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Host plant manipulation of natural enemies: leaf domatia protect beneficial mites from insect predators

Abstract Acarodomatia are small tufts of hair or invaginations in the leaf surface and are frequently inhabited by several taxa of non-plant-feeding mites. For many years, ecologists have hypothesized that these structures represent a mutualistic association between mites and plants where the mites benefit the plant by reducing densities of phytophagous arthropods and epiphytic microorganisms, and domatia benefit the mite by providing protection from stressful environmental conditions, other predaceous arthropods, or both. We tested these hypothesized benefits of domatia to domatia-inhabiting mites in laboratory and growth chamber experiments. In separate experiments we examined whether domatia on the wild grape, *Vitis riparia*, provided protection against drying humidity conditions or predaceous arthropods to two species of beneficial mite: the mycophagous species *Orthotydeus lambi*, and the predaceous species *Amblyseius andersoni*. For both taxa of beneficial mite, domatia significantly increased mite survivorship in the presence of the predatory bug, *Orius insidiosus* and the coccinellids *Coccinella septempunctata* and *Harmonia varigata*. There was no evidence for a protective effect of domatia with a third species of predatory arthropod, lacewing larvae *Chrysoperla rufilabris*. In contrast, there was no evidence for either species of beneficial mite that domatia provided any protection against low humidity. Thus in this system the primary mechanism by which domatia benefit beneficial mites is by protecting these organisms from other predatory arthropods on the leaf surface.

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Introduction

Ecologists and entomologists have long recognized that physical aspects of the leaf surface can influence the behavior and population dynamics of arthropod predators and parasitoids. Traits such as glandular trichomes (e.g., Farrar and Kennedy 1991), rolled versus un-rolled leaves (Clark and Messina 1998), leaf hairiness (e.g., Treacy et al. 1987), and the presence of cuticular waxes (Eigenbrode et al. 1998) have been demonstrated to make large differences in predator abundance and prey consumption rates. Recently, one such plant trait, the presence of acarodomatia, has received increasing attention from ecologists. Acarodomatia are small tufts of hair or invaginations of the leaf surface located on the underside of leaves, and are found on a wide number of plant species throughout the world (see Walter 1996 for a review). These structures are commonly associated with elevated densities of non-plant feeding mites (Walter and O'Dowd 1992; Walter 1996) and recent work has documented that plants with these structures are better protected against phytophagous mites (Grostal and O'Dowd 1994; Agrawal and Karban 1996; G. English-Loeb and A.P. Norton, unpublished work), and a plant pathogen (Norton et al. 2000). Thus these structures may represent a diffuse mutualism between beneficial mites and plants, where the mites attain higher densities on plants with these structures compared to plants lacking them, and plants with domatia benefit from lower levels of pathogens and/or herbivores.

Several hypotheses have been advanced to explain the mechanism by which these mites benefit from these structures (O'Dowd and Willson 1991):

1. That domatia alter leaf surface humidity levels, and thus protect these mites from desiccating conditions
2. That domatia provide physical refuge from other predaceous arthropods

3. That the dense tufts of hair on leaves with these structures are better at trapping pollen and fungal spores than plants without domatia, thus providing a higher density of food for microbivorous or generalist feeding taxa

In this paper we report the results from experiments that test the first two of these hypotheses with two separate taxa of beneficial mites on wild grape, *Vitis riparia*.

Physical characteristics of the leaf are believed to alter humidity levels on the leaf surface (Johnson 1975; Schuepp 1993), and several species of phytoseiids (including *A. andersoni*) have been shown to be sensitive to low relative humidities (Croft et al. 1993). As leaves transpire the stomata open for gas exchange, releasing air saturated with water vapor. This very humid air mixes with drier ambient humidity air creating a gradient or *boundary layer* of high humidity. Structures that disturb air movement increase the size of the boundary layer, leading to higher humidity levels at the leaf surface. Tuft form domatia, as are found on *V. riparia*, may have reduced air movement within them, resulting in higher humidity levels.

