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The influence of black bean aphid, *Aphis fabae* Scop., and its honeydew on leaf growth and dry matter production of sugar beet

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Summary

A. fabae populations, started at the 3–4 leaf-stage of sugar beet in the glasshouse and peaking at 3000 individuals per plant, reduced leaf area by 64% at the 14 leaf-stage. The size of the heavily-infested leaves number 5 to 10 was reduced by 80% or more. The rate of leaf growth regained normal values after the aphid populations collapsed, but the infested plants did not make up for the decrease in leaf area production that had been incurred during the infestation. Total dry matter production over a period of 15 weeks was reduced by 47%. Honeydew had no effect on leaf size or dry matter production. Sugar beet plants in the field became infested with *A. fabae* at the 2–3, 4–5 and 6–8 leaf stages. Maximum populations of 800, 2100 and 2200 aphids per plant were recorded, respectively. The pertinent reductions in leaf area were 91%, 67% and 34% at the 10–12 leaf-stage and 79%, 65% and 14% at harvest while the total dry matter produced was reduced by 91%, 79% and 16%. Neighbouring plants of the early-infested sugar beet plants gained significantly higher weights than control plants. Honeydew had no effect on leaf area or dry matter production. The consequences of these results for our understanding of *Aphis fabae* injury in sugar beet and aphid control in the field are discussed.

Key words: *Aphis fabae, Beta vulgaris*, damage, feeding, honeydew, leaf growth, dry matter production

Introduction

Black bean aphid, *Aphis fabae* Scop., is a major pest of sugar beet in Eastern Europe (Weismann & Vallo, 1963; Hurej, 1984). The aphid's influence on the crop is mainly due to its feeding. Virus transmission is of small importance as the aphid is a non-vector or very poor vector of beet mild yellowing virus (Russell, 1963; Thielemann & Nagi, 1979; Karl, Lehmann & Fritzsche, 1985), while its sessile behaviour prevents an important role as a vector of beet yellows virus and beet mosaic virus, viruses that *A. fabae* can transmit efficiently (Björling, 1952; Heathcote & Cockbain, 1966). There are three major periods of flight during the year: [1] spring flights from the primary host (mostly spindle trees, *Euonymus europaeus*) to herbaceous secondary hosts (sugar beets, field beans and many other dicot species), [2] dispersal flights among secondary hosts during the summer, and

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[3] autumn flights to the primary overwintering host (Kennedy, Ibbotson & Booth, 1950; Way, 1967; Opyrchalowa & Goos, 1973; Cammell, Tatchell & Woiwod, 1989). The aphids flying from the winter hosts in spring threaten sugar beet crops. They multiply quickly on young plants, producing six or seven generations before the populations collapse as a result of decreasing plant quality and increasing impact of predators, parasites and diseases (Weismann & Vallo, 1963; here a generation is defined as the time between birth of the mother and the production of the *first* offspring). Heavy and early attack causes yield losses up to 70% (Weismann & Vallo, 1963; Hurej, 1984; Capinera, 1981). Reductions in leaf biomass are of the same order: 30–70% (Hurej, 1984).

The dry matter production and sugar yield of sugar beet are closely related to the radiation intercepted during the growing season (Monteith, 1977; Milford *et al.*, 1980; Scott & Jaggard, 1985). The fraction of incident light intercepted is largely determined by leaf area. There have only been a few studies of the influence of aphids on plant leaf area. Dixon (1971*a*) showed that sycamore trees, infested early and heavily by the aphid *Drepanosiphum platanoides* (Schr.), produced 60% less leaf area than uninfested trees while the number of leaves was not affected. Lime trees infested by the aphid *Eucallipterus tiliae* L. had the same leaf area as uninfested ones during the first year of infestation, while a reduction of 41% was found in the next year (Dixon, 1971*b*). According to Forrest, Hussain & Dixon (1973), radish plants, *Raphanus sativus*, had smaller cotyledons and first leaves after 10 days of infestation by *Myzus persicae*. *Aphis fabae* occurs in the earliest stages of sugar beet canopy development. A delay in plant growth incurred in this stage postpones the period of full light interception in which the growth rate is maximal (Goudriaan & Monteith, 1991). In addition to this, it weakens the competitive position of the crop with respect to weeds and makes it more vulnerable to drought and other stresses, later in the season.

In the present paper the effect of *Aphis fabae* and its honeydew on the leaf growth and dry matter production of sugar beet in the glasshouse and in the field are described. The purpose of this work is to help unravel the mechanisms that underly the effects of *A. fabae* on sugar beet growth and provide an understanding that is necessary for the development of rational decision rules for aphid control. The decision rules, presently used, are inadequate as they do not take sufficient account of crop growth stage and other factors that affect damage.

Materials and Methods

Treatments

In the glasshouse and in the field, three treatments were compared: [1] control, [2] honeydew sprayed onto leaves, and [3] infestation with *Aphis fabae*. In the glasshouse, sugar beet plants were grown on nutrient solution. The aphid infestation was started at the 3–4 leaf stage. Artificial honeydew solution was sprayed about once a week onto leaves of the honeydew-treated plants as long as *Aphis fabae* was present in the *Aphis fabae*-treatment. Each treatment was applied to 10 replicate plants. Further details are given in an earlier paper (Hurej & van der Werf, 1993).

In a field crop of sugar beet, 150 representative and similar-looking plants were marked at the 2 leaf-stage. Following natural infestation with *A. fabae* from spindle trees in the neighbourhood, the infested plants were divided over three treatment groups: [3*a*] infested at the 2–3 leaf stage, [3*b*] infested at the 4–5 leaf-stage, and [3*c*] infested at the 6–8 leaf-stage. From the remaining plants, 2 × 25 plants were randomly selected for the [1] control and [2] honeydew treatments. The dosage and composition of the honeydew applied in the honeydew-treatment closely matched the situation in the *Aphis fabae*-treatment. The number of plants in the treatment groups 1, 2 and 3*a*-3*c* were 25, 25, 10, 7 and 25 respectively. Further details can be found in Hurej & van der Werf (1993).

