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The causes and processes of the mid-summer population crash of the potato aphids *Macrosiphum euphorbiae* and *Myzus persicae* (Hemiptera: Aphididae)

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Abstract

Populations of many phloem-feeding aphid species in temperate regions increase exponentially in early summer and then 'disappear', usually over a time-scale of a few days, in July. To understand these dynamics, empirical investigation of the causes and modelling of the processes underlying population change are required. Numbers of the aphids *Myzus persicae* (Sulzer) and *Macrosiphum euphorbiae* (Thomas), monitored over three years in commercial potato fields in the UK, increased to a maximum of 2–2.5 per leaflet on 16 July in 1999 and 2001, and then declined to < 0.25 per leaflet by 26 July. In 2000, aphid numbers remained very low (< 0.25 per leaflet) throughout the season. The onset of the crash in aphid numbers (16–19 July in 1999 and 2001) was consistently associated with changes in the phloem amino acid composition of potato leaflets. Natural enemies, including syrphids, parasitoids, coccinellids, chrysopids and entomopathogenic fungi, increased in abundance throughout the sampling period. The incidence of winged emigrant aphids prior to the crash was low (< 10%). Experimental manipulation during 2001 demonstrated that, during the crash period, the fecundity of aphids (caged on leaves to exclude natural enemies) was depressed by 25–45% relative to earlier in the season, and that presence of natural enemies reduced aphid numbers by up to 68%. Using these data, an excitable medium model was constructed, which provided a robust description of aphid population dynamics in terms of plant development-induced changes in aphid fecundity and temporal change in natural enemy pressure.

Introduction

Populations that change in size very rapidly, resulting in outbreaks or local extinction, are an abiding focus in population ecology (Gurney & Nisbet, 1998). When these fluctuations affect human health or food production, they can result in anthropogenic intervention, with poorly understood consequences at wider ecological scales. It is therefore vital that the processes governing the population dynamics, ranging from detailed physiological changes to more diffuse notions of trophic interactions, are quantified and united to form a single coherent model upon which rational management strategies can be built.

The population dynamics of many aphid species in early summer provide a reliable example of a sharp decline from relatively large numbers to apparent local extinction over a few days, usually in July. This mid-summer crash in aphid numbers occurs in the absence of insecticide application, and has been observed both on crop plants in agricultural

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landscapes (e.g. Mackauer & Way, 1976; Soroka & Mackay, 1990; Nakata, 1995a; Kift *et al*., 1998; Losey & Denno, 1999; Parker *et al*., 2000) and non-crop plants in 'natural' vegetation (e.g. Jarosík & Dixon, 1999; Müller *et al*., 1999). The crash is not followed by colonization of other plants (of the same or different species) in the same locale, and aphid numbers generally remain low or undetectable for at least 6–8 weeks after the crash. The scale and timing of the crash might contribute to the overall regulation of aphid populations, although this possibility requires formal investigation.

Three processes in aphid populations are anticipated to contribute to the mid-summer decline: reduced fecundity, increased mortality and emigration. In principle, the crash could occur by mass emigration (as when certain aphid species leave their winter host plants in the spring), or by mass mortality (e.g. by predation); and either process could be intensified by a decline in fecundity due to depressed plant quality or adverse weather conditions. The causal factors potentially underlying changes in aphid population processes include developmental changes in nutrients, allelochemicals and anatomical features of plants (e.g. Jansen & Stamp, 1997; Blackmer & Byrne, 1999), which might alter plant quality for aphids. Increased abundance of natural enemies, including parasitoids, generalist predators (e.g. carabids), specialist predators (e.g. coccinellids, syrphids) and fungal pathogens, can depress aphid numbers, as is illustrated by their use in biological control programmes (Hickman & Wratten, 1996; Michels *et al*., 2001). Furthermore, natural enemy and plant factors can interact synergistically to alter aphid performance. For example, feeding at sites of high nutritional quality might expose aphids to greater predation (Hacker & Bertness, 1995), while variation in plant architecture can influence predator foraging success (Grevstad & Klepetka, 1992). Environmental or weather conditions might enhance these interactions, and plant suitability for aphids is influenced by drought-stress (McVean & Dixon, 2001) and by nutrient-deficiency (van Emden & Bashford, 1969; Ponder *et al*., 2000).

The causal factors and population processes that might mediate the mid-summer aphid decline have been discussed in the literature (Taylor, 1955; Mackauer & Way, 1976; Chambers *et al*., 1982; Boiteau, 1986; Dixon *et al*., 1993; Ro & Long, 1999), but their relative importance in shaping the scale and speed of the crash has not been investigated. The principal aim of this study, conducted over three years in commercial potato fields in the UK, was to quantify the contribution of plant and natural enemy factors to the population crash. The specific objectives were firstly, using a combination of field monitoring, sampling and experimental manipulation, to describe the population processes underlying the decline in aphid numbers and the factors influencing those processes. The second aim was to develop a mathematical model, based on these data and existing behavioural studies, to examine population responses to host plant- and natural enemy-mediated processes. The model strategy used an excitable medium paradigm, previously applied with success to study rapid changes in phytoplankton populations (Truscott & Brindley, 1994) but not, to our knowledge, applied to address the sudden crashes in the populations of phytophagous insects. This approach exploits the differences in time scales observed between host plant, aphid, and natural enemy dynamics. The aphids are regarded as a 'fast' variable whose population typically lies close to some quasi-equilibrium (mathematically, a stable manifold), with the dynamics near these stable manifolds being driven by slower changes in plant physiology and natural enemies (Murray, 1989). The observed population outbreaks and subsequent crashes correspond, essentially, to the aphid population switching rapidly from one locally stable manifold to another. Data indicating a peak in natural enemy activity simultaneous with the aphid crash provide further evidence in favour of this approach; such behaviour is generic within excitable models.

Materials and methods

The field sites

The study sites were untreated (i.e. no insecticide) commercial field crops of potato *Solanum tuberosum* cv. Wilja in 1999 (OS 813 026), 2000 (OS 862 021) and 2001 (OS 858 022) in Shropshire, UK. Plants were fertilized with 500 kg ha^{-1} of 15:15:20 NPK and the crops were not irrigated. Fungal growth was controlled by fungicide application, which included Dithane 945 (mancozeb: 1.7 kg ha^{-1}), Curzate M68 (cymoxanil and mancozeb: 2 kg ha^{-1}) and Ripost (oxadixyl, cymoxanil and mancozeb: 2.5 kg ha^{-1}). Assessments started as soon as practicable after 80% crop emergence (mid-June) and continued until aphid populations had peaked and subsequently declined (between late July and mid-August). Monitoring and sampling was carried out twice per week (every Monday and Thursday), with 30 different plants visited across the field along a W-shape sampling line. Meteorological data for the period of sampling was obtained from local meteorological office stations at Shawbury and Penkridge.

Aphid collection and insect identification

Numbers of aphids (nymphs, apterous and alate adults) and natural enemies were recorded on the terminal leaflet of a compound leaf selected at basal, mid-axis and apical positions (referred to as 'bottom', 'middle' and 'top' positions, respectively) along the stem axis on each of the 30 plants monitored per sampling visit. In addition, one top, one middle and one bottom compound leaf was removed from an adjacent plant, and returned to the laboratory for life stage and species determination of the aphids. Aphids were removed from all leaves either by directly picking them off under a binocular microscope or, if populations were very high, by gently washing leaves in water containing 'Teepol' surfactant and straining off the aphids. Each aphid was categorized as an 'apteriform' nymph (first to fourth instar apterous nymphs and first and second instar alatiform nymphs) or an 'alatiform' nymph (third and fourth instar alate nymphs with visible wing buds), or as an alate or apterous adult. Due to the difficulty of identifying early instar nymphs, only adult apterae and alatae were identified to species.

Nutritional indices of plants

There were two elements to plant sampling. Firstly, phloem sap was collected by the EDTA exudation technique of King & Zeevart (1974). Briefly, the terminal leaflet was excised from a compound leaf mid-way along the shoot axis

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and inserted immediately into 0.2 ml 5 mM EDTA solution, pH 7.5. The samples were incubated for 60–90 min in the dark in a sealed chamber equilibrated at 25°C with a dish of saturated KH_2PO_4 to maintain high humidity. The EDTA samples were frozen at –20°C until analysis of sugar and amino acid content (see chemical analysis below). Secondly, plant developmental stage (Jefferies & Lawson, 1971) and dry matter accumulation were monitored in six plants on the first visit of each week (i.e. Monday) to the field site. The whole plants, including all aerial parts, tubers, stolons and as much fine root material as possible were dug up and returned to the laboratory. The plants were then divided into their constituent parts, i.e. compound leaves, stems, stolons, daughter tubers, fine roots, flowers and berries. All plant components were dried at 100°C to constant weight.

