Growth rate × period	Total dry matter production in a growing season, under Dutch conditions (kg ha^{-1})
1	radiation (growth rate) and temperatue (length of growing) period and weather)	200 kg ha^{-1} d^{-1} × 100 d =	20.000
2	water: e.g. 300 mm available transpiration coefficient 300 kg H_2O per kg dry matter	ca. 200 kg ha^{-1} d^{-1} × 50 d =	10.000
3	nitrogen: e.g. 50 kg N per ha available lower-limit nitrogen 1 % N		5.000
4	phosphorus: e.g. 1.5 kg P per ha available lower-limit phosphorus 0.05 % P		3.000

tors and their interactions can now be studied, provided the experimental fields are homogeneous. In addition to these measurements of end-results, analysis during the growing season is performed increasingly often. These more detailed descriptions yield more insight into the basis of the effects. However, they do not necessarily result in more understanding of the causal relations between photosynthesis, respiration or transpiration and the behaviour of the crop as a whole. More detailed studied are needed to attain such insight.

Increase of production requires both understanding and external resources. The external resources are needed for agricultural activities, such as fertilization, water management and improvements to structural conditions of the crop, and for crop protection measures. Use of these resources requires time, care and insight. Without physiological and agronomical knowledge some farmers with 'green fingers' are able to reach high production levels. Others, however, take wrong decisions, or time them wrongly. The development of the knowledge required to improve agricultural production, and the formulation of new perspectives, are the major tasks of agricultural research. Side-effects of agricultural production that may threaten its continuity should be removed, energy efficiency improved, biocide use reduced and other goals such as landscaping maintained. What has been achieved through a combined effort of research, education, extension and, last but not least, farmers' initiatives is illustrated by the increase of wheat production in the Netherlands per unit of surface since 1850 (Fig. 1). There is a continuous increase, with at two times a shift in rate of growth. The first, at the beginning of this century, resulted from the introduction of new cultivars and artificial nitrogen fertilization. The second, much greater, discontinuity in the Netherlands, but also in other parts of Europe and the United States occurred just after World War 2 and can be characterized as an unno-

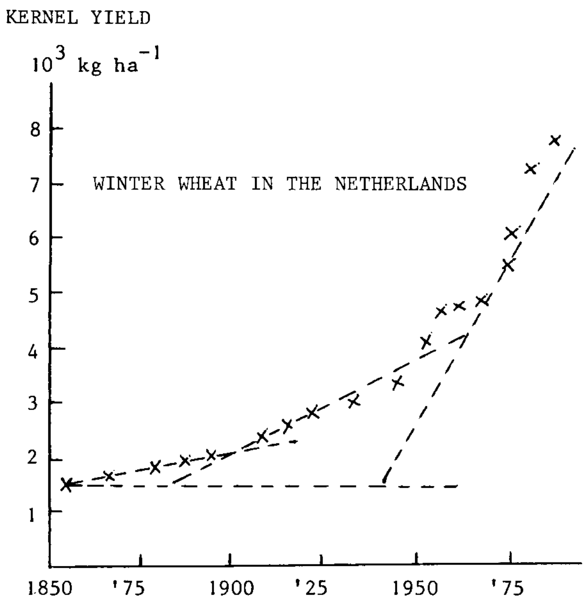

Fig. 1. Average yield of winter wheat in kernels (kg dry matter per ha) for the Netherlands from 1850 to 1985.

ticed green revolution; it was a consequence of advances in several areas. Plant breeders introduced the short-straw cultivars developed by Heine during the second World War; nitrogen fertilization and its application were improved by plant nutritionists; and herbicides (and later insecticides and fungicides) were introduced by crop protectionists.

There was not only an enormous increase in yield but also an increase in labour productivity due to mechanization and an increased use of other external resources such as fertilizers and biocides. Around 1900 the production of 1 tonne of wheat required 300 man-hours, whereas in intensive modern agriculture the same amount of wheat requires no more than 1.5 man-hours.

