Plant nutrient supply determines competition between phytophagous insects

Joanna T. Staley[1,2,*], David B. Stafford[1], Emma R. Green[1], Simon R. Leather[1], John T. Rossiter[3], Guy M. Poppy[4] and Denis J. Wright[1]

[1]*Division of Biology, Department of Life Sciences, Imperial College London, Silwood Park campus, Buckhurst Road, Ascot, Berkshire SL5 7PY, UK*
[2]*NERC Centre for Ecology and Hydrology, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire OX10 8BB, UK*
[3]*Division of Biology, Department of Life Sciences, Imperial College London, South Kensington Campus, London SW7 2AZ, UK*
[4]*School of Biological Sciences, University of Southampton, Hampshire SO16 7PX, UK*

Indirect competition is often mediated by plant responses to herbivore feeding damage and is common among phytophagous insect species. Plant-mediated responses may be altered by abiotic conditions such as nutrient supply, which can affect plant growth, morphology, and the concentration of primary and secondary metabolites. Nutrient supply can be manipulated by the type and amount of fertilizer applied to a plant. *Brassica oleracea* plants were grown in several types of fertilizer, including those commonly used in sustainable and conventional agricultural systems. The occurrence of indirect competition between two phytophagous species from different feeding guilds (a phloem-feeder and leaf-chewer) was assessed. The leaf-chewer reduced aphid populations on plants growing in most fertilizer treatments, but not on those in the ammonium nitrate fertilizer treatment, which caused the highest concentration of foliar nitrogen. The potential consequences of our findings are discussed for phytophagous species in conventional and sustainable agricultural systems.

Keywords: *Brevicoryne brassicae*; glucosinolate; induced defence; nitrogen; plant-mediated competition; *Plutella xylostella*

1. INTRODUCTION

Competition between phytophagous species sharing a host plant has been considered to play a structuring role in insect communities by some ecologists (e.g. [1]), whereas others have argued that food resources for phytophages are plentiful, and thus competition is rare (e.g. [2]; see references in [3] for full discussion). A recent meta-analysis found that competition among phytophagous insects occurred in 62 per cent of cases in which two species shared a host plant [3] and an earlier review found that 76 per cent of potential pairwise interactions were competitive [4].

Most phytophagous interactions examined involve indirect competition, whereby two species are spatially or temporally separated on the same host plant but affect each other through changes to host plant morphology or chemistry, often by inducing plant defences [3]. For example, root herbivores can alter the performance and abundance of above-ground phytophages through changes to host plant chemistry [5–7]. Kaplan & Denno [3] concluded that indirect plant-mediated mechanisms are likely to affect entire phytophage communities as well as pairwise interactions, and that their prevalence and importance may have previously been underestimated. The response of host plants to insect herbivore feeding damage may

therefore play a key role in structuring communities of phytophages and the predators and parasitoids that feed on them [8–10].

Plant responses to feeding damage often depend on the abiotic conditions in which a plant grows [11]. For example, Hawkes & Sullivan [12] found that resource availability affected plant regrowth following damage by herbivores, and increasing nutrient availability to woody plants altered their induced response to artificial damage intended to mimic herbivory [13–15]. Higher demand for sustainable agriculture and horticulture has decreased the use of high-input mineral fertilizers and increased the use of green manures and animal fertilizers that provide slow-release forms of nitrogen [16]. Organically fertilized plants may contain a higher concentration of secondary metabolites than those grown in conventional mineral fertilizers [17–19]. If fertilizer type also alters the capacity of plants to produce induced defences, it could alter host-mediated interactions between phytophages in sustainable and high-input agricultural systems.

We grew *Brassica oleracea* plants in several types of fertilizers and assessed competition between a sap-feeder (*Brevicoryne brassicae* L.; Sternorrhyncha: Homoptera) and a leaf-chewer (*Plutella xylostella* L.; Lepidoptera: Plutellidae). *Brevicoryne brassicae* feeds predominantly on the plant apex and young foliage [20], whereas *P. xylostella* larvae feed mainly on older leaves (V. Chadfield & J. T. Staley 2009, unpublished data). The two species co-occur on crucifers during the spring and early summer in the

*Author for correspondence (jnasta@ceh.ac.uk).

UK [21], but are unlikely to compete through interference owing to their different feeding modes and sites.

