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HOW TO USE COMBINATION MODELS IN CROP PROTECTION

R. RABBINGE, Department of Theoretical Production Ecology,
Agricultural University, Bornsesteeg 65,
6708 PD Wageningen, The Netherlands.

1. Introduction

Pest and disease management requires knowledge of both the crop and the pest or disease system. The dynamic character of the interrelations urges a dynamic description of the substrate and environment of the pathogenic organisms. The emphasis in most pest and disease management studies is reflected in Ruesink's review (1976); most studies emphasize the description of pest and disease population dynamics sometimes with stochastic submodels that simulate the infection and spread of the pathogenic organisms. These models have proved to be reliable predictors of pest or disease development but their value as quantitative predictors of injury to the crop is limited. For that purpose, combination models of the population dynamics of the pest or disease organism and of the growing crop are needed. Such combined models have been developed for situations in specific crops, such as cotton, alfalfa, apple and wheat (Gutierrez et al., 1976; Rabbinge, 1976; Rabbinge et al., 1981; Rabbinge et al., in prep.). In some cases, these comprehensive simulation models have led to simplified economic models for decisions about spraying or praying, but their reliability is low and their value is still limited.

2. Types of models

Multivariate regression models of the type developed by Thompson (1969) Pitter (1973) Bridge (1976) are often more reliable. With proper 'tuning', such models accommodate better to average field conditions since historical data include the variation in plant stand, diseases and pests, and nutrient and water supply, which may be the principal determinants of yield. Such regression models perform best in predicting the mean performance of a population of fields, whereas the dynamic models may work best with the individual field. Among the dynamic models, different levels of detail should be distinguished depending on the objective of the study. When an explanatory approach is aimed at, these dynamic models are based on a systems hierarchy in an effort to provide prediction of integrated behaviour from a more detailed knowledge of the underlying physiological and morphological processes (De Wit et al., 1978; De Wit & Goudriaan, 1978). Of course all such knowledge becomes descriptive at the ultimate level of reduction, but one may distinguish between descriptive and explanatory models (De Wit, 1982) on this basis. When damage assessment is the aim, less detail seems necessary as rough estimate of the effect of pathogenic organisms may suffice. However, when explanation is the aim comprehensive simulation models are needed to take into account the complex nature of the various interrelations between harmful organims and host plant. The most important characteristic of these explanatory models is their integrative capability. Knowledge from different levels of organization is brought together in such a way that it is used to explain the behaviour of crops and the pest or disease organisms in a variable environment. Some types of physiological information are readily extrapolated from lower to higher levels; others are not.

2.1 Development of models

In this paper we will discuss some simple examples of how combined plant-pest or disease models have been developed. The aim of this modelling effort is to obtain insight as to how pest or disease organisms affect crop growth and productivity. A complete understanding of the nature of the interrelations is not the objective, but enough basic knowledge on the physiological background is necessary when the final aim is a management system which requires a reliable prediction of the effect of damage-causing organisms in individual fields. Comprehensive explanatory simulation models are then indispensable as an integrative tool. By sensitivity analysis and simplification, models are developed which may be used in management systems. Thus we may distinguish three types of models which express different levels, or phases of development, of knowledge and insight. At the frontiers of knowledge, preliminary models are very common. They enable the quantification and evaluation of hypotheses and are useful as such, but seldom survive a long time. Many different hypotheses may be expressed quantitatively in these models and their consequences may be calculated and used for an evaluation. These models may help as guidelines in experimental research. Comprehensive models may be developed from these preliminary models as a result of scientific progress; more knowledge and insight become available and may promote the lucidity of the system studied. The third category of models comprises summary models. These models are derived from comprehensive models and serve as vehicles for communication, instruction and may sometimes be used for management purposes. Since summary models are derived from comprehensive models, different forms of these may exist depending on the objective and interest of its user.

Combination models of crop growth and pests and diseases may exist in each phase of model development. Some examples of preliminary models are given below.

2.2 Combination models

Few combination models in the literature are based on detailed plant physiological analysis. They are very often of a dualistic nature, combining a great deal of descriptive elements on one hand, and a great deal of experimental observations on subprocesses on the other. But if too many phenomena observed at the system level are introduced, very often the behaviour of the model is being governed merely by these descriptive relationships. Models which aim at explanation are then rapidly degenerating into sophisticated ways of curve-fitting. Some examples are given to illustrate the use of combination models. These examples should merely be seen as a way of calculating pest or disease effects on the canopy without regard for the nature of damage. In many cases, this approach suffices to get reliable estimates of crop losses due to the damage-causing organism and may serve pest management and decision making, but when explanation is the aim they are too simple and a more detailed study is needed, as demonstrated for the cereal aphid-wheat relationship (Rabbinge et al., 1981) and the cereal-stripe rust relationship (Rabbinge, in prep.).

