Ecological Entomology (2008), **33**, 45–52 DOI: 10.1111/j.1365-2311.2007.00933.x

Bottom-up cascading effects in a tritrophic system: interactions between plant quality and host-parasitoid immune responses

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Abstract. 1. Little is known about underlying mechanisms by which plants indirectly affect parasitism success in hymenopteran endoparasitoids. The hypothesis that *host-plant effects can challenge the innate immune system of an insect host* was experimentally tested in this study using a model tritrophic, crucifer – lepidopteran [*Plutella xylostella* (L.)] – parasitoid [*Cotesia plutellae* (Kurdjumov)], system.

2. The effects of host-plant suitability on herbivore performance and parasitism were examined. The bottom-up effect of plant suitability on host-parasitoid immune responses was then evaluated using measures of cellular and humoral effectors.

3. Host-plant quality showed a significant effect on the encapsulation response of *P. xylostella* to first instar but not to second instar parasitoid larvae. Encapsulation was never sufficient to prevent parasitoid emergence.

4. Poor host-plant suitability suppressed phenoloxidase activity in the absence of the parasitoid. The suppressive effect of *C. plutellae* on phenoloxidase activity was much greater and no plant effects were detectable after insects had been parasitized.

5. Despite strong plant effects on parasitism, those on immune effectors of the host were transitory or overwhelmed by the effect of the parasitoid.

6. These results demonstrated that plant-mediated variation in parasitism success by *C. plutellae* were not as a result of plant nutritional status or other attributes affecting the immune function of *P. xylostella*, nor to host-plant effects on superparasitism.

7. In these experiments, *P. xylostella* was a fully permissive host to *C. plutellae* and host-plant-mediated effects on the innate immune response appeared to play no part in parasitoid survival within hosts.

Key words. *Cotesia*, crucifer, diamondback moth, immunity, permissive host, *Plutella*, tritrophic.

Introduction

Ecological approaches to pest management, integrating technologies such as host-plant resistance and biological control, have the potential to be far more sustainable than chemical control (Verkerk & Wright, 1996; Lewis *et al.*, 1997; Verkerk *et al.*, 1998; Thomas, 1999). However, plants, herbivores and natural enemies are tightly entwined in ecological systems (Dicke, 1999; Walker & Jones, 2001) and in different tritrophic systems interactions between plants and natural enemies can be antagonistic, additive or synergistic (Wright & Verkerk, 1995; Gange & Brown, 1997; Tscharntke & Hawkins, 2002).

The role of ecological processes, such as bottom-up and top-down forces on herbivore populations, is often considered to be specific to particular ecosystems (Power, 1992), the bottom-up effects of plants being more effective in trophic interactions in terrestrial systems (Harrison & Cappuccino, 1995; Stiling & Rossi, 1997; Ostfeld & Keesing, 2000). The cascading effects of bottom-up forces (Hunter & Price, 1992; Teder & Tammaru, 2002) can be detected as indirect effects of heterogeneity (i.e. differences in species richness, abundance, productivity and

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quality) of plants on third trophic levels through herbivorous insects (Kagata & Ohgushi, 2006). However, variation in host-plant characteristics may have differential effects on a herbivore and its associated natural enemies (Teder & Tammaru, 2002). For example, plant quality can influence the higher trophic levels in the same direction (Barbosa *et al.*, 1991; Zvereva & Rank, 2003; Kagata *et al.*, 2005), such that highly nutritional (or less defensive) plants increase the performance of both the insect herbivores and their natural enemies (Kagata & Ohgushi, 2006). Other studies have shown opposite effects of plant quality on herbivorous insects and their natural enemies (Karowe & Schoonhoven, 1992; Holton *et al.*, 2003), for example, nutrient deficiencies and stresses can reduce general immunocompetence in insects against natural enemies (Brey, 1994; Suwanchaichinda & Paskewitz, 1998; Vass & Napi, 1998; Rantala *et al.*, 2003).

