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Domatia reduce larval cannibalism in predatory mites

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Abstract. 1. Acarodomatia are small structures on the underside of leaves of many plant species, which are mainly inhabited by carnivorous and fungivorous mites.

2. Domatia are thought to protect these mites against adverse environmental conditions and against predation. They are considered as an indirect plant defence; they provide shelter to predators and fungivores and these in turn protect the plants against herbivores and fungi.

3. We studied the possible role of domatia of coffee (*Coffea arabica* L.) (Rubiaceae) and sweet pepper (*Capsicum annum* L.) (Solanaceae) in reducing cannibalism in the mites inhabiting the domatia. We measured cannibalism of larvae by adults of the predatory mites *Iphiseiodes zuluagai* Denmark & Muma and *Amblyseius herbicolus* Chant on coffee leaf discs and of the predatory mite *Iphiseius degenerans* (Berl.) on sweet pepper leaf. Domatia were closed with glue or left open.

4. Cannibalism in all three species increased when domatia were closed. With *I. degenerans*, moreover, we found that the previous diet of the cannibal attenuated the effect of domatia on cannibalism.

5. We conclude that domatia can protect young predatory mites against cannibalism by adults and that the diet of cannibals affects the rate of cannibalism.

Key words. Antipredator behaviour, coffee, diet, indirect plant defence, intra-specific predation, Phytoseiidae, sweet pepper.

Introduction

Plants are known to interact with the enemies of their herbivores, thus reducing herbivory (Price *et al.*, 1980; Sabelis *et al.*, 1999; Kessler & Baldwin, 2002). To achieve this indirect defence, plants produce herbivore-induced volatiles to attract predators and parasitoids (Dicke, 1999; Janssen *et al.*, 2002; Kessler & Baldwin, 2002), offer pollen and nectar as alternative food to the enemies (Beattie, 1985; Pemberton & Lee, 1996; Sabelis & van Rijn, 1997), or provide shelter to natural enemies (Beattie, 1985; O'Dowd & Willson, 1989; Pemberton & Turner, 1989; O'Dowd & Willson, 1991; Walter, 1996). Examples of shelter provided by plants are leaf domatia. They are found in the bifurcation of veins on the underside of the leaves of many plant species (O'Dowd & Willson, 1989; Pemberton & Turner, 1989; Grostal & O'Dowd, 1994; O'Dowd & Pemberton, 1994;

Walter, 1996; Agrawal, 1997, 2000), and consist of tufts of hair, pockets, pits or pouches (Pemberton & Turner, 1989). They are mainly inhabited by predatory and fungivorous mites and are therefore referred to as acarodomatia (Pemberton & Turner, 1989; O'Dowd & Pemberton, 1998). A mutualistic interaction between plants and the mites through leaf domatia has been hypothesised, with the mites being protected inside the domatia (Norton *et al.*, 2001; Faraji *et al.*, 2002a). This would result in increased survival of the mites, resulting in an increased consumption of herbivores or plant-pathogenic fungi, thereby providing benefit to the plant (O'Dowd & Willson, 1991; Walter & O'Dowd, 1992; Grostal & O'Dowd, 1994; Walter, 1996).

Many studies have shown that plants with natural domatia or artificial domatia harbour more individuals and species of carnivorous and fungivorous arthropods (Agrawal & Karban, 1997; Agrawal *et al.*, 2000; Norton *et al.*, 2000; English-Loeb *et al.*, 2002; Matos *et al.*, 2006), but surprisingly, only a few studies have identified what kind of protection domatia actually offer to the mites. Thus far, it is clear that domatia can protect the mites against adverse abiotic conditions such as drought (Walter & O'Dowd, 1992; Grostal & O'Dowd, 1994), intra-guild predation

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(Norton *et al.*, 2001) and counterattacking prey (Faraji *et al.*, 2002a), but not whether they also offer protection against cannibalism. Cannibalism is a common ecological interaction in nature (Polis, 1981; Elgar & Crespi, 1992), and occurs frequently in predatory mites (Croft & Croft, 1996; Schausberger, 2003; Montserrat *et al.*, 2006).

In this paper, we studied the possible role of domatia in reducing cannibalism. We used two plant species, coffee plants (*Coffea arabica* L.) (Rubiaceae) and sweet pepper plants (*Capsicum annuum* L.) (Solanaceae). These two species have different types of domatia: those of coffee are pit shaped and are located in the primary vein axils on the underside of leaves (O'Dowd, 1994), whereas sweet pepper plants have tufts of hair (Faraji *et al.*, 2002a, b). For coffee, we used the two most common predatory mite species in coffee fields in Brazil (Pallini-Filho *et al.*, 1992): *Iphiseiodes zuluagai* and *Amblyseius herbicolus*. The main stages found inside the domatia in the field are eggs and moulting mites, suggesting that domatia are important sites for mite reproduction and development. However, adult predatory mites are also capable of entering the domatia. Both predatory mites are known to feed on many phytophagous mite species and adults cannibalize on young stages.

