How leaf domatia and induced plant resistance affect herbivores, natural enemies and plant performance

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Predators and plant resistance may act together to control herbivorous arthropod populations or antagonistically, which would reduce the control of pest populations. In a field experiment we enhanced predation by adding simulated leaf domatia to plants. Leaf domatia are small structures that often harbor predaceous arthropods that are potentially beneficial to the plant. We also manipulated host plant quality by inducing resistance with controlled, early season exposure of seedlings to spider mite herbivory.

Our manipulations had profound consequences for the natural community of arthropods that inhabited the plants. Leaf domatia had a direct positive effect on abundances of two species of bugs and one species of thrips, all of which are largely predators of herbivores. On leaves with domatia, each of the predators was found inside the domatia two to three times more often than outside the domatia. Eggs of predaceous bugs inside leaf domatia were protected from parasitism compared to eggs outside the domatia. The positive effects of leaf domatia on predator abundances were associated with reduced populations of herbivorous spider mites, aphids, and whiteflies. Plants with experimental leaf domatia showed significantly enhanced reproductive performance.

Induced resistance also affected the community of arthropods. Of the abundant predators, all of which also fed on the plant, only minute pirate bugs were negatively affected by induced resistance. Populations of herbivorous spider mites and whiteflies were directly and negatively affected by induction. In contrast, aphid populations were higher on plants with induced resistance compared to uninduced plants. Effects of induced resistance and domatia were additive for each of the predators and for aphids. However, spider mite and whitefly populations were not suppressed further by employing both induced resistance and domatia compared to each strategy alone. Our manipulations suggest that plant defense strategies can have positive effects on some species and negative effects on others. Negative effects of "resistance traits" on predators and positive effects on some herbivores may reduce the benefits of constitutive expression of resistance traits and may favor inducible defense strategies. Multiple plant strategies such as inducible resistance and morphological traits that aid in the recruitment of predators of herbivores may act together to maximize plant defenses, although they may also be redundant and not act additively.

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Variation in the intensity of predation, competition, host plant quality, and climatic factors have significant effects on populations of herbivorous arthropods (Karban 1989, 1992, English-Loeb 1990, Haukioja 1993, Cappuccino and Price 1995, Denno et al. 1995, Walde 1995). Although considerable debate has surrounded the relative importance of these factors in structuring ecological communities, no consensus has been reached

other than agreement that each factor can be important in some systems (Hairston et al. 1960, Strong 1984, 1992, Gange and Brown 1997). Aquatic ecologists have made considerable progress in this pursuit of understanding top-down and bottom-up forces using mesocosm experiments, and the emerging picture is that both are important in freshwater communities (Power 1992, Brett and Goldman 1996, 1997, Wallace et al. 1997). Moreover, interactions between trophic, competitive, and abiotic factors are likely to be the rule, rather than the exception (Boethel and Eikenbary 1986, Hare 1992, Hartvigsen et al. 1995, Walde 1995).

In terrestrial ecosystems, experiments are needed not only to assess the relative roles of factors such as host plant variation and predation, but also to construct sensible prescriptions for agricultural pest management with reduced pesticide inputs. Although breeding plants for resistance to herbivores and augmenting natural enemies of herbivores have traditionally been the focus of biologically-based pest management programs (DeBach and Rosen 1991, Panda and Khush 1995), interest in developing methods to induce host plant resistance has also been considered (Kogan and Paxton 1983, Karban 1991, Karban and Baldwin 1997, Karban et al. 1997, Agrawal et al. 1999a, Thaler 1999a, b, c). Unfortunately, we do not yet have a general sense for whether manipulations of host plant quality and augmentation of predaceous arthropods are compatible strategies, or whether they interact positively or negatively. In some systems it appears that plant resistance traits may have a negative effect on growth and development of predators and parasites of herbivores (e.g., Campbell and Duffey 1979, Orr and Boethel 1986, Duffey et al. 1995, Thaler 1999b); in other systems plant resistance traits appear to be beneficial in indirect ways including the attraction of predators and parasites of herbivores by volatile compounds associated with inducible resistance (Hare 1992, Eigenbrode et al. 1995, Pare and Tumlinson 1996, Takabayashi and Dicke 1996, Thaler 1999b).

In this study we manipulated levels of predation and host plant resistance simultaneously to understand their potential for control of herbivores. We manipulated levels of predation by augmenting plants with simulated leaf domatia (Putman and Herne 1964, Agrawal 1997, Agrawal and Karban 1997). Leaf domatia are tiny pockets or tufts of hair found on the undersides of thousands of perennial plant species (O'Dowd and Willson 1989, Brouwer and Clifford 1990, Walter 1996). Leaf domatia are very common and have been demonstrated to harbor predators of herbivores in many ecosystems world-wide (O'Dowd and Willson 1989, 1997, Pemberton and Turner 1989, Brouwer and Clifford 1990, Willson 1991, O'Dowd and Pemberton 1994, Rozario 1995). Such plant structures could have important consequences for populations of herbivores and plant performance (Marquis and Whelan 1996).

