Bulletin of Entomological Research (2003) **93**, 65–72 DOI: 10.1079/BER2002208

Differential parasitism of *Plutella xylostella* (Lepidoptera: Plutellidae) larvae by the parasitoid *Cotesia plutellae* (Hymenoptera: Braconidae) on two host plant species

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Abstract

Laboratory experiments were conducted to examine host selection by *Cotesia plutellae* Kurdjumov when larvae of its host, *Plutella xylostella* (Linnaeus), fed on Chinese cabbage, *Brassica campestris* L. ssp. *pekinensis* and those fed on common cabbage, *Brassica oleracea* L. var. *capitata* were provided simultaneously, and to investigate the roles of plant and host volatiles in mediating host selection. When *C. plutellae* were provided with equal numbers of host larvae on plants of the two species in one arena, the parasitoid parasitized 4- to 15-fold more host larvae on Chinese cabbage than on common cabbage. This preference changed little with host density. However, an experience of searching coupled with an oviposition in a host larva on a leaf of the less-preferred plant, common cabbage, significantly increased the preference for parasitizing host larvae on this plant and resulted in twice as many host larvae parasitized on this plant than on Chinese cabbage. Dual choice tests with a Y-tube olfactometer showed that plant volatiles from Chinese cabbage were more attractive to female *C. plutellae* than those from common cabbage when plants of both species were either intact or infested. In parallel to the increased parasitism on common cabbage following experience, oviposition in a host larva on this less-preferred plant significantly increased the response to volatiles emanating from that plant. These results indicate that host plants may strongly influence the foraging behaviour of *C. plutellae,* but their differential attractiveness to the parasitoid may be altered by experience of the parasitoid.

Introduction

Plants may mediate many of the interactions between herbivores and their insect parasitoids and thereby increase or decrease the effectiveness of natural enemies (Cortesero *et al*., 2000). Apparent levels of parasitism of herbivores by the same insect parasitoids have frequently been observed to differ between plant species or cultivars in the laboratory (Stansly *et al*., 1997; Fujiwara *et al*., 2000) and field (Benrey & Denno, 1997; Stansly *et al*., 1997; Nwanze *et al*., 1998; Joyce & Bellows, 2000; Billqvist & Ekbom, 2001). In some cases, variation in the level of parasitism among plant species or cultivars has been shown to be correlated with plant morphology (e.g. structure and density of glandular trichomes) and/or plant semiochemicals (van Lenteren *et al*., 1995; Benrey *et al*., 1997; Bottrell *et al*., 1998; Fujiwara *et al*., 2000). Understanding these multitrophic effects may help fulfill the potential for manipulating crop–pest–parasitoid interactions for improved pest management (Bottrell *et al*., 1998; Verkerk *et al*., 1998).

Insect parasitoids are important biological control agents of the diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae), a major pest of crucifer crops worldwide (Talekar & Shelton, 1993). Some laboratory and field studies have indicated that the performance of various

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parasitoids may differ between crop species, varieties or cultivars (Verkerk & Wright, 1996). Field sampling on crops of three varieties of *Brassica oleracea* L. (Brassicaceae), i.e. common cabbage, broccoli and cauliflower, in New Zealand indicated that levels of parasitism of *P. xylostella* by the larval parasitoid, *Diadegma semiclausum* Hellen (Hymenopetera: Ichneumonidae) and the pupal parasitoid, *Diadromus collaris* (Gravenhorst) (Hymenopetera: Ichneumonidae) were highest on broccoli (Beck & Cameron, 1990). Talekar & Yang (1991) demonstrated in a laboratory choice test that levels of parasitism of *P. xylostella* larvae by each of the two parasitoids, *Cotesia plutellae* Kurdjumov (Hymenoptera: Braconidae) and *Diadegma semiclausum*, differed significantly among the four *Brassica* species/varieties tested. Field observations in the Cameron Highlands of Malaysia suggested that *C. plutellae* and *D. semiclausum* showed significantly different levels of parasitism of *P. xylostella* on the same crop, and *D. semiclausum* seemed to exert more control of *P. xylostella* populations on common cabbage than on Chinese cabbage (Verkerk & Wright, 1997). Apparent variations in levels of parasitism of *P. xylostella* larvae by *C. plutellae* in the field were observed between crop species in Hangzhou, China (Liu *et al*., 2000) and between two cultivars of the common cabbage, *Brassica oleracea* L. var. *capitata*, in Chiba, Japan (Haseeb *et al*., 2001). Because the levels of parasitism in the field are usually influenced by many factors and apparent differences between plant species or cultivars may not necessarily be caused by intrinsic properties of the plants, critical behavioural observations under controlled conditions are necessary to investigate the effects of plants.