Leaf characteristics may also alter the behavior and efficiency of predaceous arthropods, and domatia may act to provide a hiding place or refuge to small mites from larger predators, reducing predation levels. Leaf trichomes and hairiness have been demonstrated to interfere with the searching efficiency of generalist predators including the coccinellid *Delphastus pusillus* on poinsettia *Euphorbia pulcherrima* (Heinz and Parrella 1994), the lacewing larva *Chrysoperla rufilabris* on cotton (Treacy et al. 1987), and the predatory mite *Phytoseiulus persimilis* in greenhouse gerberas *Gerbera jamesonii* (Krips et al. 1999). *Orius* spp. (Cloutier and Johnson 1993; Wittman and Leather 1997) and other species of predaceous mites (MacRae and Croft 1997; Schausberger 1999) have been demonstrated to feed on phytoseiid mites. Predaceous mites appear to be vulnerable to at least some species of predatory arthropods, and domatia may provide a refuge from these generalist predators.

Wild grape is abundant throughout the eastern portion of North America, growing along the edges of woodlots, creeks and roadsides. This species possesses conspicuous tuft form domatia for which there is heritable variation (G. English-Loeb and A.P. Norton, unpublished work). Associated with the domatia on wild grape are several taxa of non-plant-feeding mites. The two most common species in upstate New York, *Orthotydeus lambi* (Tydeidae) and *Amblyseius andersoni* (Phytoseiidae), have been demonstrated to benefit the plant by reducing the severity of powdery mildew (*Uncinula necator*) and European red mite (*Panonychus ulmi*) infestations respectively (English-Loeb et al 1998; Duso 1989). Further, both of these taxa are more abundant on wild grape plants with domatia than on plants where these structure have been removed (Norton et al. 2000; G. English-Loeb and A.P Norton, unpublished work). Using laboratory assays we tested two non-exclusive hypotheses to explain why the densities of these mites on plants with domatia were higher than on plants without domatia.

Materials and methods

Humidity assays

There is ample evidence that phytoseiid mites are sensitive to low humidities (e.g., Croft et al. 1993), but there are not equivalent data on the impact of humidity on tydeids. Consequentially we measured the impact of humidity on *O. lambi* in the absence of any plant effect. We caged groups of adult mites (5 per cage) in small cages made from 0.5-ml centrifuge tubes and dialysis tape, and regulated humidity by placing individual cages over solutions of glycerol and water (Braun and Braun 1958). Six humidity levels (100, 98, 95, 85, 78, and 40% relative humidity, RH, at 27°C) were created, and five *O. lambi* were placed into each cage with a small amount of cattail pollen for food. Mortality and reproduction were determined after 36 h under a dissecting microscope. These data were analyzed using a generalized linear model with a natural log link function and Poisson-distributed errors (McCullagh and Nelder 1989).

We examined the impact of low humidity on *O. lambi* or *A. andersoni* in growth chamber experiments on potted grape vines. We were interested in the ability of domatia to ameliorate the impact of low humidity conditions on mite survival and reproduction and thus used a factorial design where we simultaneously manipulated the presence of domatia and the ambient humidity level in the experiment. Two leaves on each vine were selected, and one leaf was given a domatia-present treatment and one a domatia-absent treatment. Access to domatia on the domatia-absent leaves was prevented by covering all of the domatia on the leaf with a small amount of pruning tar (Walter E. Clark and Son, Orange, Conn., USA). On domatia-present leaves we placed a small amount of pruning tar adjacent to each domatia to control for any direct effects of pruning tar on the mites or the plants. Adult mites were then transferred to each of these treated leaves (30 mites per leaf for *O. lambi*; 5 mites per leaf for *A. andersoni*) and a ring of tanglefoot was placed around the base of each petiole to prevent mites from moving off of the treated leaves. These vines (each with one domatia-absent and one domatia-present leaf) were randomly assigned to replicated low (45% RH) or high (95% RH) humidity treatments. For both experiments we placed two vines within each growth chamber, resulting in a nested design structure with two replicates of each domatia treatment within each replicated humidity treatment. We used a total of 16 growth chambers for the tydeid assay (64 leaves) and 12 growth chambers (48 leaves) for the phytoseiid assay. Natural densities of *O. lambi* on *V. riparia* average >20 mites per leaf in upstate New York by mid summer, while *A. andersoni* densities are considerably more variable. A survey of 400 wild *V. riparia* leaves in 1999 found an average of 0.7 *A. andersoni* per leaf, but more than 7% of leaves with phytoseiids had five or more mites per leaf (G. English-Loeb and A.P. Norton, unpublished work).

