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HOST LEAF SELECTION BY LEAF MINERS: INTERACTIONS AMONG THREE TROPHIC LEVELS¹

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Abstract. The influence of leaf characteristics on host leaf selection and survivorship in an endophagous insect were studied in a leaf-mining species, *Stilbosis juvantis*. Dry mass measurements of mined and unmined leaves (after abscission) showed that the leaf miner does not select leaves for oviposition and subsequent larval feeding based on leaf size, possibly because densities of *S. juvantis* are typically low and this miner consumes only a small part of a leaf. However, censuses of 18 host trees, on 6 of which the proportion of damaged leaves had been experimentally increased, revealed that these leaf miners do select significantly more intact leaves than damaged ones for oviposition. *S. juvantis* on damaged leaves experienced significantly lower survivorship, owing to increased parasitism, than did miners on intact leaves. The higher rate of attack by parasitoids is probably attributable to physical or chemical alterations in damaged leaves. Thus, damage to leaves by previous herbivores modifies leaf selection by miners. These results indicate a subtle interaction among species at three trophic levels in this plant-herbivore system. Indirect negative interactions occur between guilds (leaf chewers and leaf miners) via changes in rates of parasitism rather than through resource-based competition.

Key words: competition; habitat selection; leaf-mining insects; mortality; *Quercus*; *Stilbosis juvantis*; survivorship; trophic interactions.

INTRODUCTION

Price et al. (1980) asserted that there is a need for examining interactions among three trophic levels (plant-herbivore-enemies) when considering plant/insect interactions. In essence, their review advocated a holistic approach, since scrutiny of interactions at only one or two levels may ignore subtle organizing factors that are apparent only when one considers all three levels. For example, changes in host plant quality may directly affect survivorship of phytophagous insects through alterations in leaf nutrition or toxins, but may also indirectly affect the efficacy of parasitoids and predators by altering insect host location or vulnerability (Vinson 1976, Price et al. 1980).

Leaf selection is an important aspect of plant/insect interactions because for some phytophagous insects, such as leaf miners or gall formers, oviposition by the adult insect determines where the larva or nymph will feed (Faeth et al. 1981). Most endophagous insects cannot move to more suitable plants or leaves as many external-feeding insects can. Therefore, natural selection for oviposition should act to minimize risks associated with all three levels of interaction: the host plant, other phytophages, and natural enemies. Host plant factors influencing leaf quantity and quality include size and position of leaves, nutritional and defensive chemistry, physical barriers, and phenological changes (e.g., qualitative seasonal changes in leaves or leaf abscission). Previous or concurrent feeding by other phytophages may alter physical and chemical aspects of the leaf or reduce leaf size so that insufficient area

remains for development. Finally, attack by predators and parasitoids may render certain leaves less suitable for oviposition and development if search for hosts on different leaf types is nonrandom (Schultz 1983).

Whitham (1978, 1980) clearly demonstrated that leaf size and quality within trees strongly affect oviposition choices by phloem-feeding insects. He showed that aphid stem mothers select large leaves on *Populus angustifolia* and that fecundity is lowered on small leaves. Small leaves of *P. angustifolia* are of lower quality because they contain few resources and high concentrations of phenolics (Zucker 1982). Predation pressure is highest on galling aphids that are clumped on preferred leaves, which suggests that there are opposing selective forces for selection of leaves (Whitham 1981, 1983).

I examined selection of leaves of *Quercus emoryi* (Fagaceae) by *Stilbosis juvantis* (Hodges) (Lepidoptera: Cosmopterigidae) and ensuing survivorship or mortality on intact leaves, leaves damaged by native leaf chewers, and leaves experimentally damaged. *S. juvantis* feed as larvae for as long as 10 mo and are therefore exposed to larval mortality factors for long periods. Consequently, I hypothesized that leaf choice should be critical for this leaf miner.

MATERIALS AND METHODS

Study area

All censuses, experiments, and observations were performed at the Sierra Ancha Experimental Station (United States Department of Agriculture) in the Tonto National Forest, Gila County, Arizona. The immediate study area (1555 m elevation) is a riparian forest bordering Parker Creek, dominated by mixed oak (*Quer-*

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cus emoryi, *Q. arizonica*, *Q. turbinella*), ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Pseudotsuga taxifolia*) stands, and surrounded by chaparral vegetation.