Determination of leaf area and leaf number

The areas of all individual leaves on each plant were assessed on 20 June, 11 July and 28 July in the glasshouse and on 11 June, 23 June and 20 July in the field. The leaves were compared to a series of 30 standard images with known areas. At harvest, 22 August in the glasshouse and 29 August in the field, leaf area was measured with an electronic Licor 3100 leaf area meter. Dead and senescent leaves were disregarded in determinations of leaf area. Absolute numbers of leaves (including those that had died) were counted in the glasshouse. In the field, only the living leaves were counted.

Determination of dry matter

At harvest the plants were divided into leaf blades, petioles, crowns and tap roots. In the glasshouse, fibrous roots were also harvested. Leaf, petiole, crown and fibrous root samples were oven-dried at 105°C, while storage roots were dried at 70°C. The total organic + inorganic nitrogen (N) content of the leaf blades was determined according to Deys (1961). Sugar content in storage roots was measured with a modified Nelson & Somogi method (Vertregt & Verhagen, 1979).

Compensatory or competitive effects

Neighbour plants of sugar beet belonging to the control treatment or to the earliest *Aphis fabae*-infested group were lifted and weighed on 29 August to investigate whether the reduction in plant size due to aphids was compensated for (or perhaps partly caused) by a greater growth (and consumption of resources) by their neighbours.

Results

A. Glasshouse experiment

Aphid populations

After the introduction at the 3–4 leaf-stage on 28 May, the aphid populations reached a peak of about 3000 individuals per plant at the 10–11 leaf-stage on 20 June. Shortly thereafter, most aphids were killed by a fungal disease outbreak. The average number of aphids per plant at different times and the corresponding plant growth stages are shown in Figs 1A & 1C.

Leaf growth

Leaf area of the plants was significantly affected by *A. fabae* but not by honeydew (Fig. 2A). In all measurements of leaf area, the differences between the control and *A. fabae*-treatment were statistically significant but the greatest percentage reduction, 64%, was observed on 11 June. On 22 August, final leaf area of the aphid infested plants was still 44% lower than that of the control plants.

The aphids were predominantly found on leaves 5–10, which each carried several hundred to a 1000 aphids at the population peak. These leaves were very severely reduced in size at all dates (Figs 3A-D) and some of them died prematurely. After the collapse of the aphid

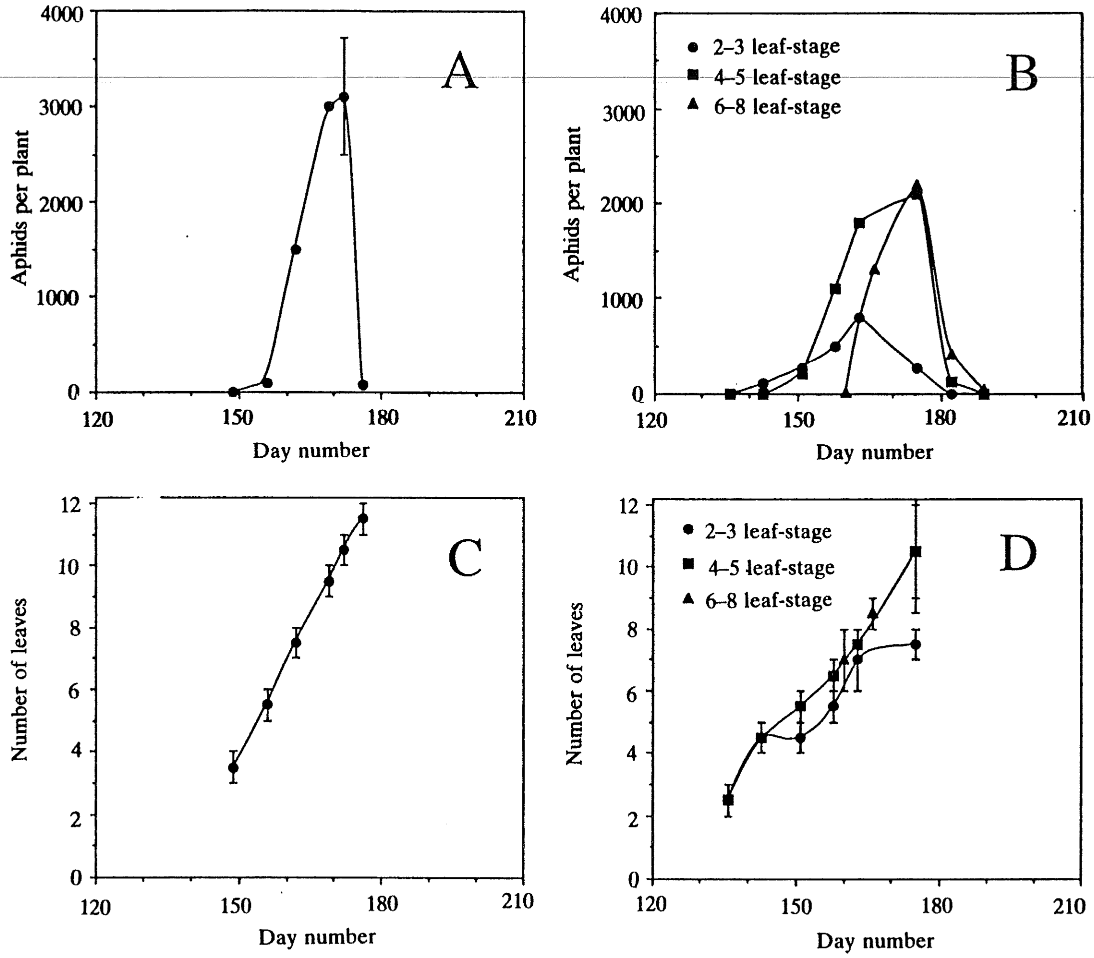


Fig. 1. Population dynamics of *Aphis fabae* in relation to the development of the sugar beet host plant in the glasshouse experiment (A) and in the field (B). In one instance the standard deviation of the sampled population is given (error bar in 1A). The numbers of leaves per plant on the sampling dates are given in Figs C & D. Error bars indicate here the ranges observed. The time axis is expressed in day of the year: 1 May = day 122; 1 June = day 153; 1 July = day 183. Figs B & D show courses of events in the field for three different periods of initial infestation with *A. fabae*.

population, the newly appearing leaves, 12 and higher, reached sizes that approached those of leaves in the control-treatment (Figs 3B,C). From about leaf 20 onwards, there was no significant difference in leaf size between the control- and aphid-infested plants. The decrease in plant leaf area growth that had been incurred during the period of aphid infestation was not made up for after the aphids had disappeared (Fig. 2A).

