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Tritrophic interactions between cabbage cultivars with different resistance and fertilizer levels, cruciferous aphids and parasitoids under field conditions

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Abstract

Tritrophic interactions involving cabbage *Brassica oleracea* var. *capitata* cultivars ± fertilizer, *Brevicoryne brassicae* (Linnaeus) and *Myzus persicae* (Sulzer), and the parasitoids *Diaeretiella rapae* (M'cIntosh) and *Aphidius* sp. were conducted in 1998 and 1999. *Brevicorne brassicae* was the dominant aphid species on all cultivars ± fertilizer, except for some treatments in late season 1998. Ruby Ball (red-leaved with antixenosis factors for *B. brassicae* alates) ± fertilizer was consistently less colonized by aphids in early stages of plant growth, although only significantly so compared with Derby Day (green-leaved, susceptible to aphids) without fertilizer for *B. brassicae* and Minicole (green-leaved with antibiosis factors for *B. brassicae*) with fertilizer for *M. persicae*. In early 1999, only *B. brassicae* was present and no significant differences between cultivars were seen. In the mid to late season 1998, the highest aphid infestations were usually found on Derby Day, although only significantly so for *B. brassicae*, in some treatments. In 1999, higher aphid infestations were observed on Derby Day in mid to late season and some significant differences were found for *M. persicae* as well as for *B. brassicae*. In both years, Ruby Ball had the greatest mummy:aphid ratios early season, with no consistent difference between the other cultivars. Later in the season, mummy:aphid ratios were generally highest on Minicole. Parasitism differed in seasonal occurrence and relative abundance. *Diaeretiella rapae* mummies were found earlier than *Aphidius* sp. There was evidence of a beneficial interaction between the degree of plant resistance and biological control in early to mid season.

Introduction

Plant cultivar, fertilizer treatment and plant age have each been shown to influence the fecundity, population density and the relative growth rate of aphids (Radcliffe & Chapman, 1965; van Emden & Bashford, 1969; Cole, 1997), and subsequent control measures (Mohamad & van Emden, 1989). For example, resistance to aphids in Brussels sprout cultivars has been linked to soluble nitrogen concentrations (van Emden & Bashford, 1969). In brassicas, the intrinsic rate of increase of *Brevicoryne brassicae* (Linnaeus) (Hemiptera: Aphididae) but not *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) has been correlated with phloem amino acid concentrations (Cole, 1997). Plant nutrition has also been found to influence the activity of aphid natural enemies (Mohamad & van Emden, 1989).

Control of *B. brassicae* and *M. persicae* is achieved commonly by repeated application of insecticides. This dependence on chemicals for the control of aphids has led to increased production costs and contributed to the development of insecticide resistance (Foster *et al.*, 1998). The use of chemicals to control aphids also poses serious hazards to natural enemies (Gamal *et al.*, 1992). There is,

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therefore, a need for a more integrated approach to the management of aphids. In aphid systems where natural enemies alone are not sufficiently effective, improvement in their efficacy through host-plant manipulation is both possible and highly desirable (van Lenteren, 1991).

The compatibility of plant resistance and biological control has been examined for several plant–herbivore (pest)–natural enemy complexes (Price *et al.*, 1980; Salto *et al.*, 1983; Ofuya, 1995; Verkerk *et al.*, 1998). In some cases, these methods of control have been found to be complementary. For example, plant resistance may slow the rate of increase of a pest population, thus allowing biological control agents to provide effective control (Starks *et al.*, 1972; Nwanze *et al.*, 1998). In other cases, plant resistance mechanisms have been shown to hinder the effectiveness of natural enemies (Campbell *et al.*, 1990; Hare, 1992).

Although antixenosis and antibiosis have been identified as defence mechanisms against aphids in the cultivars Ruby Ball and Minicole, respectively (Singh & Ellis, 1993; Ellis *et al.*, 1996), the effect of this resistance on the aphid parasitoids under field conditions is not known. This is crucial because the effects of these resistance factors are also likely to be manifested in the third trophic level, that is, on natural enemies. Other studies have shown that these cabbage cultivars influence parasitism and biological characteristics of the parasitoid, *Aphidius colemani* Viereck (Hymenoptera: Braconidae) under laboratory conditions (T. Kalule and D.J. Wright, unpublished data). However, plant growth stage, seasonal synchrony of aphid and natural enemy abundance, and abiotic factors in the field may contradict results from such laboratory studies (Obrycki & Tauber, 1984). In the present work, field tritrophic studies were conducted to evaluate the effect of different cabbage cultivars with varying levels of resistance and with different rates of fertilizer treatment on cruciferous aphids and their parasitoids for the length of the growing season.