3. Crop growth under optimal and suboptimal conditions

Much attention has been paid to develop calculation procedures based on the process of photosynthesis. Some review articles illustrate this considerable effort (Loomis et al., 1979; Penning de Vries, 1980). These calculation procedures form the backbone of simulation models of crop growth. Different classes of simulation models may be distinguished depending on the crop production level for which they are meant; a delimitation of growing crops proposed by De Wit (De Wit & Penning de Vries, 1982). This approach emphasizes dry matter production rather than morphogenetic development. Four levels of plant production may be distinguished.

Production level 1

Comprises the potential production level reached in conditions with ample plant nutrients and soil water all the time. The growth rate of the crop in these conditions is determined by weather conditions and amounts to 150-350 kg ha^{-1} d^{-1} of dry matter when the canopy fully covers the soil. In these conditions the absorbed radiation is often the factor limiting the growth rate during the growing season. In fact, this is quite a common situation in cool climates. Major elements in this class of system are the dry weights of leaves, stems, reproductive or storage organs and of roots, and the surfaces of photosynthesizing tissues; major processes are CO_2 assimilation, maintenance and growth, assimilate distribution and leaf area development. A situation with plant growth at this production level can be created in field and laboratory experiments while it is approached in practice in glasshouses and in the very intensive production of sugar-beet, potato and wheat on some Western European farms.

Production level 2

Growth is limited by water shortage at least part of the time, but when sufficient water is available the growth rate increases up to the maximum rate set by the weather. Such situations can be created experimentally by fertilization in temperate climates and in semi-arid zones; it is approached in practice in non-irrigated but intensively fertilized field, such as many Dutch pastures. The extra elements of this class of system are the water balances of the plant and soil; crucial processes are transpiration and its coupling to CO_2 assimilation and loss or gain of water by the soil through evaporation, drainage and run-off. The heat balance of the canopy needs consideration in detailed analyses at this production level because of its relation to the water balance.

Production level 3

Growth is limited by shortage of nitrogen (N) at least part of the time, and by water or weather conditions for the remainder of the growth period. This is quite a common situation in agricultural systems using little fertilizer, and is also normal in nature. Even with ample fertilization, N shortage commonly develops in crops at the end of the growing season. Important elements in these systems are the various forms of N in the soil and in the plant; important processes are the transformations of nitrogenous compounds in the soil to forms less or more available to plants, leaching, denitrification, N absorption by roots, the response of growth to N availability and redistribution of N within the plant from old organs to growing ones.

Production level 4

Growth is limited by the low availability of phosphorus (P) or by other minerals like potassium (K) at least part of the time, and by N, water or weather for the remainder of the growth period. Lack of P is particularly interesting because of its relation to the metabolism of N. Growth rates are typically only 10-15 kg ha^{-1} d^{-1} of dry matter during a growing season of 100 days or less. This situation occurs often in heavily exploited areas where no fertilizer is used, such as in the poorest parts of the world. Important elements of this class of system are the P or mineral contents of the soils and of the plants; important processes are their transformation into organic and inorganic forms of differing availabilities, absorption of minerals by roots, and the response of plant growth to their absolute availabilities. The availability of P relative to that of N is also important.

It is rare to find cases that fit exactly into one of these four production levels, but it is a very practical simplification of a study to reduce specific cases to one of them. It focuses attention on the dynamics of the principal environmental factor and on the plant's response. Other environmental factors can then be neglected, because they do not determine the growth rate; or rather, it is the growth rate that sets the rate of absorption or efficiency of utilization of the non-limiting factor. If, for example, plant growth is limited by the availability of N, there is little use in studying CO_2-assimilation or transpiration to understand the current growth rate. All emphasis should then be on N availability, the N balance and the response of the plants to N.

