

Exploitative Competition Strongly Affects the Herbivorous Insect Community on *Baccharis halimifolia*

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## Exploitative competition strongly affects the herbivorous insect community on *Baccharis halimifolia*

Eric E. Hudson and Peter Stiling

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Folivory on *Baccharis halimifolia* by larvae of the chrysomelid beetle *Trirhabda bacharidis* depresses densities of the most common insect herbivores on *B. halimifolia*: the leaf mining flies *Amauromyza maculosa* and *Liriomyza trifolii*, and the gall making fly *Neolasioptera lathami*. Larval *T. bacharidis* were excluded from *B. halimifolia* plants in a field experiment using Tanglefoot® pest barrier to stop larvae, which emerge from eggs laid in the plant bark, from feeding on the leaves. Densities of *A. maculosa*, *L. trifolii*, and *N. lathami* were significantly higher on plants from which larval *T. bacharidis* had been excluded than on controls. Laboratory experiments showed that larval *T. bacharidis* did not prefer to eat mined leaves and the miners within. Thus, observed density reductions are the result of exploitative competition with *T. bacharidis* larvae. Competition between *T. bacharidis* larvae and other folivores is probably frequent in this system because *T. bacharidis* larvae occurred on 69% of 172 *B. halimifolia* plants in the study areas and defoliated 68% of the available vegetation.

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The role of interspecific competition in structuring phytophagous insect communities has been the subject of a long and controversial debate. In the 1970s, observational studies indicated that interspecific competition was a potent force in structuring insect communities (Uekert and Hansen 1971, Waloff 1979). However, in the 1980s, interspecific competition was deemed weak and unimportant (Lawton and Strong 1981, Lawton 1982, Strong 1982, Strong et al. 1984). In his widely cited review on competition, Schoener (1983) argued that data from field experiments supported the Hairston et al. (1960) theory (HSS) that food rarely limits herbivores and that natural enemies maintain herbivore densities below competitive levels. Both Connell (1983) and Schoener (1983) noted a general lack of field experiments on competition in insect communities, and insect ecologists soon responded to this paucity of studies (Stiling and Strong 1983, 1984, Fritz et al. 1986,

Karban 1986, 1989, Crawley and Pattrasudhi 1988, Evans 1989, 1992, Faeth 1990, Gilbert and Owen 1990, Moran and Whitham 1990, Root and Cappuccino 1992). Several of these studies revealed that interspecific competition was frequent and important in nature (Karban 1986, 1989, Crawley and Pattrasudhi 1988), yet others (Evans 1989, 1992, Gilbert and Owen 1990, Root and Cappuccino 1992) found little evidence for interspecific competition. In an apparent turnaround, the most recent review of competition in phytophagous insects (Denno et al. 1995) found evidence for interspecific competition in 76% of examined cases. If competition is frequent in insect communities, researchers must now examine the effects of competition on entire communities.

Schoener (1983) noted six different forms of competition: consumptive, preemptive, overgrowth, chemical, territorial, and encounter competition. Consumptive and

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preemptive competition can be considered what Denno et al. (1995) called exploitative competition; overgrowth, chemical, territorial, and encounter competition are all mechanisms of interference or direct competition between individuals. Strauss (1991) has suggested that exploitative competition is a type of indirect effect. An indirect effect occurs when the exploitation of one species by another has a negative influence on a third species. In phytophagous insect communities, the use of plant resources by one species can have a negative effect on other herbivorous species. This may be especially true when one plant-feeding insect monopolizes the available plant resources. Schoener (1983) suggested that this type of indirect effect was the most frequent type of competition found in nature, yet Denno et al. (1995) found no significant difference between the frequency of exploitative and interference competition in phytophagous insect communities.

