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MODELLING THE EFFECT OF ASSIMILATE WITHDRAWAL BY BLACK BEAN APHID, Aphis fabae, ON THE GROWTH OF SUGARBEET PLANTS, INFECTED WITH BEET YELLOWS VIRUS

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Summary

Damage to sugarbeet plants from aphid feeding and simultaneous virus infection was studied experimentally and analysed with a simulation model.

Experiment. Sugarbeet plants, grown on nutrient solution in a glasshouse, were infested with black bean aphids in the two-leaf stage. The aphids infected the plant with beet yellows virus. In the following month, the healthy plants reached a final dry weight of 30 g and a leaf area of 0.27 m^2, whereas the aphid-infested plants reached a weight of 9 g and a leaf area of 0.12 m^2. The peak number of aphids per plant was 2700. From the collection of honeydew droplets, the rate of assimilate withdrawal by the aphids was estimated as 1.6 mg (sugar) mg^{-1} (aphid dry weight) day^{-1}.

Model. A plant growth simulation model was used to calculate the theoretical effect of the two growth reducing agents. Thereby, the assimilate withdrawal by the aphids and the decreased rate of photosynthesis and increased light scattering and respiration in yellow virus-infected leaves were taken into account. The daily assimilate production by the plants was calculated from measured leaf area, observed photosynthesis light response curves, and incoming radiation. Assimilate withdrawal was estimated on the basis of the observed dry weight of the aphid population and the assimilate requirement of the aphids. The simulation results demonstrate that the aphids absorb a significant proportion of the assimilates produced by the plant, up to *ca.* 70%. Assimilate withdrawal by the aphids and the malfunctioning of the yellow leaves quantitatively account for the observed reduction of sugarbeet growth.

Introduction

Black bean aphid, *Aphis fabae,* is a major pest of sugarbeet, *Beta vulgaris* ssp. *saccharifera* and field beans, *Vicia faba,* in Europe (Weismann and Vallo, 1963; Cammell, 1981; Hurej, 1984; Jones and Jones, 1984). The aphid overwinters on woody primary hosts, mostly *Evonymus europaeus,* and migrates to arable crops in spring. Damage to the crops depends on the growth stage at which the plants become infested, early infestation causing greater loss. The economic injury level - the population density at which the costs and profits of control are equal (Wellings et al, 1989) - increases during the season. Economic injury levels can be

established by field experimentation, by expert assessment or by theoretical analysis of the population dynamics of the pest and the mechanisms of damage, making use of simulation models and decision theory (Rabbinge and Rossing, 1988; Rossing, 1989). The present study concerns the mechanisms of damage by *Aphis fabae* in sugarbeet.

Aphids cause damage to their host plants through several mechanisms (Miles, 1989a,b). The three most important are: (1) withdrawal of assimilates, (2) leaf coverage with honeydew and (3) injection of physiologically active substances, toxins or growth regulators, with the saliva. Hurej and Van der Werf (in prep.) found no effects of honeydew coverage on leaf longevity and photosynthesis in sugarbeet. The nature and effects of tentatively physiologically active substances in the saliva of *Aphis fabae* are unknown. Therefore, in this paper, we investigate whether the effect of *Aphis fabae* on the growth of sugarbeet can be explained by the first mechanism alone.

Assimilate withdrawal by the black bean aphid on field bean has been quantified by Banks and Macaulay (1964), using a water budget approach. Their data indicate that the aphids imbibe about 2 mg phloem sap (fresh weight; FW) per mg body FW per day. Data of Llewellyn and Qureshi (1978), who constructed an energy budget for *Aphis fabae* on *Vicia faba,* also suggest a rate of 2 mg (phloem sap FW) mg^{-1} (aphid FW) day^{-1} for adults but a higher rate for larvae: $\pm$ 5 (phloem sap FW) mg^{-1} (aphid FW) day^{-1}. Relative ingestion rates in the order of 1 to 2 mg (phloem sap FW) mg^{-1} (aphid FW) day^{-1} have been found for other aphid species (Coster, 1983; Rabbinge and Coster, 1984). The rate of sap uptake by *Aphis fabae* on sugarbeet has not been investigated, so far, and it may differ from the afore-mentioned values because the ingestion rate of an aphid is affected by the quality of the phloem sap, e.g. the amino acid composition.

