Annals of Applied Biology ISSN 0003-4746

RESEARCH ARTICLE

Interaction between plant resistance and predation of *Aphis fabae* (Homoptera: Aphididae) by *Coccinella septempunctata* (Coleoptera: Coccinellidae)

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Keywords
Aphis fabae; *Coccinella septempunctata*; plant resistance.

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Received: 19 April 2007; revised version accepted: 12 December 2007.

doi:10.1111/j.1744-7348.2008.00220.x

Abstract

We investigated the compatibility of host plant resistance to the black bean aphid in the faba bean crop with the use of the predatory ladybird beetle for biological control under laboratory and greenhouse conditions. Greenhouse experiments indicated that apteriform *Aphis fabae* reproduced on *Vicia faba major* (susceptible) and on 79S4 (partially resistant) cultivars at different rates. During the entire experimental period, aphids built up higher populations on *V. faba major* than on 79S4 cultivar. Aphid numbers on 79S4 were about 37% of those on *V. faba major* after 14 days. Release of a newly hatched *Coccinella septempunctata* larva onto each plant significantly reduced aphid density to 32.8% and 57.2% on *V. faba major* and 79S4 on day 14, respectively. Partial resistance combined with predation was more effective in lessening aphid numbers on faba bean than either the predator or the plant resistance alone. Laboratory tests showed that prey, *A. fabae*, raised on susceptible cultivar was more suitable for the predator as food source, enhancing the development rate and fecundity than aphids fed on the partially resistant cultivar. Consumption of aphids reared on susceptible cultivar significantly increased the female fecundity and fertility of *C. septempunctata* by 37.7% and 33.2%, respectively, more than those fed with aphids from partially resistant cultivar. Pre-oviposition time was shortened by 4.5 days, and oviposition period was extended by 11.4 days. Feeding the predator on aphids from the partially resistant cultivar prolonged the embryonic larval developmental time and the time required from egg laying to adult emergence by 19.8, 10.1 and 32.5 h, respectively. Adult longevity was not influenced by the aphid source. The results are discussed in relation to the compatible utilisation of host plant resistance and biological control in the integrated management of aphids.

Introduction

Faba bean, *Vicia faba* L., is one of the oldest cultivated field crops. It constitutes a major protein source for human populations in many countries (FAO, 1995). The total area seeded to this crop and the annual production are considerably declining worldwide as a result of biotic and abiotic stress factors (Bond *et al*., 1994). The black bean aphid, *Aphis fabae* Scopoli, is the most destructive pest of faba bean around the world. This aphid species has become a major concern for faba bean growers in Jordan because it decreases yield severely under most conditions.

The high damage potential and unpredictable infestations by *A. fabae* often lead to extensive routine pesticide applications. This approach is somewhat effective. However, an escalating awareness of the economic, environmental and health costs associated with the broad use of chemicals has led to the search for alternative methods of pest management. In the context of sustainable pest management for aphids, host plant resistance and biological control seem to be the most suitable control methods. Some faba bean cultivars exhibited partial resistance to *A. fabae*, mainly with antibiosis effects (Bond & Lowe, 1975; Morvan, 1987; Shannag & Obeidat, 2006*a*). The mechanisms underlying the partial resistance of 79S4 to *A. fabae* is not known but the large effects on herbivores offer potential for resistance breeding. Although the population growth rate of *A. fabae* is low on the most resistant cultivars, the black bean aphid will still exceed the economic damage threshold if left undisturbed. Therefore, faba bean growers will remain dependent on other methods of pest control such as the use of natural enemies.

