Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz
Journal of Plant Diseases and Protection
87 (7), 409–422, 1980. ISSN 0340–8159
© Eugen Ulmer GmbH & Co., Stuttgart

The effect of diseases or pests upon the host[1])

Die Wirkung von Krankheiten oder Schädlingen auf den Wirt[1])

R. Rabbinge and P. H. Vereyken
Department of Theoretical Production Ecology, Agricultural University, p/a CABO, Bornesteeg 65, Wageningen, The Netherlands

Summary

A crop growth model of wheat based on a simplification of a detailed explanatory model for assimilation, respiration and transpiration of canopy surfaces is coupled to a population model of the cereal aphid *Sitobion avenae.* The crop model calculates dry matter accumulation of shoot, root and head in relation to such changing abiotic conditions as daylength, incoming radiation, temperature and humidity. It utilizes leaf area index as a driving variable. The pest model simulates the development of the aphid population, calculating both absolute numbers and age distribution, in relation to abiotic conditions like temperature and humidity and considers immigration, emigration and the different antagonists such as predators, parasites and *Entomophthora* spp. Results of model calculations show the importance of secondary effects such as honeydew production and its effect on secondary fungal parasites, which seem to account for more than 60 % of the yield losses.

Key words: models; simulation; abiotic factors; yield losses; wheat; *Sitobion avenae*

Zusammenfassung

Ein Wachstumsmodell für die Entwicklung von Weizen im Bestand, das auf einer Vereinfachung eines ausführlichen erklärenden Modells für die Assimilation, Atmung und Transpiration von Oberflächen in der oberen Bestandesgrenze basiert, ist mit einem Populationsmodell der Getreideblattlaus *Sitobion avenae* verknüpft. Das Modell für die Bestandesentwicklung berechnet die Ansammlung von Trockensubstanz des Schößlings, der Wurzel und der Ähre in Beziehung zu jenen sich ändernden abiotischen Bedingungen wie Tageslänge, auftreffende Strahlung, Temperatur und Feuchtigkeit. Es verwendet den Blattflächen-Index als eine lenkende Variable. Das Schädlingsmodell simuliert die Entwicklung der Blattlauspopulation, berechnet sowohl die absolute Anzahl als auch die Altersverteilung in Beziehung zu den abiotischen Bedingungen, wie Temperatur und Feuchtigkeit, und berücksichtigt die Einwanderung, Auswanderung und die verschiedenen Antagonisten wie Räuber, Parasiten und *Entomophthora* spp.

---

[1]) Written version of paper presented during the Symposium on "New Mathematical Approaches in Epidemiology" at the 3rd International Congress of Plant Pathology in Munich, 16–23 Aug. 1978.
Schriftliche Fassung eines Vortrages, der während des Symposiums über „Neue mathematische Ansätze der Epidemiologie" beim 3rd International Congress of Plant Pathology in München, 16.–23. 8. 1978, gehalten wurde.

Die Ergebnisse der Modellrechnungen zeigen die Wichtigkeit von sekundären Effekten wie die Honigtau-Produktion und ihre Wirkung auf sekundäre Pilzparasiten, die mehr als 60 % der Ertragsverluste zu erklären scheinen.

Stichwörter: Modelle; Simulation; abiotische Faktoren; Ertragsverluste; Weizen; *Sitobion avenae*

1 Introduction

Pest and disease control is gradually becoming a science concerned with programming of control measures through manipulation of the agricultural system. Integrated pest control requires well defined concepts of damage levels and accurate knowlege of the way a system may be changed by both chemical and biological control measures. Up till now the definition of damage levels for pests and diseases was merely empirical or based on the judgement of experienced specialists. Quantitatively well defined damage levels and accurate knowledge of the interactions of pests and diseases and their host are very rare so that studies on this topic are urgently needed. Here the problem is approached by coupling a basic model of crop growth to a simplified population model of a pest-causing organism and its natural enemies. Analysis of host and parasite behaviour in the simulation model should increase our understanding of this system through comparisons with the behaviour of real systems. This understanding of the system may pave the way for a more reliable management system of the damage-causing organism.

In this study, we consider the relation of cereal aphids with their host plant, wheat, and limit our discussion to the English green aphid *Sitobion avenae* F. on winter wheat, cv. 'Clement'. The increase in numbers of this species especially during the last decade constitutes a serious problem for wheat growing in Europe.

2 The hierarchical approach

Model development follows the hierarchical approach. Levels of organization and understanding are interrelated such that the behaviour of the system studied is explained from the way well-defined and elaborately studied processes, that constitute the system, operate. For example, the simulation of the system of crop growth can be based on detailed knowledge of the underlying processes of respiration, assimilation and transpiration and that of the population dynamics of an epidemic in the field may be based on detailed knowledge of the life cycle of the damage-causing organism that is collected in the laboratory. By comparison of model behaviour and the behaviour of the real system our understanding of the system grows. Based on this understanding, shortcuts are made; the elaborately defined processes are summarized and then incorporated in a broader model. Both crop growth and the population dynamics of the damage-causing organism are treated in this way.