Variation in plant quality can influence the preference and performance of parasitoids in several mechanisms (Hunter, 2003). One way in which endoparasitoids may benefit from tritrophic interactions involving partially-resistant plants is via effects on their host's immune system (Price, 1986; Godfray, 1994; Thomas & Waage, 1996). The insect innate immune reaction involves humoral responses, such as synthesis of antimicrobial peptides and the prophenoloxidase activation system, and cellular responses, such as phagocytosis and encapsulation; overall immunity resulting from a complex interplay of the two systems (Bulet *et al.*, 1999; Lavine & Strand, 2002; Cerenius & Soderhall, 2004). The principal immune defences against endoparasitoids are encapsulation and melanization. It has been suggested that the success of the encapsulation reaction with endoparasitoids depends on the vigour of the herbivore (Siva-Jothy & Thompson, 2002). This can be reduced by hostplant-induced stresses, such as poor nutrition, starvation or a high level of allelochemicals (Blumberg, 1997; Souissi & Le Ru, 1998; Turlings & Benrey, 1998).

Here using a model tritrophic (crucifer-lepidopteran-parasitoid), experimental system, the objective is to test the hypothesis that host-plant effects can challenge the innate immune system of an insect host. *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae) is a solitary, koinobiont, larval endoparasitoid of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae), a specialist herbivore on crucifers (Talekar & Shelton, 1993). This parasitoid species is generally regarded as being highly specific to *P. xylostella.* There is evidence that it can parasitize and develop in some other lepidopteran hosts in the laboratory (Cameron *et al.*, 1997) but this might be an overestimation of host range in the field. Previous studies have shown plant-mediated variation in parasitism success by *C. plutellae* (Talekar & Yang, 1991; Verkerk & Wright, 1994b; Karimzadeh *et al.*, 2004); however, the mechanisms by which host-plant variation influence parasitism success of the parasitoid is unclear. Using measures of the two principal immune effectors against parasitoids, encapsulation and phenoloxidase activity, it was shown that despite strong plant effects on parasitism, those on immune effectors of the host were transitory or were overwhelmed by the effect of the parasitoid. The varied levels of parasitism of *P. xylostella* mediated by plant quality are therefore likely to be an outcome of behavioural and fitness factors rather than a reduced immune challenge. The results are discussed in the aspects of plant-mediated variation in parasitism, host permissiveness and its ecological consequences in field populations.

Materials and methods

Plants and insects

Chinese cabbage, *Brassica pekinensis* cv. Tip Top (Chiltern Seeds, Ulverston, U.K.), common cabbage, *B. oleracea* var. *capitata* cvs. Wheelers Imperial and Red Drumhead (Suttons Seeds, Devon, U.K.) and cauliflower, *B. oleracea* var. *botrytis* cv. Early Green Glazed (Plant Introduction 234 599; Northeast Regional Plant Introduction Station, Geneva, U.S.A.) were grown under glasshouse conditions (25 ± 5 °C and LD 16:8 h) without the application of any pesticide. Four-week-old Chinese cabbage, 15-week-old common cabbages and 12-week-old cauliflower were used as representatives of high-, intermediate- and poor-quality host plants for *P. xylostella*, respectively (Lin *et al.*, 1984; Verkerk & Wright, 1994a). *Plutella xylostella* (ROTH, laboratory strain) and *C. plutellae* were obtained from Rothamsted Research (Harpenden, U.K.). Insects were cultured on Chinese cabbage as described previously (Karimzadeh *et al.*, 2004).

Herbivore performance

Batches of 10 second instar *P. xylostella* larvae were placed on leaf discs (4.8 cm dia.) within individual Petri dishes (5 cm dia.) containing a moistened filter paper. Leaf discs were cut from randomly selected leaves on different plants for each plant group used in experiments. To prevent starvation of larvae, the leaf discs were replaced every 24 h. Pupae were transferred to Petri dishes and kept until eclosion. The experiments were conducted under controlled environment conditions (25 ± 2 °C, 70 ± 10% RH and LD 16:8 h). Life stage and mortality were recorded every 24 h until all the insects had either died or emerged as adults. The mean time from oviposition to pupation and eclosion, and the survival percentage was calculated. Each treatment was replicated six times. This experiment was only carried out with two host-plant types, Chinese cabbage and Wheelers Imperial.