The increase in efficiency of labour was due to better knowledge and to the increased use of fossil energy for mechanization, infrastructural activities, fertilization and crop protection. However, the increase in production and labour efficiency did not lead to a decrease in energy efficiency. On the contrary, the energy efficiency increases at higher yield levels. This was demonstrated by Pimentel (1984) in a comparison of various ways of cultivating maize. A high-yielding American maize farm with a high energy consumption is three times more energy-efficient than the traditional farm in Mexico, where the work is done by hand or with the help of animal traction and no industrial fertilizers are used (Table 2). The increase in production and the higher efficiencies led de Wit in 1972 to the conclusion that higher yields per unit of surface will lead not only to a reduced use of land per unit of product, but also to more efficient use of many, perhaps all, external production

Table 2. Energy production and direct plus indirect use of energy, including human labour and animal traction, in maize cultivation under four different conditions, according to Pimentel (1984).

	N use ($kg\ ha^{-1}$)	Yield ($kg\ ha^{-1}$)	Output ($MJ\ ha^{-1}$)	Input ($MJ\ ha^{-1}$)	Output/ input
Mexico					
human labour only, no industrial fertilizers	0	1944	289	394	0.73
Mexico					
human labour, oxen, no industrial fertilizers	0	941	140	193	0.73
USA					
human labour, horses, industrial fertilizers	152	7000	1026	1118	0.92
USA					
human labour, machines, industrial fertilizers	152	7000	1026	481	2.13

sources. Calculations, experiments and the development of agriculture in some places since 1972 have confirmed de Wit's conclusion. This is a result of the effects of various agronomic measures on growth and production, such as fertilization in various conditions of production or reclamation levels (Wolf, 1986). This is illustrated in Fig. 2 (Wolf, 1986), where the relation between fertilizer application and yield is split into relations between uptake and yield and between the amount of fertilizer applied and uptake. Both relations are affected by reclamation. The uptake yield curve for a particular element is characterized by its initial slope and the maximum yield, which is achieved at high nutrient levels. The initial slope is mainly a crop characteristic and is affected only indirectly by environmental conditions. By changing the reclamation level the maximum yield is changed. The nutrient re-

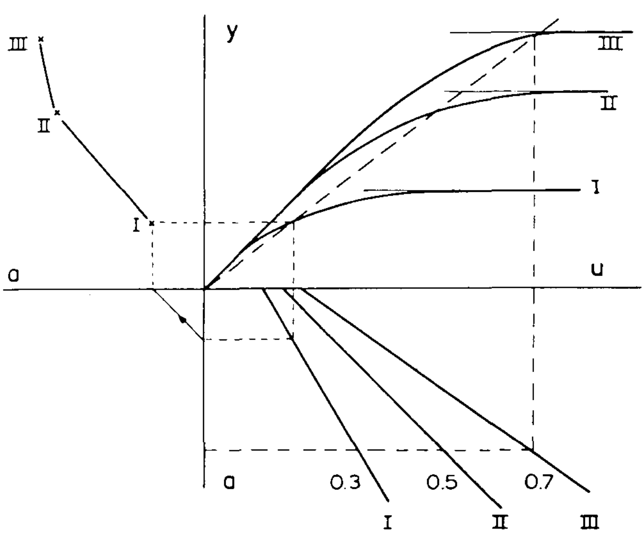

Fig. 2. The effect of various reclamation levels (I, II, III) on the relation between fertilizer uptake (u) and yield (y), on the relation between fertilizer application rate (a) and uptake, and on the relation between fertilizer application and yield (Wolf, 1986).

quirement increases linearly with that yield. The amount of fertilizer needed to meet that requirement depends on the recovery of the fertilizer and on the amount of nutrients taken up from unfertilized soil. In general, both are favourably affected by reclamation, because improved water control stimulates the activity of the root system, contributes to an increased mineralization of organic matter in the soil, reduces losses by leaching, and losses by denitrification due to waterlogging. Although there may be considerable deviation from this general pattern, it is clear that the higher the reclamation level the more efficient are measures such as fertilization. Higher efficiency of the use of energy, other external resources and labour at high yield levels than at moderate or low yield levels is reached by intelligent farming, in which excessive use of external resources is avoided. The experiments of Alberda (1972) on grass revealed that nitrogen use at yield levels of 20 000 kg ha^{-1} is very similar to that at yield levels which are 40 % lower. Well-timed and -dosed nitrogen applications result in high yields and thus have a very high efficiency. Detailed analyses by Van der Meer (1986) and Kemp (1985) (Fig. 3) have shown that the utilization of nitrogen in grassland has increased considerably during the last few years as a result of appropriate management. The potential, however, is still higher. A study by Lantinga (1985) showed that nitrogen fertilization above a well-defined minimum level, 3.0 % nitrogen in the leaves, has no effect on photosynthesis and that the only effect at higher nitrogen levels is that on leaf extension. There are, however, indications that a reduction in leaf extension due to lower nitrogen levels could be compensated by a more adequate grazing. At present, the general recommendation for N fertilization in the Netherlands is 400 kg ha^{-1}, with small adaptations for various soil types. This could be reduced considerably, and by a combination of detailed experiments and simulation studies a new underlimit could be formulated. The recommendation for nitrogen fertilization could then be