Biological control is an essential component in integrated management of aphids. Predatory ladybird beetles in the taxa of Coccinellidae are important natural enemies and often linked to biological control of aphids (Frazer, 1988). The seven-spot ladybird beetle, *Coccinella septempunctata*, is considered to be a talented predator with high biological aggressiveness, high biotic potential and great voracity. It feeds on a variety of insects during its biological cycle and occurs in several crops of economic interest (Frazer, 1988). However, this aphidophagous predator is usually found at sites where aphids are abundant (Arakaki, 1992; Winder *et al.*, 1994); thus, the abundance peak of predatory coccinellids is generally delayed in comparison with that of the prey. The impact of predator on aphid populations often becomes effective only when peak of aphid numbers is declining. Biological control and host plant resistance are often combined in integrated pest management programmes and are classically considered to be compatible, resulting in suppression of aphid population below control level with little influence on the environment (Moraes *et al.*, 2004).

As the simultaneous use of resistant plants and biological control can produce different outcomes with respect to pest management (Hare, 1992), it is of importance to verify the relationships between resistant plants, herbivores and natural enemies as a first step towards a sustainable pest management programme. Literature reviews on the third trophic level indicate that resistant plant can affect natural enemies directly by modifying their behaviour or indirectly by changing the nutritional value of the prey and/or the host (van Emden, 1995; Thomas & Waage, 1996). The impact of this interaction could be negative because of the incompatibility between the two control methods (Obrycki & Tauber, 1984) or positive through the cumulative decreasing effects on aphid density (Cortesero *et al.*, 2000; Messina & Sorenson, 2001; Kennedy, 2003). Recognition of these tritrophic effects has led to repeated calls for better integration of efforts to breed resistant crops and to implement biological control (Cortesero *et al.*, 2000).

The present study was performed to determine the combined effects of predation and plant resistance on *A. fabae* populations and to verify the selected biological characteristics of the generalist *C. septempunctata* predator feeding on black bean aphids obtained from two faba bean cultivars with different levels of resistance.

Materials and methods

Stock cultures

Black bean aphids, *A. fabae*, were gathered from an infested faba bean field in Irbid district, Jordan. Aphids were reared on faba bean plants, *Vicia faba minor*, in an insect room at a temperature of 27 ± 3°C, relative humidity (RH) of 63 ± 17% and light regime of 16L:8D.

Two other *A. fabae* colonies were then established on a partially resistant (79S4) and susceptible (*V. faba major*) cultivars for all tests for at least 30 generations. Each cultivar was planted in 20-cm diameter pots at a rate of three plants per pot under greenhouse conditions. Old and senescing plants were replaced with young ones to provide aphid colonies with a continuous suitable food supply.

The culture of ladybird beetles was derived from adult *C. septempunctata* collected from Irbid locality, Jordan. Beetles were kept in the laboratory at a temperature of 27 ± 3°C, 70 ± 10% RH and 1000 Lux at 16L:8D photoperiod. Two stock cultures of the predator were established for all experiments according to the procedure described by Pinsdorf (1977). Predator in the first culture was fed with *A. fabae* reared on the susceptible faba bean cultivar (*V. faba major)*, while the second one was nourished with aphids from the partially resistant cultivar (79S4). Each stock culture was raised for three generations.

Efficiency of predation in reducing *Aphis fabae* on susceptible and partially resistant cultivars

The combined effect of predation and plant resistance on aphid populations was assessed under greenhouse conditions. Seeds of faba bean cultivar 79S4 were provided by International Center for Agricultural Research in the Dry Areas (ICARDA) and seeds of *V. faba major* cultivar were obtained from the commercial market. Seeds of both cultivars were germinated in seed trays (40 × 40 × 5 cm) filled with peat moss under greenhouse conditions. Plants were transferred by the time two to three true leaves appeared on individual plastic pots (20-cm diameter) filled with fine loam soil. Plants were irrigated every other day and fertilised with diammonium phosphate shortly after transplanting. Each plant received the same amount of water and fertiliser.