We tested the hypothesis that the benefit of domatia to the mites was greater under the more stressful humidity conditions using mixed model analysis of variance. Relative humidity (2 levels), domatia (2 levels) and their interaction were fixed effects, and growth chamber nested within humidity along with an interaction between this nested factor and domatia were random effects. We included these random effects to account for the nested design structure and possible corelations between observations within individual growth chambers. For the tydeid data we ensured normaility and homoscedasticity by transforming the data by ln(y+1). For the phytoseiid data the low numbers of mites per experimental unit made meeting the assumptions of normally distributed errors and equal variance impossible. Thus we implemented the above design in a generalized linear model with a log link function and Poisson error distribution (McCullagh and Nelder 1989). We ensured that the transformation or error structure was appropriate by

examining plots of the residuals against predicted values and by examining the magnitude of the dispersal parameter in the generalized linear model. All analyses were carried out in either SAS proc mixed or in the SAS macro glimmix (SAS Institute 1997).

Predation assays

We used a design similar to the humidity experiments to determine if domatia could protect either mite species from predation. We examined the effect of domatia on mite survivorship in the presence and absence of predation in a 2×2 factorial design. Detached *V. riparia* leaves were placed on wet cotton inside 75-mm petri dishes and randomly selected to receive one of four treatments: (1) blocked domatia, predators present; (2) blocked domatia, predators absent; (3) intact domatia, predators present; (4) intact domatia, predators absent. We used two separate plant clones in each of these assays with equal numbers of leaves from each clone in each treatment. We transferred mites to these leaves (20 *O. lambi* adults or 5 *A. andersoni* adults) along with a small amount of cattail pollen for food and then placed these leaves in a growth chamber at 27°C, 75% RH and 18:6 h light:dark cycle. We counted the mites under dissecting microscope 24 and 48 h after the release of predators. A total of six experiments (three for each mite species) were run: *O. lambi* versus the minute pirate bug *Orius insidiosus* (adults, 1 per leaf, 18 replicates per treatment), *O. lambi* versus the lady beetle *Coccinella septempunctata* (adults, 1 per leaf, 16 replicates), *O. lambi* versus the lacewing *Chrysoperla rufilabris* (2nd instars, 2 per leaf, 16 replicates*) A. andersoni* versus *Ori. insidiosus* (adults, 1 per leaf, 32 replicates), *A. andersoni* versus the lady beetle *Harmonia varigata* (adults, 1 per leaf, 16 replicates*), A. andersoni* versus *Ch. rufilabris* (2nd instars, 2 per leaf, 16 replicates).

Source of organisms

O. lambi were collected from wild *V. riparia* growing on the Cornell University New York State Agricultural Experiment Station (NYSAES) campus in Geneva, New York, and were transferred to the experimental arenas within 48 h after collection. *A. andersoni* were collected from *V. riparia* as well, and had been maintained in a laboratory colony with *V. riparia* leaves as a rearing substrate. The colonies used for these experiments had been in culture for <8 months. *Ori. insidiosus* and both coccinellid species were collected from station plantings and then held in the laboratory on grape leaves with mites for 24 h prior to the start of each assay. The lacewing larvae used were commercially reared (Rincon Vitova insectaries, Inc., Ventura, Calif., USA) and were used immediately after we received them. We collected *V. riparia* leaves from field plantings growing in a common garden planting at NYSAES. We randomly chose leaves from two clones for the predation assays and blocked for clone when setting up the treatments. Leaves

for the assays with *Ch. rufilabris* were collected from the same two clones from greenhouse-grown material. Prior to releasing organisms, assay leaves were examined and all arthropods were removed.

Data analysis

We analyzed these data using two-way mixed-model ANOVA, with domatia treatment (2 levels), predator treatment (2 levels) and their interaction as fixed effects, and with plant clone and its interaction with domatia and predation treatments as random factors. Each predator and mite species combination was analyzed separately. Experiments with *Ori. insidiosus* and *O. lambi* and *Ori. insidiosus* and *A. andersoni* led to marginally significant results, so we repeated these experiments and the results from both trials were combined. This additional factor (assay date) and it's interactions with all fixed effects were included as random effects in these analyses. All tydeid data were ln(y+1) transformed to ensure normality and homoscedasticity. As above, the low numbers of phytoseiids used in the experimental units made meeting the assumptions for ANOVA difficult. These analyses were performed as generalized linear models with a log link function and a Poisson error structure.