Leaf number

None of the treatments had a significant effect on the number of leaves (Fig. 2B). At harvest, control plants had 32.1 ± 1.3, honeydew treated 33.3 ± 1.1 and infested ones 29.5 ± 0.9 leaves per plant. The effect of the aphids on plant leaf area was thus entirely due to an effect of the aphids on leaf size, not on leaf number.

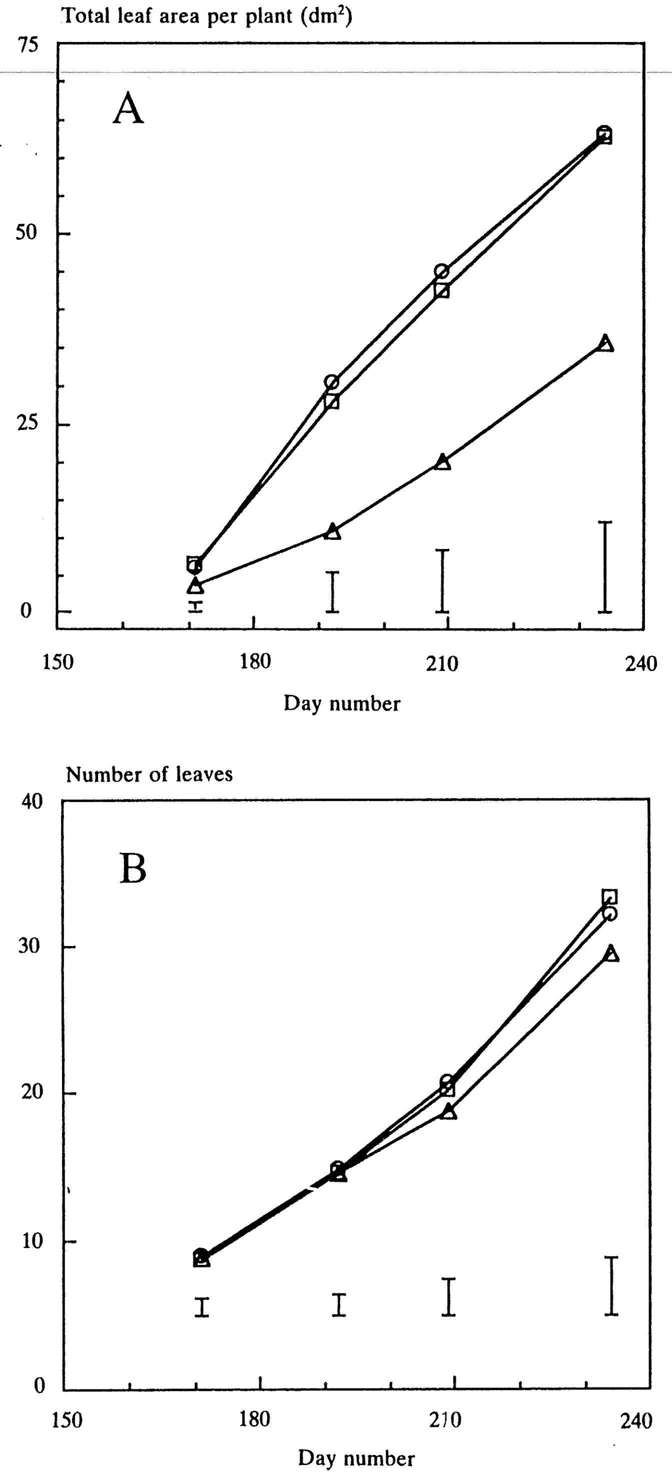


Fig. 2. Effect of *Aphis fabae* and artificial honeydew on plant leaf area (A) and leaf number (B) of sugar beet in the glasshouse. Treatments are control (○), honeydew (□) and *A. fabae* (△). Bars indicate minimum significant differences according to Tukey's procedure for multiple comparisons in ANOVA at $\alpha = 0.05$.

Table 1. *Effect of* Aphis fabae *and artificial honeydew on dry matter production and chemical composition of sugar beet plants in the glasshouse*

		Control	Honeydew	Aphids	M.S.D.[2]
Leaf blades	(g DM/plant)[1]	37.8 ± 1.9 (15) a[2]	38.1 ± 3.6 (11) a	23.8 ± 1.7 (15) b	8.0
Petioles	(g DM/plant)	28.1 ± 2.1 (15) a	28.2 ± 2.8 (11) a	16.0 ± 1.1 (15) b	6.9
Crown	(g DM/plant)	13.9 ± 1.2 (15) a	13.2 ± 1.7 (11) a	6.4 ± 0.6 (15) b	4.1
Storage root	(g DM/plant)	117 ± 7.5 (15) a	102 ± 10.2 (11) a	56.8 ± 6.3 (15) b	27.2
Fibrous roots	(g DM/plant)	5.4 ± 0.3 (15) a	4.6 ± 0.8 (11) ab	3.4 ± 0.2 (15) b	1.5
Total dry matter	(g M/plant)	203 ± 11.4 (15) a	186 ± 17.0 (11) a	107 ± 9.2 (15) b	42.4
N content of leaf blades	(mg N/g DM)	49.6 ± 0.5 (5) a	46.8 ± 2.0 (5) a	49.9 ± 0.8 (5) a	4.7
Sugar content of storage root	(mgsugar/g DM)	623 ± 14 (5) a	653 ± 5.0 (5) a	620 ± 13 (5) a	42

[1] DM: dry matter

[2] Treatment means followed by the same letter are not significantly different in Tukey's procedure for multiple comparisons in ANOVA at $\alpha = 0.05$. The minimum significant difference (M.S.D.) is given in the last column.