We manipulated host plant quality by exposing young plants to controlled spider mite herbivory. Induced plant changes following initial herbivory can reduce the performance or preference of subsequent herbivores in this and other systems (Karban and Myers 1989, Karban 1991, Karban and Baldwin 1997, Agrawal et al. 1999a). Induced resistance has been reported from over 100 plant-herbivore systems, and appears to be a common feature of anti-herbivore defenses in all walks of plant life. Induced resistance can have long lasting negative impacts on populations of herbivores and positive effects on plant performance (Agrawal 1998, 1999a, b).

In a field experiment with cotton plants and a naturally occurring community of arthropods, we manipulated leaf domatia and host plant resistance in a 2×2 factorial design to ask the following questions: 1) What are the direct effects of leaf domatia on the numbers of predaceous arthropods, and do effects on predators correlate with changes in the populations of herbivorous arthropods? 2) What percentage of predators on leaves with leaf domatia are found inside the domatia? 3) What are the effects of leaf domatia on the protection of domatia inhabitants from parasitism? 4) What are the effects of induced plant resistance on the fauna of naturally occurring herbivorous and predaceous arthropods? 5) Does induced resistance interact with predation to affect predator and herbivore populations? and 6) What are the ultimate consequences of leaf domatia and induced resistance for plant performance?

Materials and methods

We established a 0.9-ha plot of cotton plants (*Gossypium hirsutum* var. Acala Maxxa) in the San Joaquin Valley at the University of California Kearney Agricultural Center (Parlier, CA). Plants were sown from seed and spaced in rows approximately 0.2 m apart; rows were separated by furrows 0.9 m wide. We randomly selected 240 plants in a section of the field that was 20 rows wide by 23 m long. Thirty plants were chosen from each of eight rows, every other row was not used, and each experimental plant was separated by 2–3 unmanipulated plants. Plants were assigned to one of four treatments with 60 replicates of each: 1) controls, 2) domatia added, 3) induced resistance, and 4) both domatia added and induced resistance.

Plants that received the induced resistance treatment were exposed to controlled herbivory on the cotyledons. After the cotyledons were fully expanded, we infested them with approximately 30 *Tetranychus turkestani* spider mites from a colony maintained on cotton plants. Spider mites often naturally colonize cotton plants at the cotyledonary stage and previous experiments have demonstrated that *T. turkestani* are potent inducers of systemic resistance in cotton plants

Table 1. Common arthropod species found in the cotton agroecosystem in the San Joaquin Valley, California.

Common name	Species name	Feeding guild	Pest?	Life stage sampled	Egg development	Affected by induced resistance	Affected by domatia
big-eyed bug	*Geocoris* spp.	generalist predator, plant sap feeder	no	eggs	on leaf surface	no	yes
minute pirate bug	*Orius tristicolor*	generalist predator, plant sap feeder	no	nymphs	in plant tissue	yes	yes
western flower thrips	*Frankliniella occidentalis*	cell content feeder, feeds on mite eggs	no	larvae, adults	in plant tissue	no (yes, in laboratory trials)	yes
lacewing	*Chrysoperla* spp.	generalist predator (mostly aphids)	no	eggs	on leaf surface	no	no
spider mite	*Tetranychus* spp.	cell content feeder	yes	all	on leaf surface	yes	yes (indirectly)
cotton aphid	*Aphis gossypii*	phloem feeder	yes	all	n/a (live birth)	yes (positive)	yes (indirectly)
silverleaf whitefly	*Bemisia argentifolii*	phloem feeder	yes	nymphs	on leaf surface	yes	yes (indirectly)

(Karban and Carey 1984). Although several species of plant parasites have been shown to be negatively impacted by induced resistance in cotton, only recently have some of the biochemical mechanisms of induction been elucidated (Bi et al. 1997, McAuslane and Alborn 1998, Sadras and Felton 1999). Induced responses to herbivory in cotton plants included increased activity of defensive oxidative enzymes and phenolics, terpenoid aldehydes, and decreased nutritional components. After the mites fed on seedlings for seven days, all experimental plants (including the plants that were not exposed to mites) were dipped in a solution of dicofol, a non-systemic miticide (Kelthane, 100 ppm, Rohm and Haas, Philadelphia, PA). The induced resistance treatment was only imposed once at this early stage of plant growth.