Host plant

Quercus emoryi is the dominant tree in the Parker Creek riparian and surrounding chaparral area. *Q. emoryi* is an evergreen oak with leaves bursting in mid-April to early May and remaining until abscission, which occurs when new buds break the following April or May.

Leaf-mining insect and its parasites

Stilbosis juvantis is a dominant leaf-mining species on *Q. emoryi*, although relatively low in density (\bar{X} = 2.4 mines/1000 leaves, SD = 1.4). *S. juvantis* is a univoltine species and obligate winter feeder. Females oviposit minute eggs (<0.5 mm in diameter) on leaves in late July. Larvae begin feeding, in early August, on the same leaves where eggs were deposited, and do not complete larval development until leaf abscission and bud burst in mid-April to early May of the following year. Emerged larvae spin cocoons and pupate in leaf litter or soil until females emerge in July. *Stilbosis juvantis* mines a small area (<20%) of a leaf relative to most other leaf-mining species feeding on *Q. emoryi*.

Larval and pupal parasites reared from *S. juvantis* are in the families Eulophidae, Braconidae, and Ichneumonidae. Parasitic species are probably generalists since they also have been reared from 10 other leaf-mining species on *Q. emoryi* and *Q. arizonica*, a syntopic oak. Egg parasites and predators have not been discovered for this leaf miner (S. H. Faeth, *personal observation*) or for confamilial miners (Green 1979). The few egg parasites found for lepidopteran leaf miners in Europe and North America are egg-larval parasites (K. Hagen, *personal communication*). These parasites oviposit in miner eggs, but parasites do not develop until larval stages (Fulmek 1962). Therefore, if eggs are differentially parasitized, then egg parasitism is reflected in mortality of larvae.

Herbivory experiment

I experimentally altered the proportion of intact and damaged leaves on trees to test the hypothesis that herbivory by early-feeding insects affects leaf selection and survivorship of late-feeding, leaf-mining insects. Of 18 trees selected on the basis of similar height (\approx 3 m), 12 were randomly assigned as controls, and 6 as experimental trees. On 7 July 1982 I simulated herbivory by removing >10% of individual leaf area on \approx 50% of leaves of each experimental tree, using a paper punch. Both controls and experimental trees suffered \approx 25% of total leaves damaged by native leaf-chewing insects (a leaf was categorized as damaged by leaf chewers if >10% of leaf area was removed). Most of the damage by native insect chewers occurs from budbreak to early June (S. H. Faeth, *personal observation*). Thus,

after herbivory manipulation, control trees had 25% of total leaves damaged, and experimental trees had 75% leaves damaged as determined from monthly random samples of 36 to 208 leaves from each tree. When leaves from all trees were pooled, 55% of leaves were found to have been damaged in some fashion, and 45% were found to be intact. These proportions represent the damaged and intact leaves available for selection by *S. juvantis* on study trees in July.

Censusing and the fate of leaf miners

All leaves on the 18 study trees were examined for leaf mines from July through November 1982, and in February and April 1983. Each active mine (larva still feeding) was labelled with tape and the fate of individual mines determined. The last census, on 26 April 1983, occurred \approx 5 d before leaves abscised from trees. At this time, I recorded the lengths of individual *S. juvantis* mines on damaged and intact leaves. I recovered all available tagged mines on abscised leaves from the leaf litter on 15 May 1983. Over 75% of the tagged mines were recovered in the leaf litter. All miners recovered in the litter had either emerged or died; none was still feeding. For each leaf mine I recorded whether it occurred on a damaged (manually or herbivore-damaged) or an intact leaf, and its fate. Dry mass of mined leaves collected on 15 May was measured and compared to the mean dry mass of leaves of study trees to determine if leaf miners occurred on leaves lighter or heavier than mean size of leaves on trees. Leaf mass and leaf area are highly correlated in *Q. emoryi* ($r = 0.965$, $P < .001$; Bultman and Faeth 1985).