Table 2. *Effect of* Aphis fabae *and artificial honeydew on total leaf area (dm²) of sugar beet plants in the field*

			Aphis fabae		
	Control	Honeydew	Infested in 6–8 leaf-stage	Infested in 4–5 leaf-stage	Infested in 2–3 leaf-stage
11 June	10.3[1,2] ± 1.0 (10) a[3]	9.8 ± 0.8 (10) a	8.0 ± 0.9 (10) a	3.9 ± 0.45 (7) b	0.8 ± 0.13 (10) c
23 June	21.4 ± 2.5 (10) a	21.3 ± 2.5 (10) a	11.6 ± 1.2 (10) b	6.1 ± 0.94 (7) c	2.1 ± 0.34 (10) d
20 July	40.1 ± 2.1 (10) a	40.0 ± 2.2 (10) a	25.5 ± 2.4 (10) b	12.9 ± 1.4 (7) c	7.6 ± 1.1 (9)[4] d
29 August	4.4 ± 2.7 (25) a	44.6 ± 3.3 (25) a	40.6 ± 2.3 (25) a	16.6 ± 2.7 (7) b	10.1 ± 1.8 (9) c

[1] The data were log-transformed before ANOVA.

[2] The table gives sample mean (untransformed) ± S.E.M. (standard error of mean) with sample size given between brackets. Sample size is highest at final harvest.

[3] Treatment means with a common letter (compared horizontally) are not significantly different in ANOVA, using Ryan-Eino-Gabriel-Welch procedure for multiple comparisons at $\alpha = 0.05$.

[4] One early-infested plant died early-July.

Dry matter production and composition

Table 1 summarises the results of the harvest on 22 August. *A. fabae* caused a significant reduction in dry matter weight in all parts of the plants: leaf blades, petioles, crown, storage root and fibrous roots. Dry matter of storage roots was reduced by 52% and total dry matter by 47%. *A. fabae* feeding did not reduce N content in leaf blades or sugar content in storage roots (Table 1). There were no significant differences between control- and honeydew-sprayed plants.

B. Field experiment

Aphid populations

Under field conditions, *A. fabae* started to colonise seedlings at the 2–3 leaf-stage in mid-May (Fig. 1B). The earliest infestations reached a peak at the 6–8 leaf-stage, on 11 June: about 800 aphids per plant. The early infestations lasted until the end of June. The aphid populations on plants colonised at the 4–5 or 6–8 leaf-stage reached their peak values only at the 9–12 leaf-stage on 23 June. The infestations lasted until early July. The average maximum densities recorded were 2100 and 2200 aphids per plant respectively.

Leaf area

A. fabae had a very large effect on plant leaf area, especially in the first two measurements (Table 2). The effect of the aphids decreased very rapidly with later infestation: 92% reduction for plants infested at the 2–3 leaf-stage, 72% for plants infested at the 4–5 leaf-stage and 46% for plants infested at the 6–8 leaf-stage. Plants infested at the 2–3 leaf-stage were so much retarded in growth that they became overshadowed by their neighbours. One out of 10 early-infested plants died. Honeydew had no significant effect on leaf growth.