Brassica-constitutive glucosinolates respond to both fertilizer concentration and type [21–24]. The effect of fertilizer type on induced concentrations of glucosinolates has not been previously investigated. Fertilizers used in the current study included a mineral source of nitrogen (ammonium nitrate) and two fertilizers that contained nitrogen derived from animal sources: organic chicken manure, which is regularly used in organic horticulture [25,26]; and an intermediate fertilizer that contains animal-derived nitrogen (hoof and horn) and mineral-derived potassium (John Innes base fertilizer). Potassium availability can affect nitrogen uptake by plants, which has the potential to alter plant–phytophage interactions [27]. Foliar nitrogen and glucosinolate concentrations were measured to determine whether fertilizer treatments altered these key determinants of *Brassica* plant quality for phytophages [28,29].

2. MATERIAL AND METHODS

(a) *Experimental design and plant cultivation*
The experimental design consisted of fertilizer and insect-competition treatments imposed in a fully factorial design. Four resource treatments were applied: three fertilizer types (details below) and an unfertilized treatment. The insect treatments consisted of: a *Brevicoryne brassicae* L. (Sternorrhyncha: Homoptera) population (no inter-specific competition; treatment abbreviation = B); a *Plutella xylostella* L. (Lepidoptera: Plutellidae) population (=P); or populations of both herbivore species feeding on a plant in interspecific competition (=B + P). Eight plants (replicates) were used for each of the 12 combinations of the two treatment factors.

Brassica oleracea var. *capitata* cv Derby Day seeds (Tozer Seeds, UK) were planted in 22 mm diameter × 50 mm peat plugs (Jiffy 7 pellets, LBS Horticulture, UK) in a greenhouse. Minimum temperature was 20°C during the day (16 h) and 14°C at night (8 h). Screened vents opened at temperatures of 3°C above the minimum temperature. Overhead lighting (mercury halide and sodium bulbs) was supplied during the day to ensure a minimum light intensity of 300 W m^{-2}.

Seedlings were transplanted into compost consisting of 33 per cent peat, 33 per cent loam, 22 per cent sand and 12 per cent grit by volume (Monro Horticulture, UK) in 13 cm diameter × 12 cm tall pots two weeks after germination. The fertilizer treatments consisted of the addition of 9.28 g ammonium nitrate fertilizer (Nitram, AN), 62.8 g John Innes fertilizer (JI; Monro Horticulture, UK), 74.5 g chicken manure (CM; Greenvale Farms Ltd, UK) or no fertilizer (NF) to 10 l of potting compost prior to transplanting the seedlings. The AN fertilizer consists of 34.5 per cent N; chicken manure of 4.5 per cent N, 2.5 per cent P, 2.5 per cent K; and the JI fertilizer of 5.1 per cent N, 7.2 per cent P and 10 per cent K. Our treatments provided 0.32 g of total nitrogen per litre of potting compost for each fertilizer, 0.18 g phosphorus and potassium per litre of fertilizer for plants growing in chicken manure, and 0.45 g phosphorus and 0.63 g potassium per litre for plants in JI fertilizer. Plants were grown in compost for 4 weeks before being used for the experiment.

(b) *Herbivore performance under competition*
The two insect species were caged on host plants either as a single herbivore species (no interspecific competition) or together (interspecific competition). Five apterous *B. brassicae* adults were placed on the fifth leaf of 16 plants from each fertilizer treatment in a controlled environment room at 20°C (±1°C), 60 to 80 per cent relative humidity and 16 L : 8 D h photoperiod. To contain the insects, each plant was enclosed in a transparent plastic bag (24 cm diameter, 65 cm height) with perforated holes that allowed air circulation. After 48 h, groups of 10 second instar *P. xylostella* were weighed (Sartorius MP3 micro-balance, UK) and placed on each of eight plants already infested with *B. brassicae* and eight uninfested plants from each fertilizer treatment. Prior to the experiment, UK populations of *B. brassicae* and *P. xylostella* had been cultured separately on Chinese cabbage (*Brassica chinensis* L. var. *pekinensis* cv Wong Bok) for several generations under the same environmental conditions as detailed above [30]. The infestation sequence (*B. brassicae* before *P. xylostella*) was chosen to mimic the order of arrival of these species on UK *Brassica* plants [21].

