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Opposing effects of organic and conventional fertilizers on the performance of a generalist and a specialist aphid species

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Abstract

Sustainable and conventional farming systems use fertilizers that differ in the availability of nitrogen, which may affect plant quality to alter the abundance and performance of potential pest species. We grew brassica plants in several types of fertilizer, including those commonly used in conventional and sustainable farming systems, and an unfertilized control. The effects of fertilizer type on the performance of two aphid species and foliar glucosinolate content were investigated. Both aphid species performed poorly (with reduced fecundity) on the unfertilized treatment compared with those feeding on fertilized host plants. *Brevicoryne brassicae*, the brassica specialist, performed best on *Brassica oleracea* plants fertilized with an organic animal manure, with a 72% increase in fecundity and an 18% increase in intrinsic rate of increase compared with plants fertilized with ammonium nitrate. In contrast, the generalist *Myzus persicae* had an intrinsic rate of increase that was reduced by 15% on plants growing in the animal manure compared with those growing in ammonium nitrate. These results may explain earlier findings on the effects of fertilizer type on aphid populations in the field, and are discussed in the context of pest species' responses to sustainable and conventional agricultural systems.

Introduction

Interest in sustainable agricultural practices, which use alternatives to synthetic fertilizers and pesticides, is increasing (Letourneau & Bothwell, 2008). The use of animal or plant-derived fertilizers can change the amount and/ or rate of nitrogen supplied to crop plants compared to synthetic fertilizers (Staley *et al.*, 2010), as well as the concentration of other elements such as sulphur (Phelan *et al.*, 1995, 1996). Nitrogen concentration can alter the performance of individual herbivores (Fox & Macauley, 1977; De Bruyn *et al.*, 2002) and thus affect the population growth rate of phytophagous insects (Mattson, 1980; White, 1984). Sulphur is a component of glucosinolates, a group of secondary compounds that play a role in defense against herbivores (Hopkins *et al.*, 2009). Populations of some herbivore species are reduced on plants growing in organic fertilizers (Culliney & Pimentel, 1986; Ponti *et al.*, 2007), while other studies have found a higher abundance of phytophages under organic production (Letourneau *et al.*, 1996), or that herbivore species differ in their response to fertilizer type (Staley *et al.*, 2010).

Variation in the population growth of potential pest species in response to fertilizer type in a field study may be due to differences in performance (e.g. development time or fecundity), or due to differential predation or parasitism, or a combination of the two. Determining whether increased individual performance has a role in population responses to fertilizer type may be of value in the development of integrated pest management strategies (Letourneau & Bothwell, 2008). There have been few investigations into the performance of individual herbivores in response to organic and conventional fertilizers

(Phelan *et al.*, 1995; Staley *et al.*, 2009), and to our knowledge none assessing the response of more than one species.

Total foliar glucosinolate concentrations often decrease in response to increasing fertilizer or nitrogen supply (Fischer, 1992; Chen *et al.*, 2004; Aires *et al.*, 2006; Schonhof *et al.*, 2007), though individual compounds may differ in their response. For example, Rosen *et al.* (2005) found that indole glucosinolate concentrations (mainly glucobrassicin) increased in response to an increase in nitrogen, while aliphatic glucosinolate concentrations (predominantly sinigrin) decreased in one cultivar of *B. oleracea*. Glucosinolate concentrations can also differ between plants grown in organic and conventional fertilizers (Staley *et al.*, 2009, 2010), which may affect herbivore performance (Cole, 1997b).

Brevicoryne brassicae (Homoptera: Sternorryncha) is a specialist on Brassicaceae (Costello & Altieri, 1995) and is responsible for severe damage on cabbages in the UK and globally (Blackman & Eastop, 2000). It infests the leaves and shoots, and remains on herbaceous cruciferous plants throughout its life cycle (Collier & Finch, 2007). *Myzus persicae* (Homoptera: Sternorryncha) is a generalist feeder (Costello & Altieri, 1995) and a serious pest on a broad range of agricultural and horticultural crops (Cole, 1997a). *Brevicoryne brassicae* is more dependent on brassica specific glucosinolate compounds, which can act as feeding stimulants or repellents depending on the compound, than the generalist *M. persicae* (Cole, 1997b; Kim *et al.*, 2008). For example, the intrinsic rate of increase of *B. brassicae* was positively related to concentrations of progoitrin and sinigrin, and negatively related to glucobrasssicanapin and neoglucobrassicin concentrations (Cole, 1997b). The intrinsic rate of increase of *M. persicae* was less strongly related to glucosinolate concentrations (47% of the variation accounted for by glucosinolates vs. 79% in *B. brassicae*), but did relate positively to glucobrassicin and negatively to gluconapin concentrations (Cole, 1997b). Populations of these two species responded differently to organic and conventional fertilizers in a field trial (Staley *et al*., 2010). *Brevicoryne brassicae* was more abundant on *Brassica oleracea* (cabbage) supplied with organic animal manure compared with those fertilized with ammonium nitrate, while *M. persicae* was most abundant on plants fertilized with a low concentration of ammonium nitrate (Staley *et al.*, 2010).