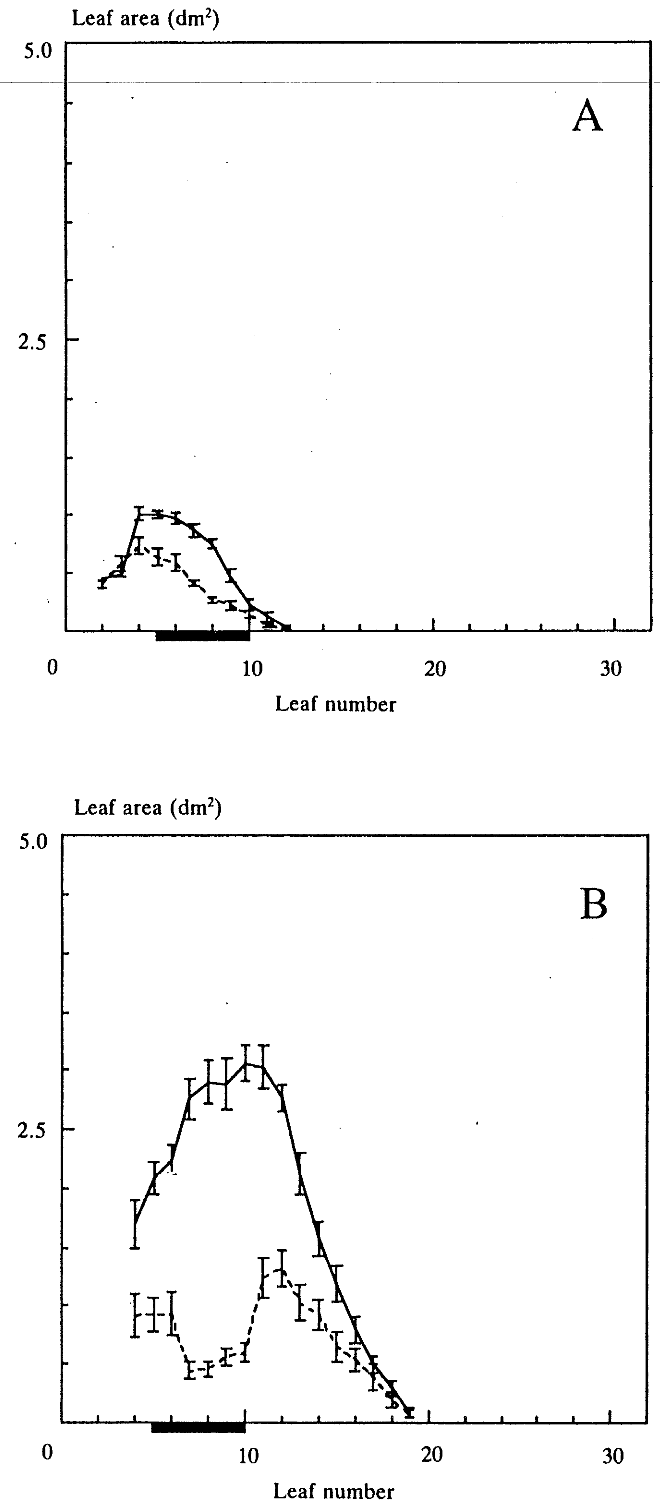
Leaf number

Under field conditions, infestation with *A. fabae* did have an effect on leaf number (Table 3). Colonisation at the 2–3 leaf-stage caused the greatest reduction. Throughout the season, the number of leaves counted on these plants was significantly lower than on the control plants. For most of the season, the plants infested at the 4–5 leaf-stage had significantly fewer leaves than control plants, but also significantly more than plants infested at the 2–3 leaf-stage. The plants, infested at the latest stage, 6–8 leaves, had initially significantly fewer leaves than control plants, but later in the season, this difference disappeared. Honeydew had no effect on leaf number.

Dry matter production and composition

Infestation with *A. fabae* at the 2–3 or 4–5 leaf-stage significantly reduced dry matter of all plant organs (Table 4). The reduction observed with the earliest infestation was significantly greater than with the infestation at the 4–5 leaf-stage. Dry matter weight of storage roots of these two infested groups was reduced by 92% and 80% and total dry matter by 90% and 79%, respectively. There were no significant differences in dry matter between control plants, plants sprayed with honeydew and those infested at the 6–8 leaf stage. *A. fabae* had no effect on N content of leaf blades but infestation at the 2–3 and 4–5 leaf-stages resulted in a lower sugar content of the storage root.

Uninfested plants adjacent to sugar beets infested by *Aphis fabae* in the 2–3 leaf-stage had advantage of the growth reduction of their neighbour and gained significantly greater total fresh weights (1513 ± 141 g; Fig. 4B) than uninfested plants adjacent to other


Leaf area (dm²)
5.0
2.5
A
0
10
20
30
Leaf number
Leaf area (dm²)
5.0
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B
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Leaf number

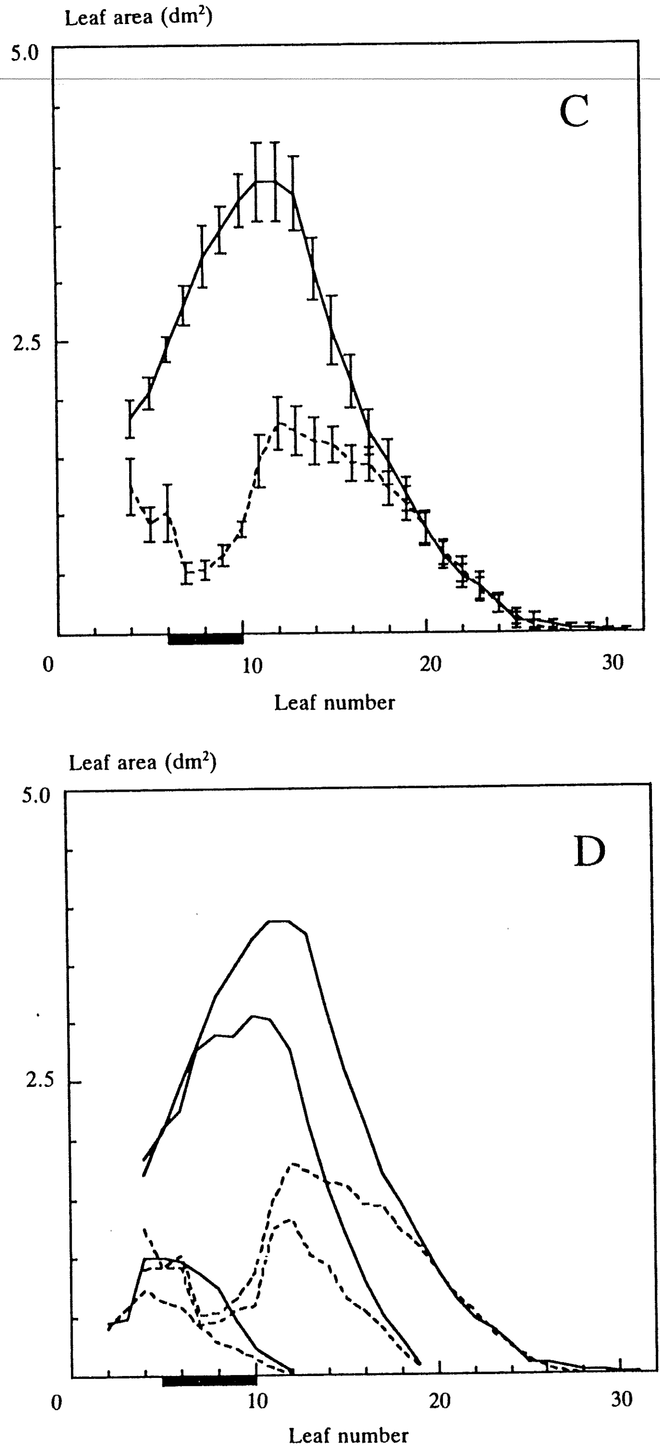

Fig. 3. Effect of *Aphis fabae* on the area of individual leaves (± S.E.M.) of sugar beet in the glasshouse, measured on 20 June (A), on 11 July (B) and on 28 July (C). Drawn lines refer to control plants, dotted lines to infested plants. The curves are presented together in D to facilitate comparisons among dates. The black bar on the abscissa indicates leaves on which black bean aphid fed in large numbers of 200–1000.

