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INDIRECT INTERACTIONS BETWEEN TEMPORALLY SEPARATED HERBIVORES MEDIATED BY THE HOST PLANT[1]

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Abstract. I tested the hypothesis that early season herbivory by leaf-chewing insects affects distribution, densities, and survivorship of late-feeding, leaf-mining insects; early chewing may physically and chemically alter quality of leaves for later leaf miners on the shared host plant, *Quercus emoryi.*

Proportions of intact leaves and leaves damaged by native leaf chewers on six control and six experimental trees were determined over two growing seasons. I manually damaged ≈50% of leaves on experimental trees to increase the total fraction of damaged leaves to ≈75%. Leaf-miner densities, distribution, survivorship, and mortality were monitored on control and experimental trees and in intact and damaged leaves within trees.

Leaf miners occurred more frequently than expected by chance on intact than damaged leaves for both control and experimental trees. Leaf-miner densities did not differ between control and experimental trees. This result suggests ovipositing leaf miners did not discriminate between damaged and undamaged trees, but selected leaves within trees.

More leaf miners survived in intact than damaged leaves in both growing seasons. Survivorship was less in damaged leaves because of significantly increased rates of parasitism on these leaves. However, death from other causes (including bacterial and fungal death) was significantly less for leaf miners on damaged leaves. This positive effect did not compensate for overall lower survivorship of leaf miners in damaged leaves due to increased parasitism. Survivorship and mortality did not differ between control and experimental trees when damaged and intact leaves were pooled within treatments. However, in 1982–1983, survival was lower and parasitism greater for leaf miners in control-damaged leaves than experimental-damaged leaves. Survival and parasitism were not different between control-intact and experimental-intact leaves. These results suggest that (1) the effect of early season herbivory on leaf miners was inversely density dependent and, (2) occurrence of leaf miners on intact leaves may be caused by avoidance of damaged leaves rather than preference for intact leaves.

Early season herbivory caused localized changes in phytochemistry within trees, and these chemical alterations were consistent with observed distributions and survivorship of leaf miners. Both early season herbivory and experimental damage resulted in higher levels of condensed tannins and lower protein content in damaged leaves within trees, but herbivory had no effect on between-tree chemistry differences. Leaf miner distributions corresponded to these localized chemical changes: leaf miners avoided damaged leaves within trees but showed no between-tree preferences.

Parasitism of miners on damaged leaves was higher, possibly because parasitoids used physical and chemical changes as cues to locate leaf-miner hosts, or because exposure of leaf miners to parasitoids was prolonged. However, when many leaves were damaged (experimental trees), the negative effect of parasites was mitigated because physical and chemical cues associated with damaged leaves were less effective. Lower leaf-miner mortality from other causes may be related to the bactericidal or fungicidal properties of increased tannins in damaged leaves.

This study demonstrates that temporally separated guilds can interact subtly at low levels of herbivory through changes in the host plant. Current theories of within- and between-guild organization of phytophagous insects may need to be re-evaluated if such interactions are common.

Key words: asymmetric interaction; community organization; competition; densities; distribution; guilds; herbivory; leaf chewers; leaf miners; mortality; protein; Quercus emoryi; *survivorship; tannins.*

INTRODUCTION

The role of competition in structuring phytophagous insect communities encompasses two distinct perspectives. Janzen (1973) proposed that insects that feed on plants "automatically compete with all other species" on the plant. Conversely, Lawton and Strong (1981) contended that "resource-based competition does not occur 'automatically' at low or even moderate levels of phytophagy," and concluded competition is relatively unimportant in structuring phytophagous insect communities (Strong et al. 1984). Experimental tests of interspecific competition (McClure and Price 1975, Rathcke 1976, Seifert and Seifert 1976, Stiling 1980, Strong 1982) generally confirm Lawton and Strong's (1981) contention that interspecific competition is rare or relatively unimportant in phytophagous insect communities. Even those who consider interspecific competition as a primary organizing force in other ecological communities now question the importance of interspecific competition in phytophagous insect communities (Schoener 1983). In cases where interspecific competition has been detected (e.g., McClure and Price 1975, Stiling 1980), intraspecific competition was considered more important in determining population densities and structuring communities (Strong et al. 1984). Connell's (1983) review of the literature on com-

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petition has showed a much higher incidence of intraspecific competition relative to interspecific competition in phytophagous insects (Connell: Table 6).

