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Influence of prey host plant on a generalist aphidophagous predator: *Episyrphus balteatus* (Diptera: Syrphidae)

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Abstract. Secondary plant metabolites (allelochemicals) play a major role in plant-insect interactions. Glucosinolates (GLS) and their degradation products from *Brassica* species are attractants and feeding stimulants for Brassicaceae specialist insects but are generally repellent and toxic for generalist herbivores. The impact of these compounds on crucifer specialist insects are well known but their effect on generalist predators is still not well documented. The influence of the prey's host plant on both development and reproduction of an aphidophagous beneficial, the hoverfly *Episyrphus balteatus*, was determined using the cabbage aphid, *Brevicoryne brassicae* (a specialist) and the peach aphid *Myzus persicae* (a generalist) reared on two crucifer plants, *Brassica napus* and *Sinapis alba* containing low and high GLS levels respectively.

The prey and its host plant differently influenced life history parameters of *E. balteatus*. The predator's rates of development and survival did not vary when it fed on the generalist aphid reared on different host plants. These rates decreased, however, when the predator fed on the specialist aphid reared on the host plant with high GLS content plant versus the host plant with lower GLS content. This aphid host plant combination also negatively affected hoverfly reproduction; lower fecundity was observed. As a result, the fitness of the hoverfly was strongly affected. This study illustrates the importance of tritrophic relations in pest management involving predators. The host plant of the prey can have a major influence on the potential of a biological agent to control herbivore species such as aphids.

INTRODUCTION

Plants of the Brassicaceae family contain secondary substances known as glucosinolates (GLS). When the plant is damaged and the cell integrity destroyed, the enzyme myrosinase catalyses the degradation of GLS to volatile molecules, mainly isothiocyanates (ITC) (Fahey et al., 2001). The latter are attractants and feeding stimulants for several crucifer specialist insects such as *Phyllotreta cruciferae* Goeze (Coleoptera: Chrysomelidae) and *Plutella xylostella* L. (Lepidoptera: Plutellidae) (Bodnaryk, 1997). Several Pieridae species such as *Pieris rapae* L. and *P. napi oleracea* Harris (Lepidoptera: Pieridae) also use GLS as oviposition stimulants (Huang & Renwick, 1994).

In contrast to their role as kairomones for insects that specialize on crucifers, the secondary plant substances are highly toxic for non-crucifer feeders and provide an efficient defence mechanism for the plant (Fenwick et al., 1983; Porter et al., 1991; Heaney & Fenwick, 1995). Sinigrin, the allyl-ITC GLS precursor, is particularly toxic for non-adapted herbivores and induces high mortality levels of generalist herbivores (Blau et al., 1978). The foliar ITC-releasing and GLS system provide some degree of plant protection against pests such as *Mamestra configurata* Walker (Lepidoptera: Noctuidae) (McCloskey & Isman, 1993) and the generalist aphid *Myzus persicae* Sulzer (Homoptera: Aphididae). The latter species generally avoids young tissues of crucifer plants, which are characterised by high GLS concentrations (Yusuf et al., 1997).

The influence of the GLS-ITC system of *Brassica* plants is not limited to the second trophic level. The odours emitted from aphid infested cabbage leaves or from the cabbage aphid *B. brassicae* alone induced positive responses of the aphid parasitod'd, *Diaeretiella rapae* M'Intosh (Hymenoptera: Braconidae). Reed et al. (1995) suggested that the source of attractants to *D. rapae* females originates from the interactions between plant and the feeding aphids. The latter absorb GLS and degrade them to ITC (Francis et al., 2001a). Here we report the allelochemical effects through the aphid prey on a generalist aphidophagous predator, *Episyrphus balteatus* De Geer (Diptera: Syrphidae). Developmental and reproductive parameters were affected depending on the prey species and its host plant. Two crucifer species, *Brassica napus* L. and *Sinapis alba* L. (with low and high GLS contents respectively) and control diet free of GLS were used to rear preys for the predator. Differential adaptations and consequences that depend on the host plant of the prey are discussed.