On sweet pepper, we used the predatory mite *I. degenerans*. This species occurs on a wide range of plants (De Moraes *et al.*, 2004) and it produces clusters of eggs inside sweet pepper domatia (Faraji *et al.*, 2002a). It is used as a natural enemy of the western flower thrips, *Frankliniella occidentalis* Pergande in a number of crops in greenhouses, including sweet pepper (Faraji *et al.*, 2002a).

We hypothesised that the presence of both types of domatia would decrease the risk of cannibalism.

Material and methods

Mite and plant rearing

Cultures of *I. zuluagai* and *A. herbicolus* were started with mites collected from a coffee field in Viçosa, Minas Gerais State, Brazil. *Iphiseiodes zuluagai* was reared on arenas made from a grey plastic sheet (25×20 cm) on top of a wet sponge in a water-containing tray. *Amblyseius herbicolus* was reared on similar arenas, but made of black plastic because it is easier to see the light-coloured mites against this background (*I. zuluagai* is dark). Paper tissue was wrapped over the edges of the arena, serving as a water source and as a barrier. Both populations were fed on a diet of cattail (*Typha* spp.) pollen. A few fibres of cotton wool were supplied under a small roof-like structure, cut from a transparent plastic sheet (3×3 cm); these served as oviposition sites.

Iphiseius degenerans was reared on arenas consisting of a grey PVC sheet (30×21 cm) on top of a wet sponge in a water-containing tray (van Rijn & Tanigoshi, 1999). Barriers and water sources were identical to those of *I. zuluagai* and *A. herbicolus*. Each arena was divided into four by three strips of filter paper (1×30 cm). The mites were fed with birch pollen (van Rijn & Tanigoshi, 1999), and cotton threads were added as oviposition substrate (0.5 mm thick, 2 cm long and black). To prevent cannibalism of juveniles by adults, threads were collected twice per week and put on a clean arena without adults.

Experimental procedure

The experiments with *I. zuluagai* and *A. herbicolus* were carried out at the Federal University of Viçosa, Minas Gerais, Brazil. Coffee leaves were collected from six plants in a coffee field (*Coffea arabica* var. Catuai), free of pesticides, in Viçosa, Brazil. Leaf discs were punched out of the mid-part of leaves (25 mm diameter), with the midribs in the middle of the discs and each disc having four domatia. The discs were checked for the presence of mites, and only discs without mites were used. Each leaf disc was embedded upside-down in agar (20 g of agar/l of water) in a small Petri dish (3.5 cm diameter), making the abaxial side with the domatia available to the mites. Domatia were blocked with a drop of glue (Tenaz®, Henkel Ltd, São Paulo, Brazil, water-based, non-toxic), discs with open domatia received a drop of glue next to the domatia. Care was taken to assign leaf discs from the same plants to all treatments.

Larvae were obtained by putting several adult females on a new rearing arena and allowing them to oviposit for 1 day. Subsequently, the adult females were removed and the eggs were allowed to hatch. Five of these newly-hatched larvae (12 h old) and one adult female mite were randomly placed on each leaf disc (20 replicates with open domatia and 20 with blocked domatia). Because each domatium can harbour several larvae, there was ample space for the larvae inside the domatia. As a control for mortality other than through cannibalism, five larvae were incubated on a leaf disc without an adult female (10 replicates with open and closed domatia each). Hence, there were two factors, resulting in four treatments: closed and open domatia crossed with the presence or absence of a cannibal. The Petri dishes were closed with Parafilm with small holes, and a mite-proof mesh was put on top of the Parafilm and secured with a rubber band to prevent escape of larvae. The Petri dishes were placed upside-down on a tray covered with mesh so that the side with domatia was facing downwards, as on leaves on a plant, but allowing air to move through the mesh and Parafilm to avoid condensation of water on the leaf discs. The coffee leaf discs were kept inside a climate cabinet at 25 °C, $60 \pm 5\%$ RH and 14 h light, corresponding to the average conditions in Viçosa. Mortality of the larvae was scored after 24 h.