On day 14, following transplanting, each pot was enclosed with a cylindrical cage made of metal wire (60 cm long and 18 cm in diameter) covered with mesh cloth. Four days later, plants were examined and any arthropods present were removed. Fine, moist camel-hair brush was used to infest plants with 2-day-old adult aphid raised on relevant cultivar at a rate of five aphids per plant. One newly hatched larva of *C. septempunctata* was introduced into each plant on day 5 after aphid infestations.

The treatments were as follows: (a) 79S4 plants with aphids; (b) 79S4 with aphids and *C. septempunctata*; (c) *V. faba major* with aphids and (d) *V. faba major* with aphids and *C. septempunctata*. Each treatment consisted of 10 pots, each one represents a replicate, and all treatments were arranged in a randomised complete block design under greenhouse conditions (26 ± 4°C and 65 ± 5% RH). Aphid density was monitored at 3-day intervals till the predator larvae became a prepupa.

Host plant and predator reproduction

Two experiments were conducted to determine the effect of bean cultivar on the suitability of *A. fabae* as prey for *C. septempunctata* in a growth chamber at 27 ± 3°C, 65 ± 5% RH and 16L:8D photoperiod regime. The first and second experiments employed predator beetles reared on *A. fabae* from susceptible cultivar and from partially resistant cultivar, respectively. Two pairs of 1-day-old ladybird adults (two males and two females) that were held at least for one generation on *A. fabae* from partially resistant or from susceptible faba bean cultivars were confined in a plastic container (18 × 13 × 8 cm) covered with transparent nylon fabric. Twenty containers were used for each treatment, each representing one replication. Predators in each container were provided daily with ample aphids from the relevant cultivar.

Small pieces of black plastic sheet were added to each container to serve as favourable oviposition sites. These oviposition sheets were replaced daily, and the number of eggs laid per container was recorded. Eggs were then transferred to another container and held until eclosion. Lifetime female fecundity was calculated as the sum of daily oviposition divided by two. Oviposition rate was computed at 3-day intervals. Female fertility was determined by the percentage of the eggs that hatched. Time needed for egg to hatch was also recorded at 3-h intervals.

Host plant, prey suitability and predator development

Time required for larval and pupal development was recorded at 3-h intervals starting at 08:00 h. Five 1-day-old larvae were placed in a plastic container and supplied with ample aphids reared on relevant faba bean cultivar. *C. septempunctata* fed aphids from 79S4 cultivar and from *V. faba major* cultivar were employed in this study using 20 containers for each treatment. No cannibalism was observed during the experiment, presumably because of plenty of food supply. Temperatures used in laboratory studies were representative to the field prevailing environmental conditions.

Data from all experiments were subjected to analysis of variance using MSTATC program (Michigan State University, East Lansing, MI, USA). Means were compared using Fisher's least significant differences test at a 0.05 probability level.

Results

Predation on *Aphis fabae* grown on two faba bean cultivars

Aphid density varied significantly in both faba bean cultivars with different levels of resistance (Table 1). When predator larvae were excluded from aphid-infested plants, both cultivars showed a steady increase in aphid population over the experimental period. However, the number of aphids on susceptible *V. faba major* was significantly higher than those on partially resistant cultivar (79S4) at all sampling dates. On day 14, aphid population on partially resistant cultivar was 36.8% of that on susceptible cultivar.

When *C. septempunctata* larva was introduced to aphid-infested plants, the aphid population significantly decreased in both cultivars in comparison with predator-free cultivars. A single predator larva reduced aphid density up to 32.8% and 57.2% in susceptible and partially resistant cultivars, respectively. On day 14, each ladybird larva consumed approximately 424 aphids developed on susceptible plant compared with 272 aphids on partially resistant 79S4. Predator larvae pupated 1 day earlier on susceptible cultivar than on partially resistant cultivar (Table 1).