Table 3. *Effect of* Aphis fabae *and artificial honeydew on number of leaves of sugar beet plants in the field*

	Control	Honeydew	*Aphis fabae* Infested in 6–8 leaf-stage	*Aphis fabae* Infested in 4–5 leaf-stage	*Aphis fabae* Infested in 2–3 leaf-stage
11 June	11.0[1,2] ± 0.5 (10) a[3]	11.1 ± 0.5 (10) a	9.1 ± 0.4 (10) b	9.4 ± 0.4 (7) ab	6.7 ± 0.4 (10) c
23 June	12.6 ± 0.4 (10) a	11.9 ± 0.4 (10) a	10.4 ± 0.4 (10) b	10.3 ± 0.4 (7) b	8.0 ± 0.6 (10) c
20 July	20.2 ± 1.1 (10) ab	20.4 ± 1.1 (10) a	17.5 ± 0.6 (10) ab	16.6 ± 1.2 (7) b	11.2 ± 0.9 (9) c
29 August	29.2 ± 1.0 (25) a	27.2 ± 0.9 (25) a	28.7 ± 0.9 (25) a	22.4 ± 1.6 (7) b	16.2 ± 1.8 (9) c

[1] The data were square root-transformed before ANOVA.
For other notes, see Table 2.

Table 4. *Effect of* Aphis fabae *and artificial honeydew on dry matter production and chemical composition of sugar beet plants in the field*

		Control	Honeydew	*Aphis fabae* Infested in 6–8 leaf-stage	*Aphis fabae* Infested in 4–5 leaf-stage	*Aphis fabae* Infested in 2–3 leaf-stage	M.S.D.[4]
Leaf blades[1]	(g DM/plant)	29.9[2] ± 2.0 (25) a[3]	27.8 ± 2.6 (25) a	24.7 ± 1.8 (25) a	7.5 ± 1.4 (9) b	4.4 ± 0.9 (9) c	
Petioles[1]	(g DM/plant)	38.8 ± 3.2 (25) a	39.2 ± 4.4 (25) a	35.4 ± 2.0 (25) a	9.1 ± 1.8 (9) b	4.6 ± 0.9 (9) c	
Crown[1]	(g DM/plant)	17.2 ± 1.5 (25) a	20.1 ± 2.3 (25) a	13.3 ± 1.4 (25) a	2.7 ± 0.4 (9) b	1.6 ± 0.4 (9) c	
Storage root[1]	(g DM/pl ant)	170 ± 14 (25) a	157 ± 17 (25) a	141 ± 122 (25) a	35 ± 7 (9) b	14.3 ± 3.4 (9) c	
Total dry matter[1]	(g DM/pl ant)	255 ± 19 (25) a	244 ± 25 (25) a	214 ± 16 (25) a	54 ± 10 (9) b	25 ± 5 (9) c	
N content of leaf blades	(mg N/g DM)	35.2 ± 1.9 (5) a	35 ± 0.6 (5) a	— ± — (0)[5]	35.4 ± 1.9 (5) a	33.0 ± 2.3 (5) a	7.2
Sugar content of storage root	(mg sugar/g DM)	788 ± 7.7 (21) a	784 ± 6.4 (17) a	769 ± 7.8 (24) a	724 ± 19 (9) b	718 ± 19 (6) b	41

[1] Dry matter (DM) data were log-transformed before ANOVA.
[4] The minimum significant difference for untransformed data (Ryan-Eino-Gabriel-Welch) is given in the right column, if appropriate.
[5] Lost samples.
For other notes *cf* Table 2.

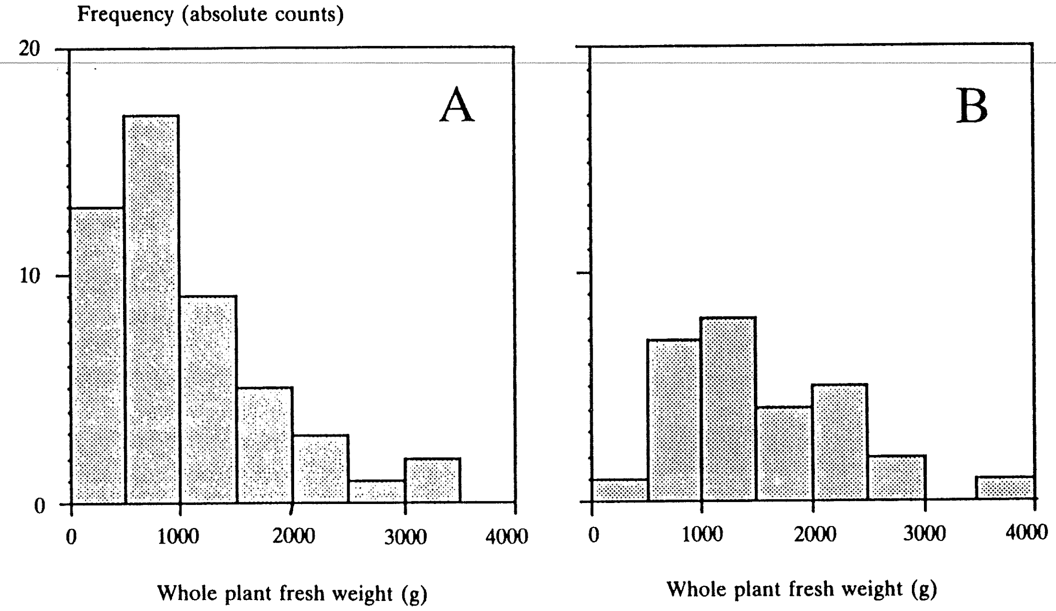

Fig. 4. Fresh weights of plants adjacent to (A) control sugar beet plants or (B) early aphid-infested plants in the field. Sugar beet plants neighbouring early aphid-infested plants became significantly heavier.

uninfested plants (1002 ± 109 g; Fig. 4A). There was also a significant difference in root fresh weights: 796 ± 75 g *vs* 469 ± 60 g. The frequency distributions of total plant fresh weight are shown in Fig. 4. A significant difference between the two distributions is indicated by the test-statistic of Kolmogorov & Smirnov at $\alpha = 0.05$.