Recently, a few studies have examined the foraging behaviour of *C. plutellae* in a tritrophic context. Bogahawatte & van Emden (1996) showed that *C. plutellae* preferred the odour of the host plant on which it had developed. Potting *et al*. (1999) demonstrated that *C. plutellae* used plant volatiles in its in-flight searching behaviour, which was modified by its experience with plant material. Shiojiri *et al*. (2000a,b, 2001) found that *C. plutellae*, being a host-specific parasitoid, showed very specific responses to volatile stimuli and exhibited differential responses between host- and non-host-plant complexes. Schuler *et al*. (1999) showed that the presence of *Bt* toxin in oilseed rape did not have direct adverse effects on the survival and host-seeking ability of *C. plutellae*, and thus the parasitoid might help to constrain the spread of genes for *Bt* resistance through parasitizing *Bt*-resistant hosts on transgenic crops. These observations indicate that host plants may influence the foraging behaviour and success of *C. plutellae*. However, a behavioural approach has not been used to compare the effects of host plant species or cultivars on the foraging and subsequent parasitism of *P. xylostella* by *C. plutellae*, or any other parasitoids of this pest.

In this study, the relative success in parasitism of *P. xylostella* larvae by *C. plutellae* on two plant species was compared in controlled conditions and the response of the parasitoid to volatiles emitted by the two host plants was investigated. To help elucidate the effects of host plants, the role of parasitoid learning was also considered in experiments. Our objective was to investigate the effects of host plants on the foraging behaviour and success of *C. plutellae* and demonstrate the roles of host plant volatiles in mediating the interactions between the host and parasitoid.

Materials and methods

Insects and plants

Three species of host plants were used in this study: (i) Chinese cabbage, *Brassica campestris* L. ssp. *pekinensis*, cv. Zaoshou No. 5; (ii) common cabbage, *Brassica oleracea* L. var. *capitata*, cv. Jingfeng No. 1; and (iii) radish, *Raphanus sativus* L. cv. Yidianhong (Brassicaceae). They were grown from seeds in potting mix in small pots (11 cm diam.) in screen houses. Plants at the 6–7 leaf growth stage were used in experiments.

Three cultures of *P. xylostella* were started from a sample collected from a cabbage field in a suburb of Hangzhou, China, and maintained on the three plant species using the procedures described by Wang *et al*. (1999).

A culture of *C. plutellae* was started from a sample collected from a radish field in a suburb of Hangzhou. The culture was maintained by exposing approximately 500 second and third instar *P. xylostella* larvae on radish plants to ten mated female parasitoids (three to four days after emergence) in a ventilated cage (55 × 55 × 55 cm, with a glass top, screen-covered opening on three sides and a clear plastic front door) for two days. The exposed larvae were reared until parasitoid cocoons developed. The cocoons were transferred to ventilated plastic containers for adult emergence and mating. The adults were fed with 10% honey solution upon emergence. To obtain parasitoids for the experiments and ensure that none of them would be reared from superparasitized hosts, individual second or third instar *P. xylostella* larvae were exposed to single mated female parasitoids and removed immediately after the first oviposition occurred. Exposed *P. xylostella* larvae were then reared on radish plants in cages until parasitoid cocoons developed. The cocoons were collected and placed in clean containers (i.e. without any plant or host material) for adult emergence and mating and provided with honey solution. Mated female wasps were collected three to four days after emergence for use in the observations. All test female parasitoids were reared from host larvae feeding on radish plants.

All insect cultures were maintained in constant temperature rooms at 25 ± 1°C, 14L:10D and 60–80% rh.