Both before and after leaf abscission, I determined survivorship of miners on damaged and undamaged leaves by the presence of characteristic emergence holes (Faeth and Simberloff 1981a, b). For nonemerged leaf miners, death was characterized as resulting from parasitism by hymenopterans, predation, other causes (including leaf nutritional quality or defenses; bacterial, fungal, or viral attack; and abiotic factors) (see Methods sections in Faeth and Simberloff 1981a, b), or leaf abscission. A larva was classed as having died through leaf abscission if it was actively mining on 26 April, a few days before abscission, was recovered in leaf litter on 15 May, and, upon dissection of the mine, appeared to have died from desiccation due to leaf abscission. Survivorship and mortality of *Stilbosis juvantis* were analyzed separately on damaged and undamaged leaves.

RESULTS

Selection of intact vs. damaged leaves: all trees

S. juvantis selected intact leaves over damaged leaves for oviposition. Of 141 mines observed, the expected distribution, based on 55% leaves damaged and 45% undamaged for all trees, is 77.5 mines on damaged and 63.5 on intact leaves; the observed distribution was

TABLE 1. Dry masses of leaves of individually numbered study trees from which tagged, abscised mined leaves were removed (based on seven sample dates, 36–208 leaves sampled for each tree at each date).

Tree number	Leaf dry mass (g, $\bar{X} \pm SE$)	Pooled* with tree(s)
1	0.053 \pm 0.002	3
2	0.108 \pm 0.005	...
3	0.057 \pm 0.002	1
4	0.064 \pm 0.002	13, 24, 25
7	0.048 \pm 0.002	10
10	0.047 \pm 0.001	7
11	0.085 \pm 0.006	15
13	0.063 \pm 0.002	4, 24, 25
15	0.088 \pm 0.005	11
18	0.073 \pm 0.003	...
20	0.095 \pm 0.002	...
24	0.068 \pm 0.003	4, 13, 25
25	0.064 \pm 0.002	4, 13, 24

* Pooling was based on nonsignificance of means according to the Least Significant Difference test (Snedecor and Cochran 1978).

significantly different: 37 on damaged and 104 on undamaged leaves ($\chi^2 = 47.12$, $df = 1$, $P < .0001$).

Selection of leaves: experimental vs. control trees

Mean densities of *S. juvantis* did not differ significantly on control vs. experimental trees (control: $\bar{X} = 1.61$ mines/1000 leaves; experimental: $\bar{X} = 3.53$ mines/1000 leaves; $t = 0.81$, $df = 16$, $P > .20$). Therefore, the leaf miner does not discriminate at the scale of entire trees, even though experimental trees had much greater proportions of damaged leaves than control trees.

Selection of leaves based on size

I compared the dry mass of mined leaves found after abscission to the mean dry mass of leaves on trees, to test whether the mean size of leaves chosen by leaf miners was different from the mean size of leaves available on trees. Tagged mined leaves were recovered from 13 of the 18 trees. Trees that did not differ sig-

nificantly in mean leaf dry mass were pooled (Table 1) because low densities of *S. juvantis* were found on each tree. The mass of the mined leaves found on pooled or individual trees was compared with the mean leaf mass of trees by binomial tests and by χ^2 tests for selection over all trees (Table 2).

S. juvantis did not select leaves different in size from those available for colonization on individual trees, pooled trees, or all trees combined. Furthermore, successful emergence (survival) was not associated with leaf size on these trees (Table 2).

Survivorship and mortality of *S. juvantis* on damaged and intact leaves

Successful emergence was greater for *S. juvantis* on intact leaves (70.2%) than on damaged leaves (51.4%) (Table 3a). Overall, leaf miners on damaged and intact leaves differed significantly in successful emergence and in the distribution of mortality factors.

Orthogonal contrasts were used to partition the total chi-square statistic independently among categories, to examine survivorship and causes of mortality more closely. Successful emergence was significantly greater for *S. juvantis* on intact than on damaged leaves (Table 3b). For those leaf miners that did not successfully emerge, parasitism was significantly greater on damaged leaves. Other causes of mortality did not differentially affect leaf miners on intact vs. damaged leaves (Table 3b). These results indicate that the lower survivorship of *S. juvantis* on damaged leaves was caused by greatly increased rates of parasitism.

Survivorship and mortality of *S. juvantis* on experimental and control trees

The proportions of leaf miners that successfully emerged on control and experimental trees were nearly equal (Table 4a). Furthermore, no significant differences were evident when mortality was partitioned into individual categories by orthogonal contrasts (Table 4b), although the rate of parasitism on experimental trees was more than twice that on control trees.