3 A basic model of assimilation, respiration and transpiration

A highly detailed model of assimilation, respiration and transpiration of crop surfaces in the vegetative phase under optimal conditions has been developed and validated by workers at the Agricultural University and the Centre of Agrobiological Research in Wageningen (De Wit et al. 1978). An outline of this model, an explanatory dynamic model using the state determined approach, is given in the very simplified relational

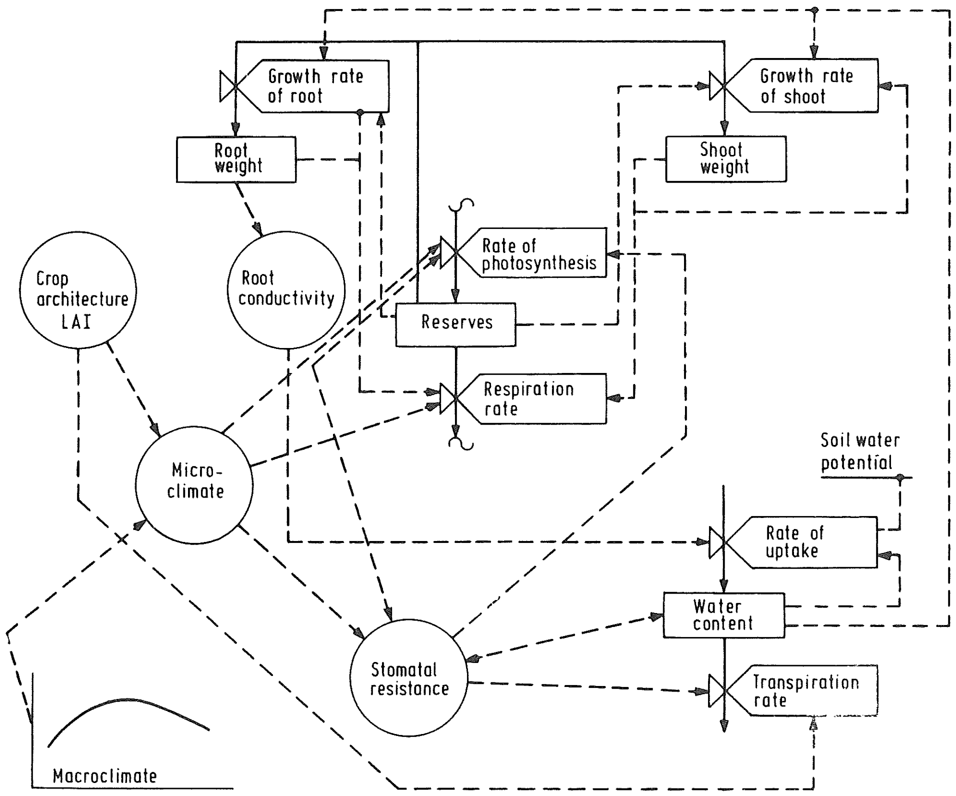


Fig. 1. Simplified relational diagram of BACROS, a basic model on respiration, transpiration and assimilation of crop surfaces.

Abb. 1. Vereinfachte Darstellung der Beziehungen im Diagramm von BACROS, einem Grund-Modell über Atmung, Transpiration und Assimilation von Pflanzenoberflächen.

diagram of Fig. 1, where rectangles represent state variables, the valves are rates and the circles auxiliary variables.

The growth of both shoot and root, defined as the increase in dry weight or structural material, is dependent on the amount of reserves present in the crop, the temperature and the water status of the crop. A functional balance, governed by the relative water content of the crop (Brouwer and De Wit 1968) determines the distribution of the newly formed material over shoot and root.

The water status of the plants is assumed to be constant with height within the canopy and is determined from the balance between transpiration and the water uptake from the soil. Transpiration is found by adding the transpiration rates of the various horizontal leaf layers that have been distinguished. These rates are calculated from the radiation absorbed by each layer, the stomatal conductivity, the resistance of the laminar layer, the turbulent resistance above the canopy and the humidity of the ambient air.

Water uptake from the soil is determined by the size of the root system, its conductivity and the difference in water potential between plant and soil, assuming the latter to be optimal (i. e. –0.1 bar). The conductivity is derived from the weight of the roots, assuming a ratio between weight, surface area and conductivity, that is dependent on soil temperature and the degree of suberization of the roots. Soil temperature and crop water status govern the growth rate of the roots. Basic models on heat transfer in the soil are available (DE WIT and VAN KEULEN 1972), but these models are not included in this basic crop growth simulator. Soil temperature is assumed to follow the air temperature with an exponential delay of 4 h.

The metabolic pool "reserves" is increased through the assimilation of carbon dioxide by the canopy. The increase is calculated by adding the assimilation rates of the variously exposed leaves in successive leaf layers. These rates are dependent on light intensity, CO_2 concentration in the ambient air and resistance to CO_2 diffusion from the atmosphere to the active sites. Transpiration and CO_2 assimilation interact strongly, not only because a relatively large transpiration may lead to loss of turgidity and subsequent closure of stomata, but also because regulation of the CO_2 concentration in the stomatal cavity may lead to closure of stomata due to a low rate of assimilation.

The metabolic pool, consisting of soluble carbohydrates and other new assimilates is decreased by the respiration rate. This rate is the sum of maintenance respiration and growth respiration. The latter is the cost of converting reserves into structural material and is, therefore, proportional to the rate of growth. The intensity of growth respiration is affected by the chemical composition of the new material, which may vary with stage of growth or other conditions. While that relationship is independent of temperature, the growth respiration is indirectly influenced by temperature through the temperature dependence of the growth rate. Usually the CO_2 evolution, resulting from the expenditure of energy in translocation of minerals and substrates, is included in the term for growth respiration. The rate of maintenance respiration depends on the turnover rates of proteins, the resynthesis of other degraded compounds, and maintenance of ionic gradients. Maintenance respiration, therefore, depends largely on the chemical composition of the plant and is considered to be sensitive to temperature. The calculation is based on the elaborated work of PENNING DE VRIES et al. (1974).