To test the hypothesis that assimilate withdrawal is responsible for the growth-reducing effect of *Aphis fabae* in sugarbeet, an experiment was performed. In the experiment, the growth of individual aphid-infested sugarbeet plants was compared to the growth of a control group. Number and size of the aphids on the infested plants were monitored to calculate the daily sugar drain due to aphid feeding. Literature estimates of the relative ingestion rate were verified by collecting the honeydew produced by some aphid colonies. The expected effect of assimilate withdrawal on the growth of sugarbeet was calculated with a simulation model. Subsequently the experimental and simulation data were compared.

In the model a second growth reducing agent, beet yellows virus (BYV), had to be introduced as the black bean aphids in the experiment accidentally transmitted this virus to all aphid-infested plants. Infection with beet yellows virus has four crop physiological effects (Van der Werf, 1988): (1) reduction of leaf size; (2) increase of light scattering by leaves; (3) impairment of photosynthesis in yellow leaves; and (4) increase of respiration. Moreover, the dry matter distribution in the plant is affected. These effects of beet yellows virus are relatively well understood and can be adequately accounted for in a plant growth model, as described elsewhere (Van der Werf, 1988). This paper concentrates on the effect of the aphids.

Experiment: materials and methods

Experimental conditions and treatments. Sugarbeet, cv. Gration, were sown in moist earth. When the plants had reached the two-leaf stage, they were transplanted in 70 l. containers, filled with 1/4 strength modified Hoagland nutrient solution (Hewitt, 1966; p. 189), supplemented with iron-EDTA. The plants were divided in a treatment group, (A), and a control group, (C), 32 plants each. The plants of both groups were randomized in blocks of 10-12 plants in a glasshouse. No additional light was provided. The temperature regime was: day/night 25/21 °C. Air humidity was kept at a minimum of 75%. Sugarbeet plants of group A were infested in the two-leaf stage, on 7 August 1989 (day 0), with three apterous adults. During the first week, some aphids that had died were replaced. Aphids migrating to control plants were removed until the fourth week. Dispersal became then too substantial to be controlled. The experiment was terminated on 8 September, before *Aphis fabae* migrating to control plants had caused significant growth reduction. The plants, being spaced at least 50 cm, did not compete for light during the 32 days of the experiment.

Aphid and virus material. Black bean aphids were a mixture of two different populations: one was collected in flowering sugarbeet near Wageningen in May 1989 and the other came from a permanent culture on *Vicia faba* (courtesy of F.L Dieleman). Before starting the experiment, several generations of this population mixture were reared on sugarbeet to avoid adaptation problems on sugarbeet. BYV was introduced accidentally and originated probably from a nearby culture of a strain causing severe symptoms: vein etch, leaf blade yellowing and necrotic leaf spots.

Growth analysis. The area of the individual leaves on each plant was determined twice a week, using transparent overlay sheets with a 1 x 1 cm^2 square grid pattern of black dots. Eight A-plants and five C-plants were harvested on day 11 and day 25, while 10 and 13 A- and C-plants were harvested on day 32. From these plants total leaf area was measured with a Licor L3100. The leaf blades, petioles, storage root (including crown) and fibrous roots were dried at 105 °C and weighed.

Aphid monitoring. Aphids on the A-plants were counted three times a week. To obtain a reasonably accurate estimate of the total aphid weight per plant, individuals were categorized in three arbitrary size classes: *small,* length 0.5 - 1.0 mm., *medium* (mostly large larvae), length 1.0 - 2.0 mm. and *large* (mostly adults), longer than 2.0 mm. Black bean aphids from harvested A-plants were dried at 105 °C and weighed to determine the average weight in each size class.