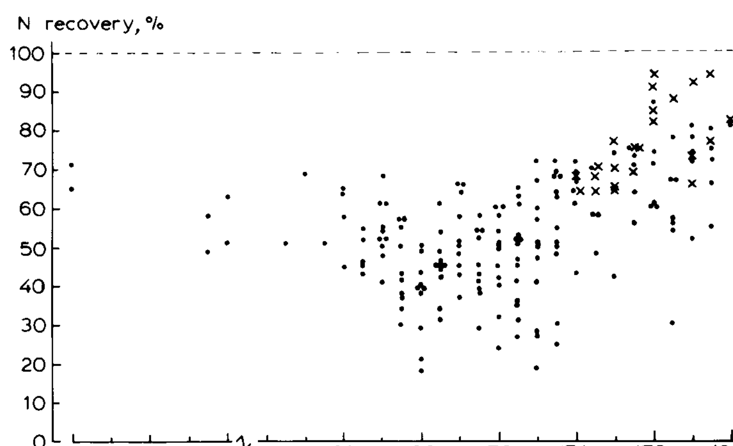

Fig. 3. Nitrogen recovery (in %) in grassland in the Netherlands from 1934 to 1982 (van der Meer et al., 1986).

tailored to the needs of individual fields and based on well tested simulation studies, rather than on a whole series of field experiments with conflicting results. The development of wuch advice requires new advisory systems that tailor recommendations to the specific needs of a field and the aims of the individual farmer. Such recommendations should be based on a combination of experience and insight, and should take into account the characteristics and perspectives of individual farms. Waste of external resources and pollution of the environment may thus be avoided.

The consequences of the anyhow continuing increase of agricultural production per unit of area for the agricultural policy of the EC is discussed elsewhere (de Wit et al., 1986).

Advisory systems and growth reduction

New advisory systems which take into account many of the objectives and characteristics of individual farms have been developed for some agronomical measures, for instance those that concern crop protection in wheat (EPIPRE). Several such systems are under development and may help farmers and extension in their 'tractical' day-to-day management decisions. The advisory systems indicate when control is needed, but also when no action is necessary. Such systems can reinforce contact between farmers and research, as the farmer is told when to make what observations and how. Research, on the other hand, is pressed to define accurate, simple, rapid observation methods and to develop appropriate damage thresholds which take into account the specific conditions in individual fields.

The effect of a growth-reducing factor may vary considerably between crop yield levels. At high levels the competitiveness of a crop relative to weeds increases in general, and control of weeds is relatively unimportant. In contrast, pests and diseases are usually more important at high yield levels. The improved condition of the crop and the favourable micro-meteorological conditions in a dense crop for a disease epidemic (as a result of appropriate water and nutrient management) may lead to higher desease and pest risks in high-yielding crops. Appropriate control is then necessary to limit biocide use and to increase energy and pesticide efficiency.

Modern pest and disease control makes use of various control techniques. Agronomic measures such as breeding and crop rotation form the basis, but are supplemented by biological control methods, sophisticated techniques involging the use of sex pheromones and sterile males, and a variety of specific and general chemical control compounds. The latter should be used only when other preventive methods have failed. This needs well-defined economic injury levels, adjusted to local conditions.