Insect performance was assessed for both species. Four days after their introduction, the *P. xylostella* larvae were removed and weighed again to assess their relative growth rate, before being reintroduced to the same plant. *Brevicoryne brassicae* populations were counted on each plant 7 and 14 days after they were first introduced. Plants were checked daily, and as each *P. xylostella* pupated, it was removed and weighed again, and the date was recorded. In total, *P. xylostella* removed approximately 10 per cent of the foliage from each plant during their development.

(c) *Plant biomass and chemistry*
A separate batch of six plants was allocated to each of the 12 treatment combinations for foliar chemical analysis. Plants were grown and infested with herbivores as described above. Ten days after infestation with *B. brassicae* (approximately halfway through the experiment) the plants were harvested for analysis. Above-ground biomass was recorded. Samples were stored at −20°C prior to being freeze-dried and milled through a 1 mm diameter mesh. Total foliar nitrogen concentration was determined using an oxidative combustion method [31] in a FlashEA 1112 analyser (ThermoScientific, USA).

Foliar glucosinolates were separated and individual compounds were identified and quantified using the methods described by Heaney *et al.* [32]. Desulphoglucosinolates were extracted as detailed by Kazana *et al.* [33]. Samples were analysed by high-performance liquid chromatography on an Agilent 1200 series instrument equipped with a Phenomenex Luna 3 micron C18(2) (150 × 2 mm) reverse-phase column. Desulphoglucosinolates were separated using a water–acetonitrile gradient (solvent A water, solvent B acetonitrile; 0–15 min, 25% B; 15–17 min, 70% B) at a flow rate of 0.2 ml min^{-1}. Retention times of known standards were used to identify desulphoglucosinolates; identification was confirmed by liquid chromatography–mass spectrometry. Glucosinolates were grouped into indole and aliphatic glucosinolates [29].

(d) *Statistical analysis*
Our statistical analyses tested the effects of fertilizer and insect competition treatments on the abundance of *B. brassicae*, the performance of *P. xylostella*, and plant biomass and chemistry. The effects of fertilizer treatment,
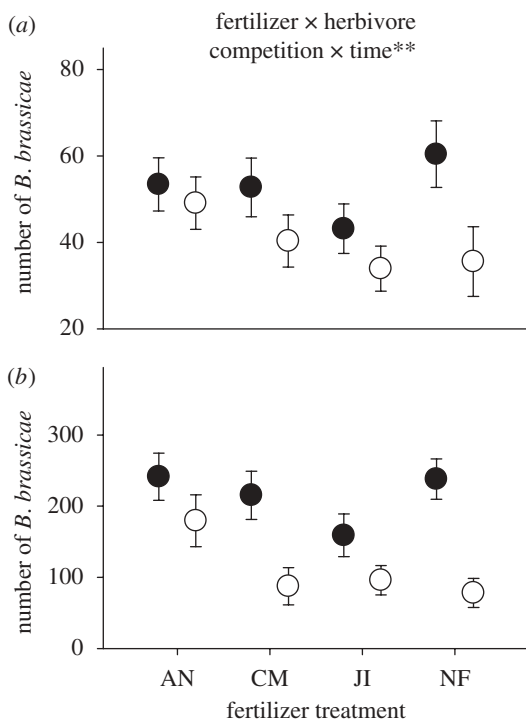
Figure 1. Mean (±s.e.) *Brevicoryne brassicae* with (B + P, open circles) or without (B, filled circles) *Plutella xylostella* per plant growing in ammonium nitrate (AN), chicken manure (CM) or John Innes (JI) fertilizer, or unfertilized compost (NF) at (*a*) 7 days and (*b*) 14 days after infestation. Significant generalized linear mixed model parameters: **$p < 0.01$.