4 Validation and sensitivity analysis of the model

An extensive description of the plant growth model and its input relations is beyond the scope of this paper; a detailed description of model and input relations is given in DE WIT et al. (1978). In that report two versions of the basic model for assimilation, respiration and transpiration of crop surfaces are presented. One that simulates the daily course of assimilation, respiration and transpiration, which needs variable timesteps of integration and another version that simulates the seasonal pattern and is programmed such that a fixed timestep of one hour is possible. To validate the model that is used to simulate the daily course under field conditions, observations have been done in the field with a mobile laboratory. Fig. 2 shows some results of measurements and simulations; the daily course of assimilation, respiration and transpiration is correctly simulated. The version of the model that simulates seasonal patterns is validated by comparison with the results of field experiments in which periodic harvests are done, using the actual weather data as the driving variables. In Fig. 3 some of these calculations are presented. Growth of a crop, in this case corn, can be simulated with an acceptable level of accuracy for the crop growing at different places in the world under variable circumstances. These results give confidence in the prediction of crop growth under optimal conditions. The crop growth under field conditions is thus explained from the input relations established in the laboratory and

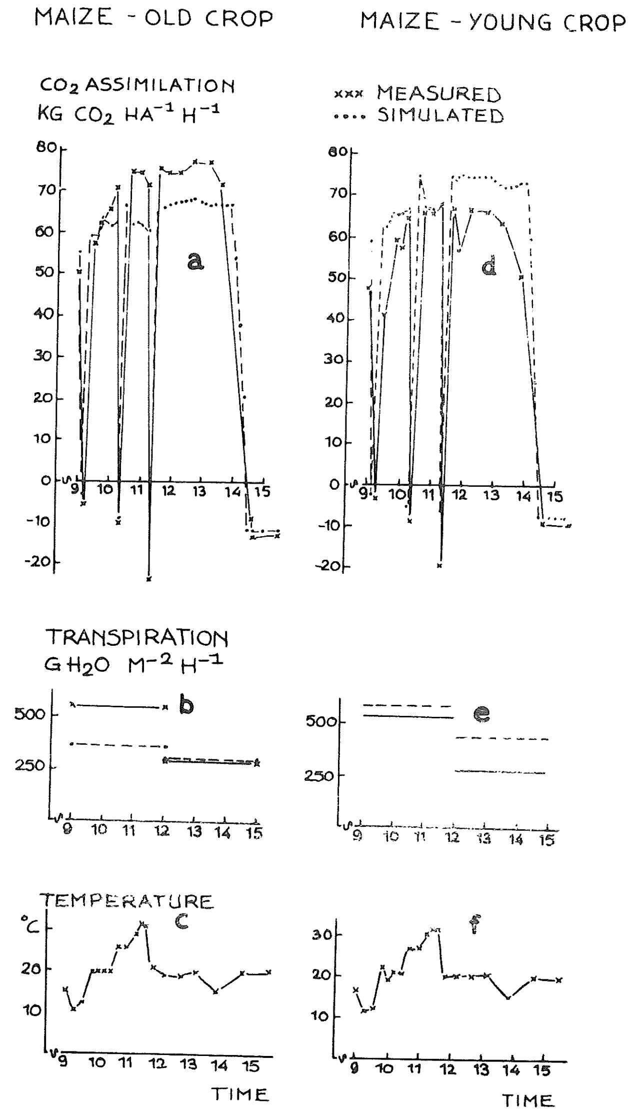
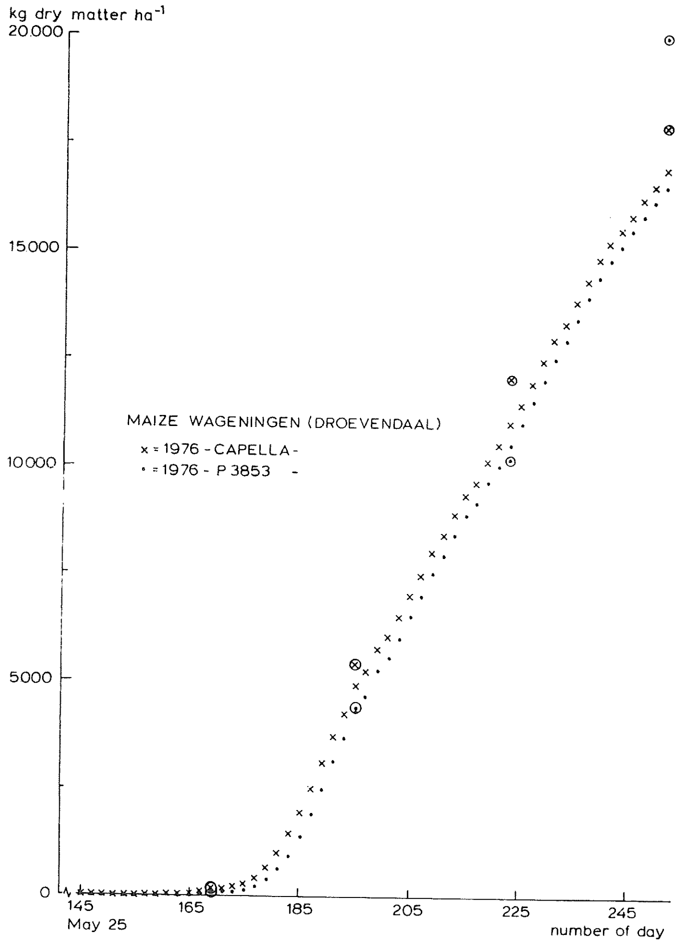


Fig. 2. Daily course of assimilation, respiration and transpiration of a corn crop under field conditions on 25 July 1976, an average summer day in the Netherlands; the dotted lines are the simulated, the solid lines the measured results.