This experiment clarified that the average infestation rate of aphids on partially resistant cultivar having a predator larva was significantly lower than that on susceptible cultivar. Partially resistant cultivar unaccompanied with predator has the potential to reduce aphid populations more than that of aphid-infested susceptible cultivar. With respect to the number of aphids on the susceptible *V. faba major*, partially resistant cultivar reduced aphid

Table 1 Mean numbers of *Aphis fabae* on susceptible *Vicia faba major* and partially resistant 79S4 cultivars of faba bean with and without predation of *Coccinella septempunctata* under greenhouse conditions[a]

Treatment	Days After Infestation 8	11	14	15
Vicia faba major + aphid	251.0 ± 20.3 a (100%)	645.8 ± 31.8 a (100%)	1292.9 ± 50.4 a (100%)	–
Vicia faba major + aphid + predator	205.8 ± 18.4 b (82.0%)	250.5 ± 21.7 b (38.8%)	868.9 ± 36.5 b (67.2%)	–
79S4 + aphid	130.2 ± 25.1 c (51.9%)	346.2 ± 25.1 c (53.6)	476.4 ± 31.8 c (36.8%)	633.3 ± 29.0 a
79S4 + aphid + predator	70.5 ± 13.7 d (28.1%)	186.2 ± 17.4 d (28.8%)	204.4 ± 18.6 d (15.8%)	239.4 ± 19.9 b

[a]Means within each column followed by the same letter(s) are not significantly different at 0.05. Each value represents mean ± SE. Percentages in parentheses represent relative values to aphids on *Vicia faba major* within each sampling date.

density to 63.2%, while *V. faba major* with predator reduced aphid population to 32.8% (Table 1).

Reproduction of *C. septempunctata* feeding on *Aphis fabae* grown on two faba bean cultivars

The pre-oviposition period of female predator fed with aphids from partially resistant cultivar extended 4.5 days in comparison with those from susceptible cultivar (Table 2). The oviposition period of ladybird reared on aphids from susceptible cultivar was 11.4 days longer than that of those fed with aphids from partially resistant cultivar.

Female oviposition followed a similar pattern, when predator adults were fed with aphids from susceptible or partially resistant cultivars (Fig. 1). The average number of deposited eggs by predator fed with aphids from susceptible cultivar increased during the first month reaching its maximum on day 21 (mean = 169.2 egg/female/3 days period). In contrast, the maximum oviposition rate for predator supplied with aphids from partially resistant cultivar was achieved on day 33 (mean = 126.8 eggs). Thereafter, oviposition rates decreased steadily in both treatments until adult's death. Differences in the reproductive rate of the predator were observed 3 weeks after oviposition. Feeding predator with aphids obtained from susceptible cultivar considerably enhanced egg depositing compared with those obtained from partially resistant cultivar. No significant differences were recorded on days 30, 33, 60, 63 and 66 of oviposition. In both treatments, oviposition continued until the adult's death.

The reproductive rate (number of eggs/female/day) did not differ significantly between the two treatments; however, predator nourished with aphids from susceptible cultivar deposited greater number of eggs (37.7%) during the lifespan than those fed with aphids from partially resistant cultivar (Table 2). In addition, the fertility of the predator was altered by prey source. The fertile eggs laid by predator fed with aphids from partially resistant cultivar were 33.2% lower than those fed with aphids from susceptible cultivar. Adults of *C. septempunctata* maintained on aphids from susceptible cultivar survived a week longer than individuals nourished on aphids from partially resistant cultivar.

Development time of *C. septempunctata* feeding on aphids kept on both cultivars

The mean time required for eggs hatching was significantly shorter for predators fed with aphids from susceptible cultivar than for those from partially resistant cultivar (Table 3). The developmental time of first and third larval instars provided with aphids from partially resistant cultivar took about 2 and 4 h longer, respectively, compared with the relevant instars in other treatment. The

Table 2 Reproduction of *Coccinella septempunctata* females when fed on *Aphis fabae* reared on two faba bean cultivars with different levels of resistance[a]