In the current study, we investigate the performance of individual *B. brassicae* and *M. persicae* on *B. oleracea* growing in a range of fertilizer types under controlled conditions, to determine whether the response of the two species to fertilizers in the field can be explained by differences in individual aphid growth rate and fecundity. We hypothesized that *B. brassicae* would have faster development and/or greater fecundity on plants fertilized with an organic animal manure compared with ammonium nitrate, while *M. persicae* would show the reverse pattern. Glucosinolate contents were analysed in a separate batch of plants to those used for aphid performance, to determine the effects of fertilizer type on constitutive glucosinolate concentrations rather than short-term induced responses to aphid feeding damage (Hopkins *et al.*, 2009).

Materials and methods

Insect cultures

Myzus persicae and *B. brassicae* were obtained from long-term laboratory cultures at Rothamsted Research (Harpenden, U.K.). The insects were cultured on *B. oleracea*, grown in unfertilized compost (33% peat, 33% loam, 22% sand and 12% grit by volume; Monro Horticulture, Kent, UK) in a controlled environment under an LD 16 : 8 h photoperiod at 20 ± 1 °C and 60 – 80% relative humidity.

Fertilizer treatments

Cabbage seeds, *B. oleracea* var. *capitata* cv Derby Day (Tozer seeds, Surrey, UK) were planted in 22 mm diameter x 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). Overhead lighting (mercury halide and sodium bulbs) was supplied during the day to ensure a minimum light intensity of 300 watts / m^2.

When the first true leaves appeared seedlings were transferred to pots with compost (as above) containing one of four fertilizer treatments: 1) an unfertilized control; 2) 6.67 g ground organic chicken manure (Westlands, Cambridgeshire, UK); 3) 5.88 g John Innes fertilizer (comprised of hoof and horn, superphosphate, limestone and potassium phosphate; Monro Horticulture, Kent, UK) and 4) 0.86 g ammonium nitrate (Nitram).

The ammonium nitrate fertilizer consists of 34.5% N, 0% P, K and S, the JI fertilizer of 5.1% N, 7.2% P,10% K and 3.1% S, and the chicken manure of 4.5% N, 2.5% P, 2.5% K and 0.2% S (Pope *et al.*, 2011). Fertilizers were added to the potting compost at a rate of 0.32 g total nitrogen per l compost as the aim was to investigate the effects of the different forms of nitrogen within the different fertilizer treatments. Each fertilizer treatment was replicated 20 times for each aphid species, using separate plants for each species. Due to space and time constraints the experiment was conducted in two temporal blocks, with 10 replicates of each treatment in each block. *Brassica oleracea* were transferred to a controlled environment room (LD 16 : 8 h photoperiod at 20 ± 1 °C and 60 – 80% relative humidity) when they had 6 – 8 true leaves (7 weeks old) and their positions were randomized.

Aphid performance

Three apterous adult aphids were placed on the underside of the fourth, fifth and sixth oldest leaves on each plant (replicate), each one contained within a clip cage (MacGillivray & Anderson, 1957). When the first nymphs were produced the date was recorded, and the adult and all but one nymph were removed. Clip cages were monitored daily to record the date when the nymph had matured to adult (development time), producing its first offspring. Every 24 h the number of nymphs produced were recorded, and the nymphs subsequently removed. The intrinsic rate of increase (r_m) of each aphid was calculated using the equation $r_m = 0.738(\log_e Md) / d$ (Wyatt & White, 1977), where d is the number of days taken to reach reproductive age and Md is the effective fecundity produced in ‘*d*’ number of days. The constant (0.738) is an approximation of the proportion of the total fecundity produced by a female in the first ‘d’ days of reproduction (Wyatt & White, 1977).