Abb. 2. Täglicher Verlauf der Assimilation, Atmung und Transpiration eines Mais-Bestandes unter Feldbedingungen am 25. Juli 1976. Die gepunkteten Linien beziehen sich auf die simulierten, die durchgezogenen Linien auf die gemessenen Ergebnisse.

the phytotron. The validated model is now used for a sensitivity analysis to evaluate the effect of structural changes in the model, to test the assumptions implicitly made in the conceptualization of the model and to determine the relative importance of the rates and the parameters.

The results of that sensitivity analysis show that the effect of changes in most input relations within the confidence interval of their measurement do not cause major perturbations in the model when run for the seasonal situation. Runs in which structural changes in the model were made such that parts of the model were replaced by short-cuts, show that these do not give larger deviations than 5 % from the results of the basic model. Simplification is, therefore, allowed and this is done to enable the coupling to a population model of the aphid.



Ad Fig. 3 on page 415.

5 Simplified crop growth model

A relational diagram of the simplified crop growth model is presented in Fig. 4. This model is, in fact, descriptive rather than explanatory. The reproductive phase of the crop was incorporated in an arbitrary simplified way. Because our understanding of the processes of form and function is insufficient, these processes have to be mimicked rather than simulated. The translocation of the reserves accumulated by photosynthesis to shoot, root or head is governed by a state variable that accounts for the development stage of the crop that is changed by a temperature-dependent development rate. Like shoot, root and head, aphids use assimilates that flow in the phloem vessels. This use is indicated by a flow mainly governed by the auxiliary variable or submodel APHI. This submodel APHI also indirectly affects the crop. With their bodies, the aphids cover photosynthesizing area and moreover their excretion product, honeydew, may act as a blanket over the leaf. The detailed calculation of respiration rate is omitted since the composition of dry matter is not considered. Only a temperature-dependent growth respiration and a temperature-independent maintenance respiration is introduced. Photosynthesis is calculated according to methods described by De Wit

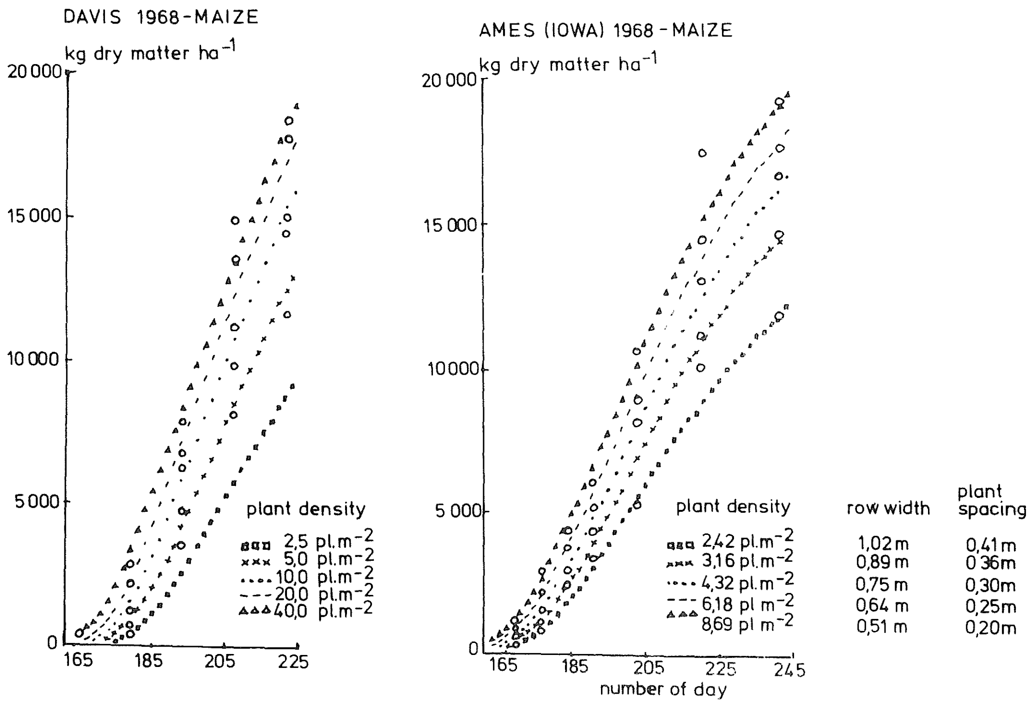


Fig. 3. Simulated and measured growth of a maize crop at different localities for different varieties and different sowing densities. The simulated numbers are given each two days, the measured numbers are given with changing intervals.

Abb. 3. Simuliertes und gemessenes Wachstum von Maispflanzen an verschiedenen Standorten bei unterschiedlichen Sorten und Aussaatdichten. Die simulierten Werte sind in 2-tägigem Abstand angegeben, die gemessenen Werte in unterschiedlichen Intervallen.

Table 1. The daily totals of radiation and photosynthesis for standard conditions at 50° Northern Latitude. (The maximum photosynthesis is assumed to be 50 kg ha^{-1} hour^{-1} and a spherical leaf distribution is assumed)

Tab. 1. Tägliche Gesamtwerte an Strahlung und Photosynthese für Standardbedingungen auf dem 50. nördl. Breitengrad. (Als maximale Photosyntheserate sind 50 kg ha^{-1} h^{-1} und eine sphärische Blattverteilung angenommen)

	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.
Total global radiation on very clear days (HC) (cal cm^{-2} day^{-1})	146.	262.	414.	608.	760.	836.	810.	688.	508.
Daily rate of gross photosynthesis on very clear days (PC) (kg CO_2 ha^{-1} day^{-1})	216.	353.	542.	764.	931.	1012.	981.	844.	636.
Daily rate of gross photosynthesis on overcast days (PO) (kg CO_2 ha^{-1} day^{-1})	64.	115.	190.	281.	352.	386.	372.	315.	229.