The leaf domatia treatments were maintained throughout the growing season. When the first true leaf of each plant had fully expanded, we added a small tuft of cotton fibers (approximate diameter 4 mm) to the underside of the leaf, where all of the veins meet near the petiole. Although *G. hirsutum* does not have domatia, several close relatives of cultivated cotton plants in the Malvaceae and plants with similar leaf morphology in the Tiliaceae have leaf domatia at the same place (Fryxell 1978, Brouwer and Clifford 1990, A. Agrawal pers. obs.). Domatia were attached by using a drop of Elmer's School glue gel (Elmer's Products, Inc., Columbus, OH), which was not found to visibly damage the leaf tissue. Leaves on the experimental plants that did not receive leaf domatia were treated with a drop of the glue to control for the possible effects of the glue itself. The domatia addition treatments were imposed every two weeks on 3–5 fully expanded leaves of each plant for the duration of the four-month growing season. Approximately 50% of the total number of leaves were treated with domatia.

Every two weeks we sampled each of the experimental plants to monitor all arthropods. Sampling dates were as follows: (1) 14 May, (2) 28 May, (3) 11 June, (4) 27 June, (5) 11 July, (6) 30 July, and (7) 21 August (all 1997). For each sample we removed one leaf, approximately five nodes down from the newest leaf, and counted all abundant arthropods on the seven sampling dates (Table 1). Because some of the arthropods are mobile, only certain life stages were sampled (see Table 1). In addition, on leaves with leaf domatia, we recorded which arthropods were inside and outside the domatia and if any arthropods were parasitized. Parasitized big-eyed bug eggs were determined by a change in color from tan to purple.

At the end of the season we recorded the number of open and closed fruits (bolls), the weight of the lint produced by the open bolls, and the number of seeds produced for each experimental plant. Although seed production may be the most relevant parameter as an indicator of plant fitness, in this agricultural variety, selection for exaggerated seed hairs (i.e., lint) is obvious. We therefore have combined our four reproductive

measures in a multivariate analysis of variance (MANOVA) analysis (see below) of plant performance.

Statistical analysis

Abundance data for each arthropod species were analyzed using a two-way repeated measures analysis of variance (ANOVA) with induced resistance and leaf domatia as fixed main effects. The first sample date was omitted from the repeated measures analysis because several plants were too small to have a sample taken. During the course of the study, two of our experimental plants died and were thus omitted from the analysis. In addition to the main effects, we were particularly interested in the interaction term to determine if the effects of domatia and induction were non-additive. We log-transformed all arthropod density data because we were interested in the multiplicative null model for the interpretation of the interaction term (Sih et al. 1998). The log-transformation allows such an interpretation, and prevents the confounding problem of arthropods allowed to be affected twice (i.e., killed) by each factor (induced resistance and domatia) as in the additive model (Sih et al. 1998). The additive and multiplicative model resulted in identical results except for one situation which is indicated in the results. For arthropod species with low abundances, we confirmed the results of our ANOVA main effects using non-parametric Kruskal-Wallis tests; however, because the interaction term was of primary interest and is unavailable when using non-parametric tests based on ranks, we have maintained our original ANOVA analysis. On leaves with domatia, we compared the numbers of arthropods (by species) inside and outside of the domatia using a chi-square test; the null hypothesis was that arthropods are equally distributed inside versus outside domatia. This is an extremely conservative hypothesis because the ratio of leaf area occupied by domatia to leaf area that is domatia-free is very small (ca 1:225). Plant performance measures were compared using a two-way MANOVA. The significant MANOVA was followed by univariate analyses which were protected from Type I errors (Barker and Barker 1984).