Aphid performance

Experiments were conducted in 2001, using young nymphs from clonal cultures of two aphid (Hemiptera: Aphididae) species, *Myzus persicae* (Sulzer) (ADAS 99/12) and *Macrosiphum euphorbiae* Thomas (ADAS 99/11), derived originally from single parthenogenetic females collected from the study site in July 1999 and maintained on immature (approximately 4–6-week-old) plants of *S. tuberosum* cv. Wilja in ventilated glass cages. Twenty replicates of single apterous adult aphids of the *M. euphorbiae* clone and the *M. persicae* clone were confined in mesh-covered clip-on leaf cages of 2.5 cm internal diameter (clip-cages) attached to the abaxial surface of a leaf mid-way along the shoot axis of *S. tuberosum* plants. Three days later, the adult and all but three nymphs were removed from each clip-cage. The experiments were monitored twice-weekly, and the dates when aphids reached adulthood, initiated reproduction and died were scored, and any offspring produced were counted on each visit and removed. Daily fecundity was quantified as (total number of offspring)/(no. adults per clip-cage) × (no. days in experimental period (3 or 4)). Where an adult died during the experimental period, she was assumed to have contributed to the reproductive output for half of the experimental period. Two replicate experiments were conducted on separate sets of plants: the first was initiated on immature plants on 11 June 2001 and the second was initiated on maturing plants on 2 July 2001.

Natural enemy exclusion

Tubers of potato cv. Wilja (Edwin Tucker and Sons Ltd, Devon, UK) were planted in John Innes No. 3 compost in 10 dm^3 pots under glass. Plants were watered daily or as required and were not fertilized. Insect control involved a single weekly spraying with nicotine (70 g dm^{-3}, applied at 600–1100 dm^3 ha^{-1}). At 3–4 weeks after planting, 20 replicate plants were inoculated with eight apterous adults of both *M. euphorbiae* clone ADAS 99/11 and *M. persicae* clone ADAS 99/12 and the infested plants were enclosed in polyester Organza™ bags and transferred into the field. Sticky traps were suspended above and placed below the bagged plants, and the plants remained in the field for one week. Mid-way through the week, the bags were removed from half of the plants for a 24-h period, exposing the aphids to natural enemy attack, and then replaced; the bags were left on the remaining ten 'unexposed' plants. The plants and the sticky traps were harvested after one week and the number of aphids and natural enemies on the plants and sticky traps were counted; unexposed bagged plants that harboured natural enemies were excluded from the analysis. Aphids collected from the plants were cultured on chitted potatoes for a further 1–2 weeks to assess the frequency of parasitism by hymenopteran wasps. The experiment was carried out in 2001, during the weeks 11–18 June (sticky traps only), 2–9 July and 23–30 July (sticky traps and exclusion experiment), which coincided approximately with the experimental periods referred to as 'initial', 'peak' and 'crash' periods, respectively, of aphid infestation (see results below).

Chemical analyses

The sucrose content of phloem exudates was quantified by the method of Dahlqvist (1984). Each 10 µl exudate sample was hydrolysed to completion with 10 U invertase (Cat. no. I-4504, Sigma-Aldrich, Gillingham, Dorset) per ml in 50 mM Na acetate buffer, pH 4.5 at 37°C for 30 min, and the glucose produced was determined by the Sigma Diagnostics glucose assay kit (GAGO-20), following manufacturer's instructions but with *o*-dianisidine concentration increased to 100 µg ml^{-1}, with glucose standards.

Amino acids in phloem exudates and aphid honeydew were separated by reverse-phase HPLC, following derivatization with *o*-phthaldialdehyde (Jones *et al.*, 1981), using a Hewlett-Packard HP1100 Series autosampling LC system with C_{18} ZORBAX™ Eclipse XDB-C8 column and fluorescence detection. Amino acids were quantified by comparison with the AA-S-18 (Sigma) reference amino acid mixture, supplemented with asparagine, glutamine and tryptophan. All protein amino acids except proline and cysteine could be detected using this method, with a detection limit of approximately 0.5 pmol. Unfortunately, due to the presence of a contamination peak in some exudates collected in 2001, the essential amino acids tryptophan and methionine could not be quantified in some 2001 samples, and hence these two essential amino acids are omitted from the comparisons between years.

Population modelling

Summer aphid population dynamics were modelled as an excitable medium (Ludwig *et al.*, 1978; Murray, 1989; Truscott & Brindley, 1994). With the aphid population A as a fast variable and the natural enemies P as the slower refractory variable, the proposed population dynamics are summarized as:

$$dA/dt = r(t).A.(1-A/K(t)) - P.R_m.(A^2/(\alpha^2+A^2)) \quad (1)$$

$$dP/dt = \gamma.P.R_m.(A^2/(\alpha^2+A^2)) - \mu.P \quad (2)$$

Thus population A grows, in the absence of P, in a logistic fashion with time-dependent growth rate r(t) and carrying capacity K(t). The P population consumes A according to a Holling Type III grazing function (Holling, 1959) with threshold α, a maximum consumption rate R_m, and assimilation efficiency γ ($\gamma << 1$, such that the time scale of P dynamics is significantly slower than that of A). The P population is subject to external mortality at a constant per capita rate μ. The property of excitability does not depend on the exact choice of the equations (Pitchford & Brindley, 1998), but does depend on a non-linear grazing response, modelled here by the Holling Type III function in (1), (2); for

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aphids, this assumption is justified by previous observational studies indicating that aphid natural enemies tend to invest effort in aphid attack only when a threshold aphid density is exceeded (as derived from Kareiva, 1986; Kindlmann & Dixon, 1993).

Simulations were performed for numbers of *M. euphorbiae*, the most abundant of the two aphid species found on potato, in each year of the study. The simulation included an initial stabilization period of 100 days to allow numbers of aphids (A: individuals plant^{-1}) and natural enemies (P: individuals plant^{-1}) to equilibrate. At day 100, aphid fecundity (r) and the carrying capacity (K) were forced from their initial values of 0.5 nymphs adult^{-1} day^{-1} and 20 aphids plant^{-1}, respectively, using data collected in this study for values of r and K. Natural enemy parameters (assimilation efficiency, γ, mortality rate, μ, and consumption rate, R_m) were varied to determine the conditions required for simulation of a crash in aphid numbers; specific values for these parameters were not known but, where possible, they were estimated from the literature, e.g. maximal daily consumption rate of approximately 0.8 aphids day^{-1} (Losey & Denno, 1998). The simulation was continued to day 200, by which time the aphid numbers had crashed in all simulations. The equations were solved numerically using a fourth order Runge-Kutta scheme with constant step length of 0.01 days (Press *et al.*, 1993). The numerics were checked for accuracy using the excitable model of Truscott & Brindley (1994) as a test system.

Statistical analysis

Parametric statistical tests were applied to data sets confirmed to be normally-distributed (Ryan-Joiner one-sample test) with homogeneous variance (Bartlett's test), which required logarithmic transformation where indicated. Regression analysis and t-tests were applied to test the impact of plant age on aphid fecundity, and survival analysis (Crawley, 1993) was employed for the examination of aphid survivorship. In the MANOVA analyses of phloem exudate amino acids, normality or homogeneity of data-sets could not be achieved for all variates (even following exclusion of outlier values identified using critical values for Dixon's test), and therefore replicate MANOVA tests were performed with and without the data for these variates. Principal components analysis (PCA) with a correlation matrix to standardize variables (Randerath, 1996) was used to explore the impact of plant age on the amino acid composition of phloem exudates. The non-parametric tests used were Kruskal-Wallis (for phloem sucrose:amino acid ratio), Mann-Whitney U-test (for phloem amino acid composition) and chi-squared (for the natural enemy exclusion experiment).

Results

Insect numbers

In all three years (1999–2001), more than 90% of the aphids on the potato leaves were *M. persicae* and *M. euphorbiae*; other aphid species observed in small numbers included *Aulacorthum solani* (Kaltenbach), *Aphis nasturtii* Kaltenbach and *Aphis fabae* Scopoli. Both *M. persicae* and *M. euphorbiae* were observed at top, middle and bottom leaflet positions on the plants, with the latter tending to support

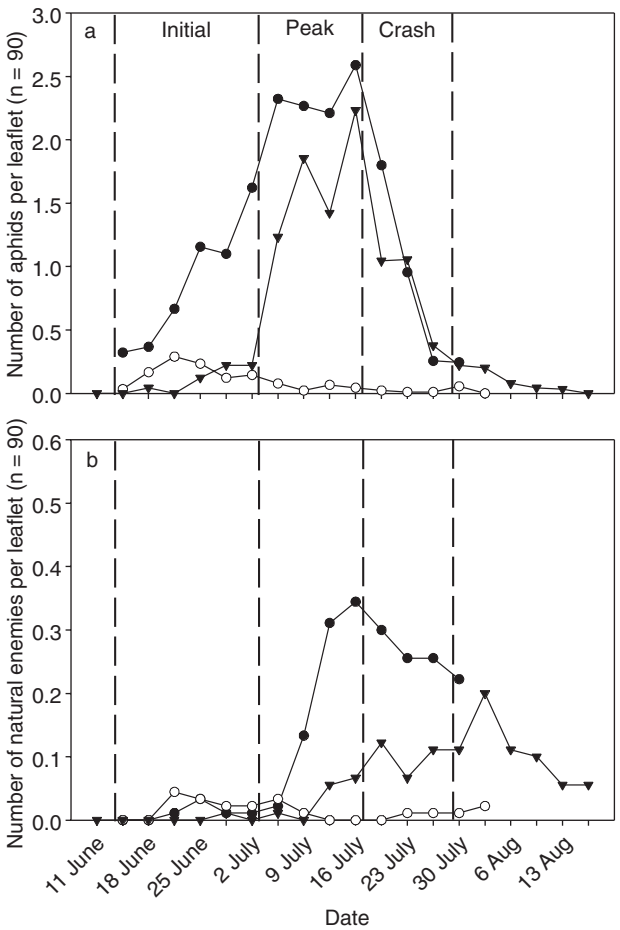

Fig. 1. Mean numbers per leaflet of (a) aphids and (b) natural enemies monitored on 90 leaflets (30 plants each sampled from top, middle and bottom leaflet positions) in summer 1999 (●), 2000 (○) and 2001 (▼). Natural enemy species included coccinellid larvae and adults, syrphid larvae, chrysopid larvae, and parasitized and fungally-attacked aphids.

higher numbers of aphids than top and middle leaflets (data not shown). Data for top, middle and bottom leaflet positions were combined because the seasonal change in aphid numbers was similar at all three leaflet positions. Maximal numbers of 2–2.5 aphids per leaflet were recorded during the second week of July (fig. 1a) in 1999 (5–16 July) and 2001 (9–16 July). In 2000, aphid numbers were consistently low, with a maximum mean value of 0.3 aphids per leaflet on 21 June. To assist with further analysis (see below), the core period of aphid infestation (14 June–26 July) was divided into three periods: 'initial', 'peak' and 'crash' (fig. 1a).