Honeydew collection. From day 9 to 11, the honeydew produced by 7 aphid colonies was collected in Petri dishes with inert mineral oil (Marcol 82; ESSO). The honeydew was pipetted from the bottom of the dish and weighed to estimate the ingestion rate of the aphids (see below).

Photosynthesis measurements. On day 30 and 31, photosynthesis-light response curves on A- and C-plants were determined in ambient light, with four different

degrees of shading by white nylon gauze or white paper, and in the dark, using an ADC LCA-2 portable system for CO_2/H_2O gas exchange measurements. Five to seven measurements were taken at sequentially lower light intensities within *ca.* 10 minutes on each leaf. On day 35, after the experiment had finished, five C-plants, then infested with 500 - 1000 aphids, were transferred to a laboratory setup for photosynthesis measurements, similar to that described by Louwerse and van Oorschot (1969). Photosynthesis was measured in the dark and at seven different light intensities in measurement sessions lasting *ca.* six h. The measured photosynthesis-light responses were characterized by fitting asymptotic exponential equations (Goudriaan, 1982):

$$P_n = (P_m + R_d) . \left(1 - e^{-(\varepsilon . H) / (P_m + R_d)} \right) - R_d$$

where

P_n = Actual net rate of photosynthesis,

P_m = Maximum photosynthesis rate at light saturation (mg (CO_2) m^{-2} (leaf) s^{-1}),

R_d = Rate of respiration, measured in the dark (mg (CO_2) m^{-2} (leaf) s^{-1}),

ε = Light use efficiency (mg CO_2 J^{-1} (absorbed PAR)), and

H = Absorbed photosynthetically active radiation (PAR; 400-700 nm; J m^{-2} s^{-1})

Experiment: results

During the first 14 days, the leaf area of the C-plants grew exponentially from 15.5 ± 0.6 (SEM) to 597 ± 20 cm^2, an increase of 30% each day (Figure 1A). Thereafter followed a period of ca. 10 days in which leaf area grew linearly at a rate of ca. 160 cm^2 d^{-1}, and finally the rate of leaf growth decreased to less than 50 cm^2 d^{-1}. The A-plants grew slower, a significant difference with the C-plants being detected for the first time on day 11: 209 ± 15 vs. 283 ± 11 cm^2. First symptoms of beet yellows virus appeared after 14 days, and finally 25% of the leaf area became yellow. The difference in leaf area between C- and A-plant steadily increased (Figure 1A). The lagging behind of the A-plants was due to decreased leaf expansion, the number of leaves being the same as in the control (Figure 1B). The relative difference between C- and A-plants was even greater when total weight is considered (Figure 2A). Translocation patterns were slightly different (Figure 2B,C), C-plants allocating a greater percentage of dry matter to the storage organ than A-plants. At each harvest, the ratio of leaf area to leaf dry weight (specific leaf area; SLA) was determined. No significant differences between dates or treatments were detected (t-test; p=5%). SLA data were pooled to yield a grand average of 250 ± 9 cm^2 (leaf) g^{-1} (leaf DW)

During the first three weeks of the experiment the aphid population grew exponentially at a rate of ca. 27% per day, thereby reaching numbers of 2700 per plant (Figure 3). After day 21 the growth rate of the population on the plants decreased, at least partly because more and more aphids left the plants. Dry weights of the aphids are given in Table 1.