TABLE 2. Probabilities of *S. juvantis* occurring and surviving on leaves greater than or less than mean size of leaves available on individually numbered study trees.

Tree number(s)	Mean leaf mass (g)	Occurrence			Surviving			Not surviving		
		>Mean	<Mean	P^*	>Mean	<Mean	P^*	>Mean	<Mean	P^*
7, 10	0.047	4	4	0.546	2	3	0.750	2	1	†
1, 3	0.055	10	5	0.183	6	5	0.451	4	0	†
4, 13, 24, 25	0.065	17	15	0.263	14	10	0.234	3	5	0.438
18	0.073	2	3	0.750	2	2	†	0	1	†
11, 15	0.087	4	2	0.469	2	1	†	2	1	†
20	0.095	1	3	†	1	3	†	0	0	†
2	0.108	5	7	0.389	1	4	0.312	4	3	0.547
All trees	obs.	43	39	$\chi^2 = 0.195$	28	28	$\chi^2 = 0.00$	15	11	$\chi^2 = 0.615$
	exp.	41	41	$P > .50$	28	28	$P > .50$	13	13	$P > .40$

* Two-tailed binomial tests.

† Sample size too small to calculate probability.

TABLE 3. Fate of *Stilbosis juvantis* leaf mines on damaged and intact leaves.

a. Percentage breakdown of survivorship and mortality factors. Numbers of mines observed are in parentheses.

Leaves	Successful emergence	Mortality source for miners not emerging			
		Parasitism	Predation	Abscission	Other
Intact	70.2% (73)	3.2% (1)	9.7% (3)	61.3% (19)	25.8% (8)
Damaged	51.4% (19)	50.0% (9)	5.6% (1)	33.3% (6)	11.1% (2)

Total $\chi^2 = 22.76$, $df = 4$, $P < .001$

b. Orthogonal contrasts of survivorship and mortality factors.

Leaves	Mortality source for miners not emerging									
	Emerged?		Parasitism?		Predation?		Abscission?		Other causes?	
	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No
Intact	73	31	1	30	3	28	19	12	8	23
Damaged	19	18	9	9	1	17	6	12	2	16
	$\chi^2 = 4.27$ $P < .05$		$\chi^2 = 15.34$ $P < .001$		$\chi^2 = 0.26$ $P > .50$		$\chi^2 = 3.56$ $P > .05$		$\chi^2 = 1.51$ $P > .20$	

DISCUSSION

Selection of leaves

S. juvantis selects leaves on the basis of damage, but not by size of the leaf. Leaf selection is at the level of individual leaves rather than trees, since densities did not differ significantly between experimental and control trees. This suggests that *S. juvantis* first locates the correct host tree, then makes oviposition decisions within that tree.

Furthermore, *S. juvantis* survivorship was not different on small vs. large leaves. This result is contrary to those of previous studies of endophagous insects, which found that leaf size is critical to survivorship and/or fecundity (Whitham 1978, 1980, 1983, Tuomi et al. 1981, Mopper et al. 1984). Mopper et al. (1984) showed that leaf size becomes crucial for a congeneric

leaf miner that reaches outbreak densities; they found a positive relationship between the number of mines per leaf and leaf area. However, when densities of miners are high, it becomes advantageous to select small leaves, because of the lower probability of sharing a leaf with another miner. Tuomi et al. (1981) demonstrated that leaf miners on multiply mined leaves occupy large leaves and that larval mass is a negative function of the number of mines per leaf. For gall-forming aphids, which are also endophagous, leaf size is also apparently critical when densities are high and more than one stem mother occupies a leaf (Whitham 1978, 1980).

However, I never encountered a leaf with more than one *S. juvantis* mine during this study. Although *S. juvantis* is a dominant leaf miner on *Q. emoryi*, it is

TABLE 4. Fate of *Stilbosis juvantis* leaf mines on control and experimental trees.

a. Percentage breakdown of survivorship and mortality factors. Numbers of mines observed are in parentheses.