Increase in natural enemy abundance was broadly similar to aphids, although densities were approximately ten-fold lower, with maximum numbers achieved after the aphid peak, except in 2000 when natural enemy abundance was low (fig. 1b). Syrphids (eggs and larvae), parasitized aphids, and fungally-attacked aphids were detected readily. Syrphid eggs were apparent in early July and their larvae in mid-July in every year. Parasitic wasp attack was evident in late June in 1999 and 2000, but was first detected in mid-July in 2001.

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Weather conditions

The mean, maximum and minimum daily temperatures during the week of the crash in aphid numbers (i.e. 16–22 July) were, respectively, 16.8, 21.0 and 12.7°C in 1999, and 14.4, 18.8 and 9.9°C in 2001. These temperatures were not elevated in comparison with the equivalent temperatures for the previous week (17.5, 22.5 and 12.4°C in 1999; 13.9, 18.1 and 9.7°C in 2001). These data do not support the suggestion of Barlow (1962) that high temperatures precipitated the July decline of established aphid infestations. Additionally, neither rainfall nor windspeed were exceptional during the week of the crash in either year (data not shown).

In 2000, the weather was marked by very high maximum daily temperatures (⩾30°C) during the initial stages of aphid infestation in mid-June; subsequently, daytime maximum temperatures were much lower (15–16°C) and this might have inhibited successful aphid establishment.

Variation in aphid performance: the host plant factor

Aphid performance over the field season

Survival to adulthood was high (> 95%) for nymphs of *M. euphorbiae* ADAS 99/11 and *M. persicae* ADAS 99/12 caged to the leaves of immature plants in June 2001 and maturing plants in July 2001. Daily fecundity (number of nymphs produced per adult per day) varied with time for both aphid species and in each experiment (fig. 2). Maximum fecundity was higher on the developmentally immature plants (early July) than on the maturing plants (late July), and this difference was significant for *M. persicae* (45% increase in nymph production: $t_{32} = 5.03$, $P < 0.001$) but not for *M. euphorbiae* (25% increase in nymph production: $t_{18} = 1.94$, $P = 0.068$: fig. 2). Fecundity was low immediately upon reaching adulthood, and the rate of increase to maximum values was significantly faster for *M. euphorbiae* on immature plants compared with maturing plants (comparison of two regression coefficients: $d_{36} = 2.276$, $P < 0.05$). A similar pattern was observed for *M. persicae*, but the regression line for initial fecundity on maturing plants was not significant, precluding the comparison with immature plants. Neither maximum fecundity nor rate of increase to maximum fecundity correlated with amount of rainfall, wind speed or sunshine hours (data not shown). However, mean, maximum and minimum temperatures were significantly lower during the increase to maximum fecundity on maturing plants compared with immature plants (e.g. two-sample t-test for minimum temperature: $t_{25} = 4.10$, $P < 0.001$). Thus the possibility cannot be excluded that temperature contributed to the difference in fecundity of aphids between the immature and maturing plants.

The mean life span of aphids, as calculated from survival analysis, did not differ significantly between the two experiments for either species (data not shown). However, production of alatae was significantly higher (Fisher's Exact Test $P < 0.05$) for *M. euphorbiae* on immature plants (13 out of 53 adults, or 24%, were alate) compared with those on maturing plants (3 out of 57 adults, or 5%, were alate); *M. persicae* did not produce any alate offspring.

Plant nutritional indices

In all three years, total plant fresh mass (fig. 3) increased throughout the sampling period (data for 2000 not shown).

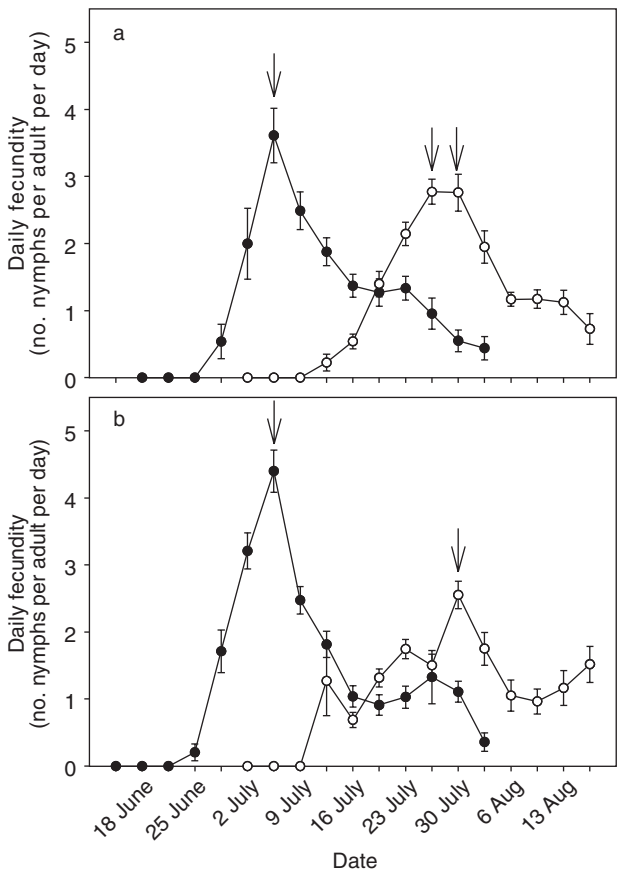

Fig. 2. Fecundity of (a) *Macrosiphum euphorbiae* and (b) *Myzus persicae* adult aphids caged onto leaves of developmentally immature (●) and maturing (○) potato plants in 2001 (mean + s.e. of between 14 and 19 cages per experiment). Arrows indicate maximum fecundity values.

Small tubers were present from the last week in June, but partitioning of mass into roots and tubers did not exceed that partitioned into the shoots until the second week in July 1999 or the fourth week of July 2000 (data not shown) and 2001. Dry matter partitioning followed a similar pattern, with biomass accumulating earlier in plants grown in 1999 compared with plants in 2000 and 2001 (data not shown). Visual inspection of the data suggests that, for both 1999 and 2001, the timing of the aphid population crash did not correlate well with the switch in biomass partitioning to tuber production (fig. 3).

The molar ratio of sucrose:amino acids in phloem exudates varied significantly across the field season in each year (see legend to fig. 4 for statistical analysis of middle leaflets). In 1999 and 2000, the sucrose:amino acid ratio was highest in exudates from top leaflets and lowest in exudates from bottom leaflets (fig. 4a,b), but ratios were similar at all three leaflet positions in 2001 (fig. 4c). In all three years, the peak sucrose:amino acid ratio in top leaflets coincided with the switch in dry matter partitioning and, with the exception of bottom leaflets in 1999, there was a general increase in sucrose:amino acid ratio at all leaflet positions during tuber filling.

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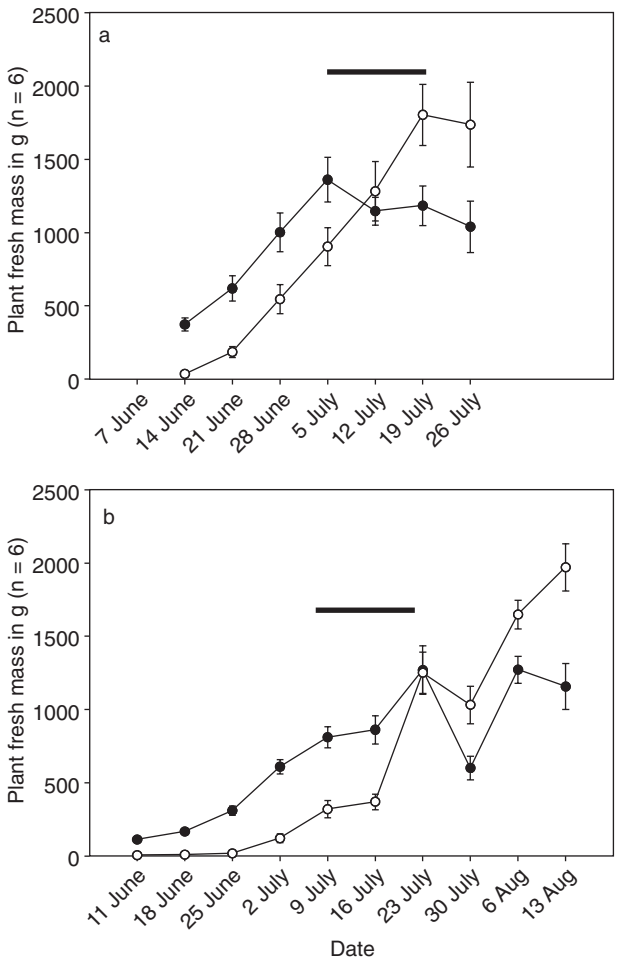

Fig. 3. Mean fresh mass of above ground (stems, leaves, flowers/berries: ●) and below ground (roots, tubers, stolons: ○) parts of potato plants cv. Wilja during summer (a) 1999 and (b) 2001. Solid bar indicates 'peak' period of aphid infestation (see fig. 1).