Parasitism and encapsulation

Two different methods were used to examine parasitism of *P. xylostella* larvae that were reared on different host plants. (i) A multiple oviposition method, where a single, mated 3-day-old adult female *C. plutellae* was placed for 1 h in a plastic Petri dish (5 cm dia.) containing 10 early third instar larvae of *P. xylostella*. Each treatment was replicated 10 times. This experiment was only carried out with two host-plant types, Chinese cabbage and Wheelers Imperial. (ii) A single oviposition method, where one early third instar larva of *P. xylostella* was

exposed to a single, mated 3-day-old female of *C. plutellae*, which was removed immediately after it had made a single oviposition. Each treatment was replicated 50 times using a fresh parasitoid each time. This experiment was carried out with all the host-plant types.

The multiple oviposition method was used to examine the plant-mediated effects on the proportion of the host larvae parasitized by *C. plutellae*, and the frequency of superparasitism and encapsulation in parasitized host larvae. However, using this method the possible reason(s) for differences in the levels of parasitism can not be clarified; as it may be because of the different proportions of parasitized hosts, the different number of parasitoid eggs laid per host (superparasitism effects), or different host's encapsulation abilities. The single oviposition method was used to eliminate any superparasitism effect on host's encapsulation ability, and in turn, on parasitism success, and to expose the direct plant effects on host immune functions.

In both methods, *P. xylostella* larvae were then allowed to feed for 72 h on the same plant type on which they had fed before parasitism under standard controlled environment conditions. The *P. xylostella* larvae were then dissected and the parasite stage(s) present determined (Lim, 1982) and a visual estimation of the encapsulation proportion of each larva was made using a 10% incremental scale (Cotter & Wilson, 2002).

The single oviposition method was used in two further experiments using all the host-plant types. In one experiment, the host larvae were dissected 5 days after parasitism (when *C. plutellae* larva was in the second instar stage) to observe possible alterations of the encapsulation proportion compared with 3 days after parasitism (when *C. plutellae* larva was in the late first instar stage). In the other experiment, the larvae were reared until the host had pupated or the parasitoid cocoon had formed to determine the effect of food plants on parasitism success. In both the experiments, each treatment was replicated 50 times using a fresh parasitoid each time.

To examine the effects of the parasitoid egg load (superparasitism) on the encapsulation ability of *P. xylostella* larvae, five early fourth instar *P. xylostella* larvae reared on Chinese cabbage were exposed to batches of five or 20 mated 3-day-old female *C. plutellae* for 1 h. The host larvae were then maintained on Chinese cabbage and dissected after 4 days. Each treatment was replicated 10 times.

Phenoloxidase assay

Batches of 10, 2-day-old unparasitised second instar *P. xylostella* larvae were placed in individual Petri dishes (5 cm diameter.) and reared on leaf discs from the appropriate host plant (as described above) until the late fourth instar larval stage but prior to cessation of feeding. For studies on parasitized larvae, the single oviposition method was used and *P. xylostella* larvae were then reared on leaf discs as above until the late fourth instar stage. Phenoloxidase (PO) activity was determined in haemolymph samples (2 μl) collected from late fourth instar larvae of *P. xylostella* by cutting off one or more prolegs and drawing up exuded haemolymph bubbles with a pulled 1-μl microcapillary tube. The haemolymph sample was quickly added to phosphate-buffered saline (PBS), pH 7.4 (30 μl), in a 0.5 ml microcentrifuge tube on ice and immediately frozen to −80 °C to disrupt haemocyte membranes. Frozen samples were then thawed to 4 °C and centrifuged at 12 000 *g* at 4 °C for 10 min. An aliquot (2 μl) of the supernatant was taken for protein assay (Bradford, 1976). A second aliquot (20 μl) was incubated for 20 min at 20 °C to activate PO activity, which was then assayed spectrophotometrically using 1 ml of 3,4-D-L-dihydroxyphenylalanine (10 mM) in PBS as a substrate (Siva-Jothy & Thompson, 2002). Negative controls contained 10% (w/v) 1-phenyl-2-thiourea, a known inhibitor of PO (Reeson *et al.*, 1998). Each treatment was replicated 10 times. This experiment was carried out with all the host-plant types.