This study investigates the competitive effect that *Trirhabda bacharidis* Weber (Coleoptera: Chrysomelidae) has on the phytophagous insect community associated with *Baccharis halimifolia* L. (Asteraceae: Asterae). *Trirhabda bacharidis* is a monophagous feeder on *B. halimifolia* (Johnson and Lyon 1976), and previous studies have shown that *T. bacharidis* larvae consume large quantities of *B. halimifolia* leaf tissue (Boldt 1989, Krischik and Denno 1990). *Trirhabda bacharidis* is rarely parasitized (Krombein et al. 1979, Hudson 1995), and predation on the larval stage is rare (Boldt 1989). There is thus little opportunity for control of *T. bacharidis* from the trophic level above, contrary to the HSS hypothesis. *Trirhabda bacharidis*, by consuming large quantities of *B. halimifolia* leaf tissue, may strongly compete with the *B. halimifolia* insect community. The main purpose of this research was to investigate the effect of *T. bacharidis* on several other members of the phytophagous insect fauna associated with *B. halimifolia*.

## Methods

### The community

*Baccharis halimifolia* is a dioecious, woody shrub that is common in marshes, shores, and disturbed areas (Tarver et al. 1979). *Trirhabda bacharidis* is a monophagous, leaf-feeding beetle on *B. halimifolia*. Adult *T. bacharidis* females lay eggs in grooves or furrows at the base of *B. halimifolia* trunks during summer and fall. In early spring larval *T. bacharidis* hatch and crawl up the trunks of *B. halimifolia* to begin feeding on leaf tissue (Hudson 1995). Larval *T. bacharidis* are not found on young *B. halimifolia* plants, because the trunks of these plants do not have the crevices in which female *T. bacharidis* lay their eggs (Boldt 1989).

In addition to *T. bacharidis*, Palmer and Bennett (1988) reported 145 species of phytophagous insects occurring on *B. halimifolia* in Florida. We have recorded many of these 145 species on *B. halimifolia* at our study sites, but few of these insects are frequently encountered. Those species that we most commonly encounter on *B. halimifolia* are two species of leaf-mining Diptera (Agromyzidae), *Liriomyza trifolii* (Burgess) and *Amauromyza maculosa* (Malloch), and a gall-forming Diptera (Cecidomyiidae), *Neolasioptera lathamii* (Gagne). Both *L. trifolii* and *A. maculosa* are polyphagous, and *N. lathamii* is a specialist on *B. halimifolia*. *Liriomyza trifolii* exhibits one spring generation on *B. halimifolia*, and *A. maculosa* has both spring and fall generations; the gall-fly *N. lathamii* is present year round in Florida (Hudson 1995).

### Field exclusion experiment

To examine the effect of *T. bacharidis* on the *B. halimifolia* insect community, we conducted a "press" experiment (Bender et al. 1984), in which we applied and maintained a perturbation to the *B. halimifolia* insect community. The experiment was conducted at two field sites: Upper Tampa Bay County Park in Hillsborough County, FL and Honeymoon Island State Recreation Area in Pinellas County, FL. *Baccharis halimifolia* often occurs in large patches (Tarver et al. 1979), and plants at these two sites were chosen in areas where 10 or more bushes occurred within a five by five-meter square, which we call a patch. Six patches were selected at Upper Tampa Bay and Honeymoon Island. Each patch was separated from all other patches by at least 50 m. Ten similarly sized plants were selected at each patch such that five could be experimentally treated and five served as experimental controls.

In January 1994, before larval hatching, Tangle-foot® pest barrier (The Tanglefoot Co., Grand Rapids, MI, USA) was applied around the trunks of treatment plants at one patch on Honeymoon Island: Enclosure-1; and two patches at Upper Tampa Bay: Enclosure-2, and Enclosure-3. All of the Enclosure plants had grooved bark at the base of the plants, in which *T. bacharidis* adults lay their eggs; the bark on higher regions of the plants is much smoother (Boldt 1989). Thus the Tangle-foot® pest barrier, applied above the furrowed regions of the bark, trapped *T. bacharidis* larvae before they could ascend and begin feeding on leaf tissue. Boldt (1989) successfully used this technique to determine the effects of *T. bacharidis* on *B. halimifolia* leaf tissue. The few larvae that emerged above the Tangle-foot® bands were removed during weekly visits to each field site. The numbers of all insects on treatment plants were compared to the numbers on similar sized, non-tanglefooted, control plants during 1994. To determine the extent of defoliation by *T. bacharidis*

larvae, the total terminal number of eight control plants at patch Exclusion-1 was counted both before the beetle larvae hatched and began feeding and after the larvae had dropped off the plants to pupate. We define a terminal as any stem greater than 3.8 cm long with living tissue. Terminals of *B. halimifolia* are five to ten cm long (Hudson and Stiling pers. obs.) and offer consistent sampling units.

