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DYNAMIC EXPLANATORY MODELS AS A TOOL IN THE DEVELOPMENT OF FLEXIBLE ECONOMIC INJURY LEVELS

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Introduction

There are several ways by which pest or disease populations may affect physiological processes in plants. They may, for example, reduce crop stands by elimination of plants, reduce inputs such as light, carbon dioxide and water, interfere with transportation of assimilates or nutrients and remove or consume previously produced structural material. Fig. 1 is a relational diagram illustrating various ways in which these crop growth reducing factors may interfere. To study the quantitative meaning of various effects, simulation studies may help. Eventually, this approach will lead to insights into the mechanisms of growth and yield reduction and into the quantification of yield reduction under various circumstances.
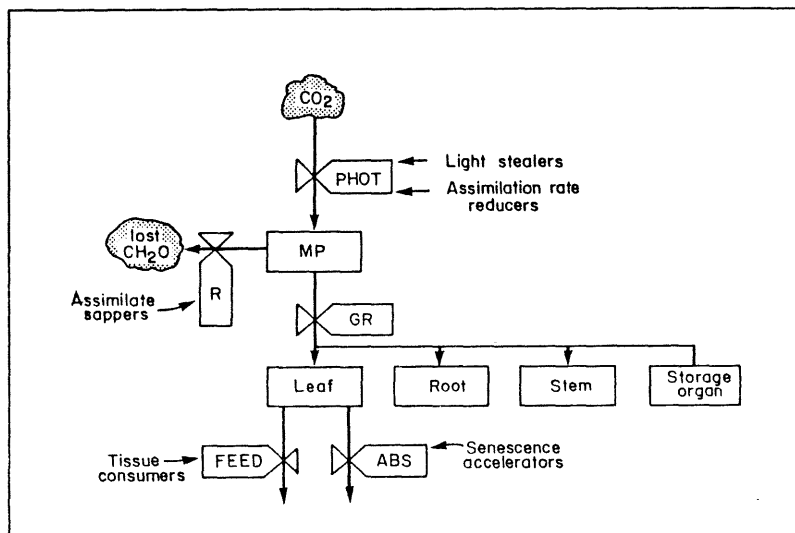

Fig. 1. Relational diagram for a Simple Universal CROp growth Simulator (MP = metabolic pool, GR = growth rate leaves, R = respiratory losses) and its interaction with various reducing factors.

Factors which define, limit and reduce crop growth

Crop growth, the accumulation of dry matter distributed between various crop organs, is determined by factors which define the physiological, phenological, optical and geometrical characteristics of the crop, providing water and nutrients are abundantly available and pests, diseases, weeds and any other crop growth-reducing factors are absent. Under these conditions, the growth of the crop is entirely governed by these characteristics and by the prevailing weather, mainly incoming radiation and temperature. Such a

situation is, however, rare since the great majority of agricultural crops suffer from water or nutrient shortage and are affected by pests, diseases and weeds.

The consequences of pests and diseases may differ considerably at different production levels. The production levels distinguished in crop growth studies have been discussed by Rabbinge (1986). He illustrated the use of combination models to evaluate the consequences of pests and diseases on crop growth and production and showed how various pests or diseases may affect different basic processes that govern growth, assuming abundant water and nutrient availability. The relational diagram in Fig. 1 illustrates this. Leaf photosynthesis may be affected by "light-stealers", or by "assimilation sap-reducers". Maintenance respiration may be increased by "assimilate and parenchyma cell-sappers". Leaf dry matter may be reduced by "tissue-consumers" or ageing may be promoted by "senescence accelerators". Some of the consequences of these perturbations are given in Table 1.

Table 1. The effects of pests and diseases on crop growth

Crop growth component	Damaging organisms	Example
(a) Rate of biomass increase	tissue consumers	Lepidopteran larvae Leaf beetles
(b) Assimilation rate:		
effects via leaf area	leaf consumers senescence promoters	leaf miners, spider mites aphids, many leaf pathogens
via incident light	light stealers	weeds, competitors, perto-trophic and saprophytic fungi
via water	turgor reducers	aphids, root-feeding coleoptera, various bacteria
via N/P/K	assimilate consumers	aphids
(c) Growth rate per organ:		
assimilate partitioning	functional balance root feeders	nematodes
assimilate conversion	assimilate consumers	aphids
(d) Leaf die-back	senescence promotors	aphids

Tissue or assimilate-consumers. An important distinction is that between tissue-consumers, which remove materials that have already been converted into plant tissue, and assimilate-consumers, which feed on unconverted assimilates. Since each kilogram of assimilate produces less than 1 kg of tissue, the tissue-consumers are more costly in terms of crop growth, although secondary damage by selective assimilate-consumers may result in higher total damage levels. Such effects are included in the rate of biomass increase as this is the net result of growth rate, rate of die-back and rate

of tissue removal by insects or other organisms. Nematodes and mites suck assimilates from host cells. The same holds for fungi which use haustoria for this purpose.