Trees	Successful emergence	Mortality source for miners not emerging			
		Parasitism	Predation	Abscission	Other
Control	63.6% (63)	13.9% (5)	8.3% (3)	52.8% (19)	25.0% (9)
Experimental	69.0% (29)	38.5% (5)	7.7% (1)	46.2% (6)	7.7% (1)

Total $\chi^2 = 4.40$, $df = 4$, $P > .20$

b. Orthogonal contrasts of survivorship and mortality factors.

Trees	Mortality source for miners not emerging									
	Emerged?		Parasitism?		Predation?		Abscission?		Other causes?	
	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No
Control	63	36	5	31	3	33	19	17	9	27
Experimental	29	13	5	8	1	12	6	7	1	12
	$\chi^2 = 0.38$ $P > .50$		$\chi^2 = 3.5$ $P > .05$		$\chi^2 = 0.01$ $P > .50$		$\chi^2 = 0.17$ $P > .50$		$\chi^2 = 1.76$ $P > .20$	

nevertheless low in density (mean density = 2.4 mines/1000 leaves). Furthermore, unlike most other miners on *Q. emoryi*, *S. juvantis* consumes relatively small areas (<20%) of individual leaves, and therefore it is unlikely that this leaf miner is resource limited. Thus, leaf size selection by endophagous insects may only become important when densities are sufficiently high that insects are forced to occupy leaves with other insects or when an individual insect requires large portions of a leaf for development.

Survivorship of S. juvantis on damaged and intact leaves

Survivorship of *S. juvantis* on damaged leaves is significantly lower than that on intact leaves, primarily because parasitism is increased on damaged leaves. Although the proximate cues for preference of intact leaves by *S. juvantis* are unknown, decreased parasitism could be an ultimate factor. The exact mechanism by which damage and intensified parasitism interact is unclear, although physical, visual, and chemical cues associated with damaged leaves may facilitate parasite search. Vinson (1976) demonstrated an association of damaged tobacco leaves and increased parasitic search for *Heliothis virescens*. I have demonstrated significant inducible changes in damaged leaves, particularly in increased condensed tannins and decreased protein content (Faeth, *in press*). I have also shown that experimentally increasing tannins on leaves without physical damage can increase rates of parasitism of leaf miners (S. H. Faeth and T. L. Bultman, *personal observation*). Condensed tannins are nonvolatile and unlikely to serve as long-range attractants to parasitoids, but may function as contact attractants (*sensu* Vinson 1975) or co-occur with compounds that are volatile.

Damage to leaves and ensuing alterations in chemical or physical aspects of damaged leaves had no effect on other categories of mortality, including death due to abscission or direct toxic effects of chemical changes (Table 3a, b). Although *S. juvantis* mines were significantly smaller on damaged leaves (damaged: $\bar{X} = 11.38$ mm; intact: $\bar{X} = 13.44$ mm; $t = 3.89$, $df = 69$, $P < .001$), individuals on damaged leaves apparently can develop sufficiently to emerge, even after leaf abscission. The area surrounding the *S. juvantis* mines often remains green, probably because the larvae exude cytokinins (Engelbrecht et al. 1969). This mechanism may prevent some deaths from desiccation and loss of photosynthate even after the leaf has abscised.

My results suggest a conciliation between two distinct perspectives regarding the role of competition in insect/plant interactions. Janzen (1973) proposed that insects feeding on plants "automatically compete with all other species" on the plant. In contrast, Lawton and Strong (1981) contended that "resource-based competition does not occur 'automatically' at low or even moderate levels of phytophagy," and concluded that competition is relatively unimportant in structuring

photophagous insect communities. My results suggest that direct resource-based competition does not occur for *S. juvantis*, since leaf size is not critical for leaf selection and survival, probably because densities are typically low and this miner uses only a small portion of the leaf. However, early-feeding, leaf-chewing insects may negatively affect members of the late-feeding, leaf-mining guild by producing physical or chemical changes when damaging leaves. This damage renders leaves less suitable for survival because of increased parasitism. This interaction between guilds occurs at relatively low levels of overall damage (<10% of total leaf area of trees was removed manually or by leaf-chewing insects). In effect, high-quality leaves in terms of survival may become limiting even at low levels of herbivory if either leaf miners fail to locate these leaves or there are constraints on extended searches. Indirect negative interactions mediated by the host plant may be common among phytophagous insects. Therefore, it may be necessary to view negative interactions between phytophagous insects in a way different from that assumed in classical resource-based competition theory.

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