Glucosinolate analysis

A separate batch of plants was grown under the four fertilizer treatments. The 5^{th} oldest leaf on each plant was excised using a sharp sterile razor, and then immediately frozen in liquid nitrogen using a pair of blunt tongs. Each leaf was placed on crushed ice, and transferred to a $-80^{o}C$ freezer prior to glucosinolate analysis.

Desulphoglucosinolates were obtained as described by Kazana *et al.* (2007) using the internal standard benzyl glucosinolate. The samples were lyophilized, and each sample was dissolved in distilled water (from EASYpure RF, Compact ultrapure water system, from this point forward referred to as H_2O). High-performance liquid chromatography (HPLC) (Agilent 1200 series) was then performed on the samples using the software Chemstation for LC 3D Systems (Copyright© Agilent Technologies). HPLC was performed on a Synergy column (15cm x 0.2cm), in a variable wavelength detector (229nm) with a flow rate of 0.2ml min^{-1}. The desulphoglucosinolates were eluted by the following gradient: H_2O 98%/ acetonitrile 2% (15min), H_2O 75%/ acetonitrile 25% (2min), H_2O 30%/ acetonitrile 70% (4min), H_2O 98%/ acetonitrile 2% (12min). The HPLC method permits the rapid separation and quantitative determination of intact individual glucosinolates under gentle conditions (Helboe *et al.*, 1980).

Statistical analyses

Mean aphid fecundity, development time and r_m were calculated per plant (replicate) and used for statistical analysis. ANOVAs were used to test the effect of fertiliser type on aphid fecundity, development time, r_m and plant glucosinolate concentrations, after ln or square root transformation if necessary. Temporal block was included in all analyses as a blocking factor. Where an ANOVA showed a significant treatment effect, posthoc Tukey HSD tests were performed to determine which treatment levels differed (Crawley, 2007). All statistical analyses were completed in the statistical package R (R Development Core Team, 2010).

Results

Aphid performance

Fertilizer treatment and aphid species interacted to affect development time significantly ($F_{3,148}$ = 3.49, P < 0.05; Figure 1a). *Myzus persicae* development was unaffected by fertilizer treatment, while development time was reduced for *B. brassicae* feeding on plants grown in chicken manure compared with unfertilized plants (Tukey HSD tests, P < 0. 05). Aphid fecundity was also affected by an interaction between species and fertilizer treatment ($F_{3,147}$ = 7.33, P < 0.001; Figure 1b). *Brevicoryne brassicae* produced more offspring on plants grown in chicken manure or John Innes fertiliser compared with those fertilized with ammonium nitrate or unfertilized (Tukey HSD tests, P < 0. 05). *Myzus persicae* fecundity was also reduced on unfertilized plants, but there was no difference between the three types of fertilizer (Tukey HSD tests, P < 0. 05; Figure 1b).

Aphid species and fertilizer treatment interacted to affect r_m ($F_{3,108}$ = 13.89, P < 0.001; Figure 1c). *Brevicoryne brassicae* r_m was greatest on plants fertilized with chicken manure or John Innes compared with plants fertilized with ammonium nitrate or unfertilized plants (Tukey HSD tests, P < 0. 05). *Myzus persicae* r_m was smallest on unfertilized plants, intermediate on plants grown in chicken manure and greatest on those in ammonium nitrate (Tukey HSD tests, P < 0. 05; Figure 1c). The r_m of *M. persicae* feeding on plants growing in John Innes was intermediate between those on chicken manure and ammonium nitrate, but not significantly different from either.

Glucosinolate analysis

Eight glucosinolates were identified. These included five aliphatic glucosinolates (derived from methionine): glucoiberin, progoitrin, glucoraphinin, sinigrin and gluconapin; and three indolyls (derived from tryptophan): 4-hydroxyglucobrassicin, neoglucobrassicin and 4 methoxyglucobrassicin.

Fertilizer treatment significantly affected foliar sinigrin concentration ($F_{3,17}$ = 3.22, $P < 0.05$; Figure 2a). There were significantly larger amounts (µmoles/g of dry weight) of sinigrin in the leaves from plants grown in unfertilized compost, compared to those grown in chicken manure or ammonium nitrate ($P < 0.05$; Figure 2a). Sinigrin concentrations in were intermediate in plants grown in John Innes (Figure 2a). There were no significant effects of fertilizer treatment on the concentration of any of the other glucosinolate compounds, or total glucosinolate concentration ($F_{3,18}$ = 2.20, $P = 0.12$; Figure 2b).