Statistical analyses

The single and multiple oviposition data were analysed independently. Differences in the levels of parasitism and survival rates between host-plant types were analysed using logistic analysis of deviance (binomial error). The developmental periods were analysed using nested ANOVA (except pupal periods, which were analysed using Student's *t*-test). The number of parasitoid larvae per host larva was compared by analysis of deviance (Poisson error). Encapsulation proportions were arcsine transformed and analysed by one-way ANOVA (for single oviposition data) and nested ANOVA (for multiple oviposition data). PO data were analysed using one-way ANOVA. Pairwise comparisons were performed using Student's *t*-test (Crawley, 2002). All statistical analyses were completed in S-Plus 6.1 (Insightful, Seattle, WA, U.S.A.).

Results

Herbivore performance

The egg-pupa ($F_{1,10} = 244.18$, $P < 0.001$) and egg-adult ($F_{1,10} = 257.47$, $P < 0.001$) development times for *P. xylostella* on common cabbage were significantly greater than on Chinese cabbage (Table 1). There was no significant difference for pupal period ($t_{10} = -0.953$, $P = 0.37$) or survival rate ($F_{1,10} = 1.4833$, $P = 0.22$) between treatments.

Parasitism and encapsulation

Cotesia plutellae eggs were not encapsulated in any of the experiments. Parasitoid larvae were encapsulated at the first or early second larval instar stage. In the multiple oviposition experiment, the proportion of *P. xylostella* larvae parasitised by *C. plutellae* was significantly greater ($F_{1,18} = 9.2923$, $P < 0.01$) when the host was on common cabbage compared with Chinese cabbage (Table 1). The number of *C. plutellae* larvae per parasitised *P. xylostella* larva feeding on common cabbage was significantly greater (d.f. = 172; *z-value* = 2.418; $P < 0.05$) than on Chinese cabbage. *Plutella xylostella* larvae reared on Chinese cabbage showed a significantly greater ($F_{1,18} = 7.5165, P < 0.05$)

Table 1. Host-plant effects on performance, parasitism (by *C. plutellae*) and encapsulation ability of *P. xylostella*.

	Parameters measured						
	Host performance (mean ± SE; $n = 6$)				Host–parasitoid interaction (mean; $n = 10$)		
	Developmental periods						
Host plant*	Egg–pupation (days)	Egg–eclosion (days)	Pupal (days)	Survival (%)†	Parasitism (%)‡	Superparasitism (rate)	Encapsulation (proportion)§
TT	10.0 ± 0.2	15.4 ± 0.2	5.5 ± 0.2	76.7 ± 7.1	56.9	1.02	0.65
WI	18.1 ± 0.5	23.8 ± 0.5	5.7 ± 0.1	66.7 ± 4.9	88.5	1.43	0.35
P	<0.001	<0.001	0.37	0.22	<0.01	<0.05	<0.05

*The abbreviations TT and WI are Chinese cabbage cv. Tip Top and common cabbage cv. Wheelers Imperial, respectively.
†Survival was measured from second instar larva to adult emergence.
‡Parasitism and superparasitism rates denote the parasitised host larvae and the number of parasitoid larvae per parasitised host, respectively.
§The encapsulation ability of host was measured against late first instar parasitoid larvae 3 days after oviposition in multi-oviposition experiment.

encapsulation proportion compared with larvae reared on common cabbage.