Stand reducers. Examples are damping-off fungi which reduce plant biomass and the number of plants. Consideration of reduced plant number is difficult and requires an approach in which competition for light or nutrients is considered similarly to an approach studying the effects of weeds. The distribution of captured plants in the field and the capacity of plants to compensate should then also be considered.

Assimilation rate-reducers. Many pathogens and pests affect CO_2 assimilation rate; they may affect the photosynthesis rate at light satiation or the light use efficiency. Mechanisms by which pathogens affect photosynthesis have been summarised by Buchanan et al. (1981). Viruses may reduce numbers of chloroplasts per unit leaf area or alter chloroplast ultrastructure, electron transport and partial resistance of photosynthesis. Fungi may alter chloroplast ultrastructure and certain components of the electron transport chain. Bacteria may also cause structural damage to chloroplasts. All these effects have been determined in detailed studies under well-defined conditions. However, the quantitative meaning of the effects in terms of crop growth and production is virtually unknown. Some pathogens and insects may accelerate leaf senescence by changing the nitrogen balance, or by excretion products affecting the activity of leaves.

Light stealers. Some leaf pathogens, for example pertotrophic and saprophytic fungi, have a 'light stealing' effect on crops by inhabiting dead host tissue which absorbs photosynthetically-active radiation. Leaf coverage by excretion products or light interception by leaves with necrotic lesions may interfere with photosynthesis. Coverage of leaves with mycelium may also affect light absorption.

Turgor-reducers. Nematodes that feed on roots and root pathogens that affect the water balance of the plant are examples. They also affect crop nutrient balance by disrupting phloem transport to roots, thus reducing the energy supply for active uptake of nutrients, such as K, and by disrupting passive flow of water and nutrients by the eventual decay of that tissue. Many root pathogens such as Pseudomonas spp., Fusarium spp. and Verticillium spp. can be classified as turgor reducers.

Stomatal functioning-disturbers. Some diseases, such as rusts and mildews, cause the stomatal guard cells to malfunction resulting in greater resistance to CO_2 uptake by well-watered plants with insufficient stomatal closure (Ayres, 1981). Whether this is a primary reaction of the plant to the host remains to be seen, as demonstrated by Rabbinge et al. (1985). They showed that mildew affects photosynthesis and transpiration as a result of an increase in carboxylation resistance. Stomatal resistance is only indirectly affected through a feedback mechanism from the internal CO_2 concentration to stomatal behaviour. Quantification is crucial for an evaluation of all these effects on crop growth and production. Such a preliminary evaluation was done in the first Bulletin of this Working Group (Rabbinge, 1983). A further analysis leading to calculated economic injury levels is given in this volume (Rabbinge, 1987).

Computation of economic injury levels using dynamic simulation models

Example 1. **Powdery mildew on winter wheat.** To quantify the consequences of powdery mildew Erysiphe graminis, a similar approach as described above could be used: mildew mycelium covering leaves could be considered as a light-stealer. However, long before a light stealing effect can be detected, the fungus affects leaf photosynthesis, as shown in Fig. 2. Mildew has an effect on dark respiration and leaf photosynthesis at light satiation;
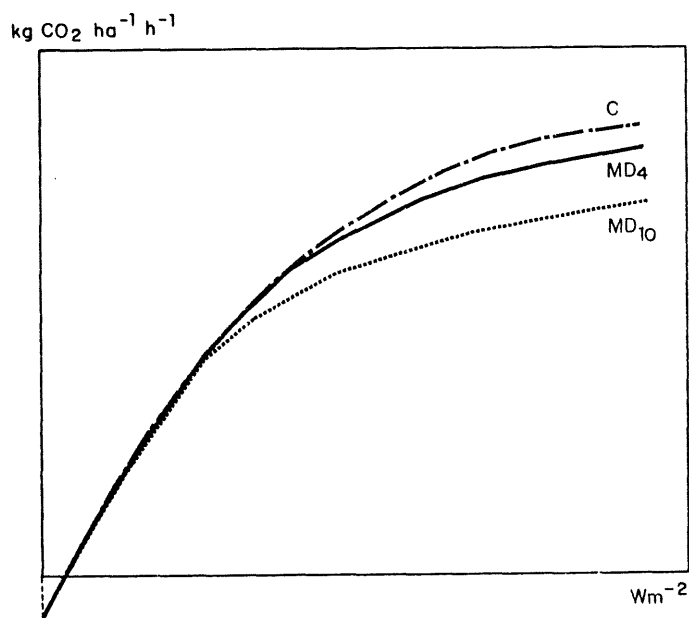