Discussion

Both aphid species had reduced fecundity and intrinsic rate of increase when feeding on unfertilized plants, and *B. brassicae*'s development time was extended on these plants. The two species, however, responded differently to the three fertilizer treatments. *Myzus persicae*'s r_m was reduced on plants growing in organic animal manure compared with those in the fertilizer typical of conventional agriculture (ammonium nitrate). In contrast, the performance (fecundity and r_m) of *B. brassicae* was reduced on plants grown in ammonium nitrate. Intrinsic rate of increase (r_m) relates the fecundity of an individual aphid to its development time, and is an estimate of future population growth based on the performance of individual aphids (Awmack & Leather, 2007). In the current study, fecundity of *B. brassicae* was more affected by fertilizer type than was development time, suggesting that fecundity may be the more important determinant of population growth in the context of fertilizer effects. The reduction in *B. brassicae* fecundity on conventionally fertilized plants may explain the smaller populations found on plants growing in ammonium nitrate in the field, compared with plants growing in organic animal manure, while the reduced *M. persicae* r_m on plants in chicken manure relates to the reduced populations of *M. persicae* on organically fertilized plants in the field (Staley *et al.*, 2010). The performance of individual aphids can therefore explain the response of aphid populations to fertilizer treatments in the field for both species.

Cole (1997b) found a stronger link between glucosinolate concentrations and the performance of *B. brassicae* on a range of brassica species than that of *M. persicae* (79%

vs. 47% of the variation in r_m accounted for by glucosinolate concentrations respectively). *Brevicoryne brassicae* is a specialist on Brassicaceae, and therefore may be more dependent on glucosinolates (including sinigrin) as feeding stimulants than *M. persicae* (Cole, 1997b). However, fertilizer effects on sinigrin or total glucosinolates differed between the current study (sinigrin increased on unfertilized plants only) and our field experiment (sinigrin and other glucosinolate concentrations greater on organic than conventionally fertilized plants; Staley *et al.*, 2010). Glucosinolate concentrations therefore do not explain the differences found in *B. brassicae* fecundity in the current study, as aphid performance and population responses to fertilizer type were similar but glucosinolate responses differed. Le Guigo & Le Corff (2011) also found that performance (longevity) of *B. brassicae* was not maximized on host plants with high total glucosinolate concentrations.

Nitrogen content may also affect herbivore performance and population growth (Mattson, 1980; White, 1984; Jansson & Ekbom, 2002; Zehnder & Hunter, 2009; Sauge *et al.*, 2010). In a separate laboratory study using *B. oleracea* grown in identical fertilizer treatments and conditions, foliar nitrogen concentration was greatest on *B. oleracea* growing in ammonium nitrate or John Innes, and reduced on those growing in chicken manure or unfertilized compost (Staley *et al.*, 2011). Total foliar nitrogen concentration thus does not explain the differences found in fecundity, as *B. brassicae* fecundity was reduced on the ammonium nitrate treatment on which foliar nitrogen concentration was maximized. *Brevicoryne brassicae*'s fecundity may have been determined by the concentration of individual amino acids in the phloem sap (van Emden & Bashford, 1971).

Plutella xylostella (diamondback moth) laid more eggs on potted plants fertilized with ammonium nitrate compared with those fertilized with organic chicken manure or John Innes, and in a field trial higher *P. xylostella* populations were found on plots fertilized with ammonium nitrate (Staley *et al*., 2010). In a greenhouse experiment, *Ostrinia nubilalis* (European corn borer) oviposition was reduced on maize grown in organic soils compared with conventional soils (Phelan *et al.*, 1995). The latter finding led Phelan *et al.* (1995, 1996) to suggest that organically managed soils result in reduced pest insect populations due to a 'biological buffering effect of organic soils' in which 'mineral relationships are optimized' (the Mineral Balance Hypothesis). Our current finding that the response of individual aphid performance to fertilizers differs between species corroborates the varying aphid population responses to organic and conventional fertilizers found in the field (Staley *et al.*, 2010), and suggests that the Mineral Balance Hypothesis may not be applicable across all herbivore species.