Parasitism of host larvae on two plant species

The day before parasitism was measured, test plants were infested with second and early third instar *P. xylostella* larvae. Chinese cabbage plants were infested with larvae previously reared on Chinese cabbage and common cabbage plants were infested with larvae previously reared on common cabbage. Two Chinese cabbage and two common cabbage plants, each bearing the same number of *P. xylostella* larvae, were placed in alternate positions at the four corners of a ventilated cage (size and structure as described above), the top of which was covered with tracing paper to diffuse the light from above. Wooden boards were placed near the four sides of each cage to avoid interference from lateral light. The cages were placed in a constant temperature room at 25 ± 1°C with minimum or no airflow. Two naïve female parasitoids (with no experience of oviposition or searching on a plant) were introduced into each cage for oviposition for 6 h and then discarded. The exposed *P. xylostella* larvae on each of the test plants were then collected and dissected to determine parasitism. The trial was conducted at four host densities (5, 10, 20 or 30 larvae per plant) with ten replicates for each level of density.

Effect of adult experience on parasitism of host larvae on different plants

The experimental set-up and procedure were similar to those used for parasitism of host larvae on the two plant species as described above. Prior to introduction into a cage, each female was allowed to search for 10 min and oviposit once in a *P. xylostella* larva on a host-damaged leaf of either the Chinese cabbage or common cabbage. Two Chinese cabbage and two common cabbage plants each bearing 20 second instar *P. xylostella* larvae were placed in alternate positions at the four corners of a cage. Two pre-treated females were introduced into each cage for 6 h and ten replicates were carried out for each pre-treatment. As these trials were done at the same time and with female parasitoids of the same generation as those for the trial of 'Parasitism of host larvae on two plant species' above, the data of the host density of 20 larvae per plant from the above trial were used here as the results of females with no experience for comparison.

Effect of previous larval-host plant on larval-host selection by the parasitoid

The experimental set-up and procedure were again similar to those above, except that the sources of host larvae used in the tests were modified. *Plutella xylostella* were reared from egg to second or early third instar larvae on Chinese cabbage, common cabbage or radish. For each of the three treatments, *P. xylostella* larvae reared from one of the host plant species were transferred to the four test plants in a cage. The two Chinese cabbage and two common cabbage plants each bearing 20 *P. xylostella* larvae that had been transferred from one of the host plant species were placed in alternate positions at the four corners of a cage. Two naïve female parasitoids were introduced into each cage for 6 h and ten replicates were carried out for each treatment.

Response to volatiles of plants and plant-host complexes

The response of female parasitoids to volatile chemicals emitted by different odour sources was investigated in a Y-tube olfactometer. The olfactometer consisted of a Y-shaped glass tube 2.8 cm in internal diameter. The stem and the two arms (at a 75° angle) of the Y-tube were 16 and 28 cm in length, respectively. Each arm was connected via a Teflon hose to an odour source chamber consisting of a glass box (25 × 25 × 35 cm), large enough to hold a whole test plant with the roots and bottom of the stems plunged in a water bottle. Air was drawn by the negative pressure of an electric pump, filtered through an activated-charcoal filter and humidified by bubbling through distilled water before being pulled into the odour source chamber at approximately 200 ml min^{-1}. The Y-tube was placed inside a box with an open front (for access of observation) and diffused light from the top, and the observations were made at 25 ± 1°C.

Female parasitoids were released individually into the base of the stem of the Y-tube, and each given 5 min to move upwind towards the ends of the arms of the tube. When a female penetrated more than 10 cm into one of the two arms and remained there for more than 30 s, it was recorded as a choice for that arm. The connections of the odour sources to the olfactometer arms were exchanged after testing five parasitoids to remove any asymmetrical bias in the set-up. The olfactometer tube was washed with alcohol and dried after testing ten females.

For each of the two plant species, the following four types of odour sources were prepared for testing in various dual comparisons: (i) intact plants; (ii) mechanically damaged plants: 20 × 5 mm holes were punched in leaves of each plant 24 h before the test and the plant was punched again in the wounds 10 min prior to the test; (iii) infested plants: each plant was infested with 20 second instar *P. xylostella* larvae 24 h prior to the test and the larvae were left on the plant during the test; and (iv) previously infested plants: the plants were infested as in (iii) but the larvae were removed 10–20 min prior to the test.