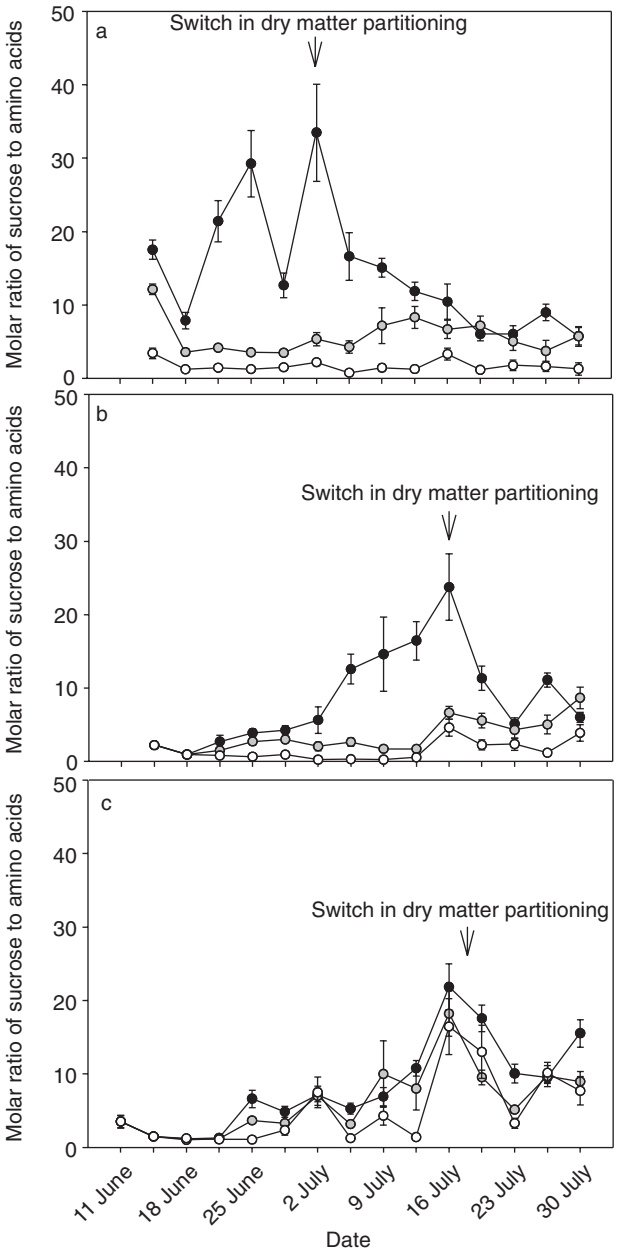

Fig. 4. The molar ratio of sucrose:amino acids from top (●), middle (◉) and bottom (○) leaflets over the field season in (a) 1999, (b) 2000 and (c) 2001. Values are means (± s.e.) of 8–15 exudate samples. Kruskal-Wallis test for variation in middle leaflet exudates over the field season in 1999: $H_2 = 0.54$, $P > 0.1$; in 2000: $H_{12} = 65.19$, $P < 0.001$; and in 2001, $H_{12} = 137.91$, $P < 0.001$. Note that sample values for 1999 were grouped into 'initial', 'peak' and 'crash' to satisfy homogeneity of variance requirements.

All protein amino acids identifiable by *o*-dianisidine conjugation were detected in every sample, and the phloem exudates were dominated by non-essentials, especially glutamine, glutamate and aspartate. In each of the three years, there was significant variation in amino acid composition over the course of the summer at all leaflet positions (table 1). To explore this variation, PCA was applied to compare data for amino acid content (expressed as mol% of total exudate amino acids) during the 'initial', 'peak' and 'crash' periods (see fig. 1a). Due to insufficient aphid numbers, data for the year 2000 were not included in this comparison. The first two principal components accounted for approximately 50% of the variation (fig. 5a,c). A plot of the amino acid attributes revealed that PC 1 tended to separate essential from non-essential amino acids, while PC 2 tended to separate the amino acids glutamate and aspartate from their amides glutamine and (to some extent) asparagine (fig. 5b,d). Other amino acids (e.g. histidine, glycine, serine, alanine) were less consistent in their associations (fig. 5b,d). These two axes achieved good, but not perfect, separation of the 'initial' and 'crash' samples (fig. 5a,c), indicating a shift during plant development in the amino acid composition of the exudates. When mol% values were compared for 'initial' and 'crash' periods, the significant shift in both years was from immature plants ('initial' period) with exudates dominated by glutamine, to

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Table 1. Results for Wilk's MANOVA for amino acid composition (log-transformed picomol amino acid data) at top, middle and bottom leaflet positions on potato plants (cv. Wilja), between mid-June and late July, in 1999, 2000 and 2001.

Year	Leaflet position		
	Top	Middle	Bottom
1999	$F_{(228, 1640)} = 9.681$, $P < 0.001$	$F_{(190, 1089)} = 6.577$, $P < 0.001$	$F_{(228, 1650)} = 5.720$, $P < 0.001$
2000	$F_{(234, 1631)} = 11.372$, $P < 0.001$	$F_{(234, 1811)} = 11.779$, $P < 0.001$	$F_{(234, 1822)} = 9.178$, $P < 0.001$
2001	$F_{(208, 1855)} = 15.190$, $P < 0.001$	$F_{(208, 1855)} = 9.724$, $P < 0.001$	$F_{(208, 1835)} = 9.572$, $P < 0.001$

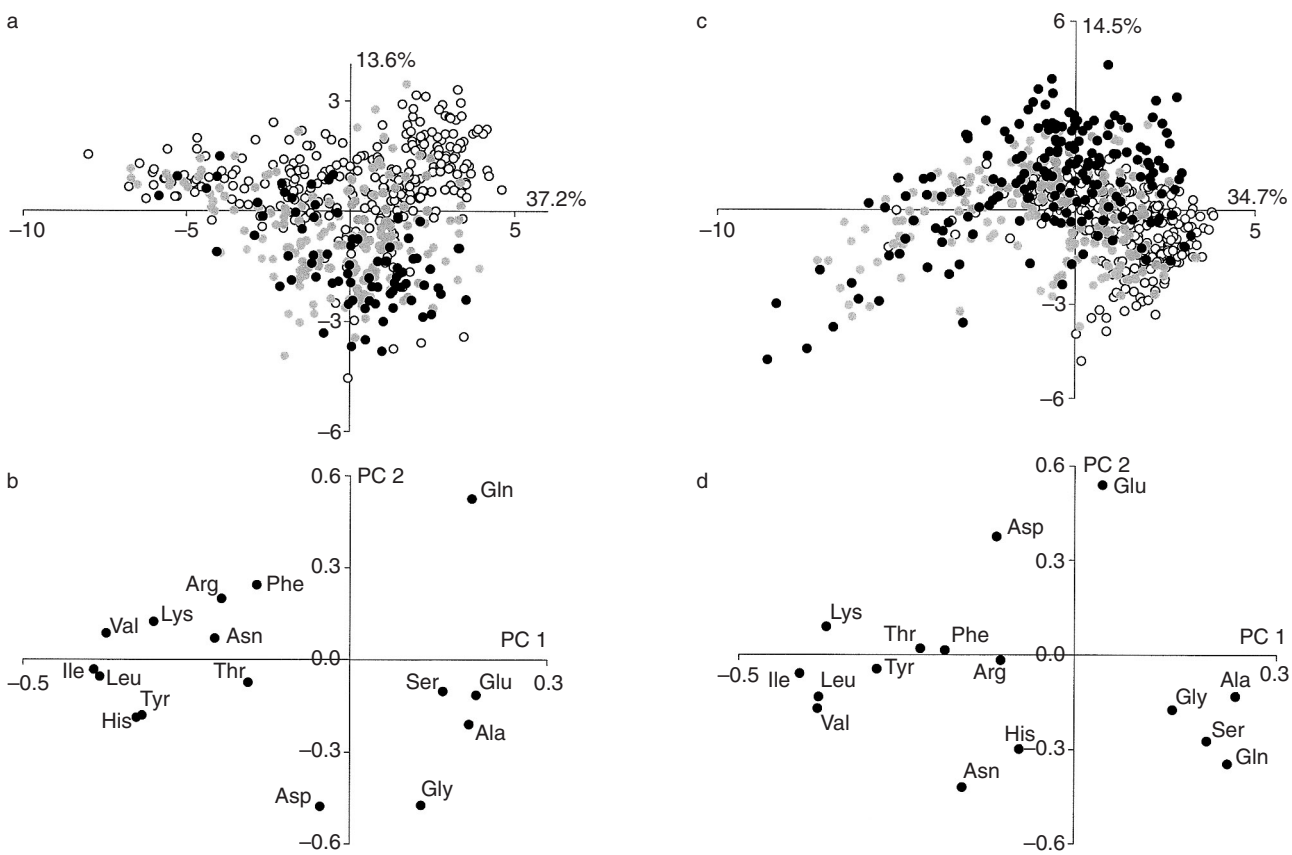

Fig. 5. Principal component analysis of amino acid mol% data in exudates sampled at all leaflet positions from plants grown in (a, b) 1999 and (c, d) 2001 during 'initial' (○), 'peak' (◎) and 'crash' (●) conditions of aphid infestation (see text for explanation). (a, c) Plot of the sample scores on the principal components. (b, d) Attribute loadings on the first two components.

maturing plants ('crash' period) with exudates dominated by glutamate, aspartate and, in 2001, most of the essential amino acids (table 2). Similar development-related trends in amino acid composition of potato leaf phloem sap were obtained in 2000 when exudate samples were analysed by date as for 1999 and 2001 (data not shown) and for glasshouse-grown potato plants (Karley *et al.*, 2002).