Discussion

Our glasshouse and field experiments showed large effects of *A. fabae* on the leaf growth and dry matter production of sugar beet, while the spraying of artificial honeydew on sugar beet leaves, at a composition and concentration similar to the natural situation, had no effect on plant growth and yield. This result refutes the notion (e.g. Cammell, 1981) that the deposition of honeydew would be one of the mechanisms underlying the damage by *A. fabae* on sugar beet. The lack of honeydew effects on leaf growth or dry matter production gives support to our finding that honeydew does not affect the photosynthesis or respiration of sugar beet (Hurej & van der Werf, 1993), because, if there was an effect on photosynthesis, it would accumulate as a growth reduction over the course of the growth period that was monitored. An absence of honeydew effects in *A. fabae*-infested sugar beet contrasts with several reports of detrimental effects of aphid honeydew on plants functioning (e.g. Wood, Tedders & Reilly, 1988; Rossing & van de Wiel, 1990).

Groenendijk, van der Werf, van Dijk & Carneiro (1990) show by means of simulation, that the assimilate consumption by black bean aphids provides sufficient explanation for the effect of black bean aphids on the growth of sugar beet plants. Some elementary calculations can illustrate this point. Black bean aphids ingest assimilates at a rate of the order of 1–2 mg (sugars) mg^{-1} (aphid dry weight) day^{-1} (Banks & Macaulay, 1964;

Groenendijk *et al.*, 1990). This rate will vary with, for example, phloem sap composition and temperature. The individual weight of black bean aphids in a colony with mixed stages may be in the order of 50–200 μg (dry weight; or 200–800 μg fresh weight), such that the daily assimilate intake per aphid is 50–400 μg (sugars). The total daily assimilate withdrawal by a colony of 2000 *A. fabae* on a young plant is then in the order of 10–80 mg (sugars). The sugar production by the plants, as a result of photosynthesis, is a function of the incoming photosynthetically active radiation (PAR; in the order of 1 MJ m^{-2} day^{-1}; but quite variable), the amount of PAR intercepted by the plant as a function of its ground cover (in the order of 500 cm^2) and an efficiency factor that accounts for the transformation of solar energy into sugars (in the order of 4 μg (sugars) per joule PAR intercepted). A sugar production of 200 mg (sugars). According to this calculation aphids could consume 5–40% of the sugars produced daily by the plant. The uncertainties in the above calculations prevent strong quantitative conclusions. It is clear, however, that the assimilate drain by aphids can be quite significant. The timing of the aphid infestation, which determines the balance between the assimilate demand of the aphids and the carrying capacity of the plant in terms of assimilates produced, has a large effect on the calculated growth reduction.
in terms of assimilates produced, has a large effect on the calculated growth reduction.

The field experiment (Table 4) showed the crucial importance of timing for the effect of *A. fabae* on individual plants. Infestations at the subsequent stages of 2–3, 4–5 and 6–8 leaves yielded dry matter productions of 9%, 21% and 84%, compared to the control. Only the last group of *A. fabae*-infested plants recovered after the aphid infestation had passed. The situation was different in the glasshouse. There, the final dry matter production of sugar beet infested at the 3–4 leaf-stage was 53% of the control. Observations of individual leaf growth (Fig. 3) showed that the normal growth pattern was resumed after the aphid infestation had passed. The more drastic effect of the aphids in the field has probably to be attributed to competitive (compensatory) effects of neighbouring plants (Fig. 4). They grew larger if the 'treatment' plant was retarded in growth due to aphid feeding. The interaction between aphid-infested and healthy plants is characterised by 'mutual causality' (Berryman, 1981): the smaller claim on resources by an aphid-infested plant (due to its slower growth) leaves better growing conditions for its neighbour, which will, in response, grow more rapidly. This is compensation. The exhaustion and pre-occupation of resources (space, light, water and nutrients) by this neighbouring plant will prevent the earlier infested plant from recovering at a later time, when the aphid infestation has passed, which is competition.

The occurrence of such compensatory effects between neighbour plants indicates that the effect of *A. fabae* on sugar beet yield has to be seen from the perspective of community production. As long as sufficient plants with an acceptable spatial distribution pattern are uninfested or late-infested, the infestation by *A. fabae* can probably be tolerated. Theoretical and empirical studies on the relation between yield and plant spacing or pest and disease incidence (Jones, Dunning & Humphries, 1955; Loomis & Bennett, 1966; Clark & Loomis, 1978; Scott & Jaggard, 1985; Smit, 1989; Hughes, Ramos Monreal & Copesal Vara, 1989) provide therefore probably the appropriate basis for determining damage thresholds for *A. fabae*.

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References

Banks C J, Macaulay E D M. 1964. The feeding, growth and reproduction of *Aphis fabae* Scop. on *Vicia fabae* under experimental conditions. *Annals of Applied Biology* **53**:229–242.

Berryman A A. 1981. *Population systems; a general introduction.* New York: Plenum Press. 222 pp.

Björling K. 1952. On the significance of different vectors of sugar beet virus yellows. *Acta Agriculturae Scandinavica II* **3**:258–278.

Cammell M E. 1981. The black bean aphid, *Aphis fabae. Biologist* **28**:247–258.

Cammell M E, Tatchell G M, Woiwod I P. 1989. Spatial pattern of abundance of the black bean aphid, *Aphis fabae*, in Britain. *Journal of Applied Ecology* **26**, 463–472.

Capinera J L. 1981. Some effects of infestation by bean aphid, *Aphis fabae* Scopoli, on carbohydrate and protein levels in sugarbeet plants, and procedures for estimating economic injury levels. *Zeitschrift für Angewandte Entomologie* **92**:374–384.

Clark A, Loomis R S. 1978. Dynamics of leaf growth in sugarbeets. *Journal of the American Society of Sugar Beet Technologists* **20**:97–113.