Results

Leaf domatia had a strong positive effect on the sampled life stages of two species of bugs and one species of thrips, the three important predators in this system (Tables 1 and 2, Figs 1, 2). On leaves with domatia, 87% of the big-eyed bug eggs were found inside leaf domatia ($\chi^2 = 65.24$, d.f. $= 1$, $P < 0.001$). We found 69% of the minute pirate bug nymphs inside domatia ($\chi^2 = 10.99$, d.f. $= 1$, $P = 0.001$) and 62% of western flower thrips inside of domatia ($\chi^2 = 9.682$, d.f. $= 1$, $P = 0.002$) (Fig. 3). In our experiment, parasitism of big-eyed bug eggs was not observed on eggs inside of leaf domatia, however, outside domatia, 32% of eggs were found to be parasitized ($\chi^2 = 60.80$, d.f. $= 1$, $P < 0.001$). The above analyses considered each insect individual to be making an independent choice; if analyses are conducted that con-
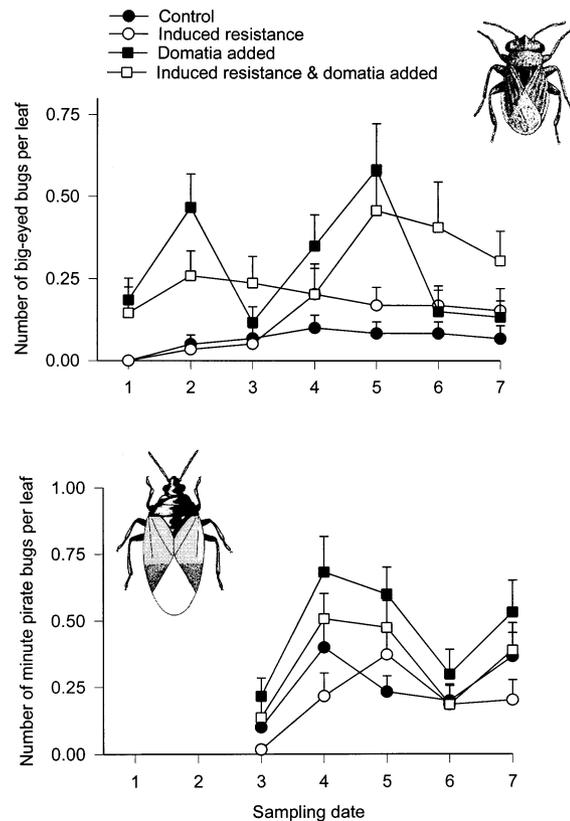

Fig. 1. The effects of leaf domatia and induced plant resistance on the abundance of big-eyed bug eggs (*Geocoris* spp.) and the minute pirate bug nymphs (*Orius tristicolor*) on seven sampling dates (mean + s.e.).
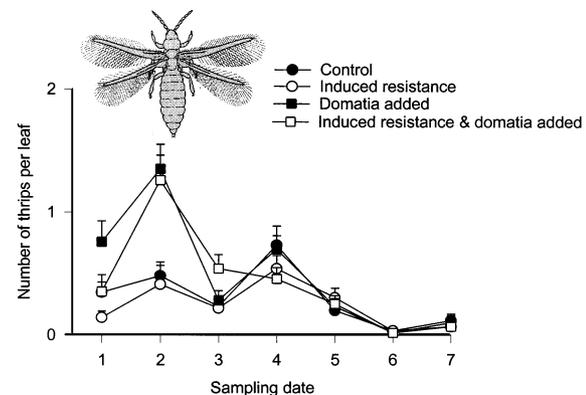

Fig. 2. The effects of leaf domatia and induced plant resistance on the abundance of the western flower thrips (*Frankliniella occidentalis*) larvae and adults on seven sampling dates (mean + s.e.).

Table 2. Repeated measures two-way analysis of variance table for effects of leaf domatia and induced resistance on the community of naturally occurring arthropods in our cotton field in the San Joaquin Valley, California. The Greenhouse-Geisser (G-G) probabilities corrected for sphericity are also presented.

Species	Source	d.f.	ms	F	P	G-G
big-eyed bugs	domatia	1	4.460	42.134	<0.001	
(eggs)	induction	1	0.094	0.892	0.346	
	domatia × induction	1	0.057	0.543	0.462	
	error	234	0.106			
	sampling date	5	0.348	3.947	0.001	0.002
	date × domatia	5	0.270	3.060	0.009	0.012
	date × induction	5	0.186	2.109	0.062	0.068
	date × domatia × induction	5	0.141	1.601	0.157	0.163
	error	1170	0.008			
minute pirate bugs	domatia	1	2.614	19.931	<0.001	
(nymphs)	induction	1	0.812	6.189	0.014	
	domatia × induction	1	0.076	0.580	0.447	
	error	234	0.131			
	sampling date	4	1.760	13.477	<0.001	<0.001
	date × domatia	4	0.163	1.246	0.290	0.291
	date × induction	4	0.057	0.438	0.781	0.763
	date × domatia × induction	4	0.085	0.654	0.624	0.609
	error	936	0.131			
thrips	domatia	1	2.060	14.320	<0.001	
(larvae, adults)	induction	1	0.110	0.762	0.384	
	domatia × induction	1	0.004	0.029	0.865	
	error	234	0.144			
	sampling date	5	6.391	47.846	<0.001	<0.001
	date × domatia	5	1.523	11.403	<0.001	<0.001
	date × induction	5	0.238	1.784	0.113	0.138
	date × domatia × induction	5	0.082	0.612	0.690	0.636
	error	1170	0.134			
spider mites	domatia	1	12.293	9.784	0.002	
(all stages)	induction	1	14.922	11.878	0.001	
	domatia × induction	1	8.511	6.774	0.010	
	error	234	1.256			
	sampling date	2	10.117	13.366	<0.001	<0.001
	date × domatia	2	0.443	0.585	0.585	0.550
	date × induction	2	3.952	5.221	0.006	0.007
	date × domatia × induction	2	0.068	0.090	0.914	0.906
	error	468	0.757			
aphids	domatia	1	3.493	5.690	0.018	
(all stages)	induction	1	0.762	1.242	0.266[+]	
	domatia × induction	1	0.017	0.028	0.866	
	error	234	0.614			
	sampling date	5	98.912	185.096	<0.001	<0.001
	date × domatia	5	0.759	1.420	0.214	0.229
	date × induction	5	0.586	1.097	0.360	0.355
	date × domatia × induction	5	0.320	0.600	0.700	0.648
	error	1170	0.534			
whiteflies	domatia	1	5.760	4.818	0.029	
(nymphs)	induction	1	3.633	3.038	0.083	
	domatia × induction	1	6.556	5.483	0.020	
	error	234	1.196			
	sampling date	3	331.751	372.960	<0.001	<0.001
	date × domatia	3	0.496	0.558	0.643	0.618
	date × induction	3	1.273	1.431	0.232	0.236
	date × domatia × induction	3	1.636	1.840	0.139	0.147
	error	702	0.890			
lacewings[++]	domatia	1	0.042	0.137	0.711	
(eggs)	induction	1	0.124	0.410	0.523	
	domatia × induction	1	1.218	4.032	0.046	
	error	234	0.302			