Materials and methods

Establishment of field experiments

Field experiments were established at Silwood Park, Berkshire, UK in the summers of 1998 and 1999. The soils are classified as Bagshot sand and are basically of acid pH and are maintained under a crop rotation of potatoes, brassicae and legumes. Nutrient analysis carried out in 1998 showed that the levels of phosphorous, potassium and nitrogen were 45, 43 and 21 mg kg^{-1}, respectively. Three cabbage cultivars, Derby Day, Minicole (both green leaved) and Ruby Ball (red leaved), were used. Derby Day is considered highly susceptible to *B. brassicae* and *M. persicae* while Minicole has shown under certain conditions to possess a degree of partial resistance (antibiosis) to *B. brassicae* (Ellis *et al.*, 1996). Ruby Ball is considered partially resistant with antixenosis factors for incoming alates of *B. brassicae* in the field (Singh & Ellis, 1993). Seeds of Derby Day and Minicole obtained from Elsoms Seeds, Spalding, UK and Ruby Ball from Nickerson Seeds, Lincoln, UK were sown separately in 7 cm square plastic trays in the greenhouse using Levingtons Multipurpose Compost® (Fisons, UK). The plants were later transplanted in the field at the 7–8 leaf stage. The experiment was a 3 × 2 factorial, in a randomized complete block design with a split plot arrangement replicated four times. The main plot factor consisted of the three cabbage cultivars. Two fertilizer levels comprised the sub-plot factor: a blanket fertilizer application of NPK at the recommended rate of 95 kg N, 78 kg P, 78 kg K ha^{-1} applied in the fertilizer plots monthly for a period of three months and no fertilizer application. A buffer zone of 2 m separated the fertilized and unfertilized blocks. Plots measured 2.8 × 2.1 m, each consisting of eight 1.5 m long rows, with cabbage being planted at a spacing of 40 × 30 cm. One seedling was planted per hill. Plots were kept free of weeds by regular hand weeding.

Effect of cultivar and fertilizer on aphid incidence

In order to assess the influence of the cabbage cultivars and fertilizer on the aphid load and species composition, plants from the inside six rows of each plot were sampled for aphids at weekly intervals by a stratified random sampling plan. One week after the first aphids had alighted on the plants, three plants per plot were scored for number of aphids as a measure of antixenosis; the aphid preference for settling on plants (Singh *et al.*, 1994). On each subsequent sampling occasion, all plants in the sample rows were inspected thoroughly and plants with five or more aphids recorded as infested. Sampling dates are presented as days after transplanting (DAT). The dates corresponded to the following plant growth stages: early stage (28–35 DAT), mid stage (42–49 DAT) and late stage (56–63 DAT). Three leaves (upper, middle and lower inner or outer leaves) were removed from three plants in the sample rows (van Emden, 1963) and the number of aphids per leaf counted. Laboratory cage experiments showed that removal of leaves did not influence the attractiveness of the plants to parasitoids (Kalule, 2000).

Effect of cultivar and fertilizer on levels of parasitism

Assessment of the number of aphids parasitized (mummy abundance) was carried out on the same plants used for estimating aphid abundance. Mackauer & Chow (1986) did not recommend the use of mummies to assess the impact of parasitoids because mummies accumulate over time. To avoid this problem, only mummies without emergence holes (full mummies) were included in the analyses. This distinction allows for assessment of newly parasitized aphids in situations where sampling is conducted on a regular basis (Fernandes *et al.*, 1998). Sample leaves were taken to the laboratory and emerging parasitoids counted. Non-emergence of mummies was low (<5%).