To determine if the Tangle-foot® treatment alone, in the absence of *T. bacharidis*, affected insect herbivores, we chose three patches of young plants with smooth bark. Boldt (1989) noted that larval *T. bacharidis* are rarely found on young *B. halimifolia* plants because the bark of these plants lacks the grooves or crevices preferred for oviposition. Two patches, Exclusion Control-1 and Exclusion Control-2, were selected at Honeymoon Island, and one patch, Exclusion Control-3, was selected at Upper Tampa Bay. These plants had experienced no herbivory by *T. bacharidis* larvae, and we could determine if the Tangle-foot® treatments alone, in the absence of *T. bacharidis* larvae, altered any aspect of community dynamics, perhaps by trapping ovipositing female insects.

A total of 60, similar-sized plants were monitored during the experiment. Each site consisted of five clumped, independent replicates (one treatment plant and one control plant). Sites were paired at Upper Tampa Bay and Honeymoon Island, with Exclusion sites adjacent to Exclusion Control sites. There was little difference in habitat between the adjacent sites, making it unlikely that habitat differences would affect insect abundance.

The insect community on *B. halimifolia* was monitored at approximately 10-d intervals from February 1994 through January 1995. One hundred haphazardly selected terminals from each plant were counted on each sampling visit, and the number and identity of every insect occurring on the leaves or stems of these terminals were recorded. Insects were identified with taxonomic keys (Spencer and Stegmaier 1973, Arnett et al. 1980, Borror et al. 1982, Gagne 1989, Spencer 1990). The identity of specimens was verified by checking with the list of reported phytophagous insects associated with *B. halimifolia* (McCoy and Rey 1981, Palmer 1987, Palmer and Bennet 1988). All terminals were counted on plants that had less than 100 terminals. To compare densities of insects on plants with different terminal numbers, the data from each field census were standardized to represent the number of insects present on 20 terminals. All data analyses were performed using these standardized densities.

Although we recorded every insect encountered on 100 terminals of both treatment and control plants, only a few species were commonly encountered. Statistical analyses was limited to these species. We classified those species that occurred on two or more plants at an individual patch and were present on any plant at that

patch for three or more consecutive sampling dates as common. By setting these criteria for abundance, we included only those species whose life cycles are closely associated with *B. halimifolia*, and excluded species that are transient or occasional community members. This exclusion was not meant to discount the possible importance that transient species might play in the dynamics of the insect community on *B. halimifolia*. Rather, it is a reflection of the difficulty associated with determining the interactions that occur when uncommon insects visit *B. halimifolia*.

Repeated measures ANOVAs were employed to test for significant differences of insect abundance between control and treatment plants. A separate ANOVA was performed for each commonly occurring community member by using the five plant totals of insect densities (number per 20 terminals) for treatment and controls at each of the six patches. Data were  $\log(x + 0.5)$  transformed before analysis to satisfy the assumptions associated with parametric statistics. *A. maculosa* second generation densities at the Honeymoon Island Exclusion-1 patch could not be transformed, and comparisons were made using a Wilcoxon Signed Rank Test.

### Field census

To determine how often *T. bacharidis* larvae infested *B. halimifolia*, we performed a wide-ranging census. On 12 February, 1995, we searched the upper regions of Honeymoon Island's salt marsh for all *B. halimifolia*. For each plant, the presence or absence of *T. bacharidis* larvae and the number of plants within a patch were recorded. Presence of *T. bacharidis* larvae was defined as greater than 10 larvae encountered on 100 terminals. This number was selected because observations in 1994 indicated that a mean of greater than 10 larvae per 100 terminals resulted in heavy defoliation and reduction in terminal number (Hudson 1995).