[+] The only result for which log transformation of data affected the qualitative result. For untransformed data, $P = 0.05$.
[++] lacewings were only abundant on one sampling date.

sider plants (not insects) to be independent units, the results are qualitatively the same. Both species of bugs are generalist predators that also feed on plant juices, and the thrips are also omnivores feeding on plant cell contents and spider mite eggs. The three major herbivores in this study, spider mites, aphids, and whiteflies were negatively affected by the addition of leaf domatia, probably due to enhanced predator numbers on plants with domatia (Table 2). Herbivores were rarely found inside the domatia.

Induced resistance had a negative impact on spider mites and whiteflies (Table 2, Figs 4, 5). Induced resistance had a positive effect on aphid populations, although this was only detectable when the untransformed data were analyzed ($P = 0.05$). Induced resistance did not affect the numbers of thrips or big-eyed bugs, but did significantly reduce the numbers of the minute pirate bugs, whose eggs are laid inside plant tissue. There was a significant domatia-by-induced resistance interaction for spider mites and whiteflies, which indicated that the effects of domatia and induction were not additive. Induced resistance and leaf domatia reduced spider mite and whitefly populations independently, but together they did not suppress numbers beyond either one alone (Fig. 4). Lacewings were only abundant on one sampling date and were not affected by our treatments.

The addition of leaf domatia to plants significantly enhanced plant performance when we considered the number of open and closed fruits (bolls), the weight of the lint produced by the open bolls, and the number of seeds produced for each experimental plant (Fig. 6, Table 3). There was no effect of induced resistance on plant performance (MANOVA: Wilks' $\lambda = 0.986$, $F_{4,231} = 0.829$, $P = 0.508$) and no interaction between domatia and induced resistance (MANOVA: Wilks' $\lambda = 0.992$, $F_{4,231} = 0.470$, $P = 0.758$) (Fig. 6).

Discussion

Herbivores in natural and managed systems are likely to be under control by a variety of ecological forces including predation and parasitism by natural enemies and plant resistance. In this study we examined the compatibility of these two forces by manipulating predation (adding small shelters to leaves which harbored predaceous arthropods) and inducing plant resistance. Leaf domatia were occupied by larvae and adults of thrips, eggs of big-eyed bugs, and nymphs of minute pirate bugs, but not by any of the herbivores. Although these three species that lived in domatia are omnivorous (Stoner 1970, Salas-Aguilar and Ehler 1977, Trichilo and Leigh 1986), none of them is considered a pest of cotton in the region where we conducted our experiments. In fact, these insects are thought to be largely responsible for the control of spider mites, which can
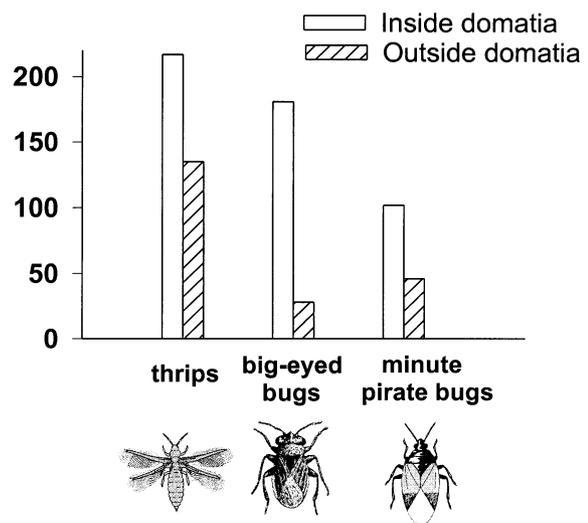