Fig. 2. Leaf photosynthesis of control (C) and powdery mildew infected winter wheat plants. MD4 and MD10 are leaves with a percentage coverage with mildew pustules of 4 and 10 percent respectively.

light use efficiency is hardly affected. The size of the effect is shown in Table 2 (Rabbinge et al., 1985). Even at a relatively low infection level (4% leaf area covered by pustules) both the assimilation and transpiration rates at light satiation were reduced up to 50%. Light use efficiency and dark respiration were not significantly affected. Evaluation of these effects with a multi-layered leaf photosynthesis module of a summary model for crop growth demonstrated that even at low infection levels considerable reductions in crop growth rate may occur. It was also shown that this effect is more pronounced when the sky is clear than when it is overcast (Table 3).

Table 2. Normalised values of maximum assimilation rate (AMAX in kg CO_2 ha^{-1} h^{-1}), light use efficiency (EFF, in kg CO_2 ha^{-1} h^{-1} W^{-1} m^2) and dark respiration (RD, in kg CO_2 ha^{-1} h^{-1}). Mildew-infected plants were grouped in classes of percentage mildew infected leaf area (PMI).

n^1	PMI class	AMAX	SD ($\pm$)	EEF	SD ($\pm$)	RD	SD ($\pm$)
11	control	100.0^2 $(45)^3$ 3.9		100.0 (.27)	0.02	100.0 (1.33)	0.21
11	0.1 - 0.5	97.1	4.4	101.5	0.03	94.0	0.20
11	0.5 - 1.0	86.5	4.1	100.4	0.03	99.2	0.29
9	1.0 - 2.0	83.6	4.9	103.4	0.02	111.3	0.37
9	2.0 - 3.0	66.8	4.1	94.0	0.03	109.8	0.25
10	3.0 - 6.0	57.5	5.2	88.8	0.04	128.6	0.29
9	6.0 -10.0	55.3	4.9	84.7	0.03	123.3	0.23
8	10.0	40.1	2.6	86.2	0.03	133.8	0.42

More detailed analysis of the effects of mildew on CO_2-assimilation and transpiration was done by measuring both rates at various external CO_2 concentrations at the same time. Assimilation rate at light satiation as well as transpiration were affected to the same extent. The assimilation rate/transpiration rate ratio (A/T) was, therefore, not significantly affected by mildew infection (Table 4).

The simultaneous reduction of assimilation and transpiration rates may have been caused by two different mechanisms: one based on an increase in carboxylation resistance (I), and a second (II) based on an increase in stomatal resistance. This is illustrated in Fig. 3. Curve A represents the response of assimilation rate (P) to the internal CO_2 concentration (CI).
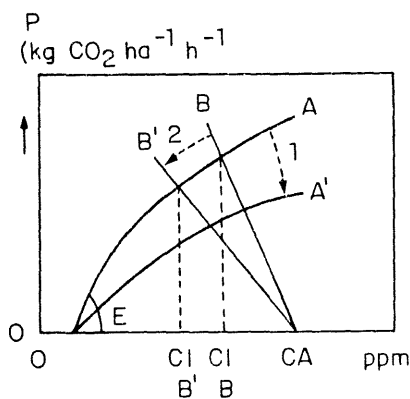

Fig. 3. Assimilation rate (P) at various internal CO_2 concentrations (CI, curve A); and the CO_2 supply function at various internal CO_2 concentrations (line B). Effects of mildew are indicated for two hypothetical mechanisms: (1) Reduction in efficiency in CO_2 absorption (ε): curve A transforms into curve A'. (2) Increase in stomatal resistance: line B transforms into line B'.