In addition to the main effects (presence or absence of domatia and presence or absence the predator species), we were interested in the interaction between these two terms. Our previous work with these organisms (Norton et al. 2000; G. English-Loeb and A.P. Norton, unpublished work) indicates that domatia increase the densities of these mite species. These experiments are designed to test the mechanism(s) for this benefit. Thus when the interaction *P*-value was <0.10 we examined the hypothesis that the effect of domatia was greater in the presence of predation than in its absence using one-tailed *t*-tests. All analyses were run in either SAS proc mixed (for the tydeid data) or the SAS macro glimmix (for generalized linear mixed models) (SAS Institute 1997).

Results

Humidity effects on *O. lambi*

When measured off of the leaf surface, there was a significant and dramatic effect of humidity on both *O. lambi* survivorship and reproduction ($F_{6,12}$=7.48, P=0.002 for survivorship, $F_{6,12}$=32.72, P<0.001 for reproduction). At 40% relative humidity, only 27% of mites survived to 36 h, and none successfully reproduced. In contrast, at 95% relative humidity more than 90% of mites survived and these mites produced an average of 1.9 progeny per mite.

Fig. 1 Effect of humidity on **A** *Orthotydeus lambi* and **B** *Amblyseius andersoni* the presence and absence of domatia (*solid circles* domatia blocked, *open circles* domatia intact). *Vertical bars* represent SEs
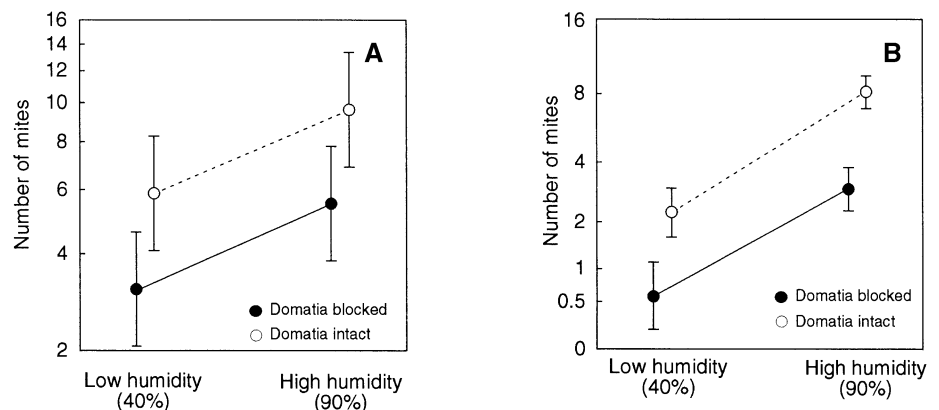
Table 1 Mixed model analysis of variance statistics for humidity experiments. We used maximum likelihood methods to analyze these mixed models (models that include both fixed and random effects). This analysis method provides more robust estimates of effect sizes and confidence intervals, particularly when data sets are unbalanced. One consequence of maximum likelihood techniques is that the usual table of sums of squares is not produced, and F-statistics are generated using an approximation method (Littell et al. 1996)

Source	df^b	Type III F	$P>F$	χ^2	$P>F$
Orthotydeus lambi					
Fixed					
Humidity	1, 14	1.40	0.2558		
Domatia	1, 46	5.27	0.0159		
Humidity×Domatia	1, 46	0.00	0.9812		
Random[a]					
Growth chamber(Humidity)	1			10.135	0.0007
GC(Humidity)×Domatia	1			0.000	0.500
Amblyseius andersoni					
Fixed					
Humidity	1, 17.86	13.86	0.0016		
Domatia	1, 16.26	19.65	0.0005		
Humidity×Domatia	1, 17.86	0.06	0.8082		
Random[a]					
Growth chamber(Humidity)	1			0.860	0.177
GC(Humidity)×Domatia	1			1.160	0.141
Dispersion[c]=1.47	42			59.83	0.0364

[a] Random effects are tested with a single degree of freedom χ^2 test of the hypothesis that the variation due the factor is greater than 0, and are thus one-tailed tests
[b] Degrees of freedom in all models were calculated using the Satterthwaite approximation, which can generate non-integer values
[c] The dispersion parameter measures the amount of residual variation in the model relative to that expected assuming Poisson errors. A value >1 indicates there is more variation than expected while a value <1 indicates there is less than expected. All test statistics and SEs have been adjusted for this greater variance