In the single oviposition experiment, at 3 days after parasitoid oviposition, there was a significant ($F_{3,155} = 111.45$, $P < 0.001$) difference in the mean encapsulation proportion of late first instar parasitoid larvae between treatments (Table 2). The encapsulation proportion was greatest (0.28), intermediate (0.08 and 0.04) and almost zero (0.01) in hosts feeding on Chinese cabbage, common cabbages and cauliflower, respectively. After 5 days the encapsulation proportion of second instar parasitoid larvae had fallen to zero for all treatments apart from Chinese cabbage ($F_{3,169} = 6.4508$, $P < 0.001$) where it was extremely low (0.01). When parasitised larvae reared until parasitoid cocoon formation, there was 100% parasitism success in all treatments ($F_{3,36} = 6.338 \times 10^{-6}$, $P = 1.0$; Table 2).

In the superparasitism experiment, at 4 days after oviposition, there were two categories of *C. plutellae* larvae in *P. xylostella* larvae (Table 3): (i) late first instar parasitoid larvae that were alive, active and not (0%) encapsulated (predominant larvae), and (ii) early first instar parasitoid larvae that were dead and fully (100 %) encapsulated (non-predominant larvae). There was a significant (d.f. = 92, *z-value* = –20.99, $P < 0.001$) difference in the number of non-predominant *C. plutellae* larvae between treatments but no significant (d.f. = 92, *z-value* = 8.37×10^{-18}, $P = 1.0$) difference in the number of predominant *C. plutellae* larvae.

Phenoloxidase assay

PO specific activity varied significantly ($F_{3,36} = 5.1968$, $P < 0.005$) between unparasitised *P. xylostella* larvae feeding on different host plants (Fig. 1). *Plutella xylostella* larvae reared on Chinese cabbage or common cabbage cv. Wheelers Imperial had greater PO activity than *P. xylostella* larvae reared on common cabbage cv. Red Drumhead or cauliflower. PO activity was greatly reduced in parasitised compared with unparasitised *P. xylostella* larvae with no significant ($F_{3,36} = 0.4857$, $P = 0.69$) difference between the host-plant treatments.

Discussion

Here, it has been shown that differences in host-plant quality do not effectively challenge immune reactions of a permissive host against an endoparasitoid. Despite clear evidence of strong host-plant-mediated effects on parasitism and superparasitism by *C. plutellae* on *P. xylostella* (as found in the present study),

Table 2. Host–plant effects on encapsulation ability of *P. xylostella* and parasitism success of *C. plutellae*.

		Host plant‡				
Experiment (towards)*	Parameter measured ($n = 50$)	TT	WI	RD	EGG	*P*
1 (dissection)	Encapsulation proportion of L_1†	0.28 a§	0.08 b	0.04 c	0.01 d	<0.001
2 (dissection)	Encapsulation proportion of L_2	0.01	0	0	0	<0.001
3 (pupation)	Parasitism success (%)	100	100	100	100	1.0

*The single-oviposition experiments, with dissection of host larvae 3 (experiment 1) and 5 (experiment 2) days after parasitism, and without dissection (experiment 3).
†L_1 and L_2 denote late first instar and second instar parasitoid larvae, respectively.
‡The abbreviations TT, WI, RD and EGG are Chinese cabbage cv. Tip Top, common cabbage cv. Wheelers Imperial, common cabbage cv. Red Drumhead and cauliflower cv. Early Green Glazed 'Plant Introduction 234–599', respectively.
§Values marked with different letters are significantly ($P < 0.05$) different.

Table 3. Effects of superparasitism by *C. plutellae* on encapsulation* ability of *P. xylostella*.