One would thus expect that negative interactions (e.g., competition) between phytophagous species of different guilds (sensu Root 1967) should be even less frequent than interactions among species of the same guild. For example, competition is expected to be greater within guilds than between guilds, because guilds, by definition (Root 1967), use a common resource in a similar fashion (Pianka 1983). If negative interactions such as competition are important for phytophagous insects, then current theory (Pianka 1983) predicts interactions should be more prevalent within the leaf-mining, leaf-chewing, or leaf-sucking guilds than between these guilds.

It is possible for guilds of phytophagous insects to interact negatively if herbivory by one guild alters plant chemistry for later feeding guilds (Janzen 1973, Strong et al. 1984). Induction of chemical changes in plants through severe herbivory is well documented (Haukioja and Niemela 1979, Rhoades 1979, Ryan 1979, Carroll and Hoffman 1980, Bryant 1981, Schultz and Baldwin 1982, Baldwin and Schultz 1983), although actual effects of inducible chemistry on herbivores are less clear (Fowler and Lawton 1985, Myers and Williams 1984). Early-feeding guilds could negatively affect late-feeding guilds not only through direct noxious effects of plant chemicals, but also by changes in leaf structure, defensive chemicals, and nutrition that may indirectly alter selection of leaves by late feeders (Faeth 1985*a*), or increase risks of parasitism and predation (Price et al. 1980, Schultz 1983, Strong et al. 1984, Faeth 1985*a*). Conceivably, early feeding guilds could affect population dynamics and community organization of late feeders under low herbivory conditions that commonly occur in nature, provided that sufficient fractions of leaves are damaged, even if total leaf area removed is small. This latter point has received little experimental attention.

I tested the hypothesis that early-feeding leaf chewers on *Q. emoryi* (Fagaceae) negatively affect the late-feeding, leaf-mining guild via changes in physical damage, inducible plant defenses (tannins), and nutrition (protein). This hypothesis was tested by experimentally increasing early-season leaf damage, and then monitoring chemical and nutritional changes in experimental and control trees and intact and damaged leaves in 1981–1982 and 1982–1983. I determined distribution, survivorship, and causes of mortality of leaf miners on two spatial scales: experimental and control trees (between trees) and intact and damaged leaves (within trees).

Materials and Methods

Study area

Experiments were conducted at the Sierra Ancha Experimental Station (United States Department of Agriculture) in the Tonto National Forest, Gila County, Arizona. The study site is a riparian forest (1555 m elevation) bordering Parker Creek and dominated by mixed oak (*Quercus emoryi, Q. arizonica,* and *Q. turbinella*), Ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Pseudotsuga taxifolia*).

Study trees

Twelve trees of *Q. emoryi* were selected on the basis of similar size (≈3 m in height); six were randomly assigned as controls, and six assigned as experimental trees. All trees were apparently disease free and located within a 150 m radius of each other. *Quercus emoryi* is an evergreen oak. Leaves burst in mid-April–early May and most remain on the tree until abscission in the following April or May when new buds burst.

Leaf-chewing guild

Leaf chewers on *Q. emoryi* were primarily Lepidoptera (Arctiidae, Noctuiidae, Lasiocampidae, Phycitidae, Geometridae, Stenomidae, Tortricidae), Coleoptera (Chrysomelidae and Curculionidae), Orthoptera (Acrididae and Tettigoniidae), and Hymenoptera (Tenthredinidae). These folivores concentrated feeding early in the growing season. In 1981–1982, almost all leaf-chewing damage occurred during the interval of budbreak to 30 d after budbreak (Faeth 1985*b*). In 1982–1983, leaf-chewing damage was distributed from late April (budbreak) to mid-October. However, most leaf damage occurred in two intervals: (1) budbreak to late May, and (2) early September to late October (Faeth 1985*b*).