Table 2 Mixed model analysis of variance statistics for predation assays with *Orthotydeus lambi*

Source	df^b	Type III F	$P>F$	χ^2	$P>F$
Orius insidiosus					
Fixed					
Predation	1, 66	13.21	0.0005		
Domatia	1, 66	13.61	0.0005		
Predation×Domatia	1, 66	4.85	0.0311		
Random[a]					
Assay	1			12.59	0.0002
Assay×Domatia	1			0.06	0.4020
Assay×Predation	1			0.00	0.5000
Assay×Domatia×Predation	1			0.00	0.5000
Coccinella septempunctata					
Fixed					
Predation	1, 59	5.02	0.0289		
Domatia	1, 59	5.14	0.0271		
Predation×Domatia	1, 59	6.37	0.0143		
Random[a]					
Clone	1			0.37	0.272
Clone×Domatia	1			0.00	0.500
Chrysoperla rufilabris					
Fixed					
Predation	1, 57	1.09	0.3009		
Domatia	1, 57.4	42.43	0.0001		
Predation×Domatia	1, 57	0.00	0.9985		
Random[a]					
Clone	1			0.005	0.4707
Clone×Domatia	1			0.000	0.5000

[a] Random effects were tested with a single degree of freedom χ^2 test of the hypothesis that the variation due the factor is greater than 0
[b] Degrees of fredom are estimated using the Satterthwaite approximation, which can give non-integer values

Table 3 Generalized linear mixed model analysis of predation on *A. andersoni*

Source	df[b]	Type III F	$P>F$	χ^2	$P>F$
Orius insidiosus					
Fixed					
Predation	1, 120.9	7.70	0.0064		
Domatia	1, 120.9	48.95	0.0001		
Predation×Domatia	1, 120.9	3.12	0.0797		
Random[a]					
Clone	1			1.93	0.082
Assay	1			0.27	0.303
Assay×Domatia	1			0.00	0.500
Assay×Predation	1			0.27	0.302
Assay×Domatia×Predation	1			0.00	0.500
Dispersion parameter[b]=1.272	119			153.54	0.018
Harmonia variegata					
Fixed					
Predation	1, 51	0.83	0.3674		
Domatia	1, 51	13.38	0.0006		
Predation×Domatia	1, 51	3.72	0.0592		
Random[a]					
Clone	1			1.76	0.0921
Clone×Domatia	1			0.00	0.5000
Dispersion parameter[c]=2.7934	50			144.51	<0.0001
C. *Ch. rufilabris*					
Fixed					
Predation	1, 60	55.30	0.0001		
Domatia	1, 60	0.61	0.4360		
Predation×Domatia	1, 60	7.64	0.0076		
Random[a]					
Clone	1			0.00	0.5000
Clone×Domatia	1			0.00	0.5000
Dispersion parameter[c]=3.8796	60			232.78	<0.0001

[a] Random effects were tested with a single degree of freedom χ^2 test of the hypothesis that the variation due the factor is greater than 0
[b] Degrees of fredom are estimated using the Satterthwaite approximation, which can give non-integer values
[c] The dispersion parameter measures the amount of residual variation in the model relative to that expected assuming Poisson distributed errors. A value >1 indicates there is more variation than expected while a value <1 indicates there is less than expected. All test statistics and SEs have been adjusted for this greater variance

Humidity×domatia interactions

For both mite taxa there was a decline in numbers with decreasing humidity and with the blocking of domatia. However, the significance of these two factors differed between the two species: For the tydeid, the domatia effect was significant but the humidity effect was not (domatia $F_{1,46}$=5.27, P=0.0159; humidity $F_{1,14}$=1.40, P=0.198) (Fig. 1A, Table 1), while for the phytoseiid both humidity and domatia were significant (domatia $F_{1,37.14}$=15.15, P=0.0004; humidity $F_{1,19.9}$=17.75, P=0.0004, Fig. 1B). For both mite taxa there was no indication of any interaction between domatia and humidity (P>0.75 in both cases). Thus while it appears that domatia benefit both species of mites and both mites are sensitive to low humidity, there is no indication that domatia protect these species from dry air.