Aphid mortality and migration: natural enemy impact

Experimental exclusion of natural enemies

The results of the natural enemy exclusion experiment are shown in fig. 6. The number of aphids on the experimental plants ('exposed' and 'unexposed' combined) was found by heterogeneity chi-squared analysis to be

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Table 2. Relative composition of key amino acids (mean ± s.e.) at 'initial' and 'crash' periods in 1999 and 2001 for phloem exudates from [a]middle leaflet positions on potato plants (cv. Wilja).

		Amino acids (% of total)		
Year		Glutamine	Glutamate+aspartate	[b]Essential amino acids
1999	Initial	25.6 ± 0.9	30.1 ± 0.7	26.1 ± 0.8
	Crash	14.23 ± 1.6	35.1 ± 2.4	27.7 ± 1.3
		[c]t_{106}=5.92, P< 0.001	t_{20}=−1.88, 0.05< P< 0.1	$W_{90,18}$=4742.0, P>0.05
2001	Initial	29.2 ± 1.1	30.3 ± 0.8	18.5 ± 0.5
	Crash	14.7 ± 0.9	44.8 ± 1.3	22.5 ± 0.8
		t_{148}=9.67, P< 0.001	t_{148}=−9.96, P< 0.001	t_{148}=−4.08, P< 0.001

[a]A fully-expanded 'source' leaf, which is developmentally equivalent across the different plant ages studied
[b]Excluding tryptophan and methionine from 2001 data
[c]Statistical analyses were performed on arcsine square root-transformed data.

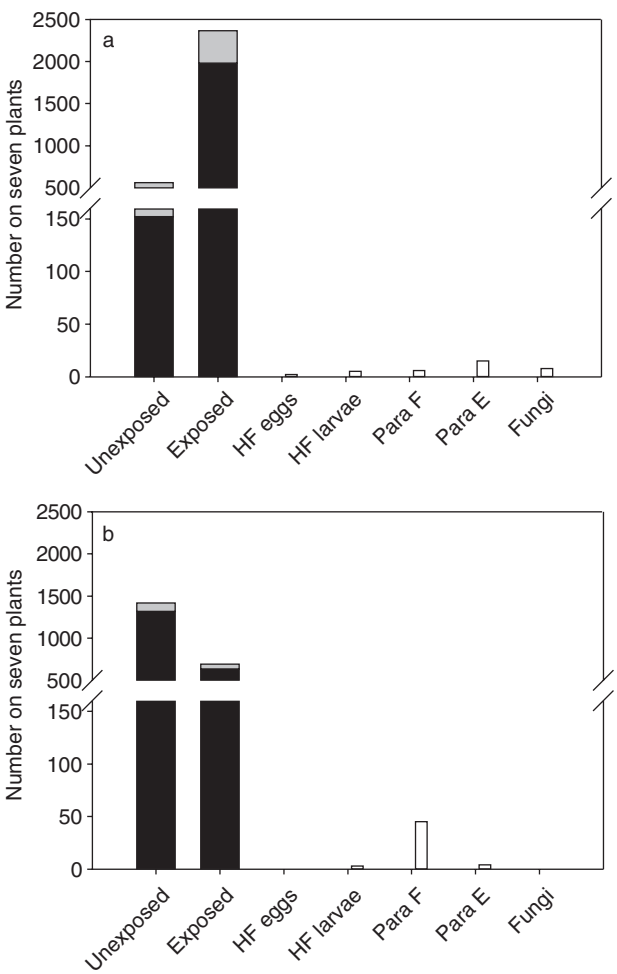

Fig. 6. Total numbers of nymphs (black bar) and adult aphids (grey bar) on aphid-infested bagged plants that were exposed for a 24 h period or remained unexposed (see text for explanation), and numbers of the dominant natural enemies counted on exposed plants (HF, hoverfly; Para F/E, parasitized aphid mummies which were full or empty, respectively). Experiments were conducted at the (a) 'peak' and (b) 'crash' periods of aphid infestation.

significantly lower in the 'crash' period, compared with the 'peak' period (fig. 6), for total aphids (χ^2_1 = 1319, P < 0.001), nymphs (χ^2_1 = 1486, P < 0.001) and adult aphids (χ^2_1 = 7.724, P < 0.01). Additionally, in the 'peak' period (fig. 6a), exposed plants supported significantly higher numbers of total aphids than unexposed plants (χ^2_1 = 1622, P < 0.001). This was due to a ten-fold increase in the number of nymphs on the exposed plants (χ^2_1 = 1566, P < 0.001), indicating that exposure resulted in nymph recruitment to the plants (fig. 6a). Although there was no significant net recruitment of adult aphids to the exposed plants, a greater proportion of the adults were alate on the exposed plants during the 'peak' period (14%, compared with 0.5% on unexposed plants) compared with the 'crash' period (5% alatae on exposed plants, and 7% alatae on unexposed plants). This correlated with increased alate catches on sticky traps (table 3: discussed below) and suggested that nymph deposition by alatae from adjacent areas might have been responsible for the increase in nymph numbers on the exposed plants. In the 'crash' period (fig. 6b), exposed plants supported significantly lower numbers of nymphs (χ^2_1 = 240.0, P < 0.001) and adult aphids (χ^2_1 = 11.61, P < 0.001) than unexposed plants, amounting to a 68% reduction in total aphid numbers. The incidence of parasitized aphids on exposed plants was 6.6% in the 'crash' period and 0.7% in the 'peak' period.

Analysis of sticky traps

The number of aphids recovered from sticky traps positioned above the plants in 2001 was maximal during the 'peak' period of aphid infestation, with an average of 75 per trap, of which 36% were alate (table 3). For traps positioned below the plant, a mean of 31 and 25 aphids were caught per trap during the 'peak' and 'crash' periods, respectively, of which 12% and 5% were alate. An index of the proportion of field aphids falling from the field plants was devised by the ratio of the mean number of aphids per trap fixed below the plant to the mean number of aphids per field plant over the same period (fig. 1a): ratio values for the 'initial' and 'peak' periods were comparable, at 3.75 and 3.76, respectively, and were lower than the ratio during the 'crash' period, at 7.0 (table 3), suggesting that a greater proportion of aphids fall from the plants during the latter period. The total number of natural enemies recorded on sticky traps increased

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Table 3. Total number of aphids (nymphs and adults), alate aphids and natural enemies caught on ten pairs of sticky traps secured above and below potato plants for weekly periods when field aphids were at 'initial', 'peak' or 'crash' numbers (see text for explanation).

	Total aphids		Alate aphids		Natural enemies	
Period of infestation	Above	Below	Above	Below	Above	Below
Initial	17	5	15	4	380	214
Peak	751	308	273	37	528	705
Crash	68	259	27	12	2203	2045

dramatically during the 'crash' period, when numbers were approximately ten-fold higher than aphid numbers (table 3). Taken together with fig. 6 (and fig. 1b), these data suggest that natural enemy activity was greater in the 'crash' period than earlier in the season.

The contribution of alatiform nymphs to the total population of aphids on the plants provides an index of the commitment of the aphid population to emigration. On all dates sampled in 1999 and 2001, the incidence of alatiform nymphs on potato leaves, expressed as a percentage of the total number of nymphs, was low, with a broad maximum of 6–10% over the 'peak' and 'crash' periods.

Model outputs

The simulations were run using the increase and decline in aphid fecundity (r) during plant development derived from fig. 2, and using the increase to maximal aphids per plant (K) as calculated from the number of *M. euphorbiae* aphids monitored per unit fresh mass of leaflet (derived from fig. 1a) and the measured increase in leaf fresh biomass (derived from fig. 3). Figure 7 shows the number of *M. euphorbiae* aphids (fig. 7a) and their natural enemies (fig. 7b) calculated from field observations to occupy the plant, and the simulated numbers of aphids (fig. 7c) and natural enemies (fig. 7d) in each year. There was good qualitative and quantitative agreement between observed and modelled aphid populations for all three years (fig. 7a,c). Good qualitative agreement was obtained for observed and modelled natural enemy numbers but the latter were approximately five-fold more abundant (fig. 7b,d); this was probably due to underestimation of natural enemy numbers using our approach of single daily observations, as was suggested from the higher abundances obtained using sticky traps (table 3).