Leaf-mining guild

Nine species of leaf miners feed within leaves of *Q. emoryi* in the riparian study site (Table 1). One of these (*Coptodisca* sp.) was never encountered on a study tree during the 2-yr study period, and therefore was not included in analyses. Leaf-mining species on *Q. emoryi* are generally late feeders, beginning to feed in late June and July, after most leaf-chewing damage has occurred. Most species also continue to feed through the winter months and exhibit very long larval developmental times (Table 1). Two species (*Stilbosis juvantis* and *Brachys cephalicus*) have single generations that begin feeding in late July and do not complete larval development until the following April or May when leaves abscise. The third generation of *Cameraria* sp. nov., *Tischeria* sp. nov., and *Stigmella* sp. mine during winter and spring months and also complete larval development near abscission.

All nine species of leaf miners are restricted to mine leaves upon which the adult female has oviposited. *Bucculatrix* sp. mines only during the first two larval instars, then feeds externally and may move to other leaves. However, at least for larval-mining stages, *Bucculatrix* is also confined to a single leaf.

TABLE 1. Taxonomy and phenology of leaf miners on *Quercus emoryi*.

Order Family Species	Generations per year	Developmental stages within mine	Begins mining	Winter feeder	Duration of mining stages (mo)
Lepidoptera					
Lyonetiidae					
Bucculatrix sp.	1–2	Some larval	late June	no	1
Gracillariidae					
Cameraria sp. nov. (Davis) (*guttifinitella* group)	3	All larval; pupal	late June	yes	1–6
Caloptilia sp.	1	Some larval	late June	no	1
Tischeriidae					
Tischeria sp. nov.	3	All larval; pupal	late June	yes	1–6
Nepticulidae					
Stigmella sp.	3	All larval	late June	yes	1–6
Unknown sp.	1	All larval	late June	yes	1–6
Cosmopterigidae					
Stilbosis juvantis (Hodges)	1	All larval	July	yes	10
Incurvariidae					
Coptodisca sp.*	1	All larval; pupal	July	yes	1–3
Coleoptera					
Buprestidae					
Brachys cephalicus (Fisher)	1	All larval; pupal	July	yes	10

* *Coptodisca* sp. was not present on study trees but was found once on a nonstudy *Q. emoryi* tree in study area.

Experimental increase of leaf damage

To test the hypothesis that previous leaf damage affects selection of leaves by leaf miners and survivorship of leaf miners, proportions of damaged leaves were artificially increased on experimental trees. On 8 July 1981 and 7 July 1982, I simulated herbivory by removing >10% of individual leaf area on ≈50% of leaves of each experimental tree, using a paper punch. Native leaf-chewing insects damaged ≈25% of total leaves on both control and experimental trees. A leaf was categorized as damaged by leaf chewers if >10% of leaf area was removed. This level of damage was selected because damage less than this amount was not always easily recognizable as resulting from insect herbivores. Estimates of proportions of intact and damaged leaves for each tree were determined from monthly leaf samples collected from the study trees (Table 2). Leaves were removed monthly in both growing seasons from each tree and returned to the laboratory. The leaves were lyophilized and then segregated into insect-damaged, manually damaged, and intact leaves. Leaves in each category were counted and weighed. Leaf mass and area are highly correlated in *Q. emoryi* (r^2 = .965, P < .001; Bultman and Faeth 1986). Amount of leaf area removed by either leaf chewers or by manual damage was determined by measuring area of damaged leaves, covering damaged areas with opaque tape, and then re-measuring with a LI-COR leaf area meter. I calculated proportions of intact and damaged leaves in both growing seasons for each tree and for control and experimental trees as groups (Table 2).