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References

Aires, A., Rosa, E. & Carvalho, R. (2006) Effect of nitrogen and sulfur fertilization on glucosinolates in the leaves and roots of broccoli sprouts (*Brassica oleracea* var. italica). *Journal of the Science of Food and Agriculture,* **86,** 1512-1516.

Awmack, C. S. & Leather, S. R. (2007) Growth and development. *Aphids as Crop Pests* (eds H. van Emden & R. Harrington), pp. 135-151. CABI, Wallingford, Oxfordshire UK.

Blackman, R. L. & Eastop, V. F. (2000) *Aphids on the World's Crops, an Identification and Information Guide.* John Wiley and Sons, West Sussex, UK.

Chen, Y. Z., Lin, L., Wang, C. W., Yeh, C. C. & Hwang, S. Y. (2004) Response of two Pieris (Lepidoptera : Pieridae) species to fertilization of a host plant. *Zoological Studies,* **43,** 778-786.

Cole, R. A. (1997a) Comparison of feeding behaviour of two Brassica pests *Brevicoryne brassicae* and *Myzus persicae* on wild and cultivated Brassica species. *Entomologia Experimentalis et Applicata,* **85,** 135-143.

Cole, R. A. (1997b) The relative importance of glucosinolates and amino acids to the development of two aphid pests *Brevicoryne brassicae* and *Myzus persicae* on wild and cultivated brassica species. *Entomologia Experimentalis et Applicata,* **85,** 121-133.

Collier, R. H. & Finch, S. (2007) IPM case studies: Brassicas. *Aphids as Crop Pests* (eds H. van Emden & R. Harrington), pp. 549 - 559. CABI, Wallingford, Oxfordshire UK.

Costello, M. J. & Altieri, M. A. (1995) Abundance, growth rate and parasitism of *Brevicoryne brassicae* and *Myzus persicae* (Homoptera, Aphididae) on broccoli grown in living mulches. *Agriculture Ecosystems & Environment,* **52,** 187-196.

Crawley, M. J. (2007) *The R Book.* John Wiley & Sons, Chichester, UK.

Culliney, T. W. & Pimentel, D. (1986) Ecological effects of organic agricultural practices on insect populations. *Agriculture Ecosystems & Environment,* **15,** 253-266.

De Bruyn, L., Scheirs, J. & Verhagen, R. (2002) Nutrient stress, host plant quality and herbivore performance of a leaf-mining fly on grass. *Oecologia,* **130,** 594-599.

Fischer, J. (1992) The influence of different nitrogen and potassium fertilization on the chemical flavour composition of Kohlrabi (*Brassica oleracea* var *gongylodes* L). *Journal of the Science of Food and Agriculture,* **60,** 465-470.

Fox, L. R. & Macauley, B. J. (1977) Insect grazing on *Eucalyptus* in response to variation in leaf tannins and nitrogen. *Oecologia,* **29,** 145-162.

Helboe, P., Olsen, O. & Sorensen, H. (1980) Separation of glucosinolates by high-performance liquid chromatography. *Journal of Chromatography,* **197,** 199-205.

Hopkins, R. J., van Dam, N. M. & van Loon, J. J. A. (2009) Role of glucosinolates in insect-plant relationships and multitrophic interactions. *Annual Review of Entomology,* **54,** 57-83.

Jansson, J. & Ekbom, B. (2002) The effect of different plant nutrient regimes on the aphid *Macrosiphum euphorbiae* growing on petunia. *Entomologia Experimentalis et Applicata*, **104,** 109-116.

Kazana, E., Pope, T. W., Tibbles, L., Bridges, M., Pickett, J. A., Bones, A. M., Powell, G. & Rossiter, J. T. (2007) The cabbage aphid: a walking mustard oil bomb. *Proceedings of the Royal Society B-Biological Sciences,* **274,** 2271-2277.

Kim, J. H., Lee, B. W., Schroeder, F. C. & Jander, G. (2008) Identification of indole glucosinolate breakdown products with antifeedant effects on *Myzus persicae* (green peach aphid). *Plant Journal,* **54,** 1015-1026.

Letourneau, D. K. & Bothwell, S. G. (2008) Comparison of organic and conventional farms: challenging ecologists to make biodiversity functional. *Frontiers in Ecology and the Environment*, **6,** 430-438.

Letourneau, D. K., Drinkwater, L. E. & Shennan, C. (1996) Effects of soil management on crop nitrogen and insect damage in organic vs conventional tomato fields. *Agriculture Ecosystems & Environment*, **57,** 179-187.