The simulations for 1999 and 2001 (fig. 7c,d) were carried out under identical parameter conditions except that maximum carrying capacity (K) was higher in 1999 (900 aphids plant^{-1}) than in 2001 (400 aphids plant^{-1}), reflecting the rapid increase in leaf fresh mass early in the season in 1999 (not shown). Natural enemy parameters were $\gamma = 0.3$ (assimilation efficiency), $\mu = 0.1$ (mortality rate), and $R_m = 0.8$ (consumption rate). The rise to maximum aphid numbers

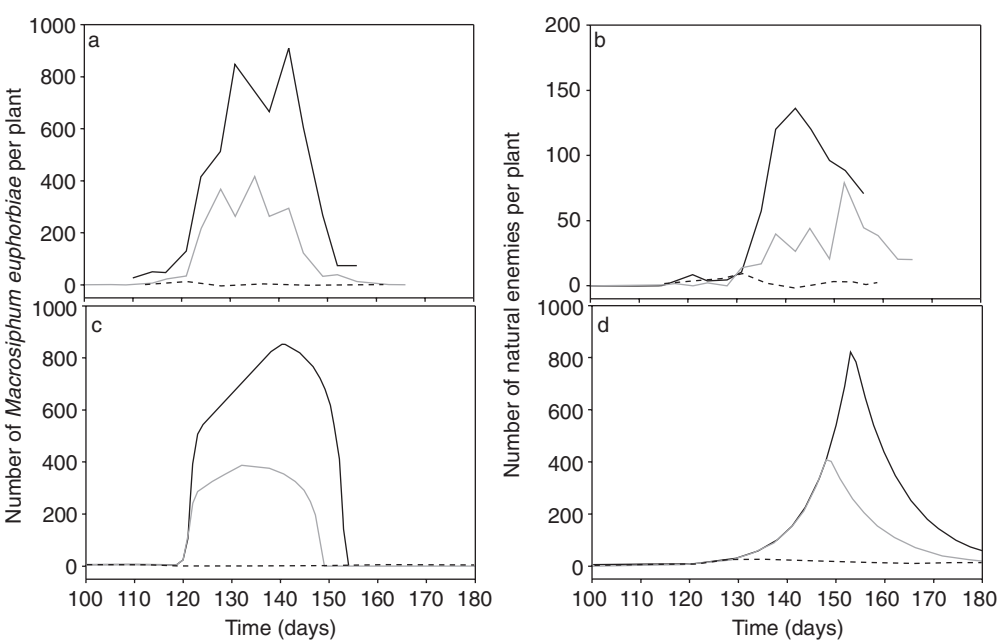

Fig. 7. Comparison of estimated numbers (a, b) and simulated numbers (c, d) per plant of *Macrosiphum euphorbiae* (a, c) and natural enemies (b, d) over the time period corresponding to the aphid population peak and decline in 1999 (—), 2000 (····) and 2001 (—). Note that the time-scale reflects the number of days after the initiation of the simulation, and not calendar date, and so differences between years in which population growth is initiated (see fig. 1a) are reflected in the timing of population crash in the model output.

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(fig. 7a,c) was shaped by the increase in K at day 100 and in aphid fecundity (r) at day 117, to reflect the time lag between leaf bulking (fig. 3) and the rise to maximum fecundity (fig. 2a). The aphid peak occurred when K reached a plateau and r declined, and the aphid crash was sustained by the increase in natural enemy abundance and activity (fig. 7b,d).

Simulation was not directly possible for aphid and natural enemy populations in 2000 as the low numbers of aphids precluded calculation of K. Instead, the parameter conditions required to prevent aphid population establishment in 2000 (fig. 7a) were investigated numerically by altering the timing of changes in r and K and by altering the intensity of natural enemy pressure. The failure to establish an aphid population could only be simulated (fig. 7c) when the increase in K was delayed until after the increase in r, and when aphid fecundity was reduced and natural enemy pressure increased. The simulated data for 2000 shown in fig. 7 shows the model output when maximum aphid fecundity was reduced to 1.8 nymphs aphid^{-1} day^{-1} (compared with 3.6 nymphs aphid^{-1} day^{-1} in 2001: fig. 2a), natural enemy mortality was reduced (μ = 0.05) and consumption rate was raised (R_m = 0.9). For comparison between years, the parameter values used in the simulations are indicated in table 4.

Discussion

Both plant and natural enemy factors shaped the changes in aphid numbers over the course of the summer; weather conditions did not appear to be a consistent defining factor. Temporal variation in aphid fecundity and survival was quantified and used to model aphid population change, satisfying our primary aim, which was to assess the relative contribution of plant developmental change and natural enemies as causal factors.

The fecundity of aphids caged to exclude natural enemies declined dramatically during potato plant development, and maximum fecundity on maturing plants during the population decline was 25–45% lower than that measured on immature plants during the increase to peak numbers. A similar reduction in aphid performance has been documented for aphids feeding on potato plants grown under controlled conditions under glass (Karley *et al*., 2002). Plant maturation involves developmental changes (e.g. flowering, filling of fruit and storage organs) which alter source-sink assimilate partitioning (Viola *et al*., 2001) and the direction and magnitude of flux of plant phloem sap (e.g. Patrick, 1997), on which aphids feed. However, there was no evidence that the large-scale change in plant biomass partitioning accompanying tuber initiation was a causal factor *per se* in the aphid decline (this study; Parker *et al*., 2000).

By contrast, the developmental changes in phloem sap composition were consistent between years, indicating a role for phloem sap quality in the aphid population crash. The decline in aphid fecundity was associated with a shift in phloem amino acid composition, principally a decline in the ratio of glutamine:[glutamate and aspartate]. Amino acids, which, together with sucrose, form the principal nutrient groups in phloem sap (Fisher, 2000), are critical for aphid feeding, nutrition and survival (e.g. Auclair, 1963; Dadd, 1985; Douglas, 1998), and a number of studies have linked aphid performance to changes in particular dietary amino acids (e.g. Weibull, 1988; Girousse & Bournoville, 1994; Sandström & Petterssen, 1994). The developmental changes in potato leaf phloem amino acid composition observed here were similar to those identified in potato plants grown under controlled conditions under glass; when mimicked in synthetic diets, these changes in phloem composition associated with plant maturation significantly reduced aphid growth and fecundity (Karley *et al*., 2002). Thus, a developmental reduction in the amino acid 'quality' of the phloem sap might be a general explanation for poor aphid performance on mature host plants of other species (van Emden & Bashford, 1971; Watt, 1979; Kazemi & van Emden, 1992; Williams, 1995; Blackmer & Byrne, 1999; McVean & Dixon, 2001). However, this interpretation is limited in the present study by the parallel changes in ambient temperatures, which could have influenced insect performance directly (e.g. Barlow, 1962) or indirectly via changes in host plant factors (e.g. Hawkins & Holyoak, 1998). A further limitation relates to the impact on aphid performance of unstudied plant factors (e.g. potato glycoalkaloids: Güntner *et al*., 1997), which might also show changes correlated with plant development, but these could not be distinguished from the developmental effects of phloem sucrose:amino acid ratio and amino acid composition studied here.

The decline in aphid fecundity on maturing potato plants (fig. 2; Karley *et al*., 2002) was insufficient to account for the observed population decline in mid-July, suggesting that natural enemy-induced mortality or emigration also contributed to the crash. During the 'crash' phase, aphid persistence on plants declined dramatically (fig. 6 and table 3), but the low abundance of alatiform nymphs prior to, and

Table 4. Parameter units, values and modelling conditions used for the simulation of aphid and natural enemy numbers in each year.

Parameter	Units	1999	2000	2001
Maximum per capita grazing rate, R_m	d^{-1}	0.8	0.9	0.8
Holling Type III parameter, α	Individuals plant^{-1}	5	5	5
Assimilation efficiency, γ		0.3	0.3	0.3
Natural enemy mortality rate, μ	d^{-1}	0.1	0.05	0.1
Initial/maximum K	Individuals plant^{-1}	20/900	20/400	20/400
Start of forcing for K	Date equivalent to simulation d 100	4 June	[a]30 June	11 June
Initial/maximum r	Nymphs adult^{-1} d^{-1}	0.5/3.6	0.5/1.8	0.5/3.6
Start of forcing for r	Date equivalent to simulation d 117	21 June	[b]20 June	28 June

[ab]Dates equivalent to d 125 and d 115, respectively (see text for explanation).

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during, the decline suggested that less than 10% of aphids were lost from plants as winged emigrants, confirming the conclusions of others for these aphid species (Nakata, 1995a; Williams *et al*., 1999). The natural enemy exclusion experiment (fig. 6) indicated that the decline in aphid numbers was due, in large part, to increased natural enemy activity. Syrphid predators and parasitoids were particularly evident in this study, although the dominant natural enemy species on unsprayed commercial potato crops can vary geographically and between years (Boiteau, 1986; Nakata, 1995b). The increased abundance of syrphids and hymenopteran parasitoids in field counts and on sticky traps, and the ten-fold increase in parasitized aphids in the natural enemy exclusion experiment support our conclusion that natural enemy activity was elevated during the 'crash' period. Further study is required for accurate quantification of natural enemy abundance and activity levels, particularly for nocturnally-active species. The overall low incidence of pathogen and parasitoid attack (i.e. fungus-infected or mummified aphids) suggests that predation might be important, although preferential consumption of parasitized aphids by other natural enemy species (Nakata, 1995b; Raymond *et al*., 2000; Colfer & Rosenheim, 2001) might have led to underestimation of parasitization levels using our approach.