Table 3. Simulated daily gross assimilation of a wheat crop for an overcast and clear sky (DGAO and DGAC, in kg CO_2 ha^{-1} d^{-1}, respectively), at several crop development stages (DC). The mildew (PMI) was homogeneously distributed in the crop. For comparison, AMAX values (in kg CO_2 ha^{-1} h^{-1}) are presented.

PMI	Day 143, DC 35, $LAI^{[1]}$ = 2			Day 160, DC 50, LAI = 4			Day 173, DC 65, LAI = 4		
	DGAO	DGAC	AMAX	DGAO	DGAC	AMAX	DGAO	DGAC	AMAX
0.0	100 (156.)[2]	100 (475.)	100 (45.)	100 (206.)	100 (644.)	100 (44.)	100 (207.)	100 (620.)	100 (39.)
0.5	99.2	96.1	91.5	99.3	96.3	91.3	99.1	95.6	90.3
1.0	98.5	92.9	85.0	98.7	93.2	84.7	98.4	91.9	82.9
2.0	97.3	87.8	75.8	97.7	88.4	75.4	97.0	86.1	72.5
4.0	95.6	81.2	65.2	96.2	82.1	64.5	95.0	78.5	60.3
8.0	93.5	74.3	55.4	94.3	75.4	54.5	92.3	70.4	49.2
16.0	91.4	68.4	48.0	92.5	69.8	47.1	89.5	63.6	40.8

[1] Leaf Area Index, in m^2 m^{-2}

[2] Normalised values, control = 100. For control plants the values calculated by the model are presented in brackets.

Line B is the CO_2 supply function, describing the diffusion of CO_2 from the atmosphere (with concentration CA) to the intercellular spaces (with concentration CI). The initial slope is made by curve A with the abscissa (E). If the first mechanism (I) is operating, then the CO_2 flow from the stomatal cavities to the carboxylation sites will decrease. Because of the feedback loop between internal CO_2 concentration, assimilation rate and stomatal conductivity, the stomata would close (Goudriaan & van Laar, 1978; Farquhar & Sharkey, 1982). Consequently the rates of gas exchange would be reduced. Investigation of this mechanism was done in a study by Rabbinge et al. (1985). In this study, the CO_2 response of assimilation rate was measured and the carboxylation resistance was calculated from the

Table 4. The ratio of assimilation (A) and transpiration rates (T) at an irradiance of 320 W m^{-2} and ambient CO_2 concentration of 340 ppm for control and mildew-infected plants at DC 50.

n^1	PMI class	A/T	SD
23	control	10.6	0.95
11	0.1 - 0.5	10.4	1.07
11	0.5 - 1.0	9.3	0.67
9	1.0 - 2.0	9.2	0.65
9	2.0 - 3.0	9.4	0.80
10	3.0 - 6.0	9.3	0.81
9	6.0 -10.0	9.6	0.74
8	10.0	8.9	0.53

[1] number of replicates

relation between internal CO_2 concentration (CI) and net assimilation rate at an irradiance of 320 W m^{-2}. Mildew had no significant effect on the ratio so that stomatal resistance was not directly affected, although the presence of mechanism II may have been masked by the strong effects of mechanism I. Nevertheless, it is concluded that there is no influence of mildew on the stomatal regulation mechanism. As a result, the efficiency of water use, expressed as the assimilation/transpiration ratio, is influenced by mildew. Whatever the exact nature of the interaction may be, quantification of the effect and its consequences is necessary. This further analysis of the consequences of the effect of mildew on crop behaviour was done with the photosynthesis module of a basic crop growth model in which the effects on assimilation rate were introduced (Spitters & van Kraalingen, 1988; Rabbinge et al., 1985). In the calculations a homogeneous distribution of mildew was assumed. However, a homogeneous distribution will rarely occur in practice. More often, infection will be initially located in lower leaf layers and spread to the top of the canopy. This location effect was mimicked assuming an overall value of percentage mildew infected as before, but with a concentration of the mildew in specific layers of the canopy (Table 5).

Table 5. Location effect of mildew infection on daily gross assimilation under an overcast sky (DGAO) and under a clear sky (DGAC) for crops with LAI^1 = 2 (DC 35) and LAI = 4 (DC 50). Starting from the top, leaf layers (LAI = 1 per layer) are numbered I to IV. The percentage mildew covered leaf area (PMI) and AMAX (in kg CO_2 ha^{-1} h^{-1}) of the diseased layers are represented by PMIL and AMAXL respectively.