4. Effects of pests and diseases

Pests and diseases may affect the growth of a crop at all production levels. However, the nature of the relation between crop and pest or disease organism may be considerably different and the crop losses, both qualitative and quantitative, may also depend on the way crop growth is affected. In a detailed study on crop losses due to ceral aphids, Rabbinge et al. (in prep.) demonstrated that the effect of a similar aphid load on the plant was considerably different at different production levels. Yield loss (kg kernels/ha) was correlated with the maximum aphid density per kernel, normally reached at crop development stage milky ripe (decimal code 77). At a production level of about 5000 wheat/ha^{-1}, a maximum aphid density of 15 $tiller^{-1}$ cau[illegible] yield depression of about 250 kg ha^{-1}; whereas, the same population density at a yield level of 7500 kg ha^{-1} caused a yield loss of 800 kg. In the analysis of this damage relation, it was demonstrated that the major reason for the progressive damage relation was the relative importance of indirect effects on yield loss. The major reason for the considerable damage at higher yield levels is found in the effect of honeydew on photosynthetic rate and promotion of senescence of leaves (Rabbinge et al., 1981). These effects are caused by the sealing of stomates and the depression of the activity of photosynthetic active enzymes.

This example has demonstrated the importance of defining the yield or production level at which the pathogen-crop relation is studied. Effects at production level 1 may be completely different from effects on production 2, 3 or 4. In the next part of this paper only effects of pests and diseases at production level 1 will be discussed. The effect of pests and diseases at other production levels may be different. It is demonstrated that pests and diseases of 'poor crops' and pests and diseases of 'rich crops' exist (Rabbinge, in prep.).

5. Simulation of crop growth

In the case of production level 1, computation of production is based on assumptions of a maximum photosynthetic activity and closed crop surfaces. Methods in which attention is spent on photosynthesis, respiration and partitioning between various plant organs are scarce. Based on knowledge about accumulation, distribution and redistribution of carbohydrates, quantitative aspects of respiration etc., Van Keulen (1976) derived a simple calculation method for potential rice production which can be applied, after some adaptation, to other crops (Penning de Vries et al., 1982) and is very suitable for interconnection with a population model of pest and disease organisms in order to study their effect.

5.1 Summary model SUCROS

The summary model (SUCROS) developed by Van Keulen comprises short cuts and descriptive tables for subprocesses, based on computations with a comprehensive crop growth simulator, BACROS, (De Wit et al., 1978).

Weight of shoot, root and ears (in the case of wheat) increases with a developmental stage-dependent rate. All organs grow from an assimilation stream, the size of which depends on the incoming radiation and the leaf surface participating in photosynthesis. Photosynthesis is diminished before partitioning between different plant organs by a rate-dependent growth respiration and a weight-dependent maintenance respiration.

Root and shoot may decrease with a rate which depends on size and a development stage.

a) Photosynthesis

The basis for the calculation of potential crop yield is the photosynthetic rate of the canopy. Assuming optimal growing conditions, De Wit's (1965) calculation procedure can be used to compute photosynthetic rates for closed green crop surfaces. Goudriaan & Van Laar (1979) demonstrate that on the basis of the photosynthesis-light response curve of a single leaf in ambient air of normal temperature and CO_2 concentration, a response curve of closed canopies may be calculated without further knowledge of the geometric characteristics of the canopy. Only the total leaf mass should be known. Effects of chloroplast distribution, nitrogen content of the leaf blade, age of the leaf and environmental conditions such as CO_2-concentration and temperature, can be found as changes in light-use efficiency or maximum photosynthesis rate of the simple leaves. In individual leaves light saturation is normally reached at values of 0.15 cal cm^{-2} min^{-1} (=104.7 J m^{-2} sec^{-1}), which is well below the values reached in the middle of a sunny day on a horizontal plane.

Goudriaan (1977) showed that it is reasonable to assume that the actual rate of gross photosynthesis is proportional to the fraction of the total energy intercepted by the canopy. To calculate this fraction an exponential extinction of the light intensity within the canopy using a fixed extinction coefficient seems reasonable (Van Keulen, 1976; De Wit, 1965; Goudriaan, 1977).

With the photosynthesis part of the comprehensive crop growth simulator BACROS (De Wit et al., 1978), Goudriaan & Van Laar (1979) calculated daily gross photosynthesis rate for completely overcast and clear skies for different geographical sites and different times of the year for a closed canopy. The actual daily gross photosynthesis rate (GFOT) in the summary model is now found by calculating the fraction overcast during a day (F), and multiplying the daily gross photosynthesis rate for overcast skies (PO) with this fraction, adding to this product the fraction clear multiplied with the gross photosynthesis rate for clear skies (PC): i.e. $GFOT = (1.0 - F) \times PC + F \times PO$.