Fig. 3. The total number of each predator species found inside and outside domatia scored on leaves with leaf domatia. These data were tallied over the whole growing season from our counts on the seven sampling dates.

reach levels of hundreds of mites per leaf and severely reduce reproduction of cotton plants (Wilson et al. 1991, Agrawal and Karban 1997). Many studies in other systems have found that beneficial arthropods inhabit leaf domatia (Putman and Herne 1964, Walter and Denmark 1991, Walter 1992, 1996, Walter and O'Dowd 1992, 1995, Norton et al. 1999), although only a few studies have shown that the enhanced levels of beneficial arthropods associated with domatia resulted in smaller herbivore populations (Grostal and O'Dowd 1994, Walter 1996, Agrawal 1997, Agrawal and Karban 1997).

Leaf domatia may benefit predaceous arthropods in many ways. Individuals inside domatia may experience a more hospitable microclimate, and be less susceptible to desiccation (Grostal and O'Dowd 1994). In addition, inhabitants of domatia may be less susceptible to their own natural enemies because the structures may provide a hiding place. In our experiment, 32% of the predaceous bug eggs outside domatia were parasitized compared to zero parasitized eggs inside domatia. These benefits of domatia may be analogous to previously reported benefits of pubescence in cotton plants for predaceous bugs (Schuster and Calderon 1986). Pubescence also reduced number of thrips and parasitism by several parasitoids of aphids and caterpillars (Schuster and Calderon 1986, Sadras and Felton 1999). However, modern cotton production has not incorporated pubescent varieties because pubescence increased herbivory by *Heliothis* spp., mites, whiteflies, and pink bollworms (Schuster and Calderon 1986, Sadras and Felton 1999). Such a trade-off between enhancing predators while also enhancing some herbivores or decreasing parasitism of herbivores does not appear to
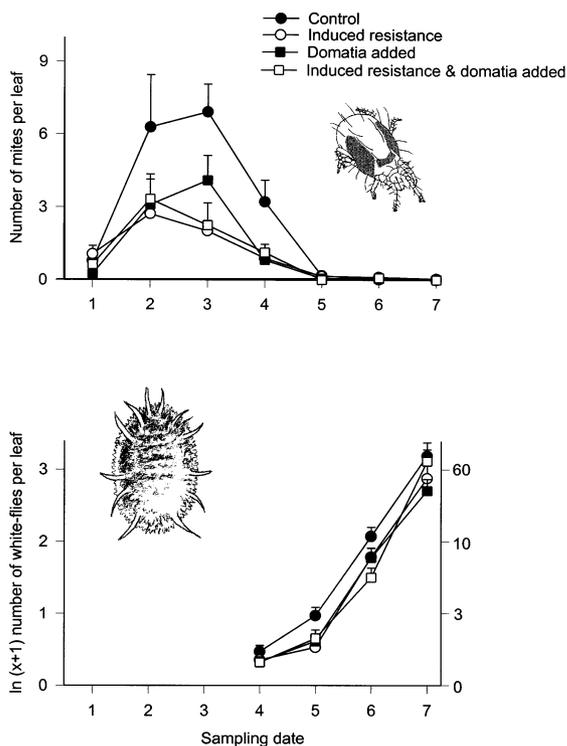
Fig. 4. The effects of leaf domatia and induced plant resistance on the abundance of two economic pests of cotton on seven sampling dates, spider mites (*Tetranychus* spp., all stages) and whitefly (*Bemisia argentifolii*) nymphs (mean + s.e.). Untransformed values for whiteflies are given on the right side of the *y*-axis.

be associated with the use of leaf domatia. Predators are able to enjoy the benefits of domatia, without creating a beneficial environment for herbivores or hindering parasitoids of herbivores, perhaps because the pubescence in a domatium is concentrated in a small area.
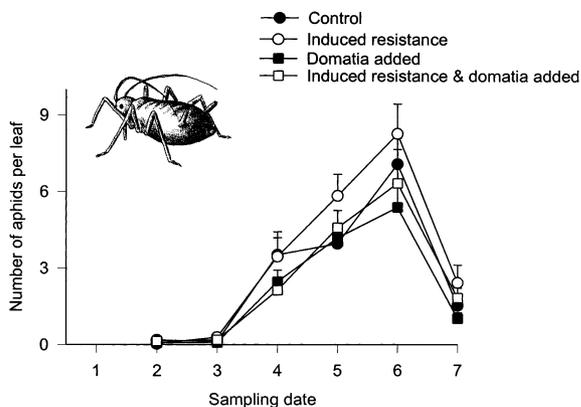

Fig. 5. The effects of leaf domatia and induced plant resistance on the abundance of aphids (*Aphis gossypii*, all stages) on seven sampling dates (mean + s.e.).