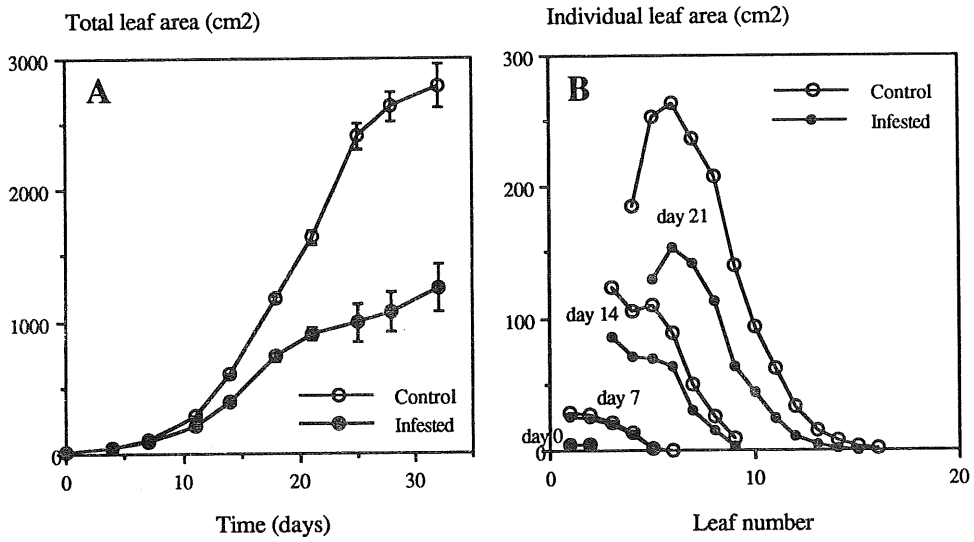

Figure 1: Growth of total (± SEM; A) and individual leaf area (B) on healthy sugarbeet plants and on plants infested with *Aphis fabae*.

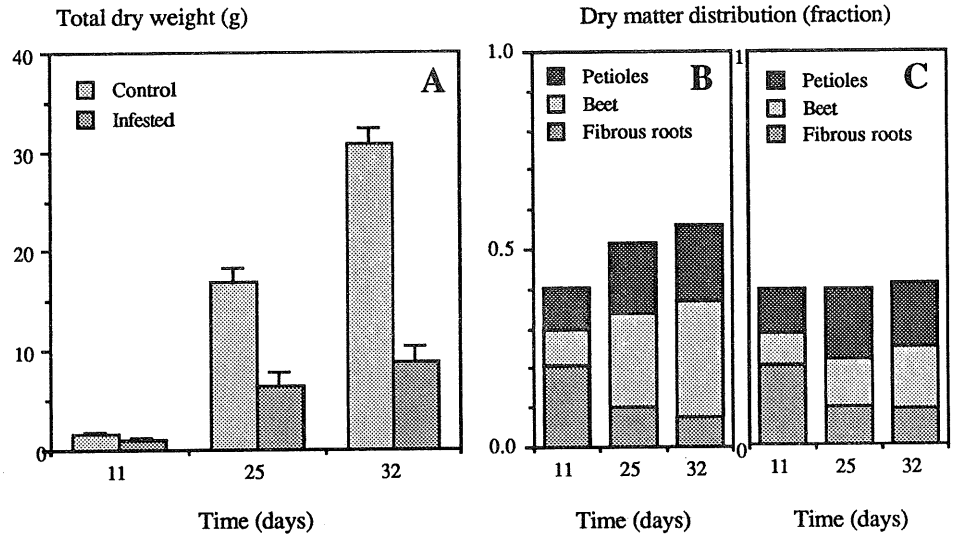

Figure 2: Increase of dry matter (± SEM) in healthy sugarbeet and sugarbeet infested with *Aphis fabae* (A), and distribution of dry matter in healthy (B) and aphid-infested plants (C). The fraction of dry matter allocated to leaf blades is the complement of the shown bars.

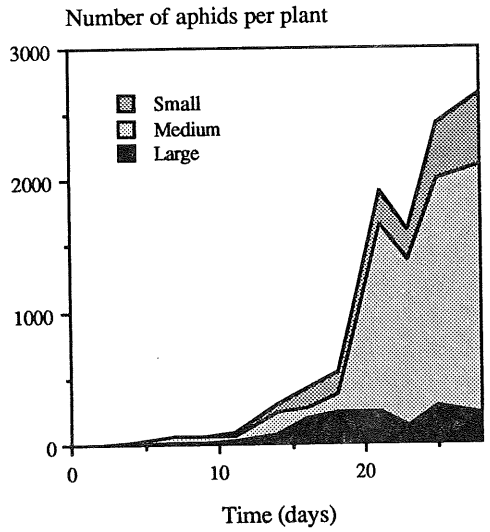

Figure 3: Number of *Aphis fabae*, classified according to size.