### Laboratory tests of *T. bacharidis* larval feeding preference

To determine if *T. bacharidis* larvae selectively feed on leaves containing larval leaf miners, and thus directly affect community structure, we performed a leaf-choice experiment similar to that of Krischik and Denno (1990). A *T. bacharidis* larva was placed in a Petri dish containing two fresh, undamaged *B. halimifolia* leaves and two *B. halimifolia* leaves that each contained an *Amauromyza maculosa* leaf miner. Larvae and the mined leaves were collected at Upper Tampa Bay County Park on 24 February, 1995. On the day of collection, mined and undamaged leaves were placed in an alternating, circular arrangement in a Petri dish lined with moist filter paper, and a single *T. bacharidis*

larva was placed in the center of the arrangement. Each larva was allowed to feed for 24 h. The area of undamaged leaves was measured before the feeding trials using a Leaf Area Meter (Model CI-201, CID, Inc. Moscow, ID, USA). To avoid destroying the mines of *A. maculosa*, the area of mined leaves was estimated after the feeding trials. If the larva had fed on the mined leaves during the experiment, we traced the leaf outline onto colored paper. The mined leaf and the tracing were then measured using the leaf area meter. We estimated the total area consumed by subtracting the area of the mined leaf (which had been fed upon) from the traced leaf (which represented the original leaf area). Never was the mined leaf totally destroyed such that we could not estimate its original area. Twenty replicates of this experiment were performed, and each trial involved a different *T. bacharidis* larva. Results were analyzed using a paired *t*-test.

## Results

### Field exclusion experiment: *Trirhabda* presence and common herbivores

*Trirhabda bacharidis* larvae hatched and defoliated many terminals on plants at patch Exclusion-1 on Honeymoon Island and at patches Exclusion-2 and Exclusion-3 at Upper Tampa Bay. The plants at the Exclusion-2 and Exclusion-3 patches died during the late summer of 1994, and data after this represent herbivore densities at patch Exclusion-1 only. Many plants at the Exclusion-1 patch reflushed leaves following *T. bacharidis* attack. Larval *T. bacharidis* were not present at any Exclusion Control patches. The mean reduction in terminal number on the eight monitored plants at patch Exclusion-1 was 67.7% (s.d.  $\pm$  23.5). The mean number of *T. bacharidis* larvae per bush at the three infested sites was 18.55 ( $\pm$  11.94), 12.25 ( $\pm$  6.11), and 11.80 ( $\pm$  7.35).

Three insect species satisfied our criteria for abundance: two species of leaf-mining Diptera (Agromyzidae), *Amauromyza maculosa* (Malloch) and *Liriomyza trifolii* (Burgess); and a gall-forming Diptera (Cecidomyiidae), *Neolasioptera lathami* (Gagne). During 1994 both leaf miners, *L. trifolii* and *A. maculosa*, were present between February and June (Figs 1–4). *Amauromyza maculosa* exhibited a second generation from September through December. *Neolasioptera lathami* were present throughout the study (Figs 5–6). Adult *T. bacharidis* emerged in April and were not present after July. *A. maculosa* densities on “Exclusion Control” patches appeared higher than those on “Exclusion” patches, suggesting that this leaf miner may prefer to oviposit on younger plants.

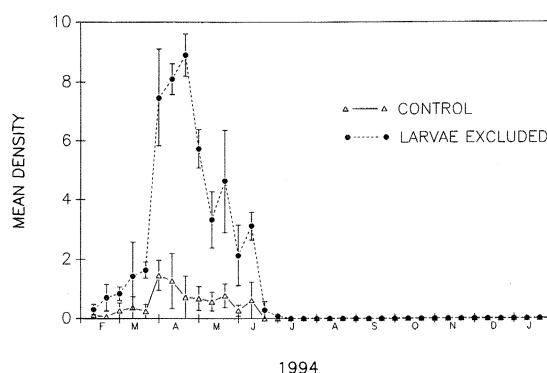


Fig. 1. Seasonal profiles of the density (mean no./20 terminals  $\pm$  SE) of the leaf miner *L. trifolii* on control and treatment plants at the patches where *T. bacharidis* larvae were present (“Exclusion” patches).