Data analysis

From the data collected, the abundance of aphids and their species composition as influenced by cultivar and fertilizer during the study period was obtained and tabulated. Variance in aphid counts was stabilized with the log(x+1) transformation (Taylor, 1970) and the data were analysed using the MSTAT-C software package (MSTAT-C, 1990). Data for each sampling date and year were analysed separately. FACTOR was used to perform the factorial analyses (MSTAT-C, 1990) to assess if there were any significant differences in the number and type of aphids on the three cabbage cultivars with and without fertilizer. Mean separation was carried out using Fisher's least significant difference (LSD) test. The abundance of mummies on each sampling date on the different cabbage treatments was also determined. Two-way ANOVA was carried out after the appropriate transformations to assess the significance of variation in parasitism as influenced by cultivar levels of resistance and fertilizer. Multiple regression analyses were also carried out to assess the relationship between parasitism and aphid populations and to partition the contribution of the respective aphid species on overall aphid mortality due to parasitism. The two aphid species were treated as multiple variables. The slope (b) of the two parasitized aphid species allowed for the assessment of the contribution of each species to total aphid mortality during different stages of crop development. The t statistic was used to test whether slope estimates differed significantly from zero, indicating a difference in relative contribution between the two aphid species to total aphid mortality (Gomez & Gomez, 1984). The level of parasitism expressed as mummy to aphid ratios, was derived from the formula by Kausalya *et al.* (1995) as: total number of mummies (m) to total number of aphids (alive and parasitized) (a + m) as follows: mummy: aphid ratio = m: a + m. Percentage values obtained to test for mean proportion parasitism were arcsine transformed and submitted to ANOVA (Gomez & Gomez, 1984). Rate of aphid population increase on treatments was calculated as: (final density − initial density) / initial density.

Results

Effect of cultivar and fertilizer on incidence and parasitism of Brevicoryne brassicae *and* Myzus persicae

In early 1998, *B. brassicae* was the dominant aphid species and it was present in lowest numbers on Ruby Ball, although this was not statistically significant except when compared with Derby Day without fertilizer plots (fig. 1). *Myzus persicae* was present in significantly ($P < 0.05$) greater numbers in the Minicole with fertilizer compared with the Ruby Ball with fertilizer plots (fig. 1). Mummy abundance was significantly ($P < 0.05$) greater on Ruby Ball without fertilizer compared with all cultivars with fertilizer when *B. brassicae* was the host and Derby Day with and without fertilizer when *M. persicae* was the host (fig. 1). In early 1999, *B. brassicae* was the only species in the field but its incidence was not significantly ($P > 0.05$) influenced by treatment (fig. 2). By mid-season (42–49 DAT), Derby Day with fertilizer had the greatest ($P < 0.05$) *B. brassicae* population compared with Minicole in 1998 and Ruby Ball and Minicole without fertilizer in 1999 (figs 1 and 2). The greatest aphid population increase from early (28–35 DAT) to mid-season (42–49 DAT) was on Derby Day with fertilizer in 1998 and Derby Day without fertilizer in 1999 (figs 1 and 2). Derby Day with fertilizer had the greatest ($P < 0.05$) *M. persicae* population compared with the other cultivars in 1999 (fig. 2). In early