Predation×domatia interactions

For each of the predator species tested there were significantly fewer *O. lambi* or *A andersoni* on treatments with predators than treatments without (Tables 2, 3). The amount of predation varied between the predator species, but was greatest for the lacewing *Ch. rufilabris* feeding on *O. lambi*. This species consumed more than 60% of the tydeids on leaves both with and without domatia within 24 h. For the two other predator species tested with *O. lambi* as prey (minute pirate bugs and seven spotted ladybeetles), we found dramatically less predation in the presence of domatia than when we had blocked them with tar (Fig. 2A–C; t_{66}=2.20, P=0.016 for *Ori. insidiosus*; t_{59}=2.52, P=0.007 for *C. septempunctata*). For lacewings however, we saw no effect of domatia either in the presence or in the absence of the predators (t_{58}=0.00, P=0.499). Domatia protected the tydeids from two of the three predators examined.

We found similar pattern of domatia×predator interactions with the phytoseiid *A. andersoni* as prey as we had with *O. lambi*. For two out of three predators examined, predation upon *A. andersoni* was greater in the absence of domatia than in the presence of these structures. Both the coccinellid beetle *H. variegata* and the minute pirate bug *Ori. insidiosus* consumed a smaller proportion of the mite population when domatia were present than when they were absent (Fig. 3A–C; t_{51}=1.93, P=0.03 for *H. variegata*; $t_{120.85}$=1.77, P=0.040 for *Ori. insidiosus*). Lacewing larvae behaved similarly in this experiment and the tydeid experiment: there was no evidence that domatia reduced the amount of predation on *A. andersoni* by this species (t_{60}=–2.76, P=0.996).
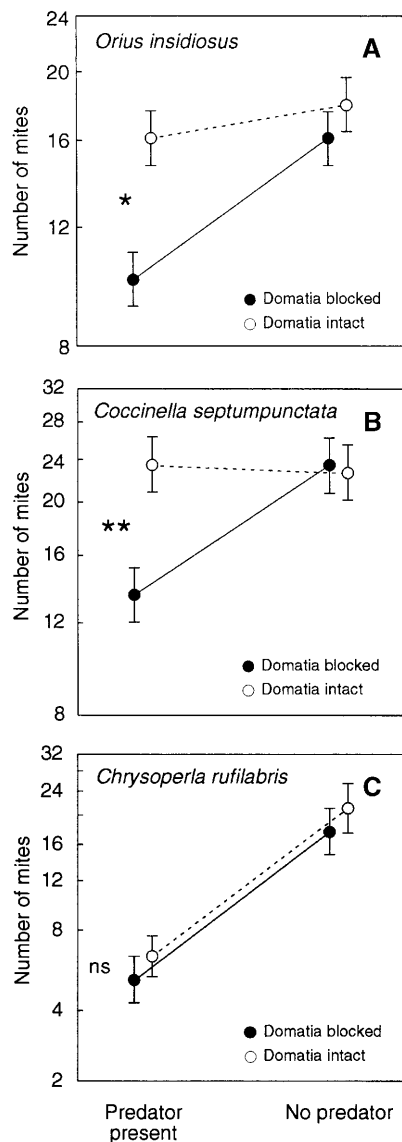
Fig. 2A–C Effect of predators on *O. lambi* abundance in the presence and absence of domatia. **A** *Orius insidiosus,* **B** *Coccinella septumpunctata,* **C** *Chrysoperla rufilabris* (*$P<0.05$, **$P>0.01$, *ns* not significant, one-tailed test of the hypothesis that there is more predation in the absence of domatia). *Bars* represent SEs
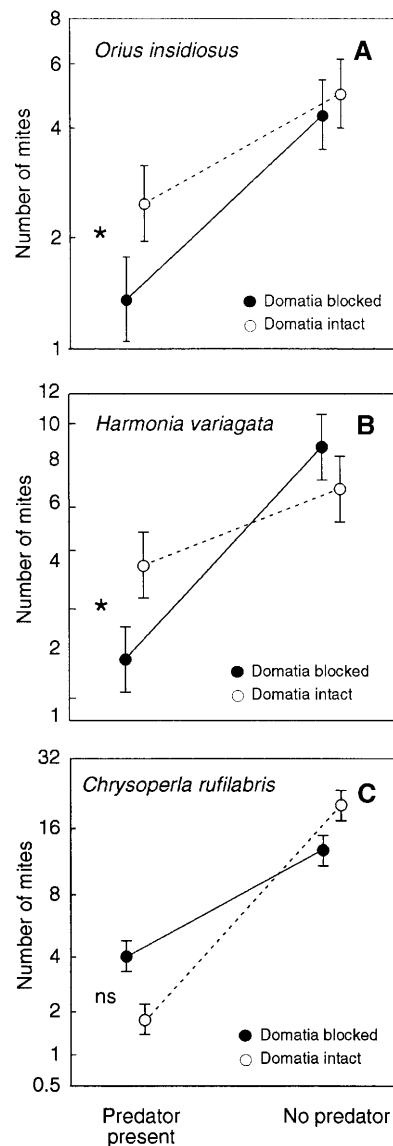