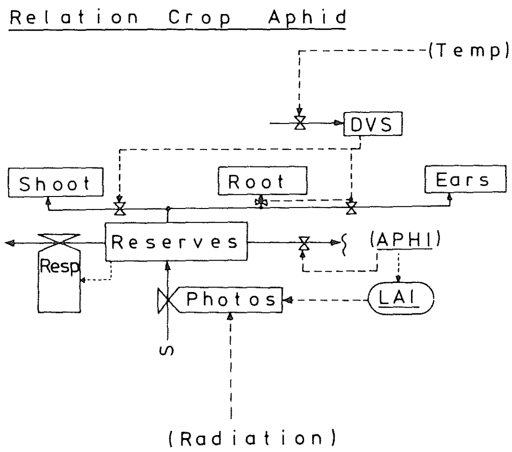


Fig. 4. Relational diagram of a simplified model of crop growth.
Abb. 4. Schematische Darstellung der Beziehungen in einem einfachen Modell für das Pflanzenwachstum.

(1965). Potential rates of dry matter accumulation are calculated with the sophisticated crop growth simulator and put in a table (Table 1) that is used to calculate the actual photosynthesis rate taking into account the actual daily radiation and the extinction of the radiation in the canopy. This calculation method is illustrated in Table 2.

6 The population model of the cereal aphids

Similar to the plant model, a detailed population model for the aphids including the effects of abiotic and biotic factors was developed and evaluated (Rabbinge et al. 1979). Simplified models were developed and coupled to the plant model. In Fig. 5 simplified relational diagram of the population model for the aphid is presented, using Forrester notation (Forrester 1961). Juvenile aphids with three larval stages develop into alatiformous or apteriformous L_4. The maturing apterous female may produce a

Table 2. Example of the calculation procedure to find the actual photosynthesis rate (Van Keulen 1976), see also text
Tab. 2. Beispiel für den Berechnungsablauf, um die aktuelle Photosyntheserate herauszufinden

(1)	Define the period of the calculations.
(1a)	Find then from Table 1, HC, PC and PO
(2)	Determine the initial value of the dry matter of the standing crop, determined from experiment.
(3)	Calculate the leaf area index (LAI) with specific leaf area and dry weight.
(4)	Find daily total global radiation (DTR) from a table of DTR versus time.
(5)	Calculate fraction overcast with: F = (DTR — 0.2 × HC)/(HC — 0.2 × HC)
(6)	Calculate gross photosynthesis: BF = f × PC + (1–F) × PO
(7)	Calculate net photosynthesis in leaf layer 1: NF1 = BF × (1.–exp(—0.6×LAI1)) — Respiration 1
(8)	Calculate net photosynthesis in leaf layer 2, 3 etc. NF2 = BF × exp (—0.6×LAI1) × (1.—exp(—0.6×LAI2)) — Respiration 2
(9)	Calculate respiration 1, 2 etc. resp. 1 = MR×DS1 (maintenance perc. × actual dry mass in this layer)
(10)	Calculate total net photosynthesis — Growth Resp.: NFOT = NF1 + NF2 + ...
(11)	Calculate new dry matter of standing crop and restart with 2.

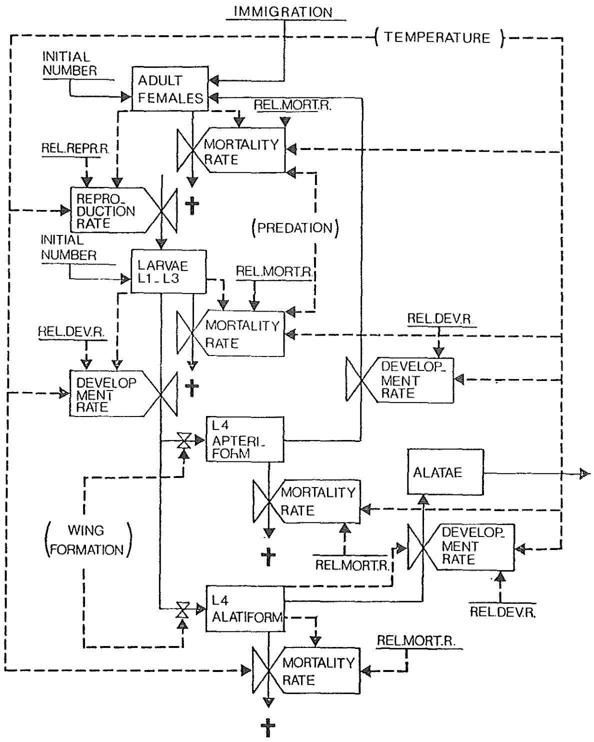


Fig. 5. Relational diagram of population growth and development of *Sitobion avenae*.
Abb. 5. Schematische Darstellung des Populationswachstums und der Entwicklung von *Sitobion avenae*.

new generation of aphids, the appearing apterae emigrate and disappear from the system. Wing formation is at first visible in the L_3 juvenile stage and is a result of the combined effects of temperature and crowding. The rate of development of juveniles is determined by temperature as shown in the relational diagram. The dispersion in time during development and ageing is mimicked with a method described by Goudriaan (1973). The different relations in the relational diagram are all dependent on temperature and food quality as quantified by literature data (Dean 1974) or own experiments and introduced in the model.