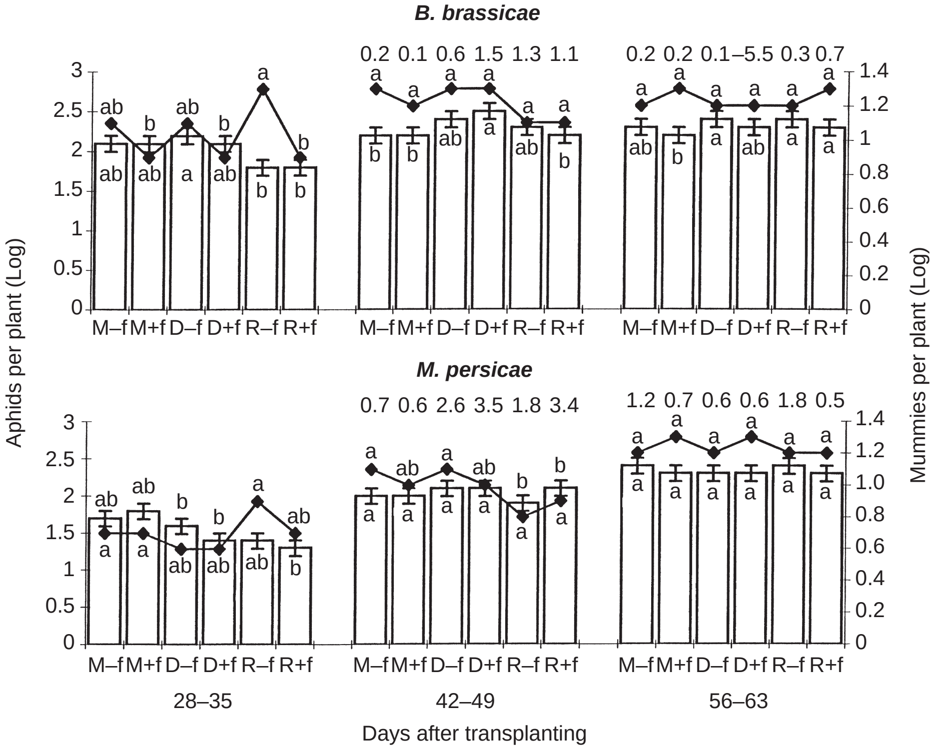

Fig. 1. Seasonal incidence (bars, left axis scale) and parasitism (mummies depicted by —◆—, right axis scale) of *Brevicoryne brassicae* and *Myzus persicae* on different cabbage cultivars at different fertilizer levels (M−f, D−f, R−f, represent Minicole, Derby Day, Ruby Ball without fertilizer and M+f, D+f, R+f represent Minicole, Derby Day, Ruby Ball with fertilizer) in the early (28–35 days), mid (42–49 days) and late (56–63 days) periods of plant growth after transplanting in 1998. Vertical lines indicate standard errors of means (aphids). Figures above line graph represent rates of aphid population increase. Means followed by same letter are not significantly ($P > 0.05$) different. Letters inside the bar graph refer to aphids while letters on line graph refer to mummies.

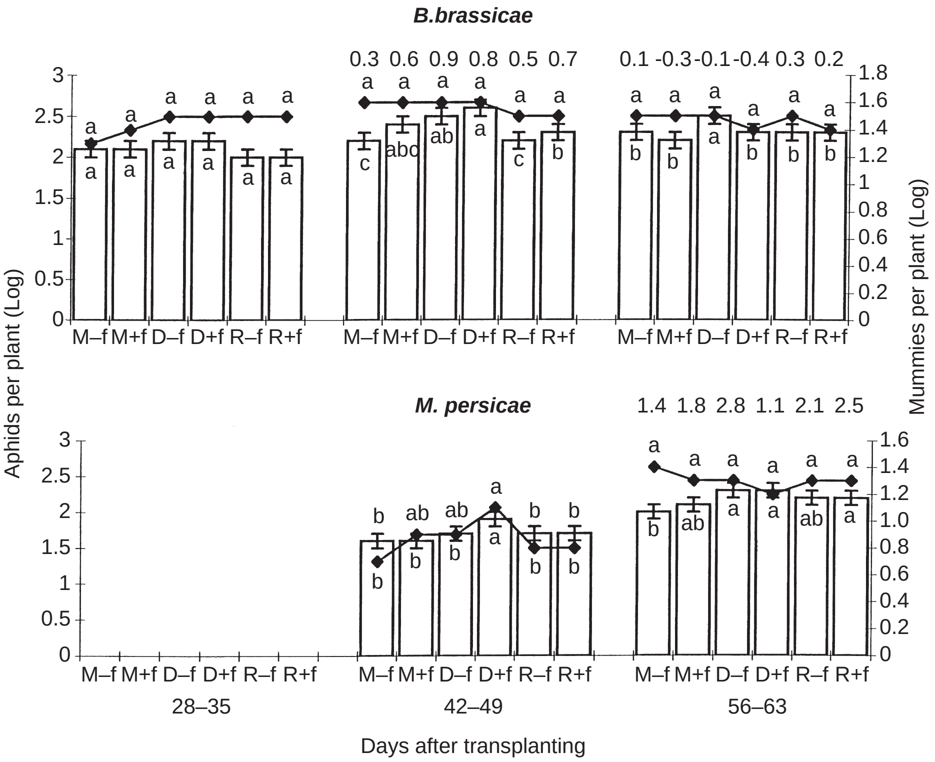

Fig. 2. Seasonal incidence (bars, left axis scale) and parasitism (mummies depicted by —◆—, right axis scale) of *Brevicoryne brassicae* and *Myzus persicae* on different cabbage cultivars at different fertilizer levels (M−f, D−f, R−f, represent Minicole, Derby Day, Ruby Ball without fertilizer and M+f, D+f, R+f represent Minicole, Derby Day, Ruby Ball with fertilizer) in the early (28–35 days), mid (42–49 days) and late (56–63 days) periods of plant growth after transplanting in 1999. Vertical lines indicate standard errors of means (aphids). Figures above line graph represent rates of aphid population increase. Means followed by same letter are not significantly ($P > 0.05$) different. Letters inside the bar graph refer to aphids while letters on line graph refer to mummies.

1998 (28–35 DAT), parasitism of both aphid species was significantly ($P < 0.05$) greater on Ruby Ball without fertilizer compared with other cultivars (fig. 3). By mid-season in both years, the two aphid species had significantly ($P < 0.05$) greater levels of parasitism on Minicole without fertilizer compared with Derby Day with fertilizer with the exception of *M. persicae* in 1999 (figs 3 and 4). In the late stages of plant growth in 1998, parasitism of both aphid species was not significantly ($P < 0.05$) different between cultivars. However, in 1999, a significantly ($P < 0.05$) greater proportion of *M. persicae* was parasitized on Minicole compared with Derby Day (figs 3 and 4).