Deys W B. 1961. De bepaling van totaal-stikstof in gewasmonsters inclusief nitraat stikstof. In *Jaarboek van het Instituut voor Biologisch en Scheikundig Onderzoek van Landbouwgewassen (IBS), Wageningen*, pp. 89–91. (In Dutch; with English summary).

Dixon A F G. 1971*a*. The role of aphids in wood formation. I. The effect of the sycamore aphid, *Drepanosiphum platanoides* (Schr.) (Aphididae), on the growth of sycamore, *Acer pseudoplatanus* (L.). *Journal of Applied Ecology* **8**:165–179.

Dixon A F G. 1971*b*. The role of aphids in wood formation. II. The effect of the lime aphid, *Eucallipterus tiliae* L. (Aphididae), on the growth of lime, *Tilia x vulgaris* Hayne. *Journal of Applied Ecology* **8**:393–399.

Forrest J M S, Hussain A, Dixon A F G. 1973. Growth and wilting of radish seedlings, *Raphanus sativus*, infested with the aphid *Myzus persicae. Annals of Applied Biology* **75**:267–274.

Goudriaan J, Monteith J L. 1991. A mathematical function for crop growth based on light interception and leaf area expansion. *Annals of Botany* **66**:695–701.

Groenendijk C A, van der Werf W, van Dijk E, Carneiro R A. 1990. Modelling the effect of assimilate withdrawal by black bean aphid, *Aphis fabae*, on the growth of sugarbeet plants, infected with beet yellows virus. *Mededelingen van de Faculteit der Landbouwwetenschappen, Rijksuniversiteit Gent* **55**:1085–1098.

Heathcote G D, Cockbain A J. 1966. Aphids from mangold clamps and their importance as vectors of beet viruses. *Annals of Applied Biology* **57**:321–336.

Hughes G, Ramos Monreal A, Copesal Vara P. 1989. Characterizing the effect of spatially heterogeneous pest injury on crop yields. *Crop Research (Horticultural Research)* **29**:37–49.

Hurej M. 1984. Biological and economical indexes of protecting of sugar beet against pests. *Zeszyty Naukowe AR we Wroclawiu* **40**:1–57. (In Polish; with English summary).

Hurej M, van der Werf W. 1993. The influence of black bean aphid, *Aphis fabae* Scop., and its honeydew on the photosynthesis of sugar beet. *Annals of Applied Biology* **122**:189–200.

Jones F G W, Dunning R A, Humphries K P. 1955. The effects of defoliation and loss of stand upon yield of sugar beet. *Annals of Applied Biology* **43**:63–70.

Karl E, Lehmann W, Fritzsche R. 1985. Eignung bzw. Effectivität von *Myzus persicae* (Schulz.) und *Aphis fabae* Scop. zur Übertragung des Virus der milden (BMYV) und der nekrotischen Rübenvergilbung (BYV). *Nachrichtenblatt für den Pflanzenschutz in der DDR* **39**:35–38.

Kennedy J S, Ibbotson A, Booth C O. 1950. The distribution of aphid infestation in relation to leaf age. II. *Myzus persicae* (Sulz.) and *Aphis fabae* Scop. on spindle trees and sugar-beet plants. *Annals of Applied Biology* **37**:651–679.

Loomis R S, Bennett C W. 1966. Competitive relationships in virus-infected sugar beet fields. *Journal of the American Society of Sugar Beet Technologists* **14**:218–231.

Milford G F J, Biscoe P V, Jaggard K W, Scott R K, Draycott A P. 1980. Physiological potential for increasing yields of sugar beet. In *Opportunities for increasing crop yields*, pp. 71–83. Eds P V Hurd, P V Biscoe and C Dennis. London: Pitman.

Monteith J L. 1977. Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society, London B* **281**:277–294.

Opyrchalowa J, Goos M. 1973. Dynamics of migrations of bean aphid (*Aphis fabae* Scop.) to sugar beet fields. *Biuletyn Instytutu Ochrony Roslin* **56**:233–247. (In Polish; with English summary).

Rossing W A H, van de Wiel L A J M. 1990. Simulation of damage in winter wheat caused by the grain aphid *Sitobion avenae*, 1. Quantification of the effects of honeydew on gas exchange of leaves and aphid population of different size on crop growth. *Netherlands Journal of Plant Pathology* **96**:343–364.

Russell G E. 1963. Some factors affecting the relative incidence, distribution and importance of beet yellows virus and sugar-beet mild yellowing virus in Eastern England. *Annals of Applied Biology* **52**:405–413.

Scott R K, Jaggard K W. 1985. The effect of pests and diseases on growth and yield of sugar beet. In *Proceedings of the 48th Wintercongress of the IIRB (Institut International de recherches Betteraviåres)*, pp. 153–169.

Smit A L. 1989. Overzaaien van suikerbieten (resowing of sugarbeet). *Arable Crops and Vegetables Research Station (PAGV), Lelystad, Report 91*. 78 pp. (In Dutch).

Thielemann R, Nagi A. 1979. Welche Bedeutung haben die zur "*Aphis fabae*- Gruppe" gehrenden Blattlausstämme fur die Übertragung des schwachen Vergilbungsvirus auf Beta-Rüben? *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz* **86**:161–168.

Vertregt N, Verhagen W. 1979. De bepaling van reservekoolhydraten in grassen. *CABO-verslag 3*. (In Dutch; with English summary), 20 pp.

Way M J. 1967. The nature and causes of annual fluctuations in numbers in *Aphis fabae* Scop. on field beans (*Vicia faba*). *Annals of Applied Biology* **59**:175–188.

Weismann L, Vallo V. 1963. *Voska makova* (Aphis fabae *Scop.)*. Bratislava: SAV. (In Czech, with German summary). 250 pp.

Wood B W, Tedders W L, Reilly C C. 1988. Sooty mold fungus on pecan foliage suppresses light penetration and net photosynthesis. *HortScience* **33**:851–853.

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