Six pairs of odour sources were compared within each of the two plant species (see figs 1 and 2 for details), and four pairs of odour sources were compared between the two plant species (see fig. 3). For each pair of odour sources, approximately 40 females were individually tested.

Effect of adult experience on response to volatiles of different plant-host complexes

The test materials and methods were the same as above, except that, 5–10 min prior to introduction into the Y-tube, each test female parasitoid was allowed to search and oviposit once in a third instar *P. xylostella* larva feeding on a host-damaged leaf of either Chinese or common cabbage. To prepare the host and plant leaf complex for each of the females to acquire experience, a third instar *P. xylostella* larva was inoculated onto a small, uninfested leaf to feed for 24 h, and then the host-infested leaf bearing the feeding larva was presented to a female to search and oviposit. The experienced females were then tested in the Y-olfactometer to observe their responses to various pairs of odour sources from the two plant species (see above). Again, as these tests were conducted at the same time and with female parasitoids of the same generation as those for the test of 'Response to volatiles of plants and plant-host complexes' above, the data of the corresponding dual treatments of the above test were used here as the results of naïve females for comparison.

Statistical analysis

A test of independence in two-way tables, with application of Williams's correction, was used to compare frequency distributions between different treatments; and a goodness-of-fit *G*-test, with application of Williams's correction, was used to analyse the numbers of females that made a choice in each pair of odour sources with the null hypothesis of no preference (Sokal & Rohlf, 1995). Comparison of two mean values was conducted by Student-*t* test. The differences between three means were analysed by one-way analysis of variance (ANOVA) and the means were compared pair-wise using Fisher protected least significance (LSD) procedure when an ANOVA indicated significant effects.

Results

Parasitism of host larvae on two plant species

When provided with equal numbers of *P. xylostella* larvae feeding on the two plant species, female parasitoids parasitized 5–16 times more larvae on Chinese cabbage than on common cabbage (table 1). While the total number of parasitized host larvae increased with higher host densities, the ratios of parasitized larvae between the two plants did not differ significantly between host densities of 5, 10 and 30 larvae per plant (G = 5.51, df = 2, $P > 0.05$). However, the relative proportion of *P. xylostella* larvae parasitized on Chinese cabbage at the host density of 20 larvae per plant was significantly higher than at the other three host densities (G = 17.15, df = 3, $P < 0.01$; table 1).

Effect of adult experience on parasitism of host larvae on different plants

The mean number of host larvae parasitized by naïve females was significantly lower than that by each of the two groups of experienced females (table 2). Compared to the naïve females which resulted in 94% of parasitized larvae on Chinese cabbage and 6% on common cabbage, females experienced on Chinese cabbage increased their preference for hosts on this plant further, resulting in parasitism on Chinese cabbage only and no parasitism on common cabbage (table 2). In contrast, females experienced on common cabbage finished with 71% of parasitized hosts on this plant and only 29% on Chinese cabbage (table 2).

Effect of previous larval-host plant on larval-host selection by the parasitoid

Irrespective of the host plant species on which the host larvae had been reared, once larvae were transferred to the respective cabbages, female parasitoids always preferred to parasitize larvae on Chinese cabbage (table 3). The frequency distributions of parasitized larvae on the two plants were similar when the larvae were previously reared on Chinese cabbage or radish (G = 0.03, df = 1, $P = 0.99$), whereas the relative frequency of parasitized larvae on common cabbage was significantly increased when the larvae were previously reared on this plant compared to larvae reared on Chinese cabbage (G = 6.31, df = 1, $P < 0.05$) or radish (G = 5.28, df = 1, $P < 0.05$). These results indicate that the parasitoids were attracted to the host plant species differentially, but their selection and acceptance of host larvae on the plants were only slightly affected by the dietary history of hosts associated with different plants.