Figure 2. Mean (±s.e.) *Plutella xylostella* (*a*) relative growth rate and (*b*) pupal weight with (B + P, open circles) or without (P, filled circles) *B. brassicae* on plants growing in ammonium nitrate (AN), chicken manure (CM) or John Innes (JI) fertilizer, or unfertilized compost (NF). Significant ANOVA factors: ***$p < 0.001$.

competition with *P. xylostella* and time on the number of *B. brassicae* were analysed using a generalized linear mixed model (GLMM) with a quasi-Poisson distribution [34]. Likelihood-ratio tests were used to test the null hypotheses [34]. Mean relative growth rate, development time and pupal weight were calculated for the 10 *P. xylostella* feeding on each plant (to avoid pseudoreplication), and these means were used in statistical analyses. Factorial two-way analyses of variance (ANOVAs) were used to test the effects of fertilizer and herbivore treatments on the relative growth rate, development time and pupal masses of *P. xylostella*, and the biomass, nitrogen, carbon and glucosinolate content of *B. oleracea* foliage. Larval relative growth rate was calculated as (larval mass after 96 h of feeding − initial larval mass)/initial larval mass [35]. Relative growth rate of *Plutella xylostella* and the concentration of indole and aliphatic glucosinolates were ln-transformed prior to analysis to meet the assumptions of ANOVA. Following a significant ANOVA result, Tukey HSD post hoc tests were conducted to determine which factor level means differed significantly [36]. All analyses were conducted using R v. 2.7.2 [37].

3. RESULTS
(a) *Herbivore performance under competition*
There was a significant interaction between fertilizer treatment, the presence of *P. xylostella* and time on the number of *B. brassicae* (GLMM likelihood-ratio test: fertilizer × herbivore competition × time: $\chi^2_3 = 12.09$, $p = 0.00708$). *Brevicoryne brassicae* populations were significantly smaller on plants also containing *P. xylostella* compared with those plants containing only aphids on
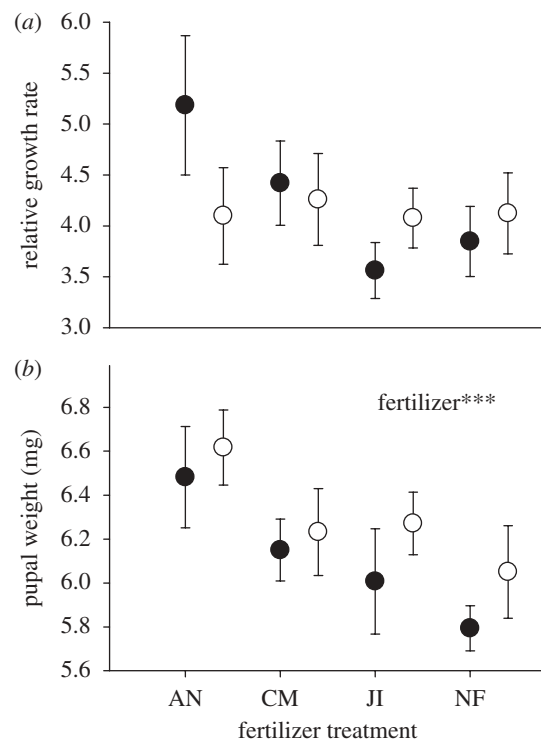
two of the four fertilizer treatments halfway through the experiment (7 days; figure 1*a*). By the end of the experiment (14 days), the presence of *P. xylostella* reduced *B. brassicae* populations on plants growing in all fertilizer treatments, except those in ammonium nitrate (figure 1*b*).

The performance of *P. xylostella* was not affected by competition with *B. brassicae*, but was altered by fertilizer treatment. Competition with *B. brassicae* did not affect the relative growth rate ($F_{1,74} = 0.78$, $p > 0.05$; figure 2*a*), larval development time ($F_{1,74} = 0.53$, $p > 0.05$) or pupal mass ($F_{1,74} = 0.71$, $p > 0.05$; figure 2*b*) of *P. xylostella*. *Plutella xylostella* pupae were significantly heavier on plants fertilized with ammonium nitrate than on unfertilized plants, and intermediate on plants growing in the other two fertilizers ($F_{3,74} = 4.24$, $p < 0.001$; figure 2*b*). Fertilizer treatment had no effect on either relative growth rate ($F_{3,74} = 1.73$, $p > 0.05$) or development time ($F_{3,74} = 2.41$, $p > 0.05$) of *P. xylostella*.