Table 1: Weight of black bean aphids (µg DW ± SEM)

Day	small	medium	large	average[a]	n
0	-	-	333 ± 11	333 ± 11	7
11	30 ± 4.2	110 ± 13	260 ± 11	70 ± 6	8
25	16 ± 3.3	65 ± 6	120 ± 10	50 ± 5	8
32	15 ± 1.4	65 ± 5	110 ± 6	50 ± 4	5

[a]Age distribution taken into account

From day 9 to day 11, the honeydew production by 7 aphid colonies was measured. The colonies consisted of 122 ± 69 ($\hat{\sigma}_{n-1}$) individuals and it was assumed that their size distribution was equal to that on the A-plants harvested on day 11. The increase in number and size during the 2-day interval was estimated with an aphid population model, based on life-history and growth data of Kennedy and Booth (1951), Banks and Macaulay (1964), and Frazer (1972). This model described the observed population growth adequately (the root of the mean squared difference between observed and simulated number after two days was 17%). The model was used to verify the relative ingestion rate of *Aphis fabae* as estimated from the literature (see introduction) and to provide an estimate appropriate to the actual experimental conditions by calibration.

The relative honeydew production rate based on data of Banks and Macaulay (1964) and Llewellyn and Qureshi (1978), 2 mg (honeydew FW) mg^{-1} (aphid FW) day^{-1} (see introduction), underestimated the observed honeydew production. A better fit was obtained with a relative honeydew production rate of 4.2 mg (honeydew FW) mg^{-1} (aphid FW) day^{-1}. This rate, divided by 0.85, the proportion of ingested sap excreted as honeydew; Banks and Macauley, 1964), yields an ingestion rate of 4.9 mg (phloem sap FW) mg^{-1} (aphid FW) day^{-1}.

Observed photosynthesis rates are given in Table 2. Rates of photosynthesis typical for healthy sugarbeet were observed on the C-plants. Yellow leaves on A-plants exhibited low rates of photosynthesis, typical of BYV-infected leaves (Hall and Loomis, 1972a,b; Van der Werf, 1988).

Table 2: Photosynthesis parameters (± SE) for leaves on aphid-infested (A) and control (C) plants

	P_m (mg m^{-2} s^{-1})	R_d (mg m^{-2} s^{-1})	ε^e (μg (CO_2) J^{-1} (PAR_{abs}))	r^2	n^f
A-plants[a]	0.24 ± 0.02	0.06 ± 0.02	11.4 ± 2.1	0.94	13
C-plants[b]	0.96 ± 0.23[d]	0.04 ± 0.02	13.3 ± 2.1	0.89	7
C-plants[c]	1.11 ± 0.04	0.05 ± 0.02	11.4 ± 0.8	0.97	12

[a]Yellow leaves, measured with portable equipment in the glasshouse

[b]Green leaves, measured with portable equipment in the glasshouse

[c]Green leaves, measured with laboratory setup

[d]High SE of P_m due to extrapolation necessitated by low ambient light intensity

[e]Assuming 85% absorption for green and 70% for yellow leaves; Van der Werf, 1988)

[f]Number of leaves sampled

Simulation model

A model was constructed to simulate the growth of sugarbeet plants with and without *Aphis fabae* under the hypothesis that assimilate withdrawal is the only damage mechanism of the aphids. To allow for the effects of the virus infection in the experiment, four damage mechanisms of beet yellows virus were taken into account in the simulations (Van der Werf, 1988). It is assumed that water and nutrients do not limit growth. The model calculates daily growth on the basis of the carbon balance of the plant, following the main concepts of the comprehensive model SUCROS87 (Spitters et al., 1989; Figure 4). The source term in this balance is photosynthesis. The sink terms are maintenance respiration, aphid assimilate consumption and growth respiration. The model is formulated in a concise way to make it lucid. It is doubtful if more detail would improve accuracy, as assimilate withdrawal, a main process, is only roughly estimated.