Synergistic interactions between plant factors and natural enemies might drive the changes in aphid numbers. While the extent to which aphids move between feeding sites varies with aphid age and species (Boiteau, 1997), aphid restlessness might be promoted by reduced plant suitability and increased natural enemy activity, resulting in further nutritional stress and increased availability for natural enemy attack. The increased proportion of aphids on sticky traps placed below plants during the 'crash' period (table 3) might be evidence of disturbance promoting aphid dropping (Gross, 1993; Losey & Denno, 1998), a behaviour which is exhibited by *M. euphorbiae* and, to a lesser extent, *M. persicae* (Pescod, 2000). This study also raises the possibility that factors contributing to the crash in aphid numbers might have operated beyond the scale of the potato field being monitored. In particular, immigrants during the 'peak' period were presumably derived from a distance, as the low incidence of alatae in the field indicated a limited potential for local (within-field) movement. The incidence, timing and magnitude of immigration from other locations, might be influenced by weather conditions (particularly wind direction and speed), plant factors and natural enemy pressures at the site of migrant origin. Research at the regional scale will be required to dissect the relative contribution of migration and local factors to changes in aphid numbers during the summer.

The second focus of this study was to use the observational and experimental data on field aphids to construct a mathematical description of aphid and natural enemy populations using an excitable medium model. This approach provided powerful support for the conclusions from the field study that both plant and natural enemy factors contribute to the aphid population decline. The model assumes that, initially, both aphids and natural enemies coexist at low densities (mathematically, at a stable equilibrium). However, the rapid increase in aphid fecundity as high quality plant material becomes available forces the system in such a way that an 'escape' trajectory is followed (Murray, 1989); aphid numbers increase rapidly toward a peak level, remaining there for some time before crashing rapidly in response to increased natural enemy activity. Under the modelling conditions used for 1999 and 2001 data, the rapid increase in fecundity will always be sufficient to cause an outbreak in aphid numbers (Truscott, 1995). While a decline in aphid fecundity is not mathematically necessary to cause a population crash (it merely slows the rate of population increase), in its absence the crash would occur long after that observed in the field, beyond any realistic timescale of potato crop and natural enemy dynamics.

The realism of any modelling depends on the reliability of the parameter values. The principal potential caveat in this study is the ecological applicability of the natural enemy parameter values used (see methods), and future research should aim to corroborate these values in the field. For our purposes, aphid consumption rates were derived from laboratory studies of single species aphid–predator interactions (e.g. Losey & Denno, 1998). However, generalist and specialist predators, parasitoids and pathogens, attack aphids; thus, the mode and efficiency of natural enemy searching (i.e. the functional response to aphids), and consumption and assimilation of aphid prey, is likely to be species-specific (see, for example, Hassell, 2000) and to be influenced by the presence of competitors. The value of the model lies in its robust mechanistic description of the key processes and interactions governing the aphid dynamics, rather than in its ability to simulate particular datasets. The model could be refined and improved: ongoing research to incorporate the processes of aphid immigration and emigration, parasitism, and changes in aphid development time into equations [(1), (2)] will strengthen the model further, without affecting the inherent excitability of the system (Truscott & Brindley, 1994; Ludwig *et al*., 1978). Also of interest is that the absence of aphid population development in 2000 could be simulated experimentally only when aphid fecundity increased more rapidly than suitable host plant material. This scenario is not unrealistic due to the unusually high maximum daily temperatures (> 30°C) experienced by aphids during the initial stages of infestation in mid-June, before any significant increase in leaf biomass; nymph output is likely to have increased initially in response to warmer temperature, until extended exposure to the high temperatures were eventually detrimental to aphid survival (Barlow, 1962).

The advantage of a modelling approach using the excitable medium paradigm is that, in addition to offering an explanation for the different scenarios observed in 1999–2001, it provides a direct and detailed mathematical description of quantifiable biological processes that govern aphid dynamics, such as aphid fecundity and mortality, thereby providing an insight into possible control strategies. This contrasts with models using indirect variables, such as ambient temperature, to predict changes in aphid population processes (Parker, 1998; Ro & Long, 1999). The timing of the aphid crash in the excitable medium model is determined by the magnitude of the aphid peak and by the intensity of natural enemy activity. Ongoing theoretical research will investigate the efficacy of potential control measures that could be applied to suppress aphid population growth or reduce the intensity of peak infestation.

In addition to its contribution to our understanding of aphid population dynamics, this study is relevant to the

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need for reduced insecticide application to crops, from the perspectives of environmental safety, public health and increasing pest resistance to conventional pesticides. Current practice involves aphicide application throughout the growing season, but mid-summer applications might be unnecessary, despite high aphid numbers, because the aphids are destined to crash independently of insecticide application. Insecticide application might even retard the crash through toxic effects on predators (e.g. Boiteau, 1986). Using the model to quantify the impact on aphid survival and performance, field-based indices of natural enemy pressure and plant nutritional 'quality' could be developed to provide growers with quantitative field-based predictors of the peak and crash in aphid numbers.

Our study of the summer aphid population crash illustrates the problems inherent in assuming a population is governed either by the trophic level immediately above ('top down' control), or that immediately below ('bottom up' control) (Hairston *et al*., 1960; Power, 1992; James *et al*., 2003). The importance of both control mechanisms may be very obvious to a field ecologist, but it is only within the context of a mathematical model that the relative importance of different mechanisms at different times can be understood. The identification of appropriate fast and slow timescales, and their interpretation in terms of changing biochemical and ecological factors, is key to this modelling process.

'Excitability' is a useful life history strategy for organisms such as aphids that exploit a transient resource; and the natural enemies of aphids are able to exploit this behaviour as long as aphid numbers increase within a time frame commensurate with natural enemy life history constraints. However, the advantage to the aphid of adopting a lifestyle likely to lead to a population crash remain elusive; by promoting natural enemy activity as aphid numbers increase, the aphid population appears to be a victim of its own success. More detailed experimental study of aphid populations that fail to increase or fail to crash will shed light on this aspect of population regulation in herbivorous insects.

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References

Auclair, J.L. (1963) Aphid feeding and nutrition. *Annual Review of Entomology* **8**, 439–490.

Barlow, C.A. (1962) Development, survival and fecundity of the potato aphid, *Macrosiphum euphorbiae* (Thomas), at constant temperatures. *Canadian Entomologist* **94**, 667–671.

Blackmer, J.L. & Byrne, D.N. (1999) Changes in amino acids in *Cucumis melo* in relation to life-history traits and flight propensity of *Bemisia tabaci*. *Entomologia Experimentalis et Applicata* **93**, 29–40.

Boiteau, G. (1986) Native predators and the control of potato aphids. *Canadian Entomologist*, **118**, 1177–1183.

Boiteau, G. (1997) Comparative propensity for dispersal of apterous and alate morphs of three potato-colonizing aphid species. *Canadian Journal of Zoology* **75**, 1396–1403.

Chambers, R.J., Sunderland, K.D., Stacey, D.L. & Wyatt, I.J. (1982) A survey of cereal aphids and their natural enemies in winter wheat in 1980. *Annals of Applied Biology* **101**, 175–178.

Colfer, R.G. & Rosenheim, J.A. (2001) Predation on immature parasitoids and its impact on aphid suppression. *Oecologia* **126**, 292–304.

Crawley, M.J. (1993) *GLIM for ecologists*. Oxford, Blackwell Science.

Dadd, R.H. (1985) Nutrition: organisms. pp. 313–391 *in* Kerkut, G.A. & Gilbert, L.I. (*Eds*) *comprehensive insect physiology, biochemistry, and pharmacology* vol. 4. Oxford, Pergamon Press.

Dahlqvist, A. (1984) α-Glucosidases (disaccharidases). pp. 208–217 *in* Bergmeyer, H.U. (*Ed*.) *Methods of enzymatic analysis* vol. 4. Weinheim, Verlag Chemie.

Dixon, A.F.G., Wellings, P.W., Carter, C. & Nichols, J.F.A. (1993) The role of food quality and competition in shaping the seasonal cycle in reproductive activity of the sycamore aphid. *Oecologia* **95**, 89–92.

Douglas, A.E. (1998) Nutritional interactions in insect-microbial symbioses: aphids and their symbiotic bacteria *Buchnera*. *Annual Review of Entomology* **43**, 17–37.

Fisher, D.B. (2000) Long distance transport. pp. 730–784 *in* Buchanan, B.B., Gruissem, W. & Jones, R.L. (*Eds*) *Biochemistry and molecular biology of plants*. Maryland, Rockville, American Society of Plant Physiologists.

Girousse, C. & Bournoville, R. (1994) Role of phloem sap quality and exudation characteristics on performance of pea aphid grown on lucerne genotypes. *Entomologia Experimentalis et Applicata* **70**, 227–235.

Grevstad, F.S. & Klepetka, B.W. (1992) The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. *Oecologia* **92**, 399–404.

Gross, P. (1993) Insect behavioural and morphological defenses against parasitoids. *Annual Review of Entomology* **38**, 251–273.

Güntner, C., González, A., Dos Reis, R., González, G., Vázquez, A., Ferreira, F. & Moyna, P. (1997) Effect of *Solanum* glycoalkaloids on potato aphid, *Macrosiphum euphorbiae*. *Journal of Chemical Ecology* **23**, 1651–1659.

Gurney, W.S.C. & Nisbet, R.M. (1998) *Ecological dynamics*. Oxford, Oxford University Press.

Hacker, S.D. & Bertness, M.D. (1995) A herbivore paradox – why salt-marsh aphids live on poor quality plants. *American Naturalist* **145**, 192–210.

Hairston, N.G., Smith, F.E., & Slobodkin, L.B. (1960) Community structure, population control and competition. *American Naturalist* **94**, 421–425.

Hassell, M.P. (2000) Host-parasitoid population dynamics. *Journal of Animal Ecology* **69**, 543–566.