Response to volatiles of plants and plant-host complexes

For each of the two plant species, the female parasitoids showed a strong preference for volatiles emanating from mechanically damaged, infested, or previously infested plants compared to intact ones (figs 1 and 2). With Chinese cabbage, the female parasitoids showed a significant preference for volatiles emanating from infested plants compared to mechanically damaged ones, although their preference between mechanically damaged and previously

Table 1. Number of *Plutella xylostella* larvae parasitized by *Cotesia plutellae* on two *Brassica* species with the same host density in choice tests for 6 h at 25°C.

Host density (larvae per plant)	No. of replicates	Mean ± SE no. of larvae parasitized per plant		
		B. campestris (a)	*B. oleracea* (b)	a/b
5	10	2.0 ± 0.2	0.3 ± 0.2	6.7
10	10	6.8 ± 0.4	0.7 ± 0.3	9.7
20	10	10.9 ± 0.9	0.7 ± 0.3	15.6
30	10	11.9 ± 1.2	2.5 ± 0.5	4.8

Note: At each host density, the mean number of *P. xylostella* larvae parasitized differs significantly between host plant species ($P < 0.01$ in all cases, Student-*t* test).

Table 2. Relative proportions of *Plutella xylostella* larvae parasitized by *Cotesia plutellae* on *Brassica* plant species in dual choice tests for 6 h at 25°C when the female parasitoids had a prior experience of searching and oviposition in a host larva on a leaf of different plants.

Prior experience of females	No. of replicates	Mean ± SE no. of host larvae parasitized per cage[1]	Mean relative percentages ± SE of parasitized larvae between the two plants	
			B. campestris	*B. oleracea*
No experience	10	23.2 ± 1.1 b	94.0 ± 7.8	6.0 ± 2.6
Search and oviposition on a host-damaged leaf of *B. campestris*	10	31.8 ± 1.2 a	100.0	0.0
Search and oviposition on a host-damaged leaf of *B. oleracea*	10	32.2 ± 1.5 a	28.6 ± 4.9	71.4 ± 4.3

[1] Number of host larvae provided: 20 per plant and 80 in total in a cage. Means in this column followed by the same letter are not significantly different at 5% level as determined by Fisher's protected LSD test.

Table 3. Number of *Plutella xylostella* larvae parasitized by *Cotesia plutellae* on *Brassica* plant species when the host larvae were reared on different plant species and then transferred to test plants for choice tests for 6 h at 25°C.

Host plant for larval rearing	No. of replicates	Mean ± SE no. of larvae parasitized per plant[1]		
		B. campestris (a)	*B. oleracea* (b)	a/b
Brassica campestris	10	10.5 ± 1.0	0.9 ± 0.3	11.7
B. oleracea	10	12.5 ± 0.8	2.2 ± 0.2	5.7
Raphanus sativus	10	9.9 ± 0.9	0.9 ± 0.4	11.0

[1] Number of host larvae provided: 20 per plant and 80 in total in a cage. In each of the three treatments, the mean number of *P. xylostella* larvae parasitized differs significantly between the two plant species ($P < 0.01$ in all cases, Student-*t* test).

infested plants, or that between infested and previously infested plants did not differ significantly (fig. 1). With common cabbage, parasitoids showed similar interest towards mechanically damaged and infested plants, or towards mechanically damaged and previously infested plants, or towards infested and previously infested plants (fig. 2).

When parasitoids were offered a choice between volatiles from the two plant species, approximately twice as many responded towards Chinese cabbage compared to common cabbage, although in the test with intact plants the difference was not significant due to the low number of females that responded (fig. 3). A test of independence in a two-way table showed that the frequency distributions between the four pairs of odour sources did not differ significantly (G = 0.03, df = 3, $P = 0.99$).

Effect of adult experience on response to volatiles of different plant-host complexes

Naïve parasitoids showed a significant preference for Chinese cabbage over common cabbage when plants of the two species were either infested or previously infested (fig. 3). Such a preference was intensified by a prior experience on Chinese cabbage (fig. 4A). More remarkably, female parasitoids experienced on common cabbage showed a significant preference for volatiles emitted from this plant over those emitted from Chinese cabbage (fig. 4B).