MacGillivray, M. E. & Anderson, G. B. (1957) Three useful insect cages. *Canadian Entomologist*, **89,** 43-46.

Mattson, W. J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics,* **11,** 119-161.

Phelan, P. L., Mason, J. F. & Stinner, B. R. (1995) Soil-fertility management and host preference by European corn borer, *Ostrinia nubilalis* (Hubner), on *Zea mays* L: a comparison of organic and conventional chemical farming. *Agriculture, Ecosystems and Environment,* **56,** 1-8.

Phelan, P. L., Norris, K. H. & Mason, J. F. (1996) Soil-management history and host preference by *Ostrinia nubilalis*: Evidence for plant mineral balance mediating insect-plant interactions. *Environmental Entomology*, **25,** 1329-1336.

Ponti, L., Altieri, M. A. & Gutierrez, A. P. (2007) Effects of crop diversification levels and fertilization regimes on abundance of *Brevicoryne brassicae* (L.) and its parasitization by *Diaeretiella rapae* (M'Intosh) in broccoli. *Agricultural and Forest Entomology,* **9,** 209-214.

Pope, T. W., Girling, R. D., Staley, J. T., Trigodet, B., Wright, D. J., Leather, S. R., van Emden, H. & Poppy, G. M. (online Sept 2011) Effects of organic and conventional fertilizer treatments on host selection by the aphid parasitoid *Diaeretiella rapae*. *Journal of Applied Entomology*.

R Development Core Team (2010) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, (URL http://www.R-project.org/).

Rosen, C. J., Fritz, V. A., Gardner, G. M., Hecht, S. S., Carmella, S. G. & Kenney, P. M. (2005) Cabbage yield and glucosinolate concentrations as affected by nitrogen and sulfur fertility. *Hortscience,* **40,** 1493-1498.

Sauge, M.H., Grechi, I. & Poessel, J.L. (2010) Nitrogen fertilization effects on *Myzus persicae* aphid dynamics on peach: vegetative growth allocation or chemical defence? *Entomologia Experimentalis et Applicata*, **136**, 123-133.

Schonhof, I., Blankenburg, D., Muller, S. & Krumbein, A. (2007) Sulfur and nitrogen supply influence growth, product appearance, and glucosinolate concentration of broccoli. *Journal of Plant Nutrition and Soil Science-Zeitschrift Fur Pflanzenernahrung Und Bodenkunde*, **170,** 65-72.

Staley, J. T., Girling, R. D., Stewart-Jones, A., Poppy, G. M., Leather, S. R. & Wright, D. J. (online Jan 2011) Organic and conventional fertilizer effects on a tritrophic interaction: parasitism, performance and preference of *Cotesia vestalis*. *Journal of Applied Entomology*. doi: 10.1111/j.1439-0418.2010.01604.x

Staley, J. T., Stewart-Jones, A., Pope, T. W., Wright, D. J., Leather, S. R., Hadley, P., Rossiter, J. T., Van Emden, H. & Poppy, G. M. (2010) Varying responses of insect herbivores to altered plant chemistry under organic and conventional treatments. *Proceedings of the Royal Society B-Biological Sciences,* **277,** 779-786.

Staley, J. T., Stewart-Jones, A., Poppy, G. M., Leather, S. R. & Wright, D. J. (2009) Fertiliser affects the behaviour and performance of *Plutella xylostella* on Brassicas. *Agricultural and Forest Entomology,* **11,** 275-282.

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 et Applicata,* **14,** 349-360.

White, T. C. R. (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia,* **63,** 90-105.

Wyatt, I. J. & White, P. F. (1977) Simple estimation of intrinsic increase rates for aphids and tetranychid mites. *Journal of Applied Ecology,* **14,** 757-766.

Zehnder, C.B. & Hunter, M.D. (2009) More is not necessarily better: the impact of limiting and excessive nutrients on herbivore population growth rates. *Ecological Entomology*, **34**, 535-543.