For example, in an experiment by Kropff et al. (1984), the presence of 100 *Chenopodium album* plants per m^2 in a maize field in 1982 caused a yield reduction of 8 %, whereas the same number of plants in a similar field in 1983 caused a yield depression of 88 % (Fig. 4). In an analysis of these experiments with a simulation model for the interaction between crop and weed it was demonstrated that the relative germination time of crop and weed was of crucial importance and explained the impressive differences (Spitters, 1984).

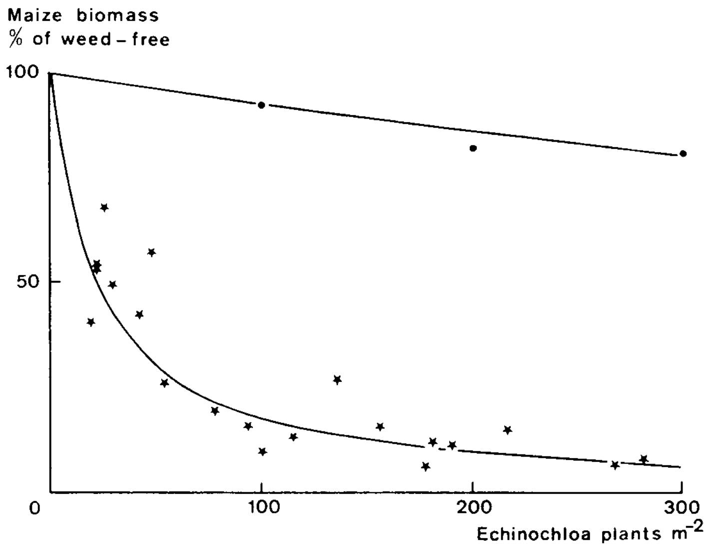

Fig. 4. Final above-ground biomass of maize in 1982 (●) and 1983 (*), expressed as % of weed-free control, in dependence of initial density of *Echinochloa*. Curves were based on a regression of the reciprocal per-plant weights of maize on weed density, including yields of weed-free maize plots (Kropff et al., 1984).

In such a case the timing of control is very important. Appropriate control measures requires knowledge, skill and experience. Insight into the early growth of crops and weeds, and the mutual interactions between them, is then indispensable.

The same holds for pests and diseases. In small grains the importance of pests and diseases has increased considerably in importance during the past years. In wheat this is due partly to the positive effect of favourable growing conditions for the crop on the development of various pathogens, and depends also on the damage relation of the crop with the pathogen. Cereal aphids caused a kernel yield loss of 250 kg ha^{-1} at a kernel yield level of 5000 kg ha^{-1} and a maximal density of 15 aphids per tiller (Rabbinge et al., 1983), whereas at a yield level of 9000 kg ha^{-1}, yield loss amounted to 900 kg ha^{-1}. Yield levels depend mainly on reclamation level and nutrient availability. With appropriate water and nutrient availability, the yield loss per pest increases. A fixed damage threshold is therefore inappropriate. This result could mean that many field experiments are needed to formulate damage relations which vary according to local conditions. This would require a lot of time and money and is vertually impossible since manipulation of a crop to a given sub-potential yield level is difficult, probably impossible. Therefore it is more feasible to consider the background of the experimental results and use this knowledge to formulate damage relations that take into account time and level of infestation, growing conditions and yield expectation.

In the case of cereal aphids, growth reduction is due to direct and indirect effects: direct effects due to uptake of phloem sap and indirect effects resulting from the injection of saliva and the excretion of honeydew. This excretion product covers the leaves and hinders gas exchange and light absorption. Both light use efficiency and CO_2 assimilation at light satiation are affected (Rabbinge et al., 1981). In addition, honeydew accelerates leaf senescence. The absolute and relative contribution of each of the damage components has been analysed with a simulation model of the interaction of crop growth and aphid population dynamics (van Roermund et al., 1986). The various direct and indirect effects were quantified on the basis of experiments or published data. Calculations with the combination model confirmed field experiments which included a detailed growth analysis (Fig. 5). It was shown that in absence of aphids as a result of chemical control a yield of 9377 kg ha^{-1} was attained, whereas aphids at an intensity of 490 aphid-days per tiller caused a yield reduction of 1241 kg ha^{-1}.