Multiple regression analysis assessed the contribution of the individual aphid species on overall aphid mortality in both seasons. When pooled across cultivar, the regression coefficient or slope (b) varied by aphid species and plant growth stage (table 1). In the early stages of crop development in 1998, the overall aphid mortality depended on *B. brassicae* and *M. persicae* (t = 3.63, $P = 0.001$ and t = 2.73, $P = 0.012$, respectively; table 1a). In mid-season of 1998, parasitism of *B. brassicae* contributed significantly ($P = 0.001$) to total aphid mortality (table 1b). The mortality of *B. brassicae* in 1998 was a significant predictor (t = 3.83, $P = 0.001$) of overall aphid mortality at this stage of plant growth. In 1999, total aphid mortality depended on both *B. brassicae* and *M. persicae* parasitism (t = 13.1, $P = 0.0001$ and t = 3.28, $P = 0.003$, respectively) although the slope was higher for the former (0.87) compared with the latter (0.19) (table 1b). In the late stages of plant growth (56 DAT), the slope estimates for both aphid species were very low for the 1998 season but were much greater in 1999 for *B. brassicae* (table 1c).

The emerging parasitoids found were mainly *Diaeretiella rapae* (M'cIntosh) (Hymenoptera: Braconidae) and *Aphidius* sp. (Hymenoptera: Braconidae). Their seasonal incidence is presented in table 2. *Diaeretiella rapae* was collected from the field earlier than *Aphidus* sp. and was more abundant. When averaged across years, species determination showed 67% *D. rapae* and 33% *Aphidius* sp. in 1998 and 69% and 31%, respectively, in 1999. *Diaeretiella rapae* was mostly collected from *B. brassicae* mummies while more *Aphidius* sp. tended to emerge from *M. persicae* (table 2). *Aphidius* sp. incidence increased with time and peaked in the late stage of plant growth while that of *D. rapae* increased more slowly (table 2).

Discussion

The present study has shown that plant cultivar can influence aphid incidence and subsequent levels of parasitism, although differences were not always consistent between years. In early 1998, the only significant difference in aphid infestations was found between Ruby Ball and any of the fertilized cultivars early in 1998. However, fertilizer treatment had only a minimal influence on aphid infestation and parasitism, unlike previous reports (van Emden & Bashford, 1969; Mohamad & van Emden, 1989). Observations on aphid incidence in the early stages of plant growth seem