Experiments with *I. degenerans* were carried out at the University of Amsterdam, the Netherlands. Ten sweet pepper plants were grown from seeds in a greenhouse inside cages ($100 \times 60 \times 100$ cm) to prevent infestation by herbivores. Leaf discs were punched out of the mid-part of leaves (24 mm diameter), with the midribs in the middle of the discs and each disc having four to eight domatia. This gave ample space inside the domatia for all larvae during the experiment. Leaf discs with and without domatia were prepared as described above for the coffee leaf discs.

One adult female mite and five eggs (30–46 h old) were placed on sweet pepper leaf discs with and without domatia. Eggs were chosen because they are more easily found in cultures of *I. degenerans* than larvae, because of the high rates of

cannibalism in these cultures. *Iphiseius degenerans* is not capable of cannibalising on eggs (Faraji *et al.*, 2002b), but we used eggs of 30–46 h old which all hatched within the experimental period. Because *I. degenerans* is capable of recognising kin (Faraji *et al.*, 2000) and cannibalise less on kin (F. Faraji, pers. comm.), we used eggs of a strain originating from Israel and adults from a Moroccan strain. Eggs from a cohort, hence, of the same age, were put inside a domatium on leaves with open domatia; on discs with closed domatia, they were placed next to the main vein. As a control for mortality other than cannibalism, eggs were placed on leaf discs without an adult female. The Petri dishes were closed with Parafilm with small holes to avoid condensation, and were placed upside-down on a box covered with a mesh to simulate the natural position of the leaf while allowing for ventilation. Leaf discs were incubated at 25 °C, 60 ± 5% RH, and 16 h light, corresponding to conditions in greenhouses in the Netherlands. After 24 h, we counted the numbers of surviving larvae that hatched from the eggs.

Because preliminary experiments with *I. degenerans* showed no effect of domatia on cannibalism, and females in the culture were unable to cannibalise (see above), we added two extra treatments, which were similar to above, except that the females were incubated with young conspecific larvae and without other food for 48 h. This group of females thus had cannibalised prior to the experiment. This resulted in six treatments: closed or open domatia, either without an adult female, with an adult female from the culture (hence, fed on pollen), or with an adult female fed with conspecific larvae. Twenty replicates were done for all treatments, but one replicate with open domatia and an adult female that was fed larvae was lost.

Larval survival in the different treatments on the coffee system were compared per predatory mite species with a generalised linear model with binomial error distributions (R Development Core Team, 2005), those in the sweet pepper system with a similar model, but with quasibinomial error distributions to correct for overdispersion (Crawley, 2007). Contrasts between treatments were assessed through model simplification by combining treatments (Crawley, 2007).

Results

On coffee leaf discs with *A. herbicolus*, there was a significant effect of the presence of a cannibalistic female and of domatia on the proportion of larvae that were found dead (Fig. 1, presence of cannibal: deviance = 83.4, d.f. = 1,57, $P < 0.0001$, domatia: deviance = 5.9, d.f. = 1,58, $P = 0.015$). The proportion of dead larvae was very low in absence of a cannibal, showing that survival of larvae was almost 100% (Fig. 1). Moreover, there was no effect of domatia being open or closed on mortality in absence of a cannibal (Fig. 1, deviance = 1.25, d.f. = 18,19, $P = 0.26$). The mortality risk was highest in the presence of a cannibal and closed domatia (Fig. 1), showing that cannibalism can cause high mortality. In the presence of a cannibal, domatia had a significant effect on mortality (Fig. 1, deviance = 8.6, d.f. = 38,39, $P = 0.003$). The interaction between the presence of a cannibal and domatia was not significant (deviance = 0.603,
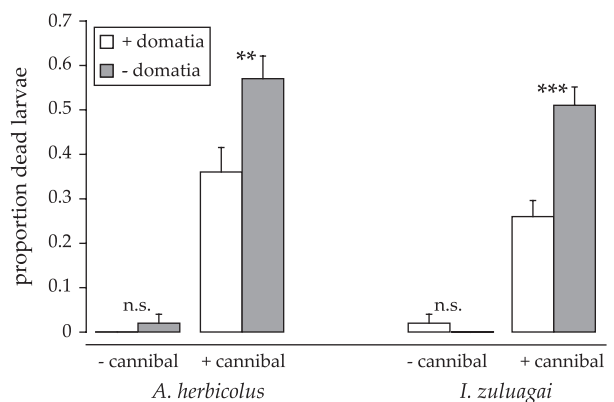

Fig. 1. Average number (+S.E.) of larvae of *Iphiseiodes zuluagai* and *Amblyseius herbicolus* killed per day in the presence (+cannibal) or absence (−cannibal) of cannibalistic adult female conspecifics on coffee leaf discs with open (white bars) and closed domatia (grey bars). The significance of the effect of open or closed domatia within cannibal treatments is indicated above the bars: n.s.: not significant; **: $P < 0.01$; ***: $P < 0.001$.