After testing, the model was used for further evaluation of growth and yield reduction. It was shown that there is a S-shaped relation between yield reduction per aphid and yield level (Fig. 6) and that yield reduction per aphid is greatest around crop development stage DC 70, watery ripe (Table 3). It was also shown that the relative importance of direct and indirect damage compounds varies greatly between yield levels. At low yield levels (< 5000 kg), more than 50% of the total yield reduction is due to assimilate consumption by the aphids, whereas at high yield levels this component is no more than 15 % of the total yield reduction. These changes are due to the way various processes are affected. For example, at low and high light intensities there is a considerable effect of honeydew excretion on photosynthesis since both light use efficiency as a result of 'light stealing' and photosynthesis at light satiation due to stomates sealing are affected. These effects increase as the leaves age. At low yield levels such effects are less important than growth duration;

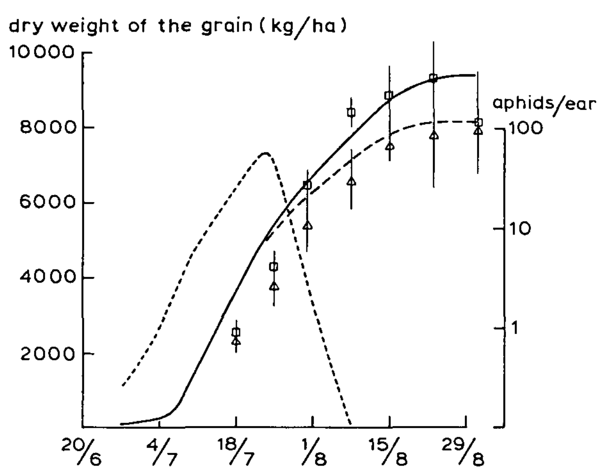

Fig. 5. Dry weight of the grain (kg ha^{-1}) in absence and in presence of aphids, and the aphid population (aphids per ear), as a function of time. ——— simulated and □ measured grain weights in absence of aphids (kg ha^{-1}) — — — simulated and △ measured grain weights in presence of aphids (kg ha^{-1}) ---- aphid population (aphids per ear).

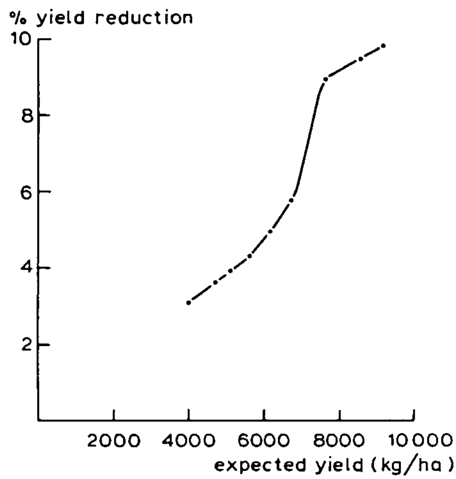

Fig. 6. Yield reduction 1 % at an aphid pressure of 490 aphid-days per tiller as a function of the expected yield level.

in particular the kernel filling period is shortened by nitrogen shortage. At very high yield levels (> 9000 kg ha^{-1}) yield reduction per unit of pest or disease no longer increases superproportionally, as nitrogen is abundantly available while the effects of aphids on photosynthesis do not increase. In addition, at high yield levels the conditions before flowering are also very important, and these are not affected by the aphids. Thus at very high yield levels yield reduction increases proportionally or subproportionally with yield. The increased understanding of the yield reduction caused by aphids has formed the basis for flexible damage relations that take into account growing conditions, yield expectation and the level and timing of the aphid infestation. Such damage relations are used nowadays in supervised control systems. For other diseases and pests similar studies have been undertaken. For example, in field studies of mildew in wheat it was shown (Daamen & van der Vliet, 1984) that at an infection level of 1 % a yield reduction of 7.5 % may occor. Detaild analysis showed that with a 4 % cover of leaves photosynthesis at light satiation was already reduced by 50 % (Rabbinge et al., 1983). This effect is due to a direct effect of mildew on carboxylation resistance. Neither stomatal behaviour nor CO_2 diffu-

Table 3. Simulated damage per aphid-day per ear as a function of the wheat growth stage.