### Field exclusion experiment: herbivore densities

Herbivore densities on treatment plants, from which *T. bacharidis* were excluded, were significantly greater than densities on control plants at the “Exclusion” patches for *L. trifolii* ( $P = 0.011$ ; Table 1), *A. maculosa* ( $P = 0.032$ ; Table 2), and *N. lathami* ( $P = 0.010$ ; Table 3). Significant time effects were found at the “Exclusion” patches for *L. trifolii* densities ( $P < 0.001$ ; Table 1) and *A. maculosa* densities ( $P = 0.012$ ; Table 2), reflecting seasonal changes in abundance. At the “Exclusion Control” patches no significant differences were found between treatment and control plants for any of the three herbivores. Significant time effects were found for *L. trifolii* ( $P = 0.033$ ; Table 1) and *A. maculosa* densities ( $P = 0.002$ ; Table 2), again reflecting seasonal changes in abundance.

Second generation densities (number of insects per 20 terminals) of *A. maculosa* from patch Exclusion-1 were significantly greater on control plants from 12 September to 12 December (Wilcoxon Signed Rank Test,  $P = 0.027$ ). At the “Exclusion Control” patches, there was no significant difference between densities of *A.*

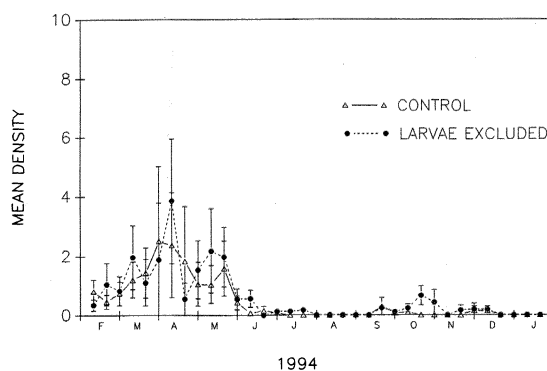


Fig. 2. Seasonal profiles of the density (mean no./20 terminals  $\pm$  SE) of the leaf miner *L. trifolii* on control and treatment plants at the patches where *T. bacharidis* larvae were absent (“Exclusion Control” patches).



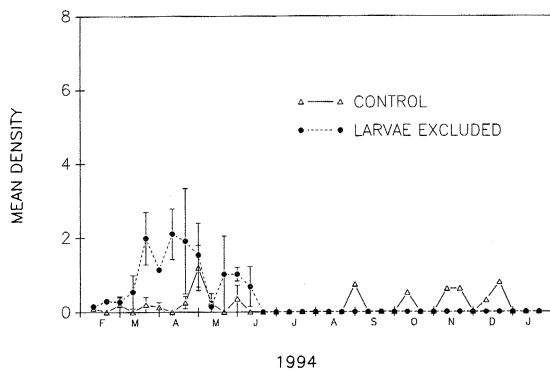


Fig. 3. Seasonal profiles of the density (mean no./20 terminals  $\pm$  SE) of the leaf miner *A. maculosa* on control and treatment plants at the patches where *T. bacharidis* larvae were present ("Exclusion" patches).

*maculosa* on treatment and control plants (Table 4). Interestingly, the densities of *N. lathami* showed an increase on control plants during the fall, although the difference between densities on control and treatment plants was not significant (Wilcoxon Signed Rank Test,  $P = 0.345$ ).

### Field census

During the large scale sampling, 172 *B. halimifolia* plants were counted at Honeymoon Island. More than 10 *T. bacharidis* larvae were present on 117 (69%) of these plants. Eighteen separate patches of *B. halimifolia* were found, and mean patch size was 9.55 plants per patch.