Leaf miner densities, distribution, and fate

All leaves on the 12 study trees were examined for leaf mines from July to April in 1981–1982 and 1982–1983. Each leaf with an active miner (larva still feeding) was labelled with tape to assure accurate determination of densities and to determine fate of individual miners. Total number of leaves on each tree was counted in July of both seasons and true densities calculated by dividing cumulative number of mines by total number of leaves on each tree (Table 2). Differences in mean densities between control and experimental trees in each season were tested with z tests.

I also recorded whether miners colonized damaged or intact leaves within trees. I used chi-square analyses to determine if leaf miners occurred on intact or damaged leaves within individual trees more frequently than expected based on estimated proportions of intact and damaged leaves. A similar chi-square analysis was used to examine leaf-miner distributions within and between control and treatment trees.

I also tested the null hypothesis that distribution of leaf miners on intact and damaged leaves was equivalent on control and experimental trees, adjusted for proportions of intact and damaged leaves observed in these treatments. The null hypothesis is:

$$H_o\colon P_{IC}/a_{IC} = P_{IE}/a_{IE}$$

where P_{IC} and P_{IE} are the fractions of leaf miners observed on control and experimental trees, respectively, and a_{IC} and a_{IE} are observed fractions of damaged and intact leaves on control and experimental trees, respectively. Assuming an approximate normal distribution, the test statistic (two-tailed) is:

$$Z = \frac{P_{IC}/a_{IC} - P_{IE}/a_{IE}}{\dfrac{a^2_{IC}P_{IC}(1 - P_{IC})}{N_C} + \dfrac{a^2_{IE}P_{IE}(1 - P_{IE})}{N_E}},$$

where the denominator is the estimated standard deviation (N_C and N_E are sample sizes of leaf miners on

TABLE 2. Percent of damaged and intact leaves on control and experimental trees in 1981–1982 and 1982–1983. N = number of leaves sampled in each season from each tree.*

Treatment	1981–1982 % leaves intact	1981–1982 % leaves damaged	1981–1982 N	1981–1982 Cumulative leaf miner density (mines/1000 leaves)	1982–1983 % leaves intact	1982–1983 % leaves damaged	1982–1983 N	1982–1983 Cumulative leaf miner density (mines/1000 leaves)
Control								
Tree								
1	75.2	24.8	946	10.0	79.6	20.4	1038	18.7
2	65.0	35.0	571	16.6	77.0	23.0	643	18.8
3	77.5	22.5	1045	14.5	77.7	22.3	1029	8.6
4	70.0	30.0	1171	7.5	88.3	11.7	1242	10.6
5	70.6	29.4	849	11.1	85.1	14.9	897	5.4
6	85.7	14.3	1129	12.7	76.6	23.4	832	9.9
All	74.9	25.1	5711	12.1 ± 3.2 ($\bar{X}$ ± SE)	81.3	18.7	5679	12.0 ± 5.5 ($\bar{X}$ ± SE)
Experimental								
Tree								
1	26.7	73.3	690	6.2	25.3	74.7	805	5.2
2	32.8	67.2	653	11.7	36.1	63.9	846	5.6
3	24.4	75.6	751	23.3	30.3	69.7	867	23.8
4	24.1	75.9	605	8.3	28.6	71.4	1004	3.7
5	25.3	74.7	546	12.5	18.1	81.8	687	8.4
6	17.5	82.5	650	7.4	29.7	70.3	785	5.2
All	25.1	74.9	3895	11.6 ± 6.25 ($\bar{X}$ ± SE)	28.4	71.6	4994	8.6 ± 7.6 ($\bar{X}$ ± SE)

* On experimental trees, ≈50% of leaves were damaged with a paper punch; the remainder were leaves that were damaged by insects.

control and experimental trees, respectively). This test was performed for distributions of leaf miners in both growing seasons.