The fraction overcast (F) is calculated according to the formula

$F = (DTRS-0.2 \times HC)/(HC-0.2 \times HC)$, in which DTRS = actual incoming radiation in $J\ m^{-2}\ s^{-1}$ and HC = incoming radiation when the sky is completely clear. The incoming radiation on overcast days equals 20 per cent of the amount of incoming radiation at clear days. PC, PO, DTRS and HC are introduced in the model as time and location-dependent variables. The gross photosynthesis rate of a crop GFT is now calculated from the gross photosynthesis of a closed canopy by multiplication with a factor that accounts for the extinction of the radiation in the canopy and thus only has considerable effect with low leaf area ($LAI < 3$): i.e. $GFT = GFOT \times (1.0 - EXP(-0.6 \times LAI))$. The LAI is not based on knowledge or measurements of the leaf area during crop development but computed from the weight of the above ground material assuming a fixed specific leaf weight of 0.5 kg m^{-2}, a figure which seems to be representative for small grains.

b) Respiration

To grow and produce new compounds, the energy fixed in the photosynthetic process is partly used, so that only a changing fraction is fixed in new compounds. Two main processes for which the just-fixed carbon is used can be distinguished.

1. Growth processes, i.e. the construction of structural plant material as proteins, fats, carbohydrates out of the primary photosynthetic products. Each of the newly formed structural compounds requires a further amount of primary photosynthetic products. In a detailed study of this growth respiration, and by means of a sophisticated way of book-keeping of all the processes involved, Penning de Vries (1975) derived the efficiency of conversion for the different structural compounds in terms of weight, namely the production value.

2. Maintenance processes. The other sink for photosynthetic material is the maintenance of already existing cells. Their structure must be maintained and this involves the turnover of protein and the sustaining of ionic gradients and membrane structures. Again the composition of the material determines the energy required; the main variable

being the protein content. The complicated character of maintenance means that accurate quantitative estimates of these processes are rare. Although the size of maintenance respiration is low in comparison with growth respiration, its presence during the plant's whole life span makes its contribution to the total energy spent for respiration comparable with the costs of growth processes (Penning de Vries, 1980). Maintenance respiration is directly affected by temperature and seems to react to temperature according to a Q 10 value of 2-3.

Since maintenance of present structures has a higher priority than synthesis of new structural material, the computations are done in such a way that growth respiration is calculated after subtraction of the respiration needed for maintenance.

c) Development

To compute how, and at what rate, carbohydrates are partitioned, the developmental phase of a plant (crop) is of high importance. In most models of crop growth, development and morphogenesis are not considered. A major reason for this is that processes of development are poorly understood and explanation of, for example, the appearance of leaves, the distinguishing between vegetative and generative phases, and flowering and heading of plants is virtually absent. Still, the development of a crop heavily interferes with its growth and thus development should be considered in a realistic crop growth simulator. To circumvent the absence of reliable data on the process of development, a description of the development of the crop is introduced in the crop model. In most crops, development is affected by temperature and day length. These governing factors may be introduced to compute the rate with which the crop develops, this is usually done by defining crop development in terms of a temperature sum i.e. the product of average temperature and time. The vagaries and implicit assumptions of this technique are too numerous in many cases and, for this reason, a more flexible approach is chosen in which development is mimicked by integrating a temperature and daylength-dependent development rate. The input relation of this rate should be determined from crop development experiments in which the average development period (for example from germination until flowering) is determined at different temperatures. Often the inverse of this period has a linear relation with temperature and thus enables the application of the temperature sum as a measure of development stage, but also the other condition of instantaneous temperature reaction should then be fulfilled. Tests on this linearity are seldom executed, so its application should be done with care.

Besides partitioning and changes in temperature response, ageing and senescence of the various plant organs is determined by development stage. To determine the ageing and senescence rate, the life span of leaves, stem and other plant organs should be determined under various abiotic conditions. Based on these measurements, temperature- and development-stage-dependent relative ageing rates for stem and root of winter wheat have been introduced. Generally it can be stated that there is a considerable shift in partitioning after flowering. This may of course be different in non-determined growing plants such as beans.