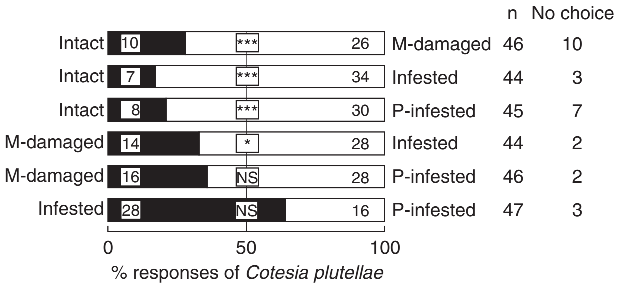

Fig. 1. Number and percentage of *Cotesia plutellae* female adults showing responses to volatiles of various combinations of *Brassica campestris* plants and host larvae in dual choice tests. Asterisks indicate statistically significant preferences in a choice test (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). NS, not significant; n, number of parasitoid wasps tested. The number of wasps that did not choose either of the odour sources is listed under 'No choice'. M-damaged, mechanically damaged; P-infested, previously infested.

Discussion

When offered a choice between Chinese cabbage and common cabbage, naïve female *C. plutellae* reared from hosts feeding on radish showed a strong preference for searching and parasitizing *P. xylostella* larvae on the former plant species (tables 1 and 2). This preference was mediated, at least in part, by the different levels of attraction to volatiles emitted from the two plant species (fig. 3). Host derived stimuli seemed to play a limited role in mediating the preference, since host larvae with dietary histories on different plant species did not induce much variation in the preference expressed by the parasitoid towards the different plants (table 3). These results indicate that the two plant species mediate the parasitoid host-selection more by influencing parasitoid attraction than they do by affecting host acceptance. Such a phenomenon of mediation of parasitoid host-selection by host plant plants has been observed in another parasitoid, *Cotesia glomerata* Linnaeus (Hymenoptera: Braconidae) (Benrey *et al.*, 1997). It was also noticeable that such a preference was much more strongly and uniformly expressed by individual females when the plants were mechanically-damaged, infested or previously infested, than when the plants were intact, as indicated by the higher proportions of females that responded when these plants were exposed in the dual choice tests (fig. 3, see also figs 1 and 2). This was not surprising, because

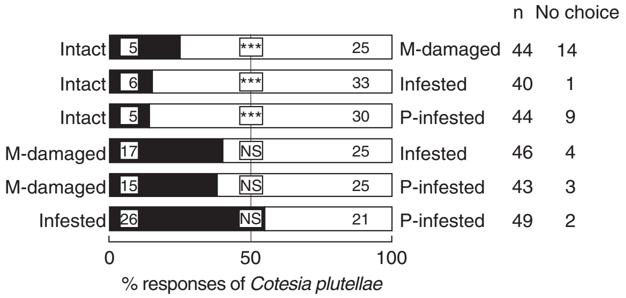

Fig. 2. Number and percentage of *Cotesia plutellae* female adults showing responses to volatiles of various combinations of *Brassica oleracea* plants and host larvae in dual choice tests. Asterisks indicate statistically significant preferences in a choice test (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). NS, not significant; n, number of parasitoid wasps tested. The number of wasps that did not choose either of the odour sources is listed under 'No choice'. M-damaged, mechanically damaged; P-infested, previously infested.

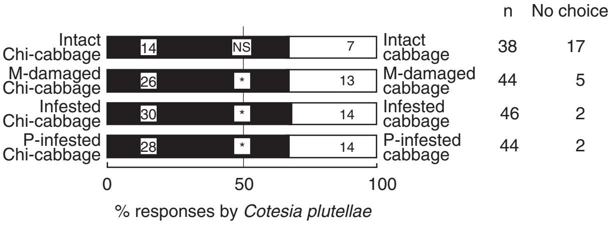

Fig. 3. Number and percentage of *Cotesia plutellae* female adults showing responses to volatiles of various plant–host-combinations including either *Brassica campestris* (Chi-cabbage) or *B. oleracea* (cabbage) in dual choice tests. Asterisks indicate statistically significant preferences in a choice test (**P* < 0.05; ***P* < 0.01; ****P* < 0.001). NS, not significant; n, number of parasitoid wasps tested. The number of wasps that did not choose either of the odour sources is listed under 'No choice'. M-damaged, mechanically damaged; P-infested, previously infested.