Infected	PMI = 4				PMI = 8			
leaf layers	PMIL	$AMAXL^2$	$DGAO^2$	$DGAC^2$	PMIL	$AMAXL^2$	$DGAO^2$	$DGAC^2$
LAI = 2, DC 35:								
none	0	100	100	100	0	100	100	100
I	8	55	95	82	16	48	93	78
II	8	55	99	92	16	48	98	90
all	4	65	96	81	8	55	93	74
LAI = 4, DC 50:								
none	0	100	100	100	0	100	100	100
I	16	47	95	83	32	42	94	81
I + II	8	55	95	80	16	47	93	75
IV	16	47	100	98	32	42	100	98
IV + III	8	55	100	96	16	47	100	95
IV + III + II	5.3	60	99	91	10.7	51	98	88
all	4	65	96	82	8	55	95	75

[1] Leaf Area Index, in m^2 m^{-2}

[2] Normalised values; disease-free = 100.

The effect on the gross assimilation rate was not marked when mildew was uniformly distributed over the canopy or concentrated in the upper leaf layers. When the mildew was concentrated in the lower leaf layers the reduction was smaller, and the effect of variation in the amount of mildew was substantial only when levels above 4% were reached.

The calculations above demonstrated the considerable effect of mildew on daily photosynthesis rate. The consequences for crop growth and production were evaluated using the same crop growth model for computations throughout the season. The outcomes were tested against field experiments which were done in 1983 by R.A. Daamen and I.J.M. Jorritsma (unpublished) at the experimental farm "Vreedepeel", situated on loamy sand and which is sensitive to dry conditions. The grain yields (total dry matter) attained in the control were 6500 kg compared to the potential 9000-12000 kg. Water limitation will cause a low growth rate during a part of the growing season. In the simulation, the yields were higher than 6500 kg but when a water balance was introduced which considered water shortage during the growing season, simulated and measured values corresponded better. The mildew, expressed as an integrated value of percentage mildew covered leaf area, was now introduced in the model and experimental and simulated relative yields at various mildew infection levels of the crop corresponded rather well (Fig. 4). The calculations are preliminary and a more detailed analysis by Daamen and Jorritsma is in preparation.
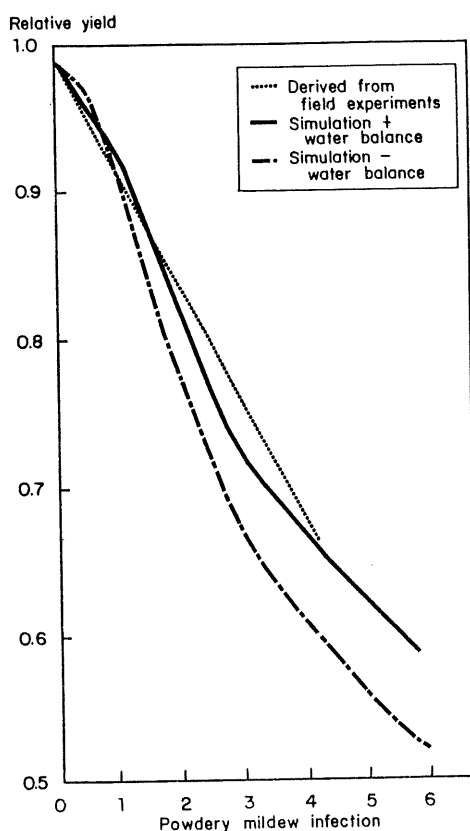
Fig. 4. Simulated and measured relative yields at various levels of mildew infection. Simulations are done with a combination model of crop growth and mildew infection, experiments are done at loamy sandy soil, (R.A. Daamen et al., unpublished)

The preliminary combination model of the growing crop and the disease has been used to evaluate the consequences of an integrated percentage of mildew severity of 3% during the growing season in crops growing at various production levels, which are dictated by water and nutrient limitations. These results (Table 6) (Schans, 1984) show that yield reduction is proportional to yield, which indicates that economic injury levels should be inversely proportional to yield.

Table 6. Simulated yield loss due to a mildew
load on the plants of 3% leaf coverage during
the growing season starting at DC 30, at various
expected yields in kg grain ha^{-1} (Schans, 1984).