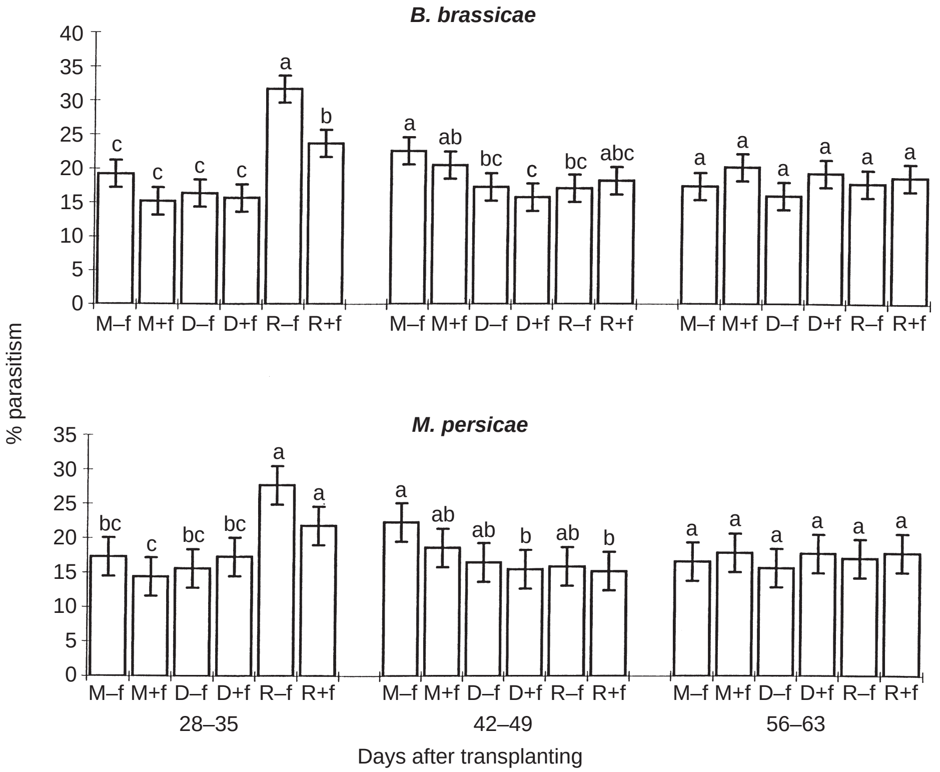

Fig. 3. Parasitism of *Brevicoryne brassicae* and *Myzus persicae* on different cabbage cultivars at different fertilizer levels in the early (28–35 days), mid (42–49 days) and late (56–63 days) periods of plant growth after transplanting in 1998. Means followed by same letter are not significantly ($P > 0.05$) different.

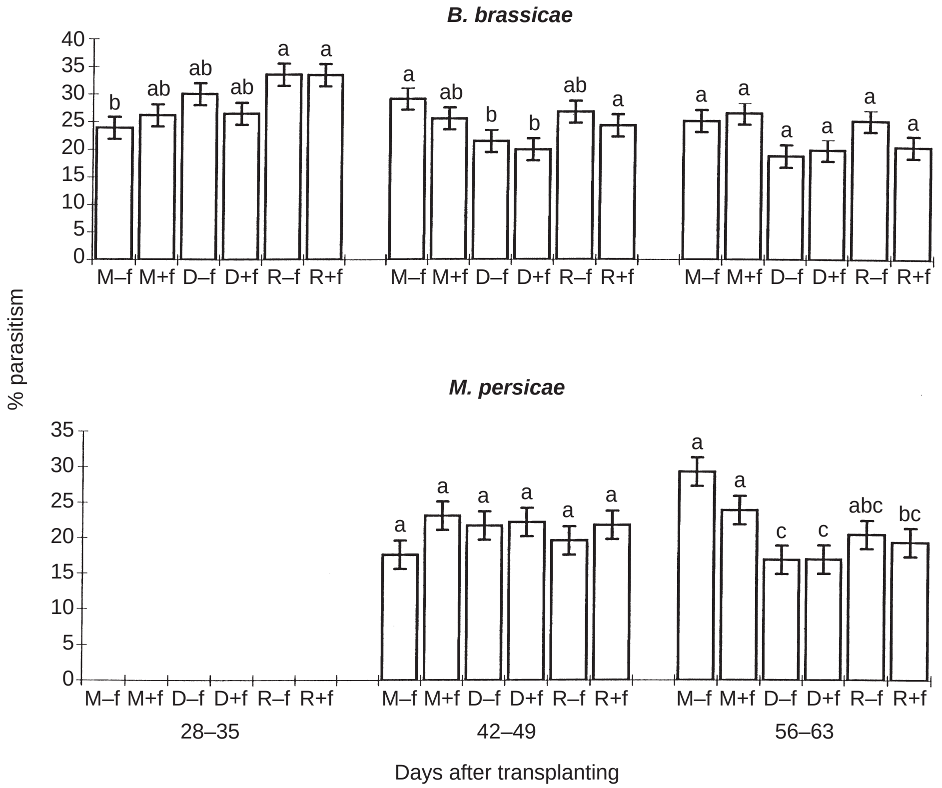

Fig. 4. Parasitism of *Brevicoryne brassicae* and *Myzus persicae* on different cabbage cultivars at different fertilizer levels in the early (28–35 days), mid (42–49 days) and late (56–63 days) periods of plant growth after transplanting in 1999. Means followed by same letter are not significantly ($P > 0.05$) different.

Table 1. Regression analysis of total aphid mortality as influenced by parasitism of *Brevicoryne brassicae* and *Myzus persicae* at early, mid and late stages of plant growth in field trials in 1998 and mid and late stages in 1999.