5.2 Combining SUCROS with population models of pests and diseases

Three examples of damage-causing organisms have been chosen to demonstrate the different effects of a disease or pest according to its relation with the host plant.
The input data in the crop model are based on winter wheat but can very easily be adapted to other crops so that this summary model is widely applicable. The calculations are all performed for a standard year, starting at 15 May and ending at 25 August. The chosen interrelations are such that the pest and disease organism dynamics are given with descriptive relationships rather than simulation with detailed population models. Mutilation of leaf mass, coverage of leaves, and leaf mass consumption are treated and each represents a group of pest or disease organisms. It is self evident that these three examples of host plant-pathogen relations are not exhaustive; many other interrelations are possible, but are not treated as they fall outside the scope of this bulletin.

a) Mutiliation of leaf mass

Many examples of leaf mass consumption by herbivores are possible. The influence of removers of leaf mass seems limited unless their numbers become very high, or their consumption rate is very considerable. For example, the effect of leaf hoppers on leaf mass is so high that sophisticated prediction and monitoring systems have been developed to prevent their disastrous effects. To demonstrate the effect of a leaf consumer on crop growth, a simplified description of population growth of the cereal leaf beetle has been attached to SUCROS and parameterised for winter wheat.

Larvae of cereal leaf beetles (Oulema melanopus) consume leaf mass and do this at a consumption rate of about 250 cm^2/day (= 2 g dry mass). Only the larvae consume leaves. After growth and development they pupate and form adults that may give rise to another generation. The rate of increase of the numbers of cereal leaf beetle larvae mainly depends on the immigration rate of the adult beetles which lay their eggs on the leaves. After hatching the larvae immediately start feeding. Their effect on crop growth is introduced as a drain on the shoot weight. This rate of decrease of shoot weight is assumed to be proportional to the number of larvae of the beetle, lumping all developmental phases of the larvae together. Consumption of leaf mass by the adults is neglected, and age and food-quality-dependent reproduction and development rates are not considered. The beetle population is introduced in a very simple way by distinguishing four morphological stages: eggs, larvae, pupae and adults. The adult population is assumed to be 50% males, so that after egg laying only 50% will grow up as females and contribute to the next generation. Reproduction of adult beetles is diminished when high larvae densities are reached, which depends on the larvae/shoot weight ratio.

Calculations with the model show that only when the population density of the larvae reaches a level of 15,000/ha or $15/m^2$ or 0.004/tiller at flowering is the effect on the yield more than 1% of the yield. It has also been shown that the time of introduction of the beetle is of high importance. A late and heavy attack of the beetles scarcely affects the final crop yield, but an early and steady attack may cause a severe decrease of the yield. For this reason it is important to determine the presence of the beetle at an early phase of crop growth and to prevent outbreaks.

b) Leaf coverage

Mildew, caused by Erysiphe graminis, is coupled to the wheat simulator to demonstrate the effect of a disease that covers the leaf surface and promotes leaf senescence. The fungus is simulated with a descriptive formula according to Vanderplank (1963) and Zadoks (1971).

Individual spores or pustules are not distinguished, but rather sites are simulated, i.e. the leaf surface is expressed in potential sites, each site representing the minimum size of a lesion (a field of 1 ha, LAI = 3, contains 10^{12} such sites). The increase of sites in course of time is simulated with the equation.

$$\frac{dN_t}{dt} = R\ (N_{t-p} - N_{t-i-p})\ (1 - \frac{N_t}{N_m})$$

in which N_t = number of visible infections at time t, R = number of daughter lesions per sporulating lesion per day, p = length of the latent period of the fungus, i = length of the infectious period and N_m = maximum number of possible infections. When the latent period approached zero and the infectious period goes to infinity the equation changes to that for logistic growth

$$\frac{dN_t}{dt} = R\ (N_t)\ (1 - \frac{N_t}{N_m})$$

in which N_m can maximally reach the value for the surface of the standing crop, in this case expressed as LAI.

Of course this representation of a mildew epidemic is too simple and a more detailed simulation model in which all morphological stages are distinguished should be used (Rijsdijk, 1978; Zadoks, 1971). However, for the present example the given equations suffice. The stimulation of respiration by the fungus is neglected and the effect of ageing of the leaves is not considered but can easily be introduced by changing the relative rate of ageing of the shoot, which is fungus-density-dependent.

Some results of the computations with the model show that the effect of leaf coverage is only of importance when the leaf area index of the crop is smaller than 3. Moreover, it is shown that a percentage of leaf area covered by mildew of 30% at early milky ripe results in a yield decrease of 10% or 700 kg of wheat. Of course these results should be considered with care as the other effects of the mildew are not introduced and high light intensities may mask these effects. A coverage percentage of more than 20% is very seldom in practice so that other damage effects are probably also very important.