Survivorship of miners was ascertained on damaged and undamaged leaves by the presence of characteristic emergence holes (Faeth and Simberloff 1981*a*, *b*) both before and after leaf abscission. For nonemerged leaf miners, death was characterized as resulting from parasitism by hymenopterans, predation, death from other causes (which included death from leaf nutrition or defenses, bacterial, fungal, or viral attack, or abiotic factors) (see Methods section in Faeth and Simberloff 1981*a*, *b*), or leaf abscission. The latter cause of mortality was invoked if a larva was actively mining a few days before abscission, recovered in leaf litter 2 wk later and, upon dissection of the mine, appeared to have died from desiccation caused by leaf abscission. Some tagged leaf mines were lost from trees during the course of the study, or some fates could not be determined accurately because of weathering of the mine. Therefore, fewer miners occur in survivorship and mortality analyses than in density and distributional analyses.

Two by five contingency tables were used to test for differences in survivorship and mortality for leaf miners occurring on damaged and intact leaves in both seasons. Similar analyses were used to test for differences in survivorship and mortality of leaf miners occurring on control and treatment trees in each season regardless of damage, and when damaged and intact leaves were considered separately within treatments. Orthogonal χ^2 contrasts were then used to partition total χ^2 independently among survivorship and categories of mortality. This method shows which categories of survivorship and mortality contribute significantly to overall χ^2 of the 2 × 5 contingency tables.

Phytochemical analyses

Insect-damaged, manually damaged, and intact leaves were analyzed separately for each experimental tree and for insect-damaged and intact leaves on control trees at each sample date for protein and hydrolyzable and condensed tannin content. Condensed tannins analyses included segregation into monomeric fractions of phenols, polymeric fractions (condensed tannins), and total vanillin positive fractions (monomers plus polymers). Only condensed tannin content is reported here; total vanillin positive content of various leaves within trees showed similar trends to condensed tannins. Randomly sampled leaves from each tree were immediately frozen in dry ice in the field and later lyophilized in the laboratory, and then ground into a fine powder. Ground samples were stored in jars at 5°C with a desiccant until analyses could be performed.

Protein content of ground, lyophilized leaf samples was determined by the BioRad Method (Richmond, California). Samples were washed twice with acetone to remove pigments and tannins that might interfere with the colorimetric reaction of the reagent (Coomassie Brilliant Blue in phosphoric acid and methanol).

Absorbances at 595 nm of samples were compared against standards using egg albumin prepared for each run. The BioRad Method is the most reliable method of determining protein content when large amounts of phenolics are present in tissue samples (Robinson 1979).

Condensed tannins were determined by a modified acidified vanillin method (Broadhurst and Jones 1978). Ground, lyophilized samples were washed three times with ether to remove lipids and pigments, and extracted with acetone. Monomeric phenol fractions were first determined by adding Sephadex LH-20 solution (Sephadex in 40% methanol) to a subset of the tissue samples. Sephadex LH-20 is a selective absorbent for tannins (Jones et al. 1976) and standardization procedures indicate >95% of condensed tannins are bound by Sephadex LH-20. Freshly prepared vanillin reagent (4% vanillin in 2 parts MeOH : 1 part concentrated HCl) was added to each sample tube from which tannins were removed and absorbance at 500 nm read after 1 h, using a catechin standard prepared for each run. Total vanillin positive was then determined by adding 40% MeOH to the remaining, rehydrated subsamples. Vanillin reagent (as above) was added to sample tubes and read at 500 nm, using a catechin standard as above.

Condensed tannins were determined by subtracting monomeric readings from total vanillin positive for each sample as above. A catechin standard overestimates condensed tannin content (Price et al. 1978). Comparison to a purified condensed tannin standard from *Q. emoryi* showed that condensed tannin equivalents could be estimated as 0.42 times tannin concentration, when that concentration was expressed as percent of leaf dry mass.

Hydrolyzable tannins were determined by a modified iodate technique (Bate-Smith 1977) and expressed as percent dry mass tannic acid equivalents as compared to a tannic acid standard curve prepared for each run. Technically, this procedure is specific only for the galloyl group of hydrolyzable tannins, not ellagitannins, but is commonly used as an estimate of hydrolyzable tannin content (Schultz and Baldwin 1982, Baldwin and Schultz 1983). Samples were read at 550 nm exactly 80 min after KIO_4 was added.