### Laboratory test of larval feeding preference

In the larval leaf-choice experiment, larval *T. bacharidis* did not prefer mined leaves over unmined leaves. Rather, larvae consumed more tissue from unmined

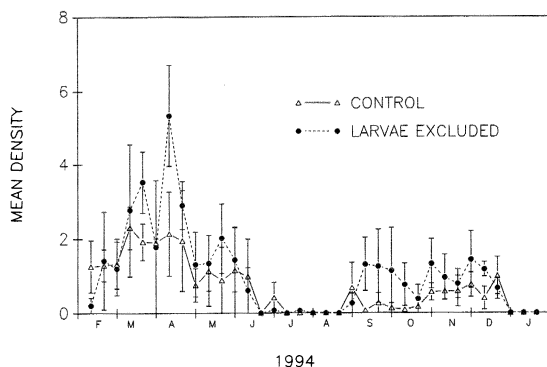


Fig. 4. Seasonal profiles of the density (mean no./20 terminals  $\pm$  SE) of the leaf miner *A. maculosa* on control and treatment plants at the patches where *T. bacharidis* larvae were absent ("Exclusion Control" patches).

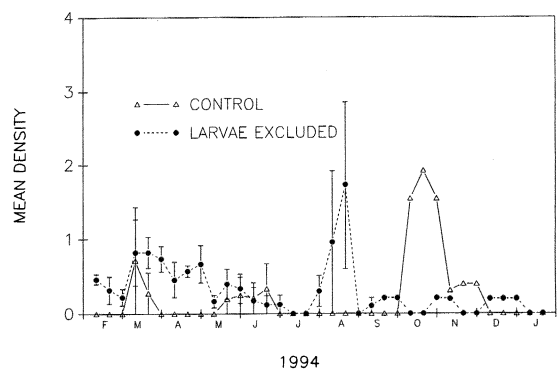


Fig. 5. Seasonal profiles of the density (mean no./20 terminals  $\pm$  SE) of the gall maker *N. lathami* on control and treatment plants at the patches where *T. bacharidis* larvae were present ("Exclusion" patches).

leaves than from leaves containing *A. maculosa* larvae during the 24-h feeding trial (paired  $t$ -test,  $P = 0.016$ , 19 df).

### Discussion

By consuming large quantities of leaf tissue on many plants, *T. bacharidis* larvae play a major role in structuring the phytophagous insect community on *B. halimifolia*. Larvae on monitored plants consumed, on average, 67.7% of living terminals. This reduction in terminal number is similar to Boldt's (1989) findings that *T. bacharidis* larvae reduced living foliage by 81%. Such a dramatic reduction in available foliage by *T. bacharidis* negatively affects several other herbivores on *B. halimifolia*.

Larvae of *T. bacharidis* were present on 69% of plants sampled in 1995, showing that herbivory by *T. bacharidis* larvae is common. Thus the gall maker *N. lathami* and the leaf miners *A. maculosa* and *L. trifolii* are likely to encounter plants defoliated by *T.*

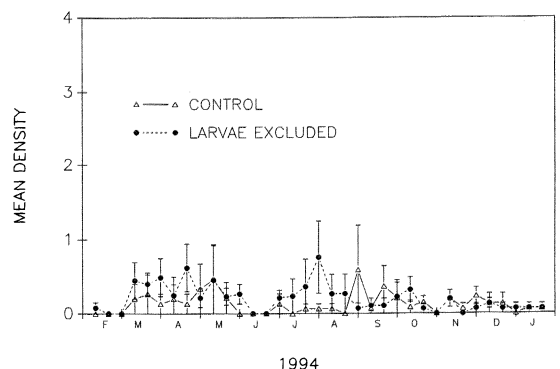


Fig. 6. Seasonal profiles of the density (mean no./20 terminals  $\pm$  SE) of the gall maker *N. lathami* on control and treatment plants at the patches where *T. bacharidis* larvae were absent ("Exclusion Control" patches).