To account for the natural enemies, a similar population model for these organisms was developed. Unfortunately, quantitative data on the natural enemies are rare. Nevertheless, an attempt is made to include these organisms. *Syrphus corollae*, the natural enemy that occurred most frequently in our experimental fields in 1976, is therefore taken as an example. The other natural enemies *Coccinella septempunctata* and the parasites *Aphidius uzbekistanicus, A. picipes* and *Praon volucre* are omitted here. Also the important fungal disease, *Entomophthora* spp. is not included.

In Fig. 6, the relational diagram for the predator *S. corollae* is given. In their life cycle adult females produce eggs that hatch into larvae. These larvae develop into pupae that give rise to a new generation of adult females and males. Like the development rates of the prey, reproduction and fecundity are affected strongly by temperature. These effects are described by Barlow (1961) and Wahby (1967) and their data are used to quantify the different relations. The rate of predation is mainly determined by prey density, predator density, temperature and the physiological condition of the predator. In a way similar to Rabbinge's method (1976), relative predation rates for each of the morphological stages are calculated and introduced

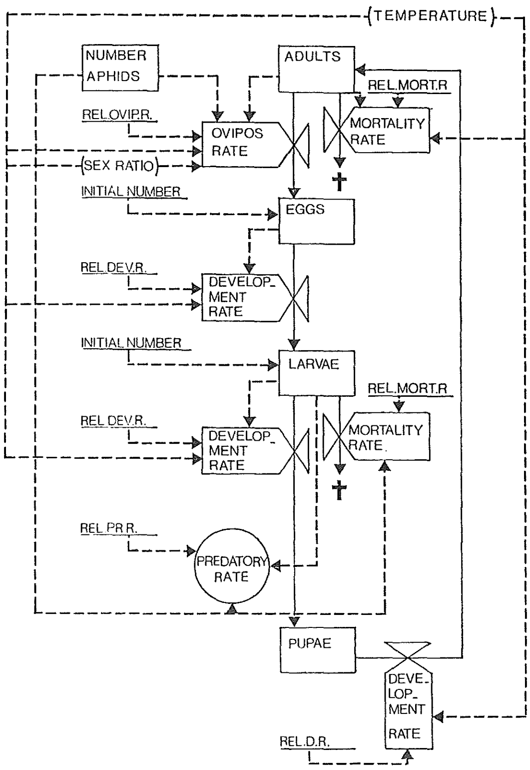
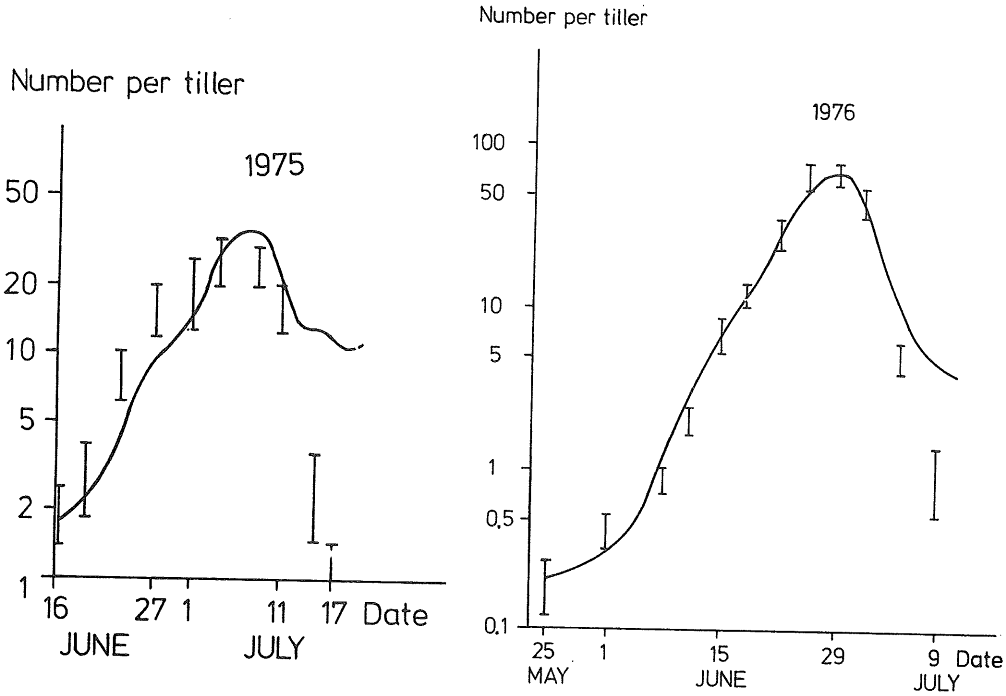


Fig. 6. Relational diagram of population growth and development of *Syrphus corollae*.
Abb. 6. Schematische Darstellung des Populationswachstums und der Entwicklung von *Syrphus corollae*.

in the model. Data from the literature were sufficient to quantify these input relations of the model for density dependence and the effect of insufficient food on the development rate of the predator and its reproductive rate (Bombosch 1962). The description of the model is necessarily short, a more extensive presentation is given by Rabbinge et al. (1979).