MATERIAL AND METHODS

Plant and insect rearing

Broad beans (*Vicia faba* L.) were grown in 20 × 30 cm trays in a mixture of perlite and vermiculite (1/1) in a controlled environment room at 20 ± 2°C and 16 h daylight photoperiod. The bean plants were used to rear *M. persicae* as control diet for hoverflies. White mustard (*Sinapis alba* L. containing high GLS level) and oilseed rape (*Brassica napus* L., containing 6 fold less GLS than *S. alba*) were grown in 10 cm diameter plastic pots containing ordinary compost in separate rooms with the same controlled conditions. The crucifer species were used to rear cabbage aphids (*B. brassicae*) and peach aphids (*M. persicae*). Each aphid species had been reared in separate rooms of the laboratory for several years.

The first generation of *E. balteatus* was provided by PK Nützlingzuchten (Welzheim, Germany). Adults were held in 100 × 60 × 60 cm cages and fed with pollen, honey and sugar. Hoverfly larvae were mass-reared in aerated plastic boxes of 11

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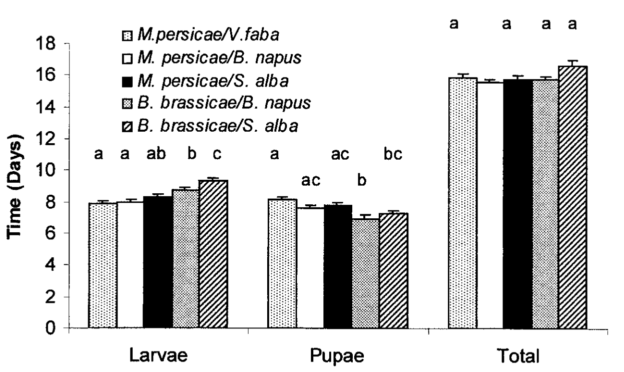

Fig. 1. Effect of different aphid host plant combinations on development durations (mean + SE) of *Episyrphus balteatus*. Letters indicate significant differences at P = 0.05, n = 60.

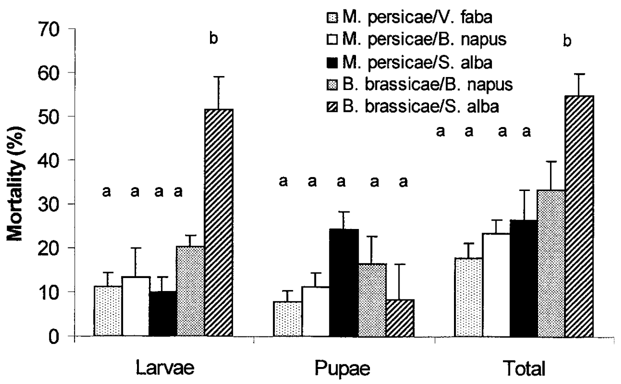

Fig. 2. Effect of different aphid host plant combinations on mortality (mean + SE) of *Episyrphus balteatus*. Letters indicate significant differences at P = 0.05, n = 60.

× 14 × 4 cm and were daily fed ad libitum with *M. viciae* on bean as standard diet.

Bioassays

For each diet, 60 newly hatched larvae (second generation) were individually placed in 5 cm Petri dishes and fed daily ad libitum with the tested host plant and aphid combination. The duration of development and mortality rates were determined for each combination of prey and host plant. Adults that emerged on a particular diet were placed as pairs in 60 × 30 × 30 cm net cages. 10 pairs were studied for each diet. Fecundity and egg viability of these pairs of hoverflies fed were recorded daily during twenty days.

The individual fitness (r) of McGraw & Caswell (1996) was selected to integrate all the larval components into a single global measure of performance. This fitness was calculated by integrating development time (D), survival (M = 1 or 0) and fecundity (V) via the equation $r = \{\mathrm{Ln}\,(M.V)\}/D$.

Data analysis

Percent mortality and egg viability were analysed by ANOVA after $\arcsin\sqrt{x}$ transformation (Dagnelie, 1975). Other results were directly analysed by ANOVA and mean comparisons by Tukey tests were performed when necessary, using the Minitab software (vs 11.2).