Table 1. Repeated measures ANOVA on first generation *L. trifolii* densities at "Exclusion" and "Exclusion Control" patches (Units = no. of insects per 20 terminals).

"Exclusion" patch					
Source	Sum of squares	df	Mean square	F-ratio	P-value
Between subjects					
Treatment	24.696	1	24.696	20.159	0.011
Error	4.900	4	1.225		
Within subjects					
Time	16.560	10	1.656	6.996	0.001
Treatment $\times$ Time	2.962	10	0.296	1.251	0.290
Error	9.468	40	0.237		
"Exclusion Control" patch					
Source	Sum of squares	df	Mean square	F-ratio	P-value
Between subjects					
Treatment	0.598	1	0.598	0.078	0.794
Error	30.781	4	7.695		
Within subjects					
Time	5.772	10	0.577	2.269	0.033
Treatment $\times$ Time	0.711	10	0.071	0.280	0.982
Error	10.173	40	0.254		

*bacharidis* larvae, and this defoliation significantly reduced herbivore densities.

Results of larval leaf choice experiments show that *T. bacharidis* larvae do not preferentially feed on mined leaves. Rather, larvae consumed more tissue from unmined leaves. This result suggests that larval *T. bacharidis*, by preferentially feeding on unmined leaves,

Table 2. Repeated measures ANOVA on first generation *A. maculosa* densities at "Exclusion" and "Exclusion Control" patches (Units = no. of insects per 20 terminals).

"Exclusion" patch					
Source	Sum of squares	df	Mean square	F-ratio	P-value
Between subjects					
Treatment	7.010	1	7.010	10.450	0.032
Error	2.683	4	0.671		
Within subjects					
Time	5.809	10	0.581	2.722	0.012
Treatment $\times$ Time	3.589	10	0.359	1.682	0.119
Error	8.538	40	0.213		
"Exclusion Control" patch					
Source	Sum of squares	df	Mean square	F-ratio	P-value
Between subjects					
Treatment	0.632	1	0.632	0.109	0.758
Error	23.151	4	5.788		
Within subjects					
Time	10.372	10	1.037	3.674	0.002
Treatment $\times$ Time	3.238	10	0.328	1.163	0.343
Error	11.292	40	0.282		

Table 3. Repeated measures ANOVA on 1994 *N. lathami* densities at "Exclusion" and "Exclusion Control" patches (Units = no. of insects per 20 terminals).

"Exclusion" patch					
Source	Sum of squares	df	Mean square	F-ratio	P-value
Between subjects					
Treatment	3.545	1	3.545	20.948	0.010
Error	0.677	4	0.169		
Within subjects					
Time	0.826	7	0.118	1.212	0.329
Treatment $\times$ Time	0.814	7	0.116	1.194	0.338
Error	2.728	28	0.097		
"Exclusion Control" patch					
Source	Sum of squares	df	Mean square	F-ratio	P-value
Between subjects					
Treatment	0.376	1	0.376	0.299	0.614
Error	5.028	4	1.257		
Within subjects					
Time	0.315	7	0.045	0.469	0.848
Treatment $\times$ Time	0.343	7	0.049	0.511	0.819
Error	2.685	28	0.096		

do not directly reduce miner densities. However, during heavy bouts of defoliation by *T. bacharidis* (i.e. 100% defoliation), larvae will feed on mined leaves (Hudson 1995). Although *T. bacharidis* larvae will feed on mined leaves when no unmined leaves are available, the preference for unmined leaves in the laboratory, shows that the reduction in densities of leaf miners and gall makers is at least partly due to exploitative resource use by *T. bacharidis* larvae. Whether deemed an indirect effect or exploitative competition, the result of larval feeding is a reduction in densities of other herbivores within the *B. halimifolia* insect community.

The differences in leaf-miner densities on control and treatment plants at the patches where larval *T. bacharidis* occurred is most likely attributable to oviposition choice by female flies. Drolet and McNeil (1984) found that the leaf-mining fly *Agromyza frontella* preferentially oviposits in younger alfalfa leaflets. Godfray

Table 4. Repeated measures ANOVA on second generation *A. maculosa* densities at the "Exclusion Control" patches (Units = no. of insects per 20 terminals).