Figure legends

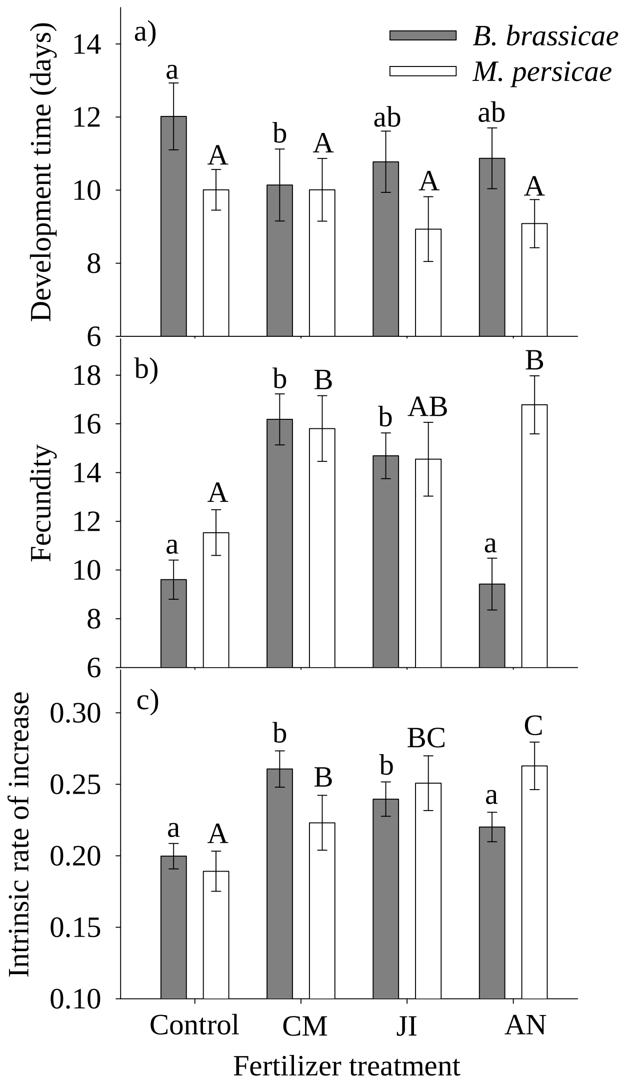
Figure 1

Mean (±SE) individual a) development time, b) fecundity and c) intrinsic rate of increase of aphids feeding on *Brassica oleracea* plants growing in compost that was unfertilized (control) or fertilized with chicken manure (CM), John Innes (JI) or ammonium nitrate (AN). Within each aphid species different letters denote treatments that differ significantly ($P < 0.05$; lower case letters for *Brevicoryne brassicae*, upper case for *Myzus persicae*).

Figure 2

Mean (±SE) foliar a) sinigrin and b) total glucosinolate concentration for *Brassica oleracea* plants growing in compost that was unfertilized (control) or fertilized with chicken manure (CM), John Innes (JI) or ammonium nitrate (AN). Different letters denote treatments that differ significantly ($P < 0.05$)

Figure 1


a)
b)
c)
B. brassicae
M. persicae
Development time (days)
Fecundity
Intrinsic rate of increase
14
12
10
8
6
18
16
14
12
10
8
6
0.30
0.25
0.20
0.15
0.10
a
A
b
A
ab
A
ab
A
b
B
b
AB
B
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A
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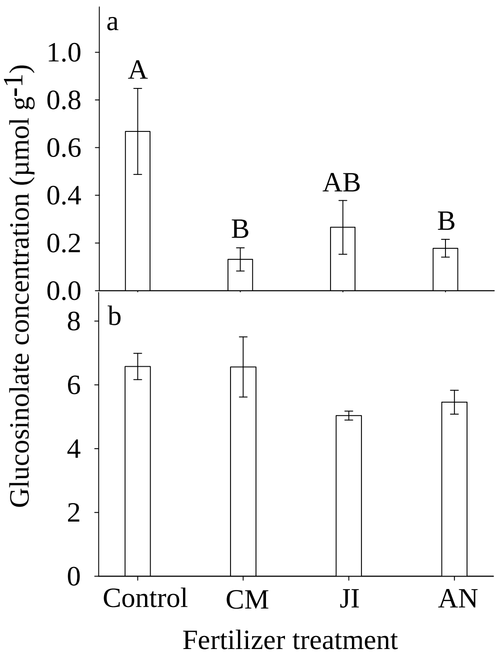
Control
CM
JI
AN
Fertilizer treatment

Figure 2


a
b
Glucosinolate concentration (µmol g-1)
1.0
0.8
0.6
0.4
0.2
0.0
A
B
AB
B
8
6
4
2
0
Control
CM
JI
AN
Fertilizer treatment