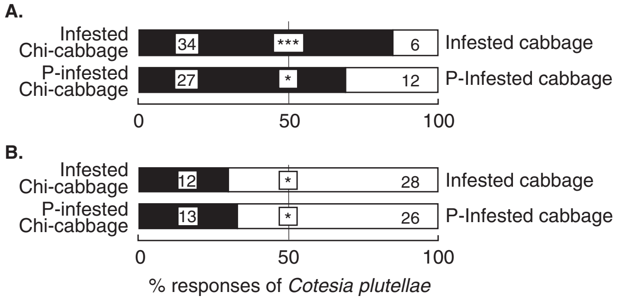

Fig. 4. Number and percentage of *Cotesia plutellae* female adults showing responses to volatiles of plant–host-combinations including either *Brassica campestris* (Chi-cabbage) or *B. oleracea* (cabbage) in dual choice tests when the female parasitoid adults had searched for 10 min coupled with an oviposition in a larva on a host-damaged leaf of either Chinese cabbage (A) or common cabbage (B). All test females responded and thus the two numbers shown on each bar make up the total number of females observed in each dual choice test. Asterisks indicate statistically significant preferences in a choice test (**P* <0.05, ***P* < 0.01, ****P* < 0.001).

parasitoids have been shown generally to respond much more strongly to herbivore-induced plant odours than to odours emitted by intact plants and use herbivore-induced plant cues in host foraging (Turlings *et al.*, 1990; Dicke & van Loon, 2000). However, the expressed preference could be immediately and significantly modified by prior experience, to the extent that a ten-minute searching coupled with a single oviposition in a host on a damaged leaf of the common cabbage resulted in higher parasitism on this plant than on Chinese cabbage (table 2). This modification of preference by experience was probably associated with learning of plant volatiles (fig. 4). It would appear that the learning of host derived stimuli were involved to a much lesser extent, as mechanically-damaged plants and infested plants had similar levels of attractiveness to the parasitoids (figs 1 and 2) and host dietary history inflicted only limited effect on the preference expressed by the parasitoid towards the different host-plant complexes (table 3).

In a separate experiment conducted during the course of this study to compare performance of the host as affected by host plant species, it was shown that cohorts of the *P. xylostella* strain reared on Chinese cabbage, common cabbage or radish used in this study were similar in development time, pupal weight, adult size and fecundity (Chapter 10 of Jiang, 2001). Thus it could be assumed that the host larvae associated with different host plant species in a given dual choice test were rather similar in size and inflicted similar amounts of damage among the two plant species. This similarity of host performance between cohorts on different host plant species would suggest that the different levels of parasitoid attraction by the volatiles from Chinese cabbage and common cabbage were mainly caused by qualitative, rather than quantitative, differences in the chemicals emitted by the two plant species.

Many parasitoids, including *C. plutellae*, have been shown to prefer the odour of the plants on which they have developed (Turlings *et al.*, 1993; Bogahawatte & van Emden, 1996). Such a preference for the original host plants has frequently been demonstrated to be the result of early adult learning rather than learning by the immature stages, because adult parasitoids that eclose from parasitoid pupae excised from their cocoons (or other plant-related chambers) and are deprived of contact with host- or plant-related materials during the process of emergence do not show such behaviour (Corbet, 1985; Herard *et al.*, 1988, Caubet & Jaisson, 1991; Turlings *et al.*, 1993; van Emdem *et al.*, 1996). In this study, the test *C. plutellae* females were reared from a third plant species to avoid the effect of early adult learning. While such a procedure could not guarantee that the early adult learning associated with radish would give absolutely unbiased experience in terms of conditioning their subsequent response to Chinese cabbage and common cabbage, it should have helped to show the innate preference of the parasitoid. Detailed behavioural observations on the effect of early adult learning by *C. plutellae* will provide further information for understanding the foraging behaviour of this parasitoid on different plants.