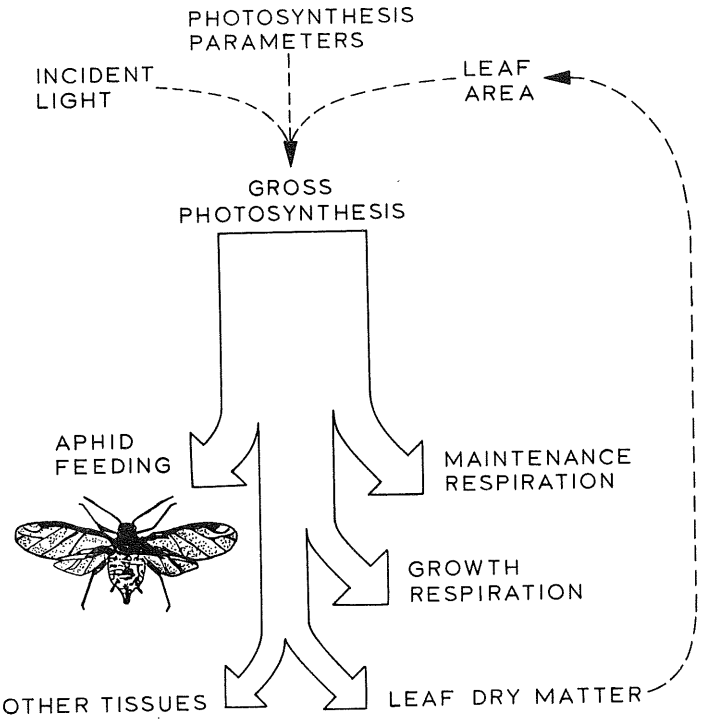

Figure 4: Schematic presentation of model structure: Part of the carbon fixed as CH_2O during photosynthesis is allocated to aphid feeding, maintenance respiration of the plant and growth respiration. The remaining dry matter is divided between leaf blades and other plant parts. The amount of leaf blade material, together with the SLA of the leaves, the incident light and the photosynthesis parameters (for green and yellow leaves) determine gross photosynthesis of the next day.

Photosynthesis is calculated for green and yellow leaves separately and then added up. For both types of leaf the daily gross photosynthesis is given by:

$$P = E \,.\, H \,.\, L$$

where

P = Daily gross photosynthesis (g (CH_2O) d^{-1}),

E = Crop light use efficiency (g (CH_2O) J^{-1} (incident PAR))

H = Incident photosynthetically active radiation (J m^{-2} s^{-1})

L = Leaf area (m^2)

The values of the coefficient E in this descriptive equation, 4.1 μg (CH_2O) J^{-1} (PAR) for green leaves and 1.9 μg (DW) J^{-1} (PAR) for yellow leaves, were calculated with the comprehensive model SUCROS87. This model integrates instantaneous rates of leaf photosynthesis over canopy depth and over the day, assuming a spherical leaf angle distribution and an exponential radiation profile in the canopy. The model was adapted for simulating free standing individual plants with a leaf area index below 1, as was the case in the experiment. As parameters in the SUCROS87-model, a maximum rate of photosynthesis, P_m, of 50 kg CO_2 ha^{-1} h^{-1} and a light use efficiency, ε, of 0.5 kg (CO_2) ha^{-1} h^{-1}/(J (absorbed PAR) m^{-2} s^{-1}) were used for healthy leaves and for green leaves on infested plants. These values are in accordance with the literature (Spitters et al., 1989) but high in comparison with the data in Table 2. For virus infected leaves, a P_m of 10 kg CO_2 ha^{-1} h^{-1} and an ε of 0.5 kg (CO_2) ha^{-1} h^{-1}/(J (absorbed PAR) m^{-2} s^{-1}) were taken. Radiation data were obtained from the nearby weather station at the Haarweg, Wageningen. Light interception by the roof and sides of the greenhouse was estimated at 30%.