The number of female parasitoids per oviposition arena	The number of parasitoid larvae present in host (mean ± SE; $n = 10$)†	
	Predominant‡	Non-predominant§
5	1.0 ± 0.0	5.7 ± 0.6
20	1.0 ± 0.0	23.5 ± 1.7
P	1.0	<0.001

*The encapsulation ability was measured 4 days post-oviposition in host larvae reared on Chinese cabbage.
†The data were calculated for each individual host larva within the batches of five.
‡Predominant denotes alive, active and non-encapsulated late first instar parasitoid larvae.
§Non-predominant denotes dead and fully-encapsulated early first instar parasitoid larvae.

underlying plant effects on measured immune effectors of the host were transitory or overwhelmed by the effect of the parasitoid. There was a significant effect of host-plant suitability on the encapsulation response of *P. xylostella* to first instar but not to second instar parasitoid larvae, which was insufficient to prevent parasitism success. Host-plant effects were also shown to partly suppress phenoloxidase activity in *P. xylostella* but the suppressive effect of *C. plutellae* on phenoloxidase activity was much greater. These results demonstrated that plant-mediated variation in parasitism success by *C. plutellae*, which was found in the previous (Talekar & Yang, 1991; Verkerk & Wright, 1994b; Karimzadeh *et al.*, 2004) and the present studies, is not as a result of plant nutritional status or other attributes affecting the immune function of *P. xylostella*, nor to host-plant effects on superparasitism.

The greater tendency for *C. plutellae* to parasitize *P. xylostella* larvae feeding on a host plant of intermediate suitability could be as a result of differential olfactory responses of the parasitoid

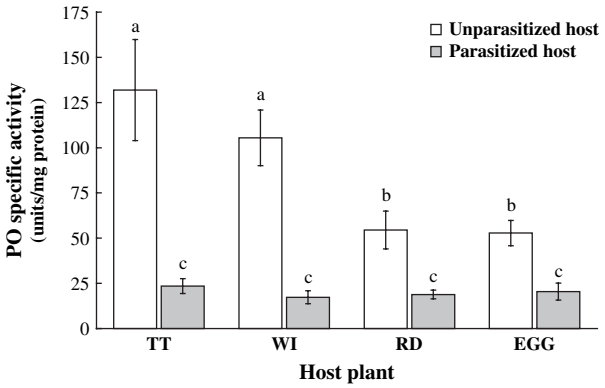

Fig. 1. Host-plant effects on specific phenoloxidase activity (mean ± SE) of unparasitised and parasitised *P. xylostella* ($n = 10$). The abbreviations TT, WI, RD and EGG are Chinese cabbage cv. Tip Top, common cabbage cv. Wheelers Imperial, common cabbage cv. Red Drumhead and cauliflower cv. Early Green Glazed 'Plant Introduction 234–599', respectively. Common letters indicate non-significant ($P > 0.05$) means. One unit represents 0.001 absorbance at 490 nm per min.

to plant-host semiochemicals (Bogahawatte & van Emden, 1996). However, double-choice olfactory experiments in our laboratory have failed to support such a hypothesis (J. Karimzadeh, J. Hardie and D. J. Wright, unpublished data). Another explanation might be reduced fitness of larvae feeding on sub-optimal host plants, resulting in a reduced ability to escape from the parasitoid attack. It has been found that extending the exposure time to *C. plutellae* in non-choice (Karimzadeh *et al.*, 2004) and double-choice (J. Karimzadeh, J. Hardie and D. J. Wright, unpublished data) studies eliminated differences in the level of parasitism between host-plant treatments. Population dynamics studies (Karimzadeh *et al.*, 2004) have also suggested that host-plant type, which influenced the population dynamics of *P. xylostella*, had no long-term effects on the *P. xylostella*–*C. plutellae* interaction. It therefore seems appropriate to suggest that plant type may affect *C. plutellae* parasitism but this effect is not persistent and disappears over long-term host–parasitoid interactions. This assumption remains to be tested under field conditions. The culturing of the insects on different host plants (rearing history) also may influence the herbivore fitness and the parasitoid performance, depending on experience- or genetically-based specialization, and needs further attention.