Ultimately, the effect of domatia on plant performance will determine its potential as an ecological tool to control herbivore populations. In the current study, predator abundances were enhanced by leaf domatia and were associated with reduced numbers of herbivores and increased reproductive output (Fig. 6). Our measures of plant performance are indicators of reproduction which are of relevance to both agricultural yield and plant fitness. Consistent results have been obtained in two separate field experiments at different sites (Agrawal and Karban 1997). Effects of leaf domatia on plant performance have not been reported for any other system.

Induced plant resistance to herbivores is a common feature of many plants and is thought to be important for herbivore population dynamics and plant fitness (Karban and Baldwin 1997, Agrawal 1998, 1999a, b). In this experiment, controlled early season herbivory induced systemic resistance in the plants. Induction had a negative impact on spider mite and whitefly populations throughout the growing season. In contrast to the negative effects of induction on spider mites and whiteflies, aphid populations were higher on induced plants compared to uninduced plants. This exemplifies an ecological cost of plant resistance, where resistance to one herbivore may confer susceptibility to another (Simms 1992). Although the mechanism is unknown in this case, such trade-offs are likely to be common in many systems (see reviews in Agrawal and Karban 1999, Agrawal et al. 1999b). An additional cost of induced resistance may be negative impacts of resistance on predators and parasites of herbivores. For example, induction had a negative impact on the numbers of minute pirate bugs in our experiment. Overall, induction did not affect plant performance (Fig. 6). The effect of the beneficial reduction in spider mite and whitefly populations, and the detrimental effects of enhanced aphids and reduced predators could have resulted in contradictory influences on the plant and no net detectable effect of induced resistance on plant performance. Additional factors may have obscured our ability to detect benefits of induction on plant performance: 1) the (imposed) early season herbivory may have reduced plant growth, and 2) the costs of induced resistance may have reduced plant performance.

Interactions between plant resistance and predation

The effects of plant resistance on natural enemies of herbivores have been of long standing interest (Campbell and Duffey 1979, Boethel and Eikenbary 1986, Hare 1992, Thaler 1999b). Although our experiment and other recent reviews (Hare 1992) do not show conclusive or consistent patterns, it appears that some predators may be vulnerable to plant resistance. We originally hypothesized that the important predators in

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Fig. 6. The effects of leaf domatia and induced resistance (IR) on four measures of plant reproductive performance: number of open and closed bolls, weight of the lint, and number of seeds produced per plant (mean $\pm$ s.e.).
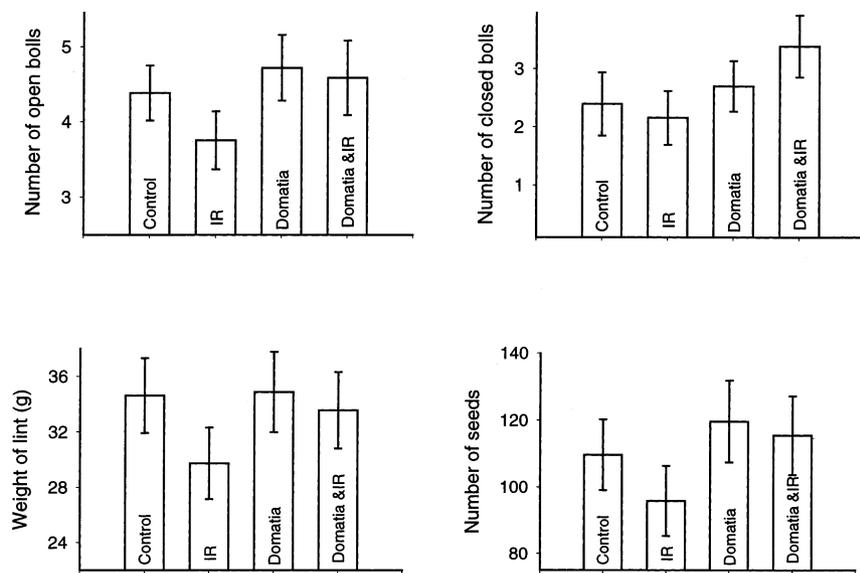
the cotton system would be particularly vulnerable to plant resistance because they are omnivorous and feed on foliage to some degree (Table 1). In addition, the eggs of minute pirate bugs and western flower thrips are placed in plant tissue. In the current experiments we consistently found fewer minute pirate bug nymphs on induced plants compared to controls. Although we did not detect overall effects of induction on thrips, thrips abundance was reduced on induced plants on the first sampling date (Fig. 2). In other experiments with western flower thrips on cotton plants, we have found that thrips on induced plants feed less than thrips on control plants (Agrawal et al. 1999c). When spider mites were available as prey for thrips, we found that the reduced feeding on induced plants was accompanied by increased feeding on spider mite eggs. Trichilo and Leigh (1988) found that populations of thrips fared poorly on genetically resistant plants without prey (spider mites) when compared to susceptible plants; however, with prey available, there was no difference in populations of thrips on resistant and susceptible plants. We can conclude, then, that induced or genetically based resistance may have negative impacts on some predaceous arthropods. When these predators are omnivorous they may shift their feeding preferences to feed more on prey than on plant tissue. Thus, induced resistance may act together with leaf domatia, or other factors which enhance predators, by decreasing herbivore populations directly, reducing plant feeding by omnivores, and increasing predation on herbivores by omnivores (Agrawal et al. 1999c). Further studies will be needed to evaluate the effects of induced resistance on the feeding choices of other omnivores.