Maintenance respiration depends on the weight of living material of the plant, on the maintenance costs of the different tissues and on temperature. Runs with the SUCROS87 model showed that for the 32 days of simulation, maintenance respiration was 1.7% of the total dry weight of the plant per day for control plants and 2.3% for infested plants (the increase due to the virus infection). These values were used in the summary model.

Aphid assimilate consumption is determined by the total aphid weight on the plant and the relative ingestion rate: 4.9 mg (phloem sap FW) mg^{-1} (aphid FW) day^{-1}. Assuming a sugar concentration in sugarbeet phloem sap of 8% (Fife et al., 1962) and an aphid dry matter percentage of 24% (Banks and Macaulay, 1964) the relative rate of assimilate intake is 1.6 mg (CH_2O) mg^{-1} (aphid dry weight; DW) day^{-1}. The numbers of aphids per plant per size class and their dry weights were introduced in the model as forcing functions.

Growth and growth respiration are determined by the amount of carbohydrates that remains after substracting maintenance respiration and aphid assimilate consumption from the gross photosynthesis. Simplifying the translocation patterns of Figure 2, 60% of the sugars are translocated to the leaf blades and 40% to the other tissues. Thereby the CH_2O costs of structural dry matter in the different organs are substracted. Using growth respiration parameters from Spitters et al (1989), a sugar requirement for synthesis of dry matter of 1.4 g (CH_2O) g^{-1} (DW) was estimated. Leaf area for the next day was calculated by multiplying simulated leaf weight with the average specific leaf area of 250 cm^2 (leaf) g^{-1} (leaf DW).

Results. The predictions of the model in comparison to the experimental data are shown in Figure 5 and Table 3. In a broad sense, model calculations and

experimental results correspond well. Apparently, the difference between the infested and control group may be explained on the basis of the damage mechanisms of beet yellows virus and assimilate consumption by *Aphis fabae*. Furthermore, in Figure 5, the control plants are grouped around the 1:1 line, indicating that differences in size between individual healthy plants are more or less explained by the model. This positive correlation is caused by the positive correlation between final weight and initial weight, which was input into the model as an initial value. Such a positive correlation is not found in the aphid-infested group. This indicates that the model does not explain differences between plants in their reaction to aphid feeding and virus infection.

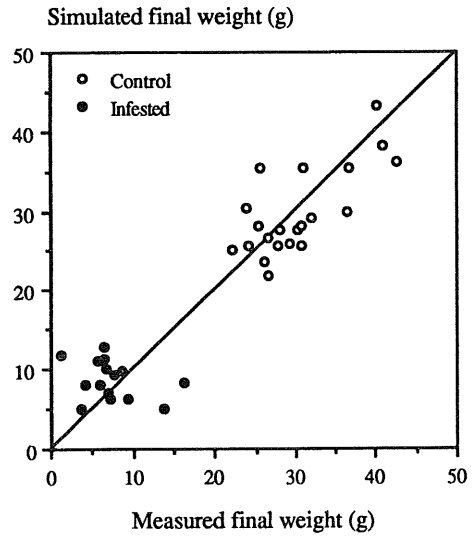

Figure 5: Evaluation of model performance; comparison of simulated and observed final dry weight of the plants.

Table 3: Observed and simulated weight, leaf area and relative growth rate (all ± SEM) of healthy and aphid-infested sugarbeet plants.

	Weight (g (DW))	Leaf area (cm^2)	RGR[a] (d^{-1})
A exp	8.92 ± 1.38	1161 ± 186	0.136 ± 0.007
A sim	6.81 ± 0.69	999 ± 101	0.139 ± 0.0018
C exp	30.2 ± 1.55	2711 ± 140	0.174 ± 0.002
C sim	24.3 ± 0.98	2890 ± 116	0.177 (equal for all plants)

[a]RGR of weight is taken. In the simulations, the RGR of weight and leaf area are equal.

In Figure 6 two representative examples of the simulated daily assimilation and assimilate withdrawal are shown. Aphid assimilate consumption means a significant assimilate drain to the plant, resulting in a large reduction of the relative growth rate (RGR; Table 3).