Cultivars	Pre-oviposition Period (days)	Oviposition Period (days)	Longevity (days)	Number of Eggs/ Female/Day	Fecundity/ Female	Fertile Eggs/ Female
Vicia faba major (susceptible)	11.20 ± 1.36 a	49.50 ± 5.56 a	60.70 ± 6.93 a	40.20 ± 6.27 a	1972.20 ± 329.71 a	1407.20 ± 234.10 a
79S4 (partially resistant)	15.70 ± 1.13 b	38.10 ± 4.37 b	53.80 ± 7.09 a	36.00 ± 4.82 a	1228.10 ± 213.02 b	940.0 ± 172.32 b

[a]Means within each column followed by the same letter(s) are not significantly different ($P \leq 0.05$). Each value represents mean ± SE.

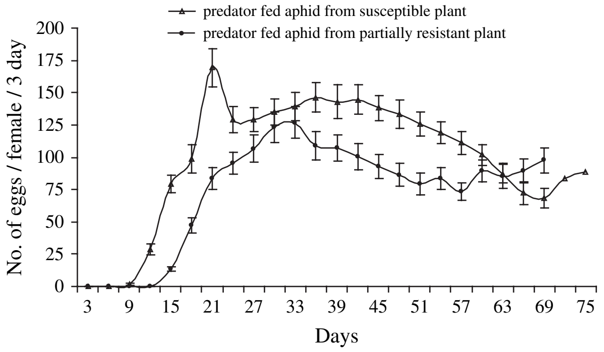

Figure 1 Mean number of eggs per *Coccinella septempunctata* female at 3-day intervals fed on *Aphis fabae* from susceptible *Vicia faba major* and partially resistant 79S4 faba bean cultivars.

average developmental time for the second and fourth instars was similar in both treatments (Table 3). Larvae consuming aphids from susceptible cultivar required significantly shorter time to complete their development (average of 161.35 h) than individuals fed with aphids from partially resistant cultivar (average of 171.5 h). Duration of the pupal stage, however, did not differ between treatments. Embryonic and postembryonic developments for *C. septempunctata* kept on aphids from partially resistant cultivar required more time (11.2%) than those from *V. faba major*.

Discussion

Resistant plants may influence the efficacy of natural enemies directly and indirectly by altering prey suitability or the host finding success (van Emden, 1995; Obrycki & Kring, 1998; Kennedy, 2003). However, coccinellids often accept the unsuitable prey as source of energy but with detrimental effects on their development, reproduction and/or survival (Hodek, 1956; Obrycki *et al.*, 1997). Therefore, suitability does differ from prey acceptability for the predator.

The results of our study indicate that *A. fabae* reared on susceptible and partially resistant cultivars represents a suitable prey for *C. septempunctata*, but they are not of equal quality. A lower suitability of aphids grown on partially resistant cultivar caused only a slight decrease in predator's development and reproduction. The mechanisms underlying the reduction in biological performance of predator on aphids from partially resistant cultivar were not identified in this study. However, in a previous study, we found an indication that *C. septempunctata* larvae appreciably devoured more *A. fabae* from partially resistant 79S4 coinciding with lower conversion efficiency of ingested food than those on aphids from susceptible

Table 3 Mean development times of different immature stages of *Coccinella septempunctata* fed on *Aphis fabae* from two faba bean cultivars with different levels of resistance[a]

	Development Time (h)							Total Period
Cultivars	Eggs	First Instar	Second Instar	Third Instar	Fourth Instar	Total Larval Development	Pupa	for Immature Stages (h)
Vicia faba major (susceptible)	46.20 ± 3.37 a	30.20 ± 0.18 a	31.20 ± 0.31 a	35.00 ± 1.59 a	64.95 ± 3.89 a	161.40 ± 3.87 a	81.6 ± 2.71 a	289.20 ± 5.11 a
79S4 (partially resistant)	66.00 ± 2.46 b	32.25 ± 1.14 b	31.45 ± 0.33 a	39.30 ± 1.62 b	68.50 ± 3.67 a	171.50 ± 4.21 b	84.20 ± 2.83 a	321.70 ± 7.45 b

[a]Means within each column followed by the same letter(s) are not significantly different ($P \leq 0.05$). Each value represents mean ± SE.