Hawkins, B.A. & Holyoak, M. (1998) Transcontinental crashes of insect populations? *American Naturalist* **152**, 480–484.

Hickman, J.M. & Wratten, S.D. (1996) Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. *Journal of Economic Entomology* **89**, 832–840.

Holling, C.S. (1959) The components of predation as revealed by a study of small mammal predation of the European sawfly. *Canadian Entomologist*, **91**, 293–320.

James, A., Pitchford, J.W. & Brindley, J. (2003) The relationship between plankton blooms, the hatching of fish larvae, and recruitment. *Ecological Modelling* **160**, 77–90.

Jansen, M.P.T. & Stamp, N.E. (1997) Effects of light availability on host chemistry and the consequences for behaviour and growth of an insect herbivore. *Entomologia Experimentalis et Applicata* **82**, 319–333.

Jarosík, V. & Dixon, A.F.G. (1999) Population dynamics of a tree-dwelling aphid: regulation and density-independent processes. *Journal of Animal Ecology* **68**, 726–732.

Jefferies, R.A. & Lawson, H.M. (1971) A key for the stages of development of potato (*Solanum tuberosum*). *Annals of Applied Biology* **119**, 387–389.

Jones, B.N., Pääbo, S. & Stein, S. (1981) Amino acid analysis and enzymatic sequence determination of peptides by an improved *o*-phthaldialdehyde precolumn labelling procedure. *Journal of Liquid Chromatography* **4**, 565–586.

Kareiva, P. (1986) Trivial movement and foraging by crop colonizers. pp. 59–82 *in* Kogan, M. (*Ed.*) *Ecological theory and integrated pest management practice*. New York, John Wiley.

Karley, A.J., Douglas, A.E. & Parker, W.E. (2002) Amino acid composition and nutritional quality of potato leaf phloem sap for aphids. *Journal of Experimental Biology* **205,** 3009–3018.

Kazemi, M.H. & van Emden, H.F. (1992) Partial antibiosis to *Rhopalosiphum padi* in wheat and some phytochemical correlations. *Annals of Applied Biology* **121**, 1–9.

Kift, N.B., Dewar, A.M. & Dixon, A.F.G. (1998) Onset of a decline in the quality of sugar beet as a host for the aphid *Myzus persicae*. *Entomologia Experimentalis et Applicata* **88**, 155–161.

Kindlmann, P. & Dixon, A.F.G. (1993) Optimal foraging in ladybird beetles and its consequences for their use in biological control. *European Journal of Entomology* **90**, 443–450.

King, R.W. & Zeevart, J.A.D. (1974) Enhancement of phloem exudation from cut petioles by chelating agents. *Plant Physiology* **53**, 96–103.

Losey, J.E. & Denno, R.F. (1998) The escape response of pea aphids to foliar-foraging predators: factors affecting dropping behaviour. *Ecological Entomology* **23**, 53–61.

Losey, J.E. & Denno, R.F. (1999) Factors facilitating synergistic predation: the central role of synchrony. *Ecological Applications* **9**, 378–386.

Ludwig, D., Jones, D.D. & Holling, C.S. (1978) Qualitative analysis of insect outbreak systems: the spruce budworm and forest. *Journal of Animal Ecology* **47**, 315–332.

Mackauer, R.H. & Way, M.J. (1976) *Myzus persicae* Sulz. an aphid of world importance. pp. 51–119 *in* Delucchi, V.L. (*Ed.*) *Studies in biological control*. Cambridge, Cambridge University Press.

McVean, R.I.K. & Dixon, A.F.G. (2001) The effect of plant drought-stress on populations of the pea aphid *Acyrthosiphon pisum*. *Ecological Entomology* **26**, 440–443.

Michels, G.J., Elliott, N.C., Romero, R.A., Owings, D.A. & Bible, J.B. (2001) Impact of indigenous coccinellids on Russian wheat aphids and greenbugs (Homoptera: Aphididae) infesting winter wheat in the Texas Panhandle. *Southwestern Entomologist* **26**, 97–114.

Müller, C.B., Adriaanse, I.C.T., Belshaw, R. & Godfray, H.C.J. (1999) The structure of an aphid–parasitoid community. *Journal of Animal Ecology* **68**, 346–370.

Murray, J.D. (1989) Mathematical biology. *Biomathematics* Vol. 19, Springer-Verlag.

Nakata, T. (1995a) Seasonal population prevalence of aphids with special reference to the production of alatoid nymphs in a potato field in Hokkaido, Japan. *Applied Entomology and Zoology* **30**, 121–127.

Nakata, T. (1995b) Population fluctuations of aphids and their natural enemies on potato in Hokkaido, Japan. *Applied Entomology and Zoology* **30**, 129–138.

Parker, W.E. (1998) Forecasting the timing and size of aphid populations (*Myzus persicae* and *Macrosiphum euphorbiae*) on potato. *Aspects of Applied Biology* **52**, 31–38.

Parker, W.E., Howard, J.J., Karley, A.J. & Douglas, A.E. (2000) Crop growth stage and the phenology of aphid populations on potato. pp. 955–960 in *The Brighton Crop and Pests Conference 2000*.

Patrick, J.W. (1997) Phloem unloading: sieve element unloading and post-sieve element transport. *Annual Reviews of Plant Physiology and Plant Molecular Biology* **48**, 191–222.

Pescod, K.V. (2000) *An investigation into escape and defence mechanisms of aphids when faced with attack by the syrphid predator* Episyrphus balteatus. MSc thesis, Imperial College of Science, Technology and Medicine, UK.

Pitchford, J.W. & Brindley, J. (1998) Intratrophic predation in simple predator–prey models. *Bulletin of Mathematical Biology* **60**, 937–955.

Ponder, K.L., Pritchard, J., Harrington, R. & Bale, J.S. (2000) Difficulties in location and acceptance of phloem sap combined with reduced concentration of phloem amino acids explain lowered performance of the aphid *Rhopalosiphum padi* on nitrogen deficient barley (*Hordeum vulgare*) seedlings. *Entomologia Experimentalis et Applicata* **97**, 203–210.

Power, M.E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* **73**, 733–746.

Press, W.H., Flannery, B.P., Tuekolsky, S.A. & Vetterling, W.T. (1993) *Numerical recipes in C*. Cambridge, Cambridge University Press.

Randerath, P.F. (1996) Ordination. pp. 251–287 *in* Fry, J.C. (*Ed.*) *Biological data analysis: a practical approach*. Oxford, IRL Press.

Raymond, B., Darby, A.C. & Douglas, A.E. (2000) Intraguild predators and the spatial distribution of a parasitoid. *Oecologia* **124**, 367–372.

Ro, T.H. & Long, G.E. (1999) GPA-phenodynamics, a simulation model for the population dynamics and phenology of green peach aphid in potato: formulation, validation and analysis. *Ecological Modelling* **119**, 197–209.

Sandström, J. & Pettersson, J. (1994) Amino acid composition of phloem sap and the relation to intraspecific variation in pea aphid (*Acyrthosiphon pisum*) performance. *Journal of Insect Physiology* **40**, 947–955.

Soroka, J.J. & Mackay, P.A. (1990) Growth of pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), populations on caged plants of six cultivars of field peas and the effects of pea aphids on harvest components of caged field peas. *Canadian Entomologist* **122**, 1193–1199.

Taylor, C.E. (1955) Growth of the potato plant and aphid colonization. *Annals of Applied Biology*, **43**, 151–156.

Truscott, J.E. (1995) Environmental forcing of simple plankton models. *Journal of Plankton Research* **17**, 2207–2232.

Truscott, J.E. & Brindley, J. (1994) Ocean plankton populations as excitable media. *Bulletin of Mathematical Biology* **56**, 981–998.

van Emden, H.F. & Bashford, M.A. (1969) A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae* in relation to soluble nitrogen concentration and leaf age (leaf position) in the Brussels sprout plant. *Entomologia Experimentalis et Applicata* **12**, 351–364.

https://doi.org/10.1079/BER2003252 Published online by Cambridge University Press

van Emden, H.F. & Bashford, M.A. (1971) The performance of *Brevicoryne brassicae* and *Myzus persicae* in relation to plant age and leaf amino acids. *Entomologia Experimentalis Applicata* **14**, 349–360.

Viola, R., Roberts, A.G., Haupt, S., Gazzani, S., Hancock, R.D., Marmiroli, N., Machray, G.C. & Oparka, K.J. (2001) Tuberization in potato involves a switch from apoplastic to symplastic phloem unloading. *Plant Cell* **13**, 385–398.

Watt, A.D. (1979) The effect of cereal growth stages on the reproductive activity of *Sitobion avenae* and *Metopolophium dirhodium*. *Annals of Applied Biology* **91**, 147–157.

Weibull, J.H.W. (1988) Free amino acids in the phloem sap from oats and barley resistant to *Rhopalosiphum padi*. *Phytochemistry* **27**, 2069–2072.

Williams, C.T. (1995) Effects of plant age, leaf age and virus yellows infection on the population dynamics of *Myzus persicae* (Homoptera: Aphididae) on sugarbeet in field plots. *Bulletin of Entomological Research* **85**, 557–567.

Williams, I.S., Dewar, A.M., Dixon, A.F.G. & Thornhill, W.A. (1999) Alate production by aphids on sugar beet – how likely is the evolution of sugar beet-specific biotypes? *Journal of Applied Ecology* **36**, 1–13.

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