Yield expected	Yield loss
6000	4800
8000	2400
10000	3000

Example 2. Cereal aphids on winter wheat. During recent decades aphids have become an important cause of yield loss in cereals, probably as a result of changes in crop husbandry (Rabbinge et al., 1983). In the Netherlands, the English grain aphid Sitobion avenae (F.), is usually the most abundant species on cereals.

Experiments have revealed the complex effects of S. avenae on yield loss. To quantify the effects of various dynamic processes on the growth of winter wheat, the various effects of cereal aphids (Table 7) were determined in detailed laboratory studies and introduced in a comprehensive simulation model of winter wheat of which a preliminary version is described by van Roermund et al., 1986. This was based on a detailed model of growth and development of spring wheat (van Keulen & Seligman, 1987).

Table 7 Damage components of cereal aphids
on winter wheat

1. Direct

    Assimilate consumption
    - carbohydrates
    - proteins (amino acid)
2. Indirect
    Saliva injection
    - Honeydew production
    - reduction photosynthesis (AMAX and
      EFF.)
    - promoting senescence

The model has been extended by incorporating a model describing the influence of S. avenae on various plant physiological parameters. Actual grain yield depends on environmental conditions, such as radiation and temperature, and on the availability of carbohydrates and nitrogen. The carbohydrate source is built up by net photosynthesis. The nitrogen source consists of translocatable nitrogen in the plant which is supplemented by nitrogen uptake from the soil. Carbohydrates and nitrogen are taken up by the grain and the competing aphids, which together form the sink. Both are characterised by their potential uptake rates.

Primary aphid damage is caused by withdrawal of phloem sap, which contains carbohydrates and nitrogen. This results in a reduction of the carbohydrate and nitrogen supply available for the grains. Secondary aphid damage is caused by the aphid excretion product, honeydew , on leaves. Honeydew reduces the maximum gross assimilation rate at light saturation (AMAX) and the light use efficiency (EFFE), resulting in a decrease of gross photosynthesis (Rabbinge et al., 1981). Recent detailed observations on the background of such effects on photosynthesis parameters have revealed some of the mechanisms (Rossing, in preparation). These effects were quantified in detailed laboratory studies, and
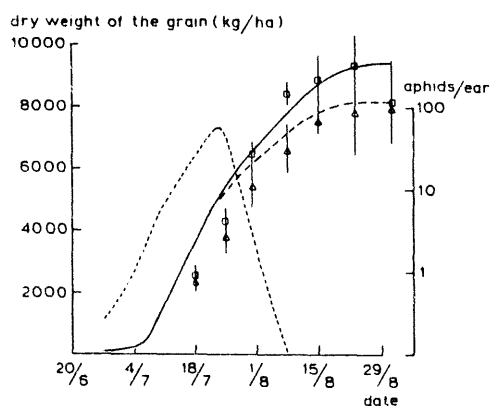

Fig. 5 Simulated (———) and measured (□) dry weight of the grain in the absence of aphids, simulated (— — —) and measured (Δ) dry weight of the grain in the presence of aphids and the aphid population (------), as a function of time

introduced into the simulation model. The simulations start at anthesis (DC 60, Zadoks et al., 1974). The model is initialised with the dry weights and nitrogen fractions of the plant organs at anthesis. Measured daily minimum and maximum temperature, daily total radiation and aphid densities are used as forcing functions. A field experiment with winter wheat (Triticum aestivum (L.) cv. Arminda) was carried out at the experimental farm 'De Eest' in Nagele, Noord-Oost Polder in 1984 to test the model. The experiment consisted of four treatments in six replicates; control of aphids by a selected aphicide (250 g pirimicarb in 600 l water per hectare) starting at development stages DC 71 (at the onset of the aphid infestation), DC 75 and DC 77, and an untreated control. Aphid numbers were recorded at weekly intervals, the method and sample size depending on the density (Ward et al., 1985). Growth analysis of the crop was carried out weekly on 50 haphazardly chosen culms per replicate.

In the field, an aphid damage (at harvest) of 994 $\pm$ 322 ha^{-1} was found. Aphid damage of 1241 kg ha^{-1} is simulated at a yield in the absence of aphids of 9377 kg ha^{-1} (Fig. 5).