c) Parenchyma cell consumption

This way of plant damage is probably best represented by mites. Plant mites can be considered as a major pest. Mites are found from the Arctics to the Tropics and frequently attack horticultural and agricultural crops. In many cases mites are considered to be secondary pests as they often become a serious pest when insect sprays are introduced. Predators (ladybirds, predatory mites, syrphids) probably regulated the numbers of the mites before that time, but were killed by the sprays, leaving the spider mites unharmed due to rapidly developing resistance (Huffaker et al., 1970). Spider mites seldom cause severe damage in wheat, only in very hot spells does the two spotted spider mite *Tetranychus urticae* cause, very locally, rapid senescence of leaves and decrease of photosynthetic activity. The increasing usage of pesticides in winter wheat may lead to mite problems in wheat when abiotic conditions are favourable. Most plant mites cause this damage by injection of their stylets through the epidermis in the parenchyma cells and swallowing the contents. The attacked cells may die and the surrounding cells often show phenomena like suberization of cell walls, decrease of photosynthetic activity and increased maintenance respiration. The crop model is changed at two places to introduce these effects. Firstly the maintenance respiration is increased with a term that accounts for the mites. This respiration term is considered to be proportional to the mite density. Although this may be true at relatively low densities, this way of introduction overestimates the effects of the mites at high densities. Secondly, an effect of the mites on the photosynthetically-active leaf mass is introduced. This effect is also mite-density-dependent, the basis of these effects being derived from damage data of Sabelis (pers. comm.) on roses. The density of the mites is simulated by way of three age classes, lumping the different morphological stages together. A more realistic population dynamic model should consider the different morphological stages and the sensitivity of development rate to temperature and food quality (Rabbinge, 1976). This effect, and that of temperature and other abiotic factors on reproduction, mortality etc., are not considered. Computations with the model show that a minor change in the simulation of the maintenance respiration due to the presence of the mites causes a major effect on the growth of the canopy, and does interfere considerably with yield. The same holds for the effect on leaf senescence, an increase in average leaf senescence of 4 days results in a yield loss of 500 kg of wheat.

6. Use of combination models

The examples of combination models described are used as a research tool to obtain better insight and understanding of the effects of a pest or disease on its host. When necessary, detailed models of the population dynamics of the pest or disease organism can be combined with detailed models of crop growth. An example of such a detailed study is given by Gutierrez et al. (1976) and Rabbinge et al. (1981; in prep.).

The detailed population-dynamic crop and combination models themselves are seldom used for actual decision-making in crop protection. Their role is to test hypothesis, to gain insight and to pin-point the most decisive variables for the rate of development of pests and diseases. They are used to compute the range of acceptable disease or pest levels according to the weather, the crop production level and the condition and developmental stage of the plants. These calculations have been made for different diseases and pests in winter wheat and have resulted in simplified summary models and/or decision rules, which are used to determine whether control measures are needed.

In the Netherlands these results are used in a supervised control system called EPIPRE (EPIdemics PREvention) (Rijsdijk et al., 1981). EPIPRE is developed for wheat farmers. It works on a field-by-field basis and gives recommendations for every individual wheat field included. This was done in 1979-1980 by a team of research workers for 1000 fields and based on field information. This information is stored in a data bank and includes data on location, sowing time, cultivar, a few simple physical and chemical soil characteristics, herbicide application and nitrogen (N) fertilization. The information per field is updated whenever additional information is supplied by the farmer or the research team.

This information is used to run the simplified combination or the decision-rule models to obtain recommendations that are then sent immediately to the farmers. This EPIPRE supervised control system is now operational in several European countries and has led to an improved economic plant protection system with reduced pesticide use and with optimal economic results. This optimal yield may be different from maximum yield as cost-benefit analyses are used as the basis for advice.

At present this supervised control system of pests and diseases in winter wheat does not supply information and advice on supervised weed control or on N and P fertilization. Reliable simulation models on N in soils and crops are gradually becoming available, and may be used in future to advise on the timing and amount of N added to winter wheat. The same holds for weed control. In this way an integrated crop protection system may be developed, in which costs are reduced and economic yields are optimized.

7. Conclusions

An introduction on combination models of pests and diseases and crop growth has been given. The examples presented are still of a preliminary nature but serve as an illustration of how these models can be used. Specialists from different fields, such as entomologists, phytopathologists, plant physiologists and crop ecologists, may contribute to the further development of combination models. Both comprehensive and summary models are needed in this process of gaining knowledge and insight in the pathogen-crop relationship. These efforts are indispensable for the development of supervised control systems.

The need for supervised crop management studies [illegible] lead to the rapid development of this type of model. [illegible] interdisciplinary effort of plant pathologists, agronomists and extension people will help to achieve reliable crop management systems in the near future.

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