Dependent variable	Variables in model	Slope (b)	Standard error	t	Probability
(a) Early stage of plant growth (1998)					
Total aphid mortality	*B. brassicae* mortality	0.40	0.11	3.68	0.001
	M. persicae mortality	0.30	0.11	2.73	0.012
(b) Mid stage of plant growth					
1998					
Total aphid mortality	*B. brassicae* mortality	0.57	0.15	3.83	0.001
	M. persicae mortality	0.31	0.19	1.62	0.118
1999					
Total aphid mortality	*B. brassicae* mortality	0.87	0.07	13.1	0.0001
	M. persicae mortality	0.18	0.06	3.28	0.003
(c) Late stage of plant growth					
1998					
Total aphid mortality	*B. brassicae* mortality	0.19	0.15	1.29	0.20
	M. persicae mortality	0.14	0.13	1.08	0.29
1999					
Total aphid mortality	*B. brassicae* mortality	0.84	0.08	11.0	0.0001
	M. persicae mortality	0.17	0.07	2.37	0.03

Table 2. The incidence (%) of parasitoids emerging from *Brevicoryne brassicae* and *Myzus persicae* at the various sampling dates in field trials in 1998 and 1999

Aphid species	Sampling date (DAT)[a]	Parasitoids emerging (%)			
		Diaeretiella rapae		*Aphidius* sp.	
		1998	1999	1998	1999
B. brassicae					
	35	80	95	20	5
	42	86	89	14	11
	49	70	80	30	20
	56	60	67	40	33
	63	53	60	47	40
M. persicae					
	35	71	79	29	21
	42	66	62	34	38
	49	68	64	32	36
	56	64	51	36	49
	63	49	45	51	55

[a] DAT, days after transplanting.

to suggest that the different cultivar characteristics interfered with aphid colonization and infestation. Relatively low aphid infestations were observed on the red cabbage cultivar, Ruby Ball, compared with the green cultivars, Minicole and Derby Day. Although no count was made on the number of landing alates, the very low aphid populations on Ruby Ball relative to the other two cultivars seem to suggest that it was more resistant to initial aphid colonization and infestation. Singh & Ellis (1993) had earlier shown that the red coloration in red leaved cabbages was an important resistance mechanism as an antixenosis factor for incoming alates. The susceptibility of Ruby Ball, however, increased with time and by mid-season it was as susceptible as Minicole. This suggests a time related shift in the effect of this resistance (Radcliffe & Chapman, 1965). Furthermore, time of season played a key role in aphid species composition and distribution. *Brevicoryne brassicae* was associated with cabbage from the early stages of crop development and fed on tender leaves. *Myzus persicae* was not observed in the field until the third sampling occasion and fed mainly on older leaves (35 DAT).

Radcliffe & Chapman (1965) working with both red and green cabbage cultivars, proposed three factors which may explain the seasonal shifts in relative susceptibility of the red cultivars to aphid infestation: (i) their nutritional susceptibility as host plants; (ii) lack of toxic constituents (antibiosis); and (iii) less parasitism or predation. In the present study, it appears that the nutritional susceptibility of Ruby Ball increased with time. However, the present results on aphid parasitism on Ruby Ball do not agree with the above proposals, as aphids on Ruby Ball did not, in most cases, show significantly less parasitism than on the other cultivars. Indeed, aphid mortality as depicted by mummy:aphid ratios was greatest on Ruby Ball in the early stages of plant growth. The most plausible reason for this shift in susceptibility could, therefore, be due to lack of toxic constituents (lack of antibiosis) in Ruby Ball, hence explaining the mid-season breakdown of resistance. Clearly, the alterations in the levels of resistance or susceptibility of the cultivars at different phenological stages influenced the plant–aphid–parasitoid relationship.

The low mummy to aphid ratios on Derby Day compared with the other cultivars could be that due to its high susceptibility, the increase in aphid numbers outstripped that of the parasitoids. This in turn may have reduced parasitoid efficiency. In early–mid stage of 1999, for example, the weekly increase in the *B. brassicae* population on Derby Day was much greater than that of the parasitoid in plots with and without fertilizer. This contrasts sharply with Minicole, where the weekly increase in its population was equal to or less than in the parasitoid (fig. 2). In the partially resistant Minicole, therefore, parasitoid efficiency was not masked, which explains the high mummy to aphid ratios. Thus, it appears that parasitoids could not cope with high aphid numbers, results that are consistent with those of Farid *et al*. (1998) who reported that *D. rapae* was more effective at low aphid densities. It is also possible that mortality due to other environmental factors may be important in this interaction. The present results show a trend towards greater levels of parasitism on cultivars which support lower aphid populations or on which aphid population growth was slower. This supports the hypothesis that any plant condition that lowers the growth rate of an insect herbivore increases the duration of their availability to natural enemies and hence the probability of mortality (Feeny, 1976).