(b) *Plant biomass and chemistry*
Plant biomass was affected both by fertilizer treatment and by which herbivore species fed on them. Plants grown in ammonium nitrate or JI fertilizer were significantly larger than those grown in CM or unfertilized compost (table 1; Tukey HSD post hoc tests all $p < 0.05$). Plants with only *B. brassicae* were also larger than those with only *P. xylostella* or both herbivores (table 1; Tukey HSD post hoc tests all $p < 0.05$). Fertilizer and herbivore competition treatments did not have interacting effects on plant size (figure 3*a* and table 1).
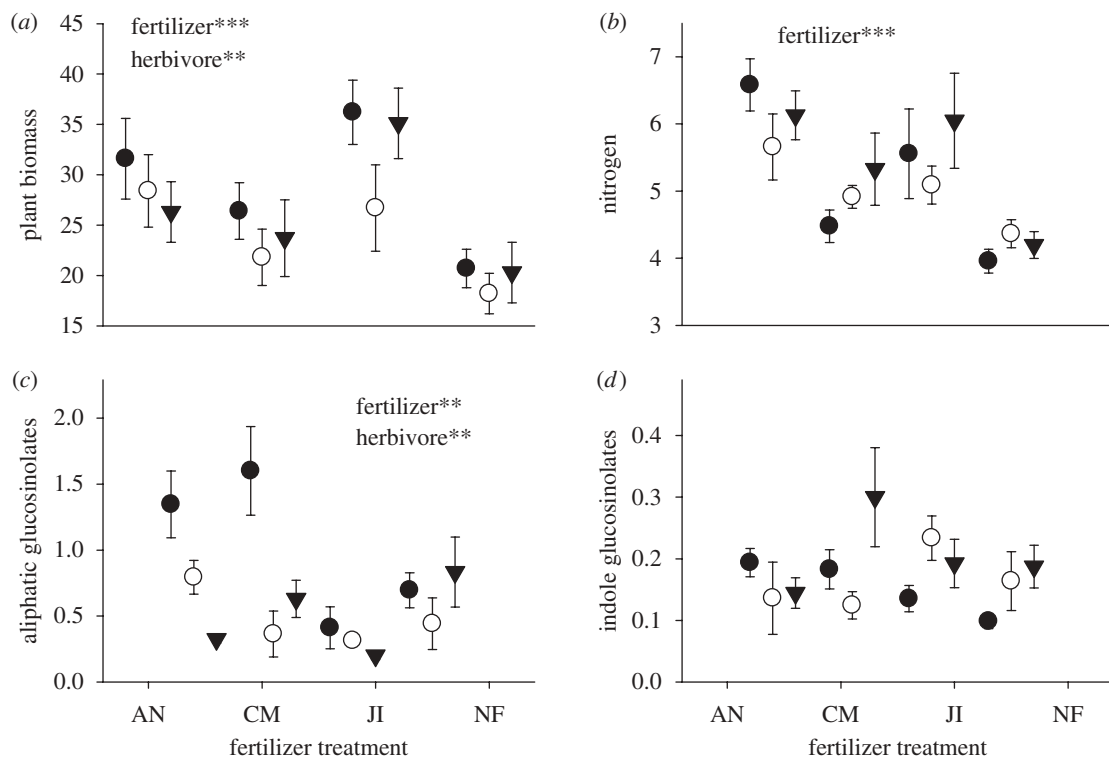
Figure 3. Mean ($\pm$ s.e.) of (*a*) fresh biomass, (*b*) nitrogen, (*c*) total aliphatic glucosinolate and (*d*) total indole glucosinolate content (% dry weight) of *Brassica oleracea* foliage growing in ammonium nitrate (AN), chicken manure (CM) or John Innes (JI) fertilizer, or no fertilized compost (NF) with *Brevicoryne brassicae* (B, filled circles), *Plutella xylostella* (P, open circles) or both herbivores (B + P, filled inverted triangles). Significant ANOVA factors: ***$p < 0.001$; **$p < 0.01$.