One of the benefits of our factorial design is that we could detect statistical interactions between the effects of inducing plant resistance and the effects of having

leaf domatia. Although it appears that plant resistance can affect predators (see above), the effects of plant resistance and domatia were additive on the three abundant predators in our system. We found a significant interaction between effects of domatia and induced resistance on two of the major herbivores, spider mites and whiteflies. The results indicate that domatia and induced resistance reduced herbivore populations independently, but together, there was no additional control of these herbivores. These non-additive effects may have been due to the effect of plant resistance on the predator-prey interaction via spatial aggregation effects (Haukioja 1993). Induced resistance can alter the distribution of herbivores (in addition to their abundance). There is considerable evidence that herbivores will feed in a more dispersed manner on induced plants (Edwards et al. 1991). Given that many predators feed more on aggregated prey, we predict that induction may have been important in making prey less available due to a distributional shift.

At least two alternative explanations exist to explain why induced plant resistance and enhanced predation did not have additive effects on spider mites and whiteflies in our system. The nasty host – nasty prey hypothesis posits that if induced resistance in our plants involved noxious chemicals, these same chemicals accumulated in the herbivores (by sequestration or passive accumulation) and may have deterred predation (Haukioja 1993). In other words, herbivores growing on induced plants may gain some protection from ingesting the induced chemicals. Previous studies have documented such an indirect benefit of plant resistance traits for herbivores (e.g., Dyer 1995), even when such traits have a directly negative effect on the herbivore (Björkman and Larsson 1991). Another explanation posits that if the same herbivore individuals that are

Table 3. Analysis of variance of the effects of leaf domatia on plant performance measures. The overall MANOVA is followed by protected univariate analyses.

Source	Wilks' λ	d.f.	ms	F	P
MANOVA	0.957	4,231		2.564	0.039
Number of seeds		1	13041.413	1.714	0.192
Error		234	7609.326		
Open bolls		1	20.147	1.885	0.171
Error		234	10.686		
Closed bolls		1	35.533	2.413	0.122
Error		234	14.724		
Weight of lint		1	247.851	0.560	0.455
Error		234	442.903		

susceptible to host plant resistance are also more likely to be subject to predation, then employing both strategies together may not have an additive effect (J. S. Thaler pers. comm.). For example, if newly hatched spider mites are very susceptible to plant resistance and predation, then these factors together may not result in additive control.

Conclusion

Plant resistance traits may harm some herbivores although these same traits may benefit other herbivore species. Plant resistance may also hinder predators and parasites of herbivores. The current experiment demonstrates that induced resistance reduced populations of two herbivores (spider mites and whiteflies), although it benefited aphid populations. Because plants, herbivores, and their natural enemies are a diverse and dynamic group of interacting and evolving organisms, it is no surprise that no single defense is completely effective against all species. Furthermore, we are now beginning to recognize that "defensive" tactics may be beneficial to plants in some environments and detrimental in others (Linhart 1991, van der Meijden 1996, Agrawal and Karban 1997).

Successful biological control of herbivores in natural and managed systems is usually based on employing several plant defense strategies (Lewis et al. 1997). Here we have shown that plant traits can have a direct "resistance based" impact on herbivores, but also an indirect impact via enhanced predation. Across the community of arthropods that visit cotton plants, the effects of leaf domatia were large, enhancing the abundance of each of the common predators and reducing populations of each of the common species of herbivores. Induced resistance also had large effects on the arthropod community, but the effects were mixed in their direction: negative effects of induction were observed on the abundance of one species of predator and two species of herbivores, while positive effects of induction were observed on a third herbivore species. Effects of induced resistance were additive for the predators, but not additive for two out of the three

herbivores. Use of leaf domatia and induced resistance together were no more effective than using each strategy independently to control spider mites and whiteflies.

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