Fig. 6 shows the different damage components simulated by the model, and their relative importance in total aphid damage at a yield in the absence of aphids of 8562 kg ha^{-1}. Although the aphid infestation started

at the end of June (with a population peak at 25 July, see Fig. 5), the simulated damage did not start until the second half of July. This is due to the reduction of the reserves in the stem at that time, i.e. when the grain growth changes from sink-limited to source-limited.
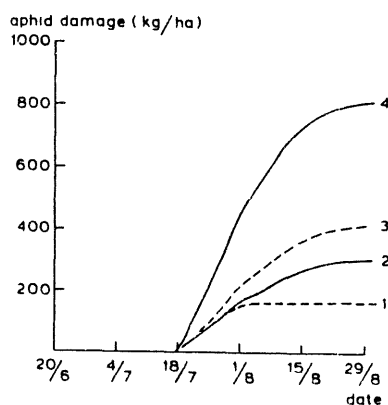

Fig. 6 Simulated damage components (kg ha^{-1} at an aphid intensity of 490 aphid-day and a yield in the absence of aphids of 8562 kg ha^{-1} as a function of time.
1 - carbohydrate withdrawal
2 - carbohydrate and nitrogen withdrawal
3 - carbohydrate and nitrogen withdrawal + AMAX reduction
4 - carbohydrate and nitrogen withdrawal + AMAX and EFFE reduction

Primary damage caused by removal of phloem sap forms 37% of the total damage. Carbohydrate and nitrogen withdrawal are of equal importance, although the time at which damage occurs is different; nitrogen withdrawal has a delayed effect on yield reduction.

Secondary damage, caused by AMAX and EFFE reduction resulting from honeydew deposits, is 63% of the total damage. The combination of withdrawal of phloem sap and AMAX reduction causes 51% of the total damage. The remainder is caused by EFFE reduction. Thus the reduction of EFFE caused by honeydew is the most important single component of the total aphid damage, according to this model. This is because EFFE is more sensitive to honeydew than AMAX, as has been shown in laboratory experiments (Rabbinge et al., 1981) and because the simulated growth is more sensitive to EFFE than to AMAX. These results have been partially confirmed by ecophysiological field and laboratory studies of Rossing (in prep.).

The simulated damage per aphid-day is highest during anthesis of wheat, (5.1 kg ha^{-1} per aphid day between DC 60 and DC 69 at a yield in the absence of aphids of 8562 kg ha^{-1}), and decreases during the grain-filling period (0.8 kg ha^{-1} per aphid-day between DC 75 and DC 77). From the field data of the four treatments, a weighted mean of 2.5 kg ha^{-1} per aphid-day has been calculated over the whole period in which aphids are present (between DC 71 and DC 79).

According to the simulation model, aphid damage increases more than linearly with the yield level in the absence of aphids up to a level of 8000 kg ha^{-1} (Fig. 6). Various yield levels are simulated by changing the initial values of the nitrogen level in the soil, the dry weight of the plant organs, their nitrogen fraction and the AMAX. At a high nitrogen level, plants take up more nitrogen, leading to a higher nitrogen and carbohydrate content in the crop, which stimulates photosynthesis. As a result, aphids take up more carbohydrates and nitrogen, and thus cause greater primary damage. Because of a longer period in which the leaf surface is productive, more green leaf area is covered by honeydew and secondary damage is higher. With increasing yield level, the relative effect of primary damage decreases and secondary effects due to honeydew excretion are more important. Beyond a yield level in the absence of aphids of 8000 kg ha^{-1}, aphid damage no longer increases more than linearly with yield level, and saturation occurs. This is because the crop parameters affected by aphids (e.g. nitrogen fraction, leaf area index, AMAX, EFFE) are now relatively less important in limiting grain growth. These high yields are also determined by other crop, soil and meteorological parameters before anthesis, which are not affected by aphids.

Thus, the economic injury levels in cereal aphids are changing relatively as well as absolutely with increasing yield levels. This has major consequences for supervised control as the tolerable aphid density may vary from >14 tiller^{-1} at yields of 5000 kg grains ha^{-1} and <3 tiller^{-1} at yield levels of 9000 kg ha^{-1}.

Conclusion

The examples of combination models of crop growth and a pest and a disease have shown how they may help to gain insight into the nature and level of yield reduction, and can be used to derive economic injury levels for various crop growth conditions. These flexible economic injury levels have considerable consequences for the practical application of integrated pest and disease control. Simple clues are becoming impossible and this will lead to the use of decision-supported management tools as described in the last section of this Bulletin.

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