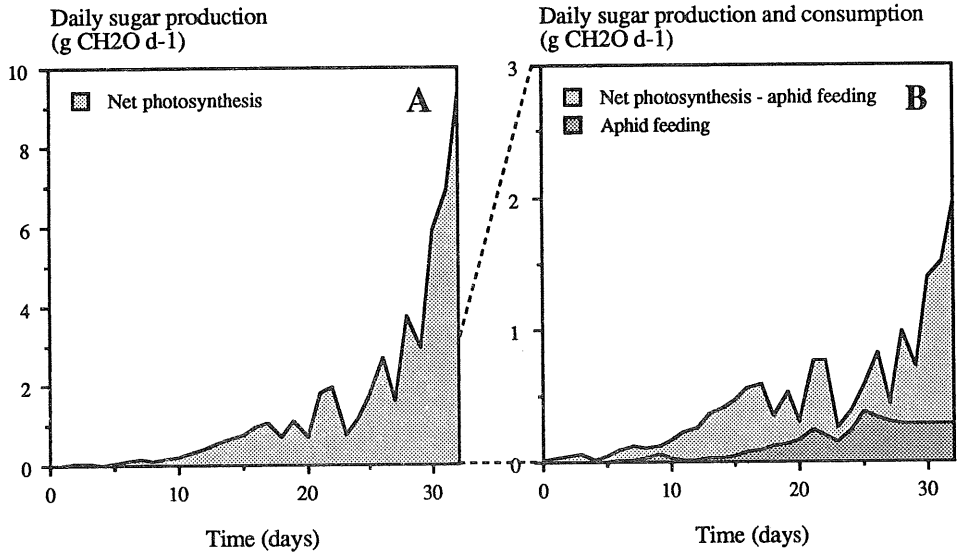

Figure 6: Simulated pattern of assimilate production through photosynthesis and consumption by aphids in a representative healthy (A) and aphid-infested sugarbeet plant (B).

Discussion

The present study shows that assimilate consumption by *Aphis fabae* constitutes an important drain of assimilates to the sugarbeet plant and causes severe growth retardation. The simulation approach allowed for a mechanistic separation of the effects of viral infection and aphid assimilate sapping. The model explains growth reduction on the basis of damage mechanisms. Retardation of early growth in the field results in a weakening of the competitive position of the plant with respect to conspecific neighbours or weeds, such that they become overgrown (Spitters, 1989; Tilman, 1989; Hurej and Van der Werf, in prep.). The deceleration of early leaf expansion will by itself reduce yield as it decreases radiation interception (Monteith and Elston, 1983; Haverkort and Bicamumpaka, 1986; Waggoner and Berger, 1987).

The model described in this paper needs expansion and further testing under different conditions. Effects of nitrogen withdrawal by the aphids were neglected. It remains to be seen whether a fixed relative ingestion rate, as used in the present model, can account for the feeding behaviour of *Aphis fabae* on sugarbeet under

different circumstances. This seems unlikely as aphids probably regulate their feeding rate as to absorb a sufficient amount of limiting nutrients, often amino-acids. Compounds in the phloem sap that are in excess, such as sugars, are excreted as a by-product of this amino-acid acquisition (Mittler, 1988). Thus the feeding rate may be higher on plants grown with little N-fertilizer if the low N-supply results in a low amino-acid content in the phloem. In the experimental setup the infested plants were infected with beet yellows virus. As infection with BYV affects the nutritional quality of sugarbeet for aphids (Baker, 1960), an effect on the ingestion rate may be expected. Such effects can be included in a model, but at the present state of knowledge such models will be rather speculative.

Validated models may be used in establishing economic injury levels (EILs) for *Aphis fabae* (Rabbinge and Rossing, 1988). The model presented in this study indicates that the EIL increases sharply with the growth stage of the plant, as the damage by the aphids depends on the balance between assimilate production by the plant, which is a function of leaf area, and assimilate consumption by the aphids, which is function of aphid number and size and possibly phloem sap quality. In the determination of EILs, the population dynamics of the aphid as affected by the weather, the host and natural enemies must be taken into account.

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