$P = 0.437$). In conclusion, domatia protect against cannibalism of larvae of *A. herbicolus* by adult females.

For *I. zuluagai*, a similar pattern was found; again there was a significant effect of the presence of a cannibalistic female and of domatia on the proportion of larvae that died (Fig. 1, presence of cannibal: deviance = 67.2, d.f. = 1,57, $P < 0.0001$, domatia: deviance = 8.6, d.f. = 1,58, $P = 0.003$). The interaction between the presence of a cannibal and domatia was again not significant (deviance = 3.0, $P = 0.084$), and the proportion of dead larvae was again very low in absence of a cannibal (Fig. 1). Moreover, there was no effect of domatia on mortality in absence of a cannibal (Fig. 1, deviance = 1.54, d.f. = 18,19, $P = 0.21$). The mortality risk was again highest in the presence of a cannibal and closed domatia (Fig. 1). Domatia had a significant effect on mortality when a cannibal was present (Fig. 1, deviance = 13.4, d.f. = 38,39, $P < 0.001$). Hence, domatia also offer protection against cannibalism in *I. zuluagai*.

For *I. degenerans* on sweet pepper plants, there was also a significant effect of cannibal treatment (cannibal absent, cannibal previously fed pollen, cannibal previously fed conspecific larvae) on the fraction of dead larvae (Fig. 2, deviance = 119.9, d.f. = 2,115, $P < 0.0001$), but there was no significant effect of domatia (deviance = 1.66, d.f. = 1,117, $P = 0.239$). However, there was a significant interaction between the presence of a cannibal and domatia (deviance = 12.4, d.f. = 2,113, $P = 0.006$), indicating that the effect of domatia depended on the cannibal treatment. Contrast analysis showed that the proportion of dead larvae differed significantly among all three cannibal treatments (Fig. 2, all *P*'s < 0.05). Within the treatments without cannibal or with a cannibal previously fed pollen, there was no significant effect of domatia (without cannibal: $F = 0.43$, d.f. = 38,39, $P = 0.52$, with cannibal from pollen: $F = 0.93$, d.f. = 38,39, $P = 0.34$), but when cannibals had previously fed on conspecific larvae, there was a highly significant effect of domatia ($F = 8.39$, d.f. = 37,38, $P = 0.006$), with domatia again reducing the risk of cannibalism (Fig. 2). We
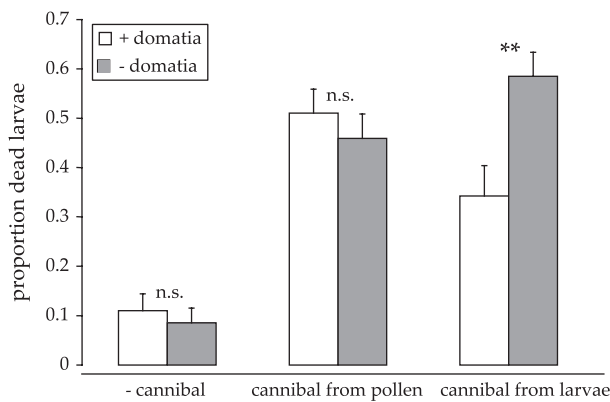
Fig. 2. Average number (+S.E.) of *Iphiseiodes degenerans* larvae killed per day in the absence (−cannibal) or presence (+cannibal) of cannibalistic adult female conspecifics that were either fed pollen (cannibals from pollen) or conspecific larvae (cannibals from larvae) on sweet pepper leaf discs with open (white bars) and closed domatia (grey bars). See legend to Fig. 1 for further explanation.

conclude that the domatia of sweet pepper can also protect against cannibalism. Moreover, in *I. degenerans* this protection depends on the previous diet of the cannibal.

Discussion

Our results show that domatia on leaves of coffee and sweet pepper can decrease cannibalism on larvae of predatory mites. In the system of *I. zuluagai* and *A. herbicolus* on coffee leaves, domatia decreased cannibalism. In the system of *I. degenerans* on sweet pepper leaves, domatia also decreased cannibalism, but only when the previous diet of the adult predatory mite consisted of conspecific larvae (instead of birch pollen). Our paper is the first to report on the effects of domatia on cannibalism, as well as on the interaction between predator diet and the protection of prey by domatia. Moreover, our study shows that both pit-shaped domatia and tuft-shaped domatia can affect the risk of cannibalism.