For protein and tannin analyses, all extraction solutions, reagent concentrations, temperatures, and time of reactions were empirically determined to standardize and optimize reactivity. Repeated measures ANOVA (Winer 1971) were used to test for differences in protein and hydrolyzable and condensed tannin content between control and treatment trees in both seasons (between-trees factor). Repeated measures ANOVA were also used to test for effects of damage and seasonality in phytochemical parameters (within-trees factors).

Results

Selection of damaged and intact leaves

Individuals of the leaf-mining guild generally selected intact leaves within trees over damaged leaves (Tables 3 and 4). For control trees, leaf miners occurred more frequently than expected ($P < .05$) in intact leaves within three of six trees in both seasons. On the other three trees, leaf miners were also found more often in intact leaves, but not significantly (Tables 3 and 4). On experimental trees, which had higher proportions of damaged leaves than control trees, leaf miners selected intact leaves over damaged leaves on all six trees in 1981–1982 and four of six trees in 1982-1983. Heterogeneity χ^2 tests (Sokal and Rohlf 1981) on pooled

TABLE 3. Distribution of leaf miners on damaged (D) and intact (I) leaves at the scale of individual trees and treatments in 1981–1982. Expected distributions are based upon proportions of damaged and intact leaves in Table 2.

Control						Experimental					
Tree	Damage	Obs.	Exp.	χ^2	Signif.	Tree	Damage	Obs.	Exp.	χ^2	Signif.
1	I	20	16.5	2.97	NS	1	I	5	2.4	3.84	*
	D	2	5.5				D	4	6.6		
2	I	38	30.6	5.13	*	2	I	24	10.8	23.15	*
	D	9	16.4				D	9	21.2		
3	I	42	36.4	3.82	*	3	I	18	8.8	12.73	*
	D	5	10.6				D	18	27.2		
4	I	48	38.5	7.81	*	4	I	13	4.1	25.46	*
	D	7	16.5				D	4	12.9		
5	I	15	12.0	2.55	NS	5	I	10	4.8	7.54	*
	D	2	5.0				D	9	14.2		
6	I	23	21.4	0.83	NS	6	I	7	2.4	10.54	*
	D	2	3.6				D	7	11.6		
All control trees						All experimental trees					
	I	186	159.5	17.53	*		I	77	32.1	83.83	*
	D	27	53.5				D	51	95.9		
Heterogeneity $\chi^2 = 5.58$					NS	Heterogeneity $\chi^2 = 0.57$					NS

* $P < .05$, NS = not significant.

TABLE 4. Distribution of leaf miners on damaged (D) and intact (I) leaves at the scale of individual trees and treatments in 1982–1983. Expected distributions are based upon proportions of damaged and intact leaves in Table 2.

Control						Experimental					
Tree	Damage	Obs.	Exp.	χ^2	Signif.	Tree	Damage	Obs.	Exp.	χ^2	Signif.
1	I	51	43.8	5.81	*	1	I	6	2.5	6.53	*
	D	4	11.2				D	4	7.5		
2	I	62	54.7	4.24	*	2	I	14	7.6	8.45	*
	D	9	16.3				D	7	13.4		
3	I	35	28.7	6.16	*	3	I	25	14.8	10.07	*
	D	2	8.3				D	24	34.2		
4	I	98	91.8	3.57	NS	4	I	7	2.9	8.16	*
	D	6	12.2				D	3	7.1		
5	I	10	9.4	0.26	NS	5	I	5	3.1	1.42	NS
	D	1	1.6				D	12	13.9		
6	I	23	19.9	2.00	NS	6	I	5	3.9	0.44	NS
	D	3	6.1				D	8	9.1		
All control trees						All experimental trees					
	I	279	247.2	21.89	*		I	62	34.1	31.89	*
	D	25	56.8				D	58	85.9		
Heterogeneity $\chi^2 = 0.15$					NS	Heterogeneity $\chi^2 = 3.18$					NS

* $P < .05$, NS = not significant.

data for control and experimental trees show that deviations from expected are in a uniform direction, i.e., distribution on each tree is toward more miners on intact leaves, and distributions are not significantly different between trees. The heterogeneity χ^2 are not significant for control or experimental trees in either season (Tables 3 and 4).