To validate the model, field experiments were done in which the numbers of prey and predator were counted throughout the season. Fig. 7 shows some of the results of the calculations in relation to field data for three years, the latter being given as confidence intervals (95 %). In all 3 years, the simulated and observed population density curves are in good correspondence during the phase of unlimited growth, and during the period of flattening of the curve, mainly due to wing formation which results in emigration. Only the collapse of the aphid population is not simulated properly. This collapse was especially noticeable in 1977 when the aphid population was attacked by an epizootic of *Entomophthora* spp. This poor agreement for the effect of the natural enemies indicates a need for more detailed biological information on these aspects. The reliability of the model during the first two phases of population growth is confirmed by calculations for other localities and by simulation of historical data on the course of the aphid population densities curve and enables its use for predictive purposes. These calculations and a sensitivity analysis with this explanatory model enable a simplification of the model using only the first phases of aphid population growth and the onset of population collapse as describing factors. These simplifications include the elimination of the detailed age structure of the aphid; the densities are now expressed in terms of biomass instead of numbers and in a generalized



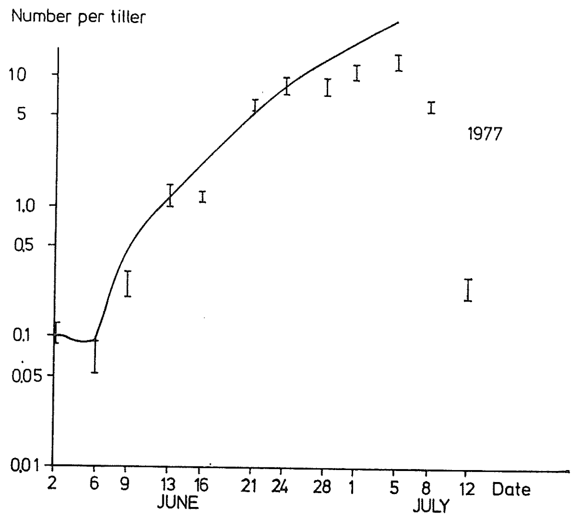


Fig. 7. Simulated and counted total number of *S. avenae* in 1975, 1976 and 1977. The counted numbers are given in terms of 95 % confidence intervals and the simulated numbers are given as solid lines.
Abb. 7. Simulierte und gezählte Gesamtmengen von *S. avenae* in den Jahren 1975, 1976 und 1977. Die Zählwerte sind in Form von Konfidenz-Intervallen mit einer statistischen Sicherheit von 95 % angegeben, während die durch Simulation gewonnenen Werte als durchgehende Linie dargestellt sind.

formulation of the natural enemies. The outcomes of this simplified model describe quite well the experimental curves (Fig. 8).

7 Coupling of aphid and plant model

To couple the two simplified models, detailed knowledge on suck rate, weight and food use efficiency of the aphids is needed. Such information was collected by VEREYKEN (1979). The average weight of an aphid in the field is 0.4 mg fresh weight and the

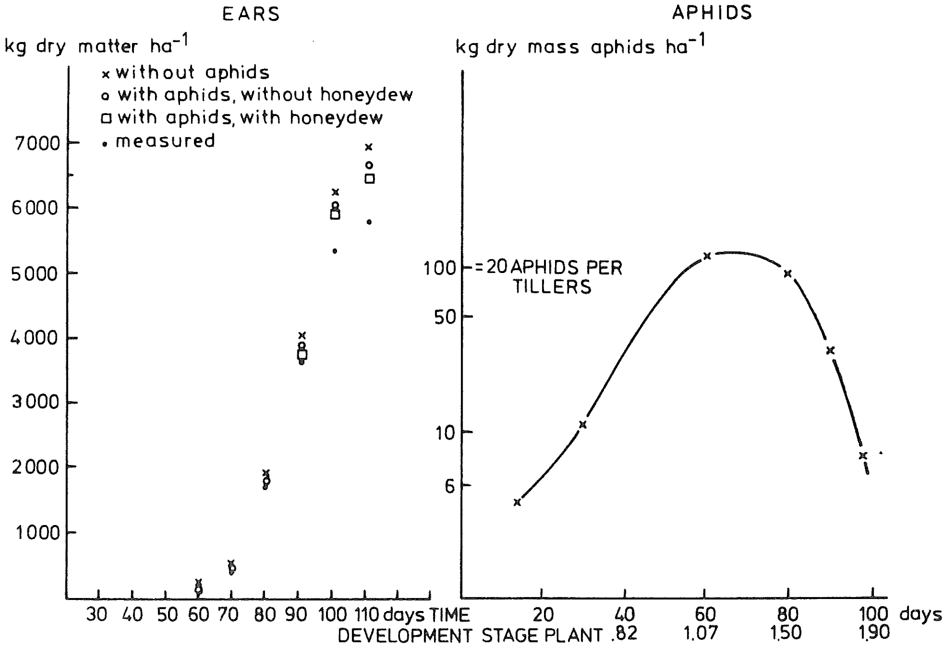


Fig. 8. Simulated effects of the presence of *S. avenae* on growth of winter wheat variety 'Clement', with and without the effect of leaf covering effects of honeydew.

Abb. 8. Simulierte Wirkungen über den Einfluß von *S. avenae* auf das Wachstum der Winterweizensorte 'Clement', mit und ohne die Wirkung eines blattbedeckenden Effektes durch Honigtau.

average production of honeydew amounts to 0.88 mg $aphid^{-1}$ day^{-1}. The surface area covered by an adult aphid is 0.4 mm^2, and the younger stages cover a smaller area proportional to their weight. The coverage of the leaves by honeydew is very heavily influenced by the air humidity. In dry air the honeydew crystallizes and has no effect; in humid air a thin cover of honeydew solution is seen. The assumption is made that a droplet of honeydew weighing 1 mg covers 0.5 cm^2 of leaf area.