The probability of at least one egg surviving encapsulation in solitary parasitoids is considered to be greater when the host contains several eggs (multiple target hypothesis; Berberet *et al.*, 1987; Blumberg, 1997; Sagarra *et al.*, 2000). In the present study, superparasitism on the most favourable host plant for *P. xylostella* indicated that the *C. plutellae* egg load was not determinative; one predominant first instar parasitoid larva always survived encapsulation. The host was able to fully encapsulate and kill all other *C. plutellae* larvae at the early first instar, regardless of the number of the parasitoid larvae in the host's haemocoel. It was also clear from single oviposition data that *P. xylostella* were not able to successfully encapsulate the only available *C. plutellae* larva in the haemocoel. These data support the idea that the multiple target hypothesis is unlikely to be responsible for increased parasitism success in hosts that have several parasitoid eggs (Vinson, 1990). The complete encapsulation of non-predominant *C. plutellae* larvae is most likely to be as a result of being attacked by the predominant larva; damaged larvae being easily targeted by the host immune system (Godfray, 1994). Parasitoids have evolved various strategies for avoiding and combating the host immune response (Schmidt *et al.*, 2001; Beckage & Gelman, 2004). For example, several *Cotesia* spp. have demonstrated polydnavirus-induced inactivation of encapsulation to overcome host immune systems (Glatz *et al.*, 2004; Kroemer & Webb, 2004). The effects of *C. plutellae* on the host immune response are likely to involve polydnaviruses injected by the parasitoid during oviposition (Bae & Kim, 2004).

The present work showed that host-plant effects on the immune response of *P. xylostella* were either transitory or overwhelmed by the effect of *C. plutellae*. The immune response was thus effectively surmounted in our system even in very well-nourished host larvae, indicating the ROTH strain of *P. xylostella* is a fully permissive host of *C. plutellae*. The lack of an effective immune response in ROTH may be as a result of inbreeding in laboratory culture although the superparasitism experiment suggested this

strain has retained a robust ability to encapsulate non-predominant parasitoid larvae. In contrast to our findings, using an implant inserted into the pupal haemocoel, Kapari *et al.* (2006) found an effect of host-plant quality on the immune defence of the geometrid *Epirrita autumnata*. Their study, however, has neglected the fact that the success of the host cellular immune response depends on the genetic status of both the host and parasitoid (resistant-virulence coevolution; Carton & Nappi, 2001; Dupas *et al.*, 2003). Field populations of an insect herbivore and its parasitoids may vary in host resistance and parasitoid virulence. Such differences have been found along clines of *Drosophila melanogaster* and its parasitoid *Asobara tabida* (Kraaijeveld & Godfray, 1999) and between two *Cotesia sesamiae* (Cameron) biotypes in Kenya, only one of which could suppress encapsulation in the noctuid *Busseola fusca* (Fuller) (Mochiah *et al.*, 2002).

The stability and persistence of host–parasitoid interactions in the field depend on host susceptibility to parasitoid attack (Sasaki & Godfray, 1999; Tuda & Bonsall, 1999), which in turn, varies with differences in host physiology (Kraaijeveld *et al.*, 1998), and temporal and spatial distributions of the host and the parasitoid (Godfray *et al.*, 1994; Hassell, 2000). Genetic variability of the host defence against parasitism between and within populations of a host species (Kraaijeveld & Godfray, 1997; Dupas *et al.*, 2003), and the trade-offs between fitness components and resistance (or virulence) can promote the stability of the host–parasitoid interaction by providing a refuge for the host population (Holt & Hochberg, 1997; Tuda & Bonsall, 1999). However, when costs of resistance are relatively high and costs of virulence are relatively low, modelling suggests that the host is selected not to invest in resistance (Sasaki & Godfray, 1999; Fellowes & Travis, 2000). Given this, the possible presence of host permissiveness of field populations for *C. plutellae* would risk the establishment and persistence of the parasitoid as an effective natural check and remains an area for future work.

Acknowledgements

J. Karimzadeh was sponsored by the Agricultural Research and Education Organisation (AREO) of Iran. We thank Toyoshi Yoshiga (Saga University, Japan) for assisting with the enzyme assay and Alex R. Kraaijeveld for comments on the draft manuscript.

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Accepted 23 July 2007
First published online 27 November 2007