In general, plant growth stage, cultivar and seasonal synchrony of aphid and parasitoids influenced the plant–aphid–parasitoid relationships. In the early stages of crop development, when the plant was more vulnerable to aphid infestation, the antixenotic factors of Ruby Ball complemented the activities of parasitoids by having a significant proportion of dead aphids and favourable mummy to aphid ratios compared with the other cultivars. It is possible, therefore, that the lower number of aphids utilizing Ruby Ball contributed to the favourable ratio. The present study, therefore, provides evidence of a beneficial interaction between plant resistance and biocontrol at this crucial stage of crop development. This beneficial effect generally declined as the plant became older. However, the partially resistant Minicole had a more stable complimentary effect from mid season and was able to maintain a high proportion of dead aphids and favourable mummy to aphid ratios throughout the season. In contrast, Derby Day, because of its high susceptibility, had the lowest rate of parasitism and mummy to aphid ratios throughout the study period.

Various workers (Wyatt, 1970; Starks *et al*., 1972; Ofuya, 1995) have reported complimentary interactions between biological control and host plant resistance since this was first proposed by van Emden & Wearing (1965). The factors that may account for this beneficial interaction have been summarized by van Emden (1991) and Gowling & van Emden (1994) and include, among others, higher pest mortality and increased natural enemy to pest ratios on resistant cultivars and that natural enemies foraging on leaf surfaces dislodge potential prey to a greater extent on partially resistant compared with susceptible host plants. The level of parasitism and the higher mummy to aphid ratios found on Ruby Ball and Minicole at various stages of crop development support these hypotheses.

While cultivar type was crucial in influencing aphid parasitism, it was also evident that differential rates of parasitism occurred between the different aphid species, with *B. brassicae* being more prone to parasitism than *M. persicae*. A number of factors could explain this variance. Firstly, the parasitism levels could be a response to the respective aphid species population densities. Throughout the season, *B. brassicae* populations were generally greater than those of *M. persicae* and this could account for the consistently greater rates of parasitism of the former especially during the early to mid stages of plant growth. It is also possible that *D. rapae* (which had a numerical advantage over the *Aphidius* sp.) showed a preference for *B. brassicae* (Hafez, 1961) hence the differential parasitism observed in the study.

The observed variations in seasonal occurrence of the parasitoids could be another factor for the observed differences in aphid parasitism. In both seasons, *D. rapae* occurred in the field earlier and in greater numbers than *Aphidius* sp. The earlier incidence of *D. rapae* may be important in the suppression of *B. brassicae* in the early stages of crop development when it is the most abundant aphid species. *Brevicoryne brassicae* feeding on cabbage plants is very damaging at this stage as it attacks the newly emerging leaves thereby obstructing head formation (Schepers, 1989). Thus, the compatibility of plant resistance and parasitoid activity becomes particularly relevant at this stage of crop development. The late arrival of *Aphidius* sp. means that numbers of this parasitoid species required to provide effective biological control may develop too late to be of practical value. The lack of synchronization of the aphids and *Aphidius* sp. is the main reason for this inefficiency. The increasing frequency of *Aphidius* sp. relative to that of *D. rapae* may therefore not contribute significantly to seasonal aphid regulation. However, this increase may be important in the long term aphid population regulation. It is evident, therefore, that parasitism was influenced by qualitative differences in cultivar and qualitative and quantitative differences in aphids and parasitoids.

The results reported here are not in full agreement with earlier studies, which showed that enhancing the nutritional status of plants influences herbivore vigour or the subsequent control measures (van Emden & Bashford, 1969; Mohamad & van Emden, 1989). This low response to fertilizer treatments was unexpected, given that van Emden & Bashford (1969) found a positive correlation between *M. persicae* and *B. brassicae* fecundity and leaf nitrogen. In the present study, the fertilizer levels applied above the base level in the field may not have been high enough to influence the above factors. Jansson & Smilowitz (1986) also reported that population growth rate for *M. persicae* on potatoes increased with the rate of nitrogen applied while Loader & Damman (1991) found that larvae of the cabbage white butterfly, *Pieris rapae* (Linnaeus) (Lepidoptera: Pieridae) grew more slowly under low nitrogen conditions and were therefore more susceptible to ground dwelling predators.

The present work has shown that while the parasitoids alone were unable to effect aphid control at the various stages of plant growth, parasitoid activity in combination with partially resistant cultivars could be important in the regulation of aphid populations. Thus, the wide range of plant resistance in cabbage cultivars is an obvious characteristic to exploit in limiting the increase of cruciferous aphids. For example, the antixenosis factors in Ruby Ball can reduce the initial aphid population allowing time for the parasitoids to act. It is also possible that the relatively low population increase for aphids on Minicole in the mid to late stages of plant growth was due to antibiosis factors. The latter is another factor that could be exploited.

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Insects on Palms

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