Table 1. Analysis of variance results for the effects of herbivore treatment and fertilizer type on *B. oleracea* biomass, foliar nitrogen, carbon, total aliphatic glucosinolate and total indole glucosinolate content.

	fertilizer	herbivore competition	fertilizer $\times$ herbivore competition
plant biomass	$F_{3,53} = 19.02$***	$F_{2,53} = 6.31$**	$F_{6,53} = 0.89$
nitrogen	$F_{3,53} = 13.95$ ***	$F_{2,53} = 1.03$	$F_{6,53} = 1.07$
carbon	$F_{3,53} = 0.39$	$F_{2,53} = 1.23$	$F_{6,53} = 0.08$
aliphatic glucosinolates	$F_{3,53} = 4.96$ **	$F_{2,53} = 5.96$ **	$F_{6,53} = 2.14$
indole glucosinolates	$F_{3,53} = 1.42$	$F_{2,53} = 1.66$	$F_{6,53} = 2.13$

***$p < 0.001$.
**$p < 0.01$.

Foliar nitrogen content was altered by the fertilizer treatment but not by the insect competition treatment (figure 3*b* and table 1). Foliar nitrogen was significantly more concentrated in plants fertilized with AN than those fertilized with CM or unfertilized plants (table 1; Tukey HSD post hoc tests all $p < 0.05$). Nitrogen content was intermediate in plants fertilized with JI fertilizer, but not significantly differently from those fertilized with AN.

Aliphatic glucosinolate concentration was affected both by the fertilizer and the herbivore treatments (figure 3*c* and table 1). Aliphatic glucosinolates were more concentrated in plants grown in AN or CM than those grown in JI fertilizer (Tukey HSD post hoc tests $p < 0.05$), and in intermediate levels in the unfertilized plants. Aliphatic glucosinolate concentration was also greater in plants with just *B. brassicae* than in plants with both *B. brassicae* and *P. xylostella*, or *P. xylostella* alone (Tukey HSD post hoc tests $p < 0.05$; figure 3*c*). Foliar carbon and indole glucosinolate contents were

not affected by either the fertilizer or the herbivore treatments (figure 3*d* and table 1).

4. DISCUSSION

Asymmetric competition occurred between *P. xylostella* and *B. brassicae*, as *P. xylostella* reduced populations of *B. brassicae* but there was no reciprocal effect, in common with most studies of interactions between phytophagous insect species [3]. The interaction was altered by the type of fertilizer available to the plant as competition occurred under three treatments but not when AN was supplied (figure 4). The effect of fertilizer on the interaction is not explained by the quantity of plant biomass available to the phytophages, as plants grown in AN and JI fertilizers had more biomass than those grown in the other two treatments, but *B. brassicae* populations did not differ significantly between the four fertilizer treatments.
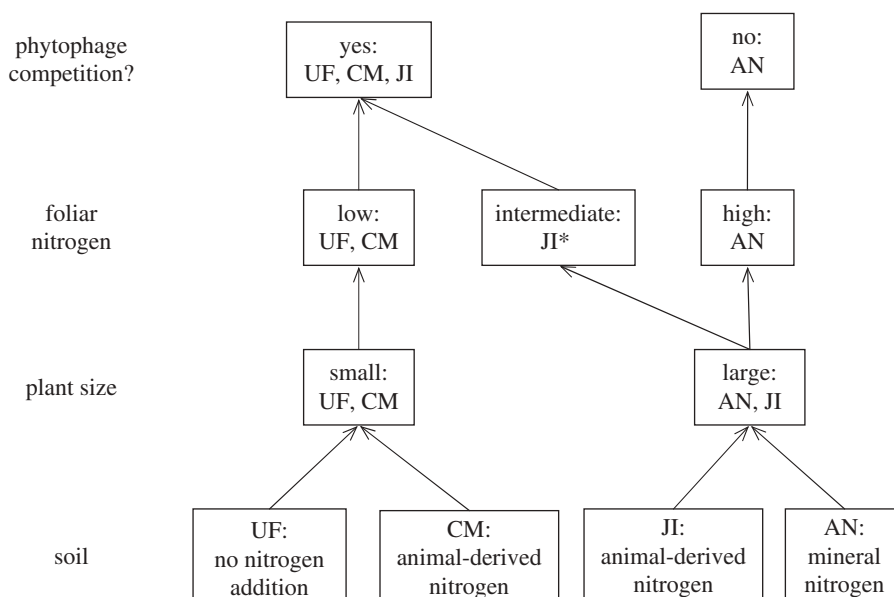
Figure 4. Summary of fertilizer treatment (UF, unfertilized; CM, addition of organic chicken manure; JI, John Innes fertilizer; AN, ammonium nitrate) effects on *Brassica* plant size and foliar nitrogen concentration and competition between a leaf-chewing and sap-feeding phytophage. Asterisk (*) denotes no significant difference in foliar nitrogen concentration of plants growing in JI compared with the other three fertilizer treatments (all other differences are statistically significant).