Fig. 3A–C Effect of predators on *A. andersoni* abundance in the presence and absence of domatia. **A** *Ori. insidiosus,* **B** *Harmonia variegata,* **C** *Ch. rufilabris* (*$P<0.05$, **$P>0.01$, *ns* not significant, one-tailed test of the hypothesis that there is more predation in the absence of domatia). *Bars* represent SEs

Discussion

We tested two hypotheses that have been proposed to explain the generally higher densities of beneficial mites on plants with domatia than plants without domatia. We found no support for a microclimate benefit from domatia, but strong support for the hypothesis that these structures protect small mites from other arthropod predators. For three out of four taxa of predaceous arthropods examined, predation on the tydeid or on the phytoseiid was significantly lower on leaves with domatia than on leaves without these structures. The magnitude of this effect was quite large: on leaves with the four predator taxa for which we found a benefit, intact domatia leaves averaged 72% more mites than leaves with blocked domatia. However, domatia did not protect against all species of predator. There was no effect of these structures in protecting either mite species against the actions of first instars of the lacewing *Ch. rufilabris.*

Both mites are sensitive to low humidity but domatia did not seem to protect them from this stress. In both assays there were fewer mites on leaves at low humidity than on leaves in high humidity, and this effect was significant for the phytoseiid *A. andersoni.* This suggests (at least for the *A. andersoni* assay) that these dry conditions made a difference to the humidity levels at the leaf surface and that leaf transpiration did not compensate for the dry air conditions of this treatment. Although the ef-

fect of humidity on *O. lambi* in the presence of a transpiring leaf was not significant, there was a strong and significant effect of low humidity on the mite in the absence of transpiring leaves. This difference between humidity effects on *O. lambi* in the presence and absence of transpiring leaves may indicate that either this species is capable of obtaining water from plant tissues or that the boundary layer surrounding the leaf was always large enough to keep humidity levels on the leaf surface high, or both. The fact that domatia did not reduce the deleterious effect of ambient humidity on the mites may mean that humidity levels inside of domatia are not much different from the levels outside of these structures. Domatia are hypothesized to have higher humidity levels inside them because the physical structure of domatia is thought to disrupt the movement of air across the leaf surface, resulting in a larger boundary layer. From these data we have no evidence that the tuft-form domatia found on *V. riparia* have this effect. We tested the effect of domatia at the extreme ranges of humidities that would commonly be found in the field. If domatia only increase leaf surface humidity by a small amount, it may be that at more moderate humidities domatia would have a measurable effect in protecting the mites. Our results also contrast with the results of Grostal and O'Dowd (1994) who found that there was a greater effect of domatia on reproduction by the phytoseiid *M. occidentalis* at low humidity than at high humidity.

Intraguild predation (where two predators that share a common prey species also feed on each other) and higher order predation more generally, may at times result in higher herbivore and pest densities and less effective biological control (reviewed by Rosenheim et al. 1995; Rosenheim 1998). Beneficial mites are vulnerable to predation (Cloutier and Johnson 1993; MacRae and Croft 1997), and larger arthropods may play a large role in their population dynamics. Determining when intraguild predation is an important component of herbivore population dynamics and what factors can alter the strength of predator-predator interactions is important for understanding arthropod population dynamics in both applied and basic systems. Our results suggest that domatia can reduce the effects of intraguild predation and/or predator-predator interactions on beneficial mite abundance.

In the *V. riparia* system, the presence of domatia has been demonstrated to result in higher densities of both beneficial mite taxa and to result in lower powdery mildew (*U. necator*) and lower European red mite (*P. ulmi*) densities. Thus if our laboratory results are representative of patterns in the field, host plants may be capable of reducing the impact of intraguild predation on beneficial taxa (via domatia) and thus providing greater protection against herbivores and pathogens.

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