When control trees are considered collectively, leaf miners overwhelmingly preferred intact to damaged leaves in both seasons (Tables 3 and 4). This selection occurred when leaf chewers damaged 25.1 and 18.7% of control tree leaves in 1981–1982 and 1982–1983, respectively (Table 2). For experimental trees combined, leaf miners also preferred intact leaves to damaged ones in both seasons (Tables 3 and 4). As a group, experimental trees had 74.9 and 71.6% leaves damaged in 1981–1982 and 1982–1983, respectively.

Selection of experimental vs. control trees

Leaf miners did not preferentially select control or experimental trees. Mean densities of leaf miners (Table 2) did not differ significantly between control and experimental trees in either season (1981–1982, $Z = 0.17$, $P > .50$; 1982–1983, $Z = 0.37$, $P > .50$).

Although densities did not differ between control and experimental trees, leaf miners occurred more frequently on intact leaves within experimental trees than within control trees. In 1981–1982, the observed and expected fractions of leaf miners on intact leaves within control trees were 0.873 and 0.749, respectively, and 0.602 and 0.251, respectively, on experimental trees. In 1982-1983, the observed and expected fractions of leaf miners on intact leaves within control trees were 0.918 and 0.813, respectively, and 0.517 and 0.284, respectively, on experimental trees. In both growing

TABLE 5. Fate of leaf miners in damaged and intact leaves in 1981–1982.

a. Pattern of leaf miner fates.

	No. mines observed	% successful emergence	% mortality (categorical) for nonemerged miners			
			Parasitism	Predation	Abscission	Other
Intact leaves	214	46.7	21.1	12.3	17.5	49.1
Damaged leaves	72	27.8	44.2	11.5	19.2	25.0

Overall $\chi^2 = 21.48$, df = 4, $P < .001$

b. Breakdown and analysis by fate category.

	Emergence		Cause of mortality of nonemerged miners							
			Parasitism		Predation		Abscission		Other causes	
	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No
Intact leaves	100	114	24	90	14	100	20	94	56	58
Damaged leaves	20	52	23	29	6	46	10	42	13	39
	$\chi^2 = 7.95$, $P < .001$		$\chi^2 = 9.45$, $P < .001$		$\chi^2 = 0.02$, $P > .50$, NS		$\chi^2 = 0.07$, $P > .50$, NS		$\chi^2 = 8.56$, $P < .001$	

TABLE 6. Fate of leaf miners in damaged and intact leaves in 1982–1983.

a. Pattern of leaf miner fates.

	No. mines observed	% successful emergence	% mortality (categorical) for nonemerged miners			
			Parasitism	Predation	Abscission	Other
Intact leaves	243	36.6	20.1	9.7	24.7	45.5
Damaged leaves	99	23.0	56.6	2.6	15.8	25.0

Overall $\chi^2 = 39.98$, df = 4, $P < .001$

b. Breakdown and analysis by fate category.

	Emergence		Cause of mortality of nonemerged miners							
			Parasitism		Predation		Abscission		Other causes	
	Yes	No	Yes	No	Yes	No	Yes	No	Yes	No
Intact leaves	89	154	31	123	15	139	38	116	70	84
Damaged leaves	23	76	43	33	2	74	12	64	19	57
	$\chi^2 = 5.73$ $P < .05$		$\chi^2 = 30.98$ $P < .001$		$\chi^2 = 3.76$ $P > .05$, NS		$\chi^2 = 2.36$ $P > .05$, NS		$\chi^2 = 8.97$ $P < .001$	

seasons, the observed distributions of leaf miners on intact leaves were significantly different between control and experimental trees (1981–1982, $Z = 3.08$, $P < .01$; 1982–1983, $Z = 5.49$, $P < .001$). Since frequency on damaged leaves is simply a reciprocal test, it follows that leaf miners occurred less frequently on damaged leaves within experimental trees than control trees.