RESULTS

Hoverfly development parameters

E. balteatus larval durations were significantly different depending on the prey and its host plant (F = 15.69 and P < 0.001, DF: 4 & 213; Fig. 1). Larvae fed *M. persicae* had the same developmental durations whatever the prey host plant. Feeding on *B. brassicae* reared on *B. napus* caused an intermediate duration of larval development not different from feeding on *M. persicae* reared on *S. alba*. When the latter plant served as host of the cabbage aphid, the predator had the longest development duration. Durations of pupal development differed depending on the aphid and host plant combination (F = 9.19 and P < 0.001, DF: 4 & 187). Total development time did not differ significantly among aphid host-plant combinations, however, the shortest larval development durations were compensated by the longest pupal development (F = 1.15 and P = 0.335, DF: 4 & 141).

Larval mortality of the hoverfly was significantly affected by the prey and its host plant (Fig. 2). Larval predators that fed on *B. brassicae* reared on *S. alba* had higher mortality rates than those with other diets (F = 16.33 and P < 0.001, DF: 4 & 9). Whereas pupal mortality rates did not vary significantly with diet (F = 3.26 and P = 0.059, DF: 4 & 9), the mortality rates from egg hatch through pupation was greater for predators that fed on the cabbage aphid reared on mustard than for predators on all other diets (F = 10.49 and P = 0.001, DF: 4 & 9).

Hoverfly reproduction parameters

E. balteatus fecundity differed significantly depending on the larval prey and the related host plant (F = 24,27 and P < 0.001, DF: 4 & 49; Fig. 3). The lowest fecundity was observed when syrphid larvae were fed *B. brassicae* reared on *S. alba*. Feeding the same aphid species reared on *B. napus* resulted in a less negative effect on fecundity, which did not differ from the fecundity observed for predators fed *M. persicae* reared on both *Brassica* hosts. No differences in fecundity were observed among predators fed peach aphid reared on different host plants. Egg viability was not affected by the host plant of the hoverfly larval prey (F = 1.64 and P = 0.181, DF: 4 & 49).

As the rank order of aphid suitability as food differed for different larval components we had to integrate them in a single measure, the fitness (r) of McGraw & Caswell (1996). The fitness of *E. balteatus* fed *B. brassicae* reared on *S. alba* was lower than that of the predator fed other diets (F = 27.16 and P < 0.001, DF: 4 & 49; Fig. 4).

DISCUSSION

Studies on the chemical ecology of host plant selection by herbivores have largely been carried out to explain the diversity of secondary plant chemicals and host specialisation of herbivores (Dicke, 2000). Multitrophic perspectives have been developed over the last twenty years to integrate natural enemies of phytophagous insects and determine the role of allelochemicals in mediating interactions. Parasitoids, including those associated with Brassicaceae, have been used as model organisms for the third trophic level (Lamb, 1989; Vet & Dicke, 1992), whereas predator species have often been neglected. Rather few studies have been conducted on the influence of different aphid species and prey host plant on development and reproduction of syrphid species.

Our results show that not only the prey species but also the host plant had a significant effect on duration of the larval and pupal development of *E. balteatus*. Feeding on *B. brassicae* reared on *S. alba* resulted in higher larval predator mortality compared either to feeding on the aphid reared on its other host plant, *B. napus*, or feeding on another aphid species (*M. persicae*) reared on *Brassica* or on a GLS free plant. Francis et al. (2000) previously demonstrated that toxicity of *B. brassicae* for *A. bipunctata* larvae increases with the increasing glucosinolate contents of the host plants. The present study reveals that the

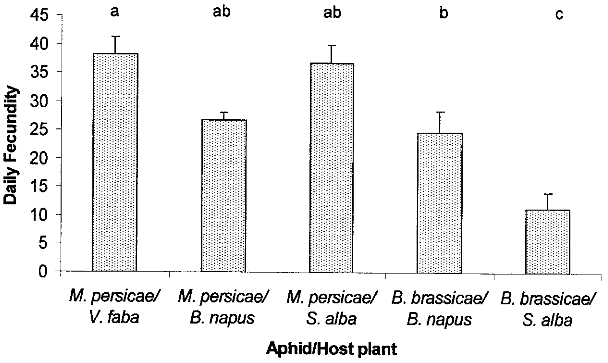

Fig. 3. Effect of aphid host plant combination during larval development of *Episyrphus balteatus* on subsequent daily fecundity (mean + SE). Letters indicate significant differences at P = 0.05, n = 10.