The same total amount of nitrogen was applied to each plant for three of the four fertilizer treatments; however, the higher foliar nitrogen concentration in plants grown in AN indicates higher uptake for this treatment when compared with the other two fertilizers. Application of the AN treatment also resulted in no effect of *P. xylostella* on *B. brassicae* population size and maximal pupal size for *P. xylostella*. Nitrogen is a key limit on herbivore population growth for a range of feeding guilds [28,38,39]. No changes in glucosinolate concentration were detected in response to *P. xylostella* feeding damage in the current study, but the concentrations of other secondary compounds or of specific amino acids essential for *B. brassicae* population growth may have been altered under the *P. xylostella* treatment. The greater uptake of nitrogen by AN-fertilized plants may have allowed *B. brassicae* to overcome any negative effects of an induced plant response to *P. xylostella* feeding.

Two studies support the hypothesis that herbivory is less likely to induce production of secondary chemicals under high resource availability, reducing the incidence of plant-mediated competition. Bryant *et al*. [13] found that complete artificial defoliation of birch (*Betula resinifera*) increased tannin concentrations in plants in a low-nutrient treatment, but had no effect on those under high nutrients. Previous damage by gypsy moth populations increased phenolic concentration in unfertilized *Quercus pinus* foliage, but not in fertilized trees [40].

Brevicoryne brassicae increased the concentration of aliphatic glucosinolates, but this had no effect on *P. xylostella* performance, whereas *P. xylostella* feeding did not induce increased glucosinolate concentration. When both species fed on the same plant, the presence of *P. xylostella* prevented the increase in aliphatic glucosinolates found on plants with *B. brassicae* feeding on their own. Feeding by several Lepidoptera species on *B. oleracae* var *alba* induces the expression of *LOX2*, a gene that plays a key role in inducing the signalling compound jasmonic acid,

which mobilizes diverse plant defences [41]. Feeding by *P. xylostella* did not induce *LOX2* gene expression, so Poelman *et al*. [41] suggested that *P. xylostella* has a mechanism for suppressing plant defences in response to its own feeding. The suppression by *P. xylostella* of a defence normally induced by a second herbivore species has not previously been shown, and may allow *P. xylostella* to avoid potentially detrimental competitive interactions.

We found that the occurrence of competition between two phytophagous species was altered by the type of fertilizer supplied to the host plant, perhaps mediated by foliar nitrogen concentration. Whether competition structures phytophagous insect communities in natural and semi-natural habitats has been much debated (e.g. [1−4]), but the potential for the occurrence of competition to vary with the availability of key resources, such as nitrogen, has not been considered. Nitrogen concentration did not differ greatly between the four fertilizer treatments, with means between 4 and 6.5 per cent dry weight, yet the occurrence of competition differed. Angiosperm foliar nitrogen content typically ranges from 1.5 to 7 per cent dry weight [28]. Competition may therefore play an even stronger role in structuring insect herbivore communities in environments with limited resources than in resource-rich environments.

The move to sustainable agricultural and horticultural practices in Europe and North America includes a reduced use of chemical-based fertilizers, and an increased application of slow-release sources of nutrition based on animal or green manures [16]. Sustainable agricultural practices may have a greater role in ensuring global food security under altered climatic conditions [42]. Our findings suggest that phytophagous species may be released from competition using synthetic fertilizers, which could allow the build-up of pest populations. Proponents of organic agriculture have claimed that organically fertilized plants are 'better defended' against insect pests [17−19]. Our results

provide little support for a consistent direct effect of fertilizer type on herbivore populations (see also [21]), but a release from competition on plants supplied with synthetic fertilizers might indirectly allow greater population growth under conventional agricultural practices.

Kaplan & Denno's [3] finding that indirect competition occurs more often than exploitation or interference competition in communities of phytophagous insects demonstrates the importance of induced plant responses to herbivory. Historically, most of the focus on competition between insect phytophages has come from entomologists, and the roles of plant chemistry and physiology under different abiotic conditions have been largely ignored. Future studies on competition between phytophages may benefit from the inclusion of abiotic treatments, such as the source of nutrients available to plants.

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