Growth stage DC		Damage (kg ha^{-1})
60-69	anthesis	5.05
70-73	watery ripe	2.44
73-75	early-medium milky ripe	1.54
75-77	medium-late milky ripe	0.83
77-79	late milky ripe	0.39

sion in the boundary layer or the mesophyll is directly affected by the presence of mildew. This was demonstrated in detailed studies on photosynthesis at various external CO_2 concentrations. The consequences of the effects of mildew were again evaluated with a simulation model. The predictions were in good agreement with the field results of Daamen et al. (in prep.), so it was possible to use the model for further hypothesis testing and computation of damage relations. It emerged that mildew, in contrast to aphids, has a damage relation that is proportional to yield expectation. This is due to the absence of secondary effects. In another disease in wheat, *Septoria nodorum*, similar studies have indicated that a subproportional damage relation may exist (Leemans et al., in prep.).

As a result of the differences between the effects of the various diseases and pests on photosynthetic parameters and other growth characteristics, great differences in yield reduction may occur. Traditional agronomic studies would require an enormous input of labour and a considerable number of experiments to formulate dynamic and flexible responses. Simulation studies that quantify the various effects of pathogens on the basic processes that govern crop growth may lead to better insight and a faster and more accurate result. They permit extrapolation and prediction. Such predictions are used nowadays to improve supervised control such that biocide use and yield reduction are limited. The positive results in the Netherlands in comparison with England, on average about 50 % less biocides per unit of area in winter wheat at even a little bit higher yield levels, are already illustrative.

Simulation and systems analysis

The examples given above for research in crop protection illustrate how simulation models can be used to integrate knowledge from different disciplines. They also demonstrate that the results of these model studies must be tested. For the descriptive relations which are used as input for the models, as well as for testing of the explanatory models against data at systems level, experiments are needed. Most descriptive relations will be derived from detailed experiments under well known conditions and verification or validation experiments are done in most cases in the field. These experiments are needed as our knowledge both at the descriptive and the explanatory level are far from complete. It is for this reason that simulation and experiment must move in tandem to yield insight into the way the system operates and increase confidence in the model. Well-tested models can be used for extrapolation and prediction. This heuristic way of working was introduced into the agricultural and biological sciences by de Wit (1968). Modelling and simulation is used in many sciences, but the agriculturist and biologist are in the unenviable position that neither the physicists and chemists nor the economists and sociologists can be of much help — the first group because they do not need this heuristic way of working for the development of their models and theories, because of the extensive knowledge of processes and systems, the latter group because the various levels of knowledge with various characteristic recovery times after a peerturbation are often poorly defined, so model testing is difficult. The application of heuristic methods in agricultural and biological sciences has been very successful. An understanding of biological systems together with structured testing, has led to models requiring little further verification.

Several stages of model development can be distinguished: conceptual models, comprehensive explanatory models and summary models. Conceptual models are usually explicit formulations of various hypotheses on the way the underlying processes govern the behaviour of the total system. After studying of these processes it it possible to construct a quantitative model that increases insight into the functioning of the system. On the basis of these comprehensive quantitative models development of a summary model is possible through simplification. Such models are used for prediction and agronomic management and may form parts of sophisticated management structures that use dynamic programming techniques or other methods developed in operations research.

This sequence of steps has been followed in various disciplines of the agricultural sciences, and this has yielded recommendations or advisory systems which may be of use in day-to-day decision making of the farmer (tactical models) or may be a useful tool in policy making (strategic models). In crop ecology the use of models is of crucial importance. The long road of descriptive experiments is hortened considerably by the repeated structured testing of models. Even so, many experiments are still necessary: process experiments to quantify relations within the system and between rate variables and external conditions, and experiments at the system level to test the outcomes of simulation models. A clear definition of priorities in various phases of model development is possible and helps to limit the need for experimental work.

Application of the models for development of practical agronomic measures is also possible, and various results from crop protection and land evaluation have shown how useful this may be.

Thus, crop ecological studies help to optimize agricultural production at the various levels, i.e. the crop level, the farm level and the regional, national or supranational level. The considerable change in the aims of agricultural production during the last years has made it clear that there is an urgent need for such integrative studies, which are quantitative and testable, and based on knowledge and insight rather than belief or conviction.

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