Interestingly, the larvae experienced reduced risks of cannibalism in the presence of domatia, even though the adults can also enter the domatia. It has been suggested that prey do not use domatia because they would run a higher risk of encountering predators that use the domatia for shelter (Sabelis *et al.*, 1999). For reasons as yet unknown, this argument does not seem to hold for potential victims of cannibalism. Perhaps the increased spatial structure of leaves with domatia reduces cannibalism. Several studies have shown that the presence of a spatial structure decreases the effects of predation and intra-guild predation (Langellotto & Denno, 2004; Janssen *et al.*, 2007). If this also holds for domatia, this suggests that even slight increases in spatial structure, such as domatia, may have large effects on predatory interactions. Similar findings with respect to leaf hairs were reported by Roda *et al.* (2000).

For *I. degenerans*, the predator on sweet pepper, we found that diet of the cannibals affected the effect of domatia. There are several explanations for this. First, the behaviour of the

cannibalistic adult female may change with previous diet. For example, the cannibals may be more or less motivated to cannibalise depending on their previous diet. In this case, it would be expected that the cannibals kill different numbers of larvae, even in absence of domatia, and this was indeed the case: with closed domatia, cannibals that were previously fed larvae killed more larvae than cannibals previously fed pollen (Fig. 2, deviance = 4.9, d.f. = 1,38, P = 0.048). It would then be expected that they would also do so in the presence of domatia, but here cannibals from pollen killed more larvae than cannibals fed larvae (Fig. 2, deviance = 5.6, d.f. = 1,37, P = 0.031). We therefore tentatively reject the idea that diet affected cannibalism through the behaviour of the cannibal.

The second explanation for the effect of diet on cannibalism is that the behaviour of the larvae changed as a function of the diet of the cannibals. It is known that predator diet is important in inducing anti-predator behaviour in prey (Mathis & Smith, 1993; Venzon *et al.*, 2000; Persons *et al.*, 2001; Magalhães *et al.*, 2005), and *I. degenerans* larvae may show the same behaviour with respect to cannibalism. In this case, we would expect the larvae to seek more refuge in the domatia when cannibals had previously fed on conspecific larvae than with cannibals that had fed on pollen. Unfortunately, we could not observe behaviour of the larvae during the experiment to verify this, because the leaf discs had to remain sealed to prevent escapes. It could be argued that the diet of both groups of cannibals would become more similar in the course of the experiment, because the present diet would only consist of larvae. It is known that both past and present diet affect behaviour of prey (Meng *et al.*, 2006), but it is still unclear whether prey would be able to track changes in predator diet instantaneously. Possibly, changes in the diet of a cannibal can only be perceived by its prey after some time.

These considerations raise the question why there was an effect of domatia on cannibalism in the coffee system, even when the cannibals were not specifically reared on a diet of larvae. The answer may well lie in differences in rearing methods. Eggs of *I. degenerans* were taken from the rearing units and incubated in absence of adults. The adults therefore only fed on pollen. In contrast, the rearing units of predatory mites from the coffee system contained all stages of the predator, and the adult predators possibly did feed on juvenile conspecifics. Hence, it is possible that the diet of the cannibals also played a role in the coffee system. This remains to be investigated.

It has been hypothesised that leaf domatia mediate mutualistic interactions between plants and predatory and fungivorous mites because they protect the mites against adverse conditions (Pemberton & Turner, 1989; O'Dowd & Willson, 1991; Grostal & O'Dowd, 1994; Walter, 1996) and against other predators or omnivores (Norton *et al.*, 2001; Faraji *et al.*, 2002a, b). Owing to this protection, the survival of predators on plants with domatia would be higher than on plants without domatia (Agrawal & Karban, 1997; Agrawal *et al.*, 2000; English-Loeb *et al.*, 2002). Our work confirms the hypothesis of protection through domatia: through the use of domatia, larvae of predatory mites can escape from conspecific adults, thus decreasing the risk of cannibalism. It remains to be investigated whether this reduced cannibalism results in decreased populations of herbivores. This

is not immediately obvious, because cannibalism can also serve to increase persistence of predator populations when food is scarce (the so-called life-boat mechanism, van den Bosch *et al.*, 1988). In this case, reduction of cannibalism might decrease persistence of predators on the plant. However, such a life-boat mechanism only holds when juveniles and adults feed on different food sources, and this is not the case in our system. We therefore expect that reduction of cannibalism through domatia would result in a decrease of herbivore density on the plant.

Acknowledgements

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