Cotesia plutellae is a specific larval parasitoid of *P. xylostella*, which can feed and reproduce on plants of at least 28 genera of the family Brassicaceae (Talekar & Shelton, 1993). In fact, *P. xylostella* has been observed to occur in high numbers on crops of many *Brassica* species in many parts of the world in the last 30 years (Talekar & Shelton, 1993; Sivapragasam *et al.*, 1997). Such an association between the three trophic levels, i.e. specific connection between the parasitoid and herbivore but diverse connections between the herbivore and its host plants, has been speculated to favour the evolution of learning by the parasitoid to deal with the variability of plant cues (Vet *et al.*, 1995). Our observations of the effects of plant volatiles and experience on the foraging behaviour of *C. plutellae* agrees with the earlier reports by Bogahawatte & van Emden (1996) and Potting *et al.* (1999) in that this parasitoid mainly uses plant volatiles in its orientation towards infested plants and experience of plant volatiles dramatically increases the order of preference to these cues. Thus, the behaviour of *C. plutellae* offers support for the above theory. In some parasitoids, including several *Cotesia* species, the learned responses have been shown to wane and disappear in a time that is short relative to adult longevity as a consequence of another experience (Vet *et al.*, 1995; Fukushima *et al.*, 2001). If this happens in *C. plutellae*, one may expect that the parasitoid would be more efficient at parasitizing *P. xylostella* on Chinese cabbage than on common cabbage when small plots of each are grown in close proximity, but that it may perform more similarly on the two plants when they are grown apart in time and space. Evidence to support such an inference is still scant. Liu *et al*. (2000) showed that in crop systems characterized by a mixture of small plots of different plant species or cultivars, levels of parasitism of *P. xylostella* larvae by *C. plutellae* varied between crop species/cultivars. For example, parasitism rates on mustard, *Brassica juncea* L. Czernjaew (Brassicaceae), a species more closely related to Chinese cabbage than to common cabbage, were usually higher than on common cabbage, when crop growth periods and levels of host density were similar between fields of the two plant species. Similarly, Haseeb *et al*. (2001) reported consistent differences in the level of parasitism of *P. xylostella* by *C. plutellae* between closely-situated small plots of two cultivars of common cabbage. Interestingly, in a different setting, Talekar & Yang (1993) found no difference in parasitism of *P. xylostella* by *C. plutellae* and *D. semiclausum* between cabbage monoculture and a mixed cropping of cabbage with eight non-crucifer vegetable crops.

Learning in parasitoids can increase their foraging efficiency (Papaj & Vet, 1990; Turlings *et al*., 1993). In *C. plutellae*, experienced females parasitized significantly higher numbers of host larvae on either Chinese cabbage or common cabbage than naïve ones, indicating that learning can aid the wasps in their foraging effort (table 2). The increased efficiency through learning in *C. plutellae* may be utilized to increase its effectiveness for biological control. For example, mass-reared parasitoids pre-treated with odour of a target crop may help them search more efficiently in the field of release.

Using chromatography Jiang (2001) analysed the volatiles of the three test plant species collected from their headspace by solid phase micro-extraction. The chromatographic profiles of the extractions illustrated apparent differences in volatiles between the three plant species when they were either intact or infested. However, detailed and meaningful comparison of volatile components between the three plant species has yet to be performed. Reddy *et al*. (2002) showed that *C. plutellae* was attracted to a variety of green leaf volatiles of the common cabbage as well as to a variety of chemical cues associated with *P. xylostella* including sex pheromone and frass volatiles, and some components of the green leaf volatiles were particularly active. While the present study showed that plant volatiles play a significant role in determining the foraging success by *C. plutellae* on different plant species, much more detailed knowledge of these volatiles will be required before we can attempt to use various plant characteristics or manipulate plant attributes to enhance biological control of *P. xylostella* by *C. plutellae* and other parasitoids.

Acknowledgements

This work was funded jointly by the National Natural Science Foundation of China (Project No. 39930120) and the Australian Centre for International Agricultural Research (Project No. ACIAR CS2/1998/089). The authors thank Myron Zalucki and Michael J. Furlong, Department of Zoology and Entomology, the University of Queensland, Australia for thoughtful comments on the manuscript.

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(Accepted 9 September 2002)