8 Results of the preliminary calculations

Calculations with the combined model and those in which no aphids were present are compared in Fig. 8. The input relations for this and the other models are presented in Table 3. In the three seasons of observations, the densities of the aphid populations were never so large that the dry matter yield of the ears decreased more than 10 %. Nevertheless, in these years the total load of aphids on the wheat crop was considerably higher than the generally accepted damage level of 15 aphids per tiller after flowering. The observed yields, however, showed that in some way or another the presence of the aphid must have caused considerable damage. Neither the direct effects of sucking damage, nor reduced photosynthesizing leaf area can account for the observed damage. This is shown in Fig. 8, where runs with and without effects of the leaf coverage by

Table 3. Input data for the simplified crop growth model coupled to a simplified model of the population dynamics of *S. avenae*
Tab. 3. Eingabewerte für das vereinfachte Pflanzenwachstumsmodell, das mit einem einfachen Modell für die Populationsdynamik von *S. avenae* verbunden ist

Crop growth model	
(1) Latitude site, day of the year, initial dry mass crop and development state.	
(2) Daily maximum and minimum temperature.	
(3) Daily total global radiation.	
(4) Specific leaf area.	
Aphid model	
(1) Initial quantity of aphids.	
(2) Initial number natural enemies.	
(3) Daily maximum and minimum temperature.	
Coupling simplified crop growth simulator and simplified population dynamics model of aphid	
(1) suck rate of the aphid	kg CH_2O (honeydew)/kg CH_2O (aphid) day $^{-1}$
(2) honeydew production of the aphid	kg CH_2O (honeydew)/kg CH_2O (aphid) day $^{-1}$
(3) area weight ratio of the aphid	m^2 kg CH_2O (aphid)
(4) area weight ratio of the honeydew	m^2 kg CH_2O (honeydew)
(5) food use efficiency of the aphid	kg CH_2O (aphid)/kg CH_2O (aphid) day^{-1} consumed

aphids and honeydew are made. Apparently secondary effects due to the presence of honeydew on the leaves promoting leaf senescence or serving as a food source for black fungi and thus introducing all kinds of other fungal attacks are the major source of the loss in yield. Another reason for the disagreement between model calculations and actual experiments may be the uncertainty in the present conceptualization of the system. Partitioning coefficients in the growth model may be incorrect or the assumed insect-plant relations may be too simplified since compensatory effects and detailed location of the aphids, be it leaf or ear, were omitted. These characteristics should be determined more carefully before conclusive remarks on the management of the system can be made. The effect of the aphids may also have been amplified by the phase of presence, a small load of aphids in the crucial phase of ear setting may have a relatively large effect on final yield. In most cases the indirect effect of aphids may, however, be absent since spraying against fungi active during the maturing phase of the wheat is done anyway, so that the development of fungi on the honeydew is prevented. More detailed studies on all these aspects are required before general statements on the aphid-host plant system can be made and the objective of a reliable warning system may be reached.

A combination of these detailed studies with quantitative hypothesis formulation by means of computer simulation models and testing of these models in independent validation experiments appeared to be up till now a very promising scientific method.

Literature

Barlow, C. A.: On the biology and reproductive capacity of *Syrphus corollae* Fab. in the laboratory. – Ent. exp. appl. 4, 91–100, 1961.

Bombosch, S.: Über den Einfluß der Nahrungsmenge auf die Entwicklung von *Syrphus corollae* Fab. – Z. angew. Ent. 150, 40–45, 1962.

Brouwer, R., C. T. de Wit: A simulation model of plant growth with special attention to root growth and its consequences. – Proc. 15th Easter School Agric. Sci., Univ. of Nottingham, 224–242, 1968.

DEAN, G. J.: Effect of temperature on the cereal aphids *Metopolophium dishodum* (Wlk.), *Rhopalosiphum padi* (L.) and *Macrosiphum avenae* (F.). – Bull. ent. Res. **63**, 401–404, 1974.

FORRESTER, J. W.: Industrial dynamics. – MIT Press, Boston 1961.

GOUDRIAAN, J.: Dispersion in simulation models of population growth and salt movement in the soil. – Neth. J. agric. Sci. **21**, 269–281, 1973.

KEULEN, H. VAN: A calculation method for potential rice production. – Contr. cent. Res. Inst. Agric., Bogor, Indonesia, No. 21, 1976.

PENNING DE VRIES, F. W. T., A. H. M. BRUNSTING, H. H. VAN LAAR: Products, requirements and efficiency of biosynthesis: a quantitative approach. – J. theor. Biol. **45**, 339–377, 1974.

RABBINGE, R.: Biological control of fruit-tree red spider mite. – Simulation Monographs, Pudoc, Wageningen, The Netherlands, 228 pp., 1976.

RABBINGE, R., G. W. ANKERSMIT, G. PAK: Cereal aphids epidemiology and simulation of population development in winter wheat. – Neth. J. Pl. Path. **85** 197–220, 1979.

VEREYKEN, P. H.: Feeding and multiplication of three cereal aphid species and their effect on yield of winter wheat. – Versl. landbouwk. Onderz. Ned. **888**, 58 pp., 1979.

WAHBI, A. A.: Untersuchungen über den Einfluß der Temperatur und der relativen Luftfeuchtigkeit auf das Fraßvermögen von Syrphidenlarven (Diptera, Syrphidae). – Diss. Georg-August-Universität, Göttingen 1967.

WIT, C. T. DE: Photosynthesis of leaf canopies. – Agric. Res. Rep. **663**, Pudoc, Wageningen 1965.

WIT, C. T. DE, H. VAN KEULEN: Simulation of transport processes in soils. – Simulation Monographs, Pudoc, Wageningen, 109 pp., 1972.

WIT, C. T. DE, J. GOUDRIAAN, H. H. VAN LAAR, F. W. T. PENNING DE VRIES, R. RABBINGE, H. VAN KEULEN, W. LOUWERSE, L. SIBMA, C. DE JONGE: Simulation of assimilation, respiration and transpiration of leaf canopies. – Simulation Monographs. Pudoc, Wageningen, the Netherlands, 140 pp., 1978.