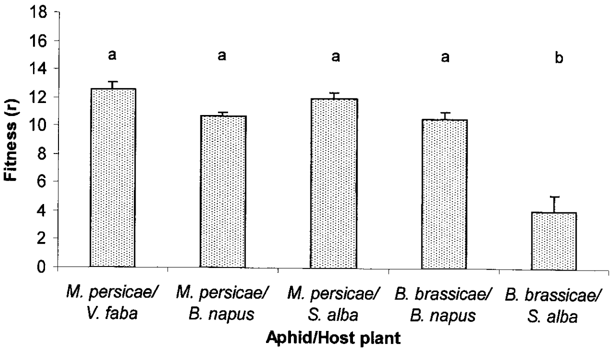

Fig. 4. Effect of aphid host plant combination during larval development of *Episyrphus balteatus* on fitness (mean + SE). Letters indicate significant differences at P = 0.05, n = 10.

hoverfly *E. balteatus* is much less sensitive than the two-spot ladybird. Thus, while in the study of Francis et al. (2000) none of the ladybird larvae fed *B. brassicae* reared on *S. alba* reached the adult stage, 45% of syrphids did in the present study. The higher mortality rate of both predator species on a diet of *B. brassicae* reared on *S. alba* compared to those fed other diets suggests a transfer of the plant's secondary metabolites through the specialist aphid prey. Indeed, chemical analysis of aphids revealed the presence of GLS and ITC toxic molecules in *B. brassicae* reared on *B. napus* and *S. alba* (Francis et al., 2001a). Such sequestration of allelochemicals has previously been reported for *Macrosiphum albifrons* Essig (Homoptera: Aphididae) (Wink & Römer, 1986; Emrich, 1991). Increasing alkaloid content of *Lupinus* spp. induced prolonged development and higher mortalities of *E. balteatus* when larvae fed on *M. albifrons* sucking this host plant. *Neodiprion sertifer* Geoffroy (Hymenoptera: Diprionidae) was also shown to sequestrate terpenoïds from *Pinus sylvestris* (Harborne, 1993).

In addition to a relatively weak effect on *E. balteatus* development through the aphid prey, secondary substances of Brassica may also be responsible for the observed decrease in the hoverfly fecundity, but appear to have no negative impact on egg viability. Sadeghi and Gilbert (2000) suggested that differences in quality among aphids, even within the same species, were directly linked to host plant chemistry. Indeed, variable amounts of various secondary substances can be found in aphids both intra- and interspecifically depending on the host plants. Here we confirmed this hypothesis by showing different biological responses, in terms of development, fecundity and overall fitness patterns, of an aphidophagous predator depending on the prey host plant combination. Not only the insect pest species but also the cultivated host plants have an influence on the efficacy of a beneficial insect (van Emden, 1995). One notes, therefore, that even if *E. balteatus* and *A. bipunctata* contribute to pest population limitation as efficient biological control agents in integrated pest management programs, the two-spot ladybird appears to have a higher prey specificity being more sensitive to variable aphid quality.

The efficacy of the hoverfly to control aphid populations in cereal fields has been described previously (Chambers & Adams, 1986; Tenhumberg, 1995). What is more, *E. balteatus* is the most abundant aphidophagous predator in vegetable crops such as broad beans and carrots, where it respectively represents more than 70% and 80% of the aphidophagous species (Colignon et al., 2001, 2002, in press). A certain resistance to Brassicaceae allelochemicals in *E. balteatus* and the influence of this hoverfly species on the population dynamics of the cabbage aphid in Brussels sprouts (Chandler, 1968; Vidal, 1997) probably enables its wide use as biological agent. In contrast, although *A. bipunctata* has been used with success in apple orchards and in glasshouses (Hodek & Honěk, 1996; Brown & Glenn, 1999), the two-spot ladybird does not appear to be adapted to control aphid pests of crop plants such as Brassicaceae.

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