V. faba major (Shannag & Obeidat, 2006*b*). Thus, we conclude that the negative effect of partially resistant cultivar on predator is not credited to predation rate but most likely because of lack of the dietary balance and/or presence of plant-derived toxins in prey.

Literature dealing with the combined use of host plant resistance and biological control give several examples of the negative influence of resistant plants on natural enemies. Stadler & Mackaur (1996) stated that great modification in aphid quality occurring under resistance conditions could be detrimental to natural enemies. The nutritional value of the same aphid species may vary from one host to another too (Smith, 1978). Mobile stages of *Tetranychus urticae* were found to differ in suitability as food source for *Phytoseiulus persimilis* on different gerbera cultivar, as they contain undigested leaf material in their gut (De Moraes & McMurtry, 1987). *Aphis gossypii* accumulated greater fatty acid while feeding on high gossypol cotton cultivar than those on low gossypol-containing cultivars. This may make them suitable as prey for predator *Propylaea japonica*, enhancing larval developmental period and adult weight (Du *et al*., 2004). Predation on suboptimal aphids has been reported to harm the development and fecundity of several species of coccinellids and chrysopids (Obrycki & Orr, 1990; Hodek, 1993; Albuquerque *et al*., 1997; Evans *et al*., 1999).

Furthermore, toxic allelochemicals occurring in plants are often sequestered in the herbivores' haemolymph, and their presence can negatively affect the biology of natural enemies (Schaffner *et al*., 1994; van Emden, 1995). *Aphis sambuci* prey impaired both larval and adult fitness of *C. septempunctata* through the passage of plant glycoside (sambunigrin) up the trophic pyramid (Hodek, 1956). Transgenetic potatoes expressing the anti-aphid plant protein (snowdrop lectin, Galanthus nivalis agglutinin) adversely influenced the longevity and reproduction of natural enemy, *Adalia bipunctata*, through aphids *Myzus persicae* in its food chain (Birch *et al*., 1999).

Integration of partially resistant cultivar and *C. septempunctata* augmented aphid control more than either varietal resistance alone or predator on susceptible cultivar. Various works indicated that the two management strategies act independently, so that their combined effects are strictly additive. Khalghani (1994) found that the relative reduction in *Sitobion avenae* because of predation by *C. septempunctata* was greater on wheat resistant genotypes. Also, the interaction between resistant sorghum genotypes and biological control with *Chrysoperla externa* was positive and permitted 80% control of *Schizaphis graminum* (Figueira & Fernando, 2004). Cumulative effect of the two management tactics have been recorded by Kartohardjono & Heinrichs (1984) for *Nilaparvata lugens* and several predators on resistant rice varieties and *Diuraphis noxia* and *Chrysoperla plorabunda* on resistant wheat plants (Messina & Sorenson, 2001).

Despite the fact that plant resistance and nutritional value of prey are detrimental to natural enemies (Stadler & Mackaur, 1996), our results illustrated that partially resistant cultivar to aphid does not entirely prohibit *C. septempunctata* from a nutritional standpoint. Ladybird predator accepts and utilises aphids from both cultivars as a food source, but aphids kept on partially resistant cultivar harmed, to some extent, the development and reproduction of the predator. Because the combined effect is accumulative, plant resistance and natural enemies would continue to play a role in naturally occurring and human-assisted biological control. The function of these natural regulation factors in insect pest management can be greatly enhanced with a return to the conceptual framework of integrated controls. Furthermore, a better understanding of resistance mechanisms would be of great significance before determining how the mode of resistance might affect the compatibility of plant resistance and natural enemies in the control of *A. fabae*.

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