Source	Sum of squares	df	Mean square	F-ratio	P-value
Between subjects					
Treatment	2.133	1	2.133	0.896	0.398
Error	9.256	4	2.382		
Within subjects					
Time	3.358	11	0.305	1.193	0.320
Treatment $\times$ Time	1.974	11	0.179	0.701	0.730
Error	11.258	44	0.256		

(1985) also found that populations of *A. frontella* prefer to oviposit in young foliage. Quiring and McNeil (1987) examined the foraging behavior of *A. frontella* and found that female flies rank plants in regards to oviposition quality; *A. frontella* flies ranked unexploited plants as the most desirable for oviposition.

Faeth (1985) found that *Stilbosis juvantis*, a lepidopteran leaf miner on *Quercus emoryi*, select more intact than damaged leaves for oviposition, possibly because individuals on damaged leaves suffer increased parasitism rates compared to individuals on undamaged leaves. Faeth (1986) later showed that the entire leaf-mining guild, consisting of nine species, preferred undamaged to damaged leaves on *Q. emoryi*. Again, miners had significantly higher survivorship on undamaged leaves, owing to increased parasitism rates on damaged leaves. West (1985) found that *Phyllonorycter harrisella*, a leaf miner on *Quercus robur*, had lower survivorship on damaged leaves than on undamaged leaves. In this case the reduced survivorship of *P. harrisella* on damaged leaves was attributable to an induced response, primarily a decrease in nitrogen content of damaged leaves, by *Q. robur*. The fact that *T. bacharidis* also reduces densities of gall makers suggests that some type of induced chemical change may be occurring on *B. halimifolia* plants damaged by *T. bacharidis*. Higher densities of *A. maculosa* on "Exclusion Control" patches also suggest that female leaf miners are selecting young host plants where *T. bacharidis* are less likely to occur.

It is interesting that there were significantly higher densities of *A. maculosa* on control plants after 12 September, suggesting that female flies select young leaf tissue for oviposition: leaves reflushed on control plants but not on treatment plants. Several studies show that insect herbivores prefer young leaves over mature leaves (Cates 1980, Auerbach and Simberloff 1984, Bernays and Chapman 1994). On *B. halimifolia*, these younger leaves may have lower concentrations of secondary compounds (Kraft and Denno 1982). *Baccharis halimifolia* contains a triterpenoid compound, baccharis oxide (Anthonson et al. 1970), and triterpenoids are known to deter herbivory (Mabry and Gill 1979, Bernays and Chapman 1994). Kraft and Denno (1982) found that an acetone soluble secondary chemical increases in concentration over the growing season, and that leaves of *B. halimifolia* increase in toughness and thickness and decrease in moisture and crude protein content throughout the growing season. Auerbach and Simberloff (1984) found that two species of leaf-mining Lepidoptera are restricted in feeding on young, newly flushed leaves of water oaks. Densities of both Lepidoptera species greatly increased when water oaks reflushed late in the season, and Auerbach and Simberloff (1984) suggested that leaf-miner abundance may be limited by the availability of new leaves. Densities of the leaf miner *A. maculosa* on control plants at patch

Exclusion-1 may thus be affected by both new leaf tissue and increases in plant secondary compounds. The increase in late season (after 12 September) densities of the gall maker *N. lathamii* at patch Exclusion-1 suggest that the increases in secondary compounds may occur in many parts of the plants, not just the leaves.

In summary, *T. bacharidis* play a major role in the phytophagous insect community on *B. halimifolia*. Larval *T. bacharidis* are commonly found on *B. halimifolia*, and both leaf miners and gall makers are likely to encounter the effects of *T. bacharidis* herbivory. Where defoliation by larval *T. bacharidis* occurs, densities of leaf miners and gall makers are reduced. The reduced densities of leaf miners and gall makers is the result of interspecific, exploitative competition facilitated by *T. bacharidis* herbivory.

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