Survivorship and mortality on intact and damaged leaves

The pattern of mortality factors and successful emergence was significantly different for leaf miners on intact and damaged leaves in both growing seasons (Tables 5a and 6a). Successful emergence was significantly greater for leaf miners in intact than in damaged leaves in both seasons (Tables 5b and 6b). For leaf miners that died, parasitism was significantly greater in damaged leaves than undamaged ones in both seasons (Tables 5b and 6b). However, death from other causes (including viral, fungal, or bacterial attack, plant chemistry, and abiotic factors) was significantly less for leaf miners on damaged than intact leaves (Tables 5b and 6b). Other categories of mortality (predation and abscission) did not differ for leaf miners on intact and damaged leaves (Tables 5b and 6b).

Survivorship and mortality on control and experimental trees

The pattern of mortality factors and successful emergence did not differ significantly between leaf miners on control and experimental trees when damaged and intact leaves were combined in either season (Table 7).

Comparison of mortality and survivorship between experimental and control trees by pooling leaf miners on intact and damaged leaves may obscure differences for the following reason. Although a larger proportion of leaf miners occurred on intact leaves within experimental than control trees based on fractions of damaged leaves, absolute numbers of leaf miners on intact leaves within experimental trees were less than on intact leaves within control trees (Tables 3 and 4). Therefore, the nondifference between experimental and control trees may be attributed to greater absolute numbers of leaf miners on intact leaves within control trees, or to differences between experimental and control trees in mortality associated with either intact or damaged leaves. Testing the latter possibility is problematic because subdividing survivorship and mortality for leaf miners on intact and damaged leaves within treatments reduces sample sizes such that statistical tests are not valid for some comparisons.

Sample sizes remain large enough for valid tests after subdivision of leaf miners on damaged and intact leaves into two categories, successful emergence and parasitism, but not for other categories of mortality. In 1981–1982, successful emergence and parasitism on damaged leaves were not significantly different in control vs. experimental trees (Table 8). In 1982–1983, leaf miners experienced significantly lower survivorship and higher parasitism on damaged leaves within control than within experimental trees. For leaf miners in intact leaves, successful emergence and parasitism did not differ between control and experimental trees in either season (Table 8).

Phytochemistry

Protein content was generally lower in manually damaged and insect-damaged leaves than in intact leaves within experimental and control trees in both seasons (Fig. 1). However, there was no overall treatment difference between experimental and control trees (1981–1982, $F = 1.76$, df = 1,10, $P > .20$; 1982–1983, $F = 0.76$, df = 1,10, $P > .50$), although there was a significant effect of damage (1981–1982, $F = 26.19$, df = 1,10, $P < .001$; 1982–1983, $F = 53.52$, df = 1,10, $P < .001$). Thus, insect-produced and experimental increases in leaf damage did not alter overall levels of

TABLE 7. Fate of leaf miners on control and experimental trees in 1981–1982 and 1982–1983. Leaf miners in intact and damaged leaves are pooled within treatments. N = number of mines observed.

	Successful emergence		Nonemergence		Mortality (categorical) for nonemerged miners							
					Parasitism		Predation		Abscission		Other	
Treatment	%	N	%	N	%	N	%	N	%	N	%	N
1981–1982												
Control	43.5	87	56.5	113	24.8	28	15.0	17	15.9	18	44.2	50
Experimental	38.4	33	61.6	53	35.8	19	5.7	3	22.6	12	35.8	19
				Overall χ^2 = 6.55, df = 4, NS								
1982–1983												
Control	33.0	76	67.0	154	29.9	46	9.7	15	22.1	34	38.3	59
Experimental	31.9	36	68.1	76	36.8	28	2.6	2	21.1	16	39.5	30
				Overall χ^2 = 4.34, df = 4, NS								

protein between control and experimental trees, but did decrease protein content on damaged leaves within trees. Protein content in control and experimental trees changed significantly throughout the growing seasons (1981–1982, $F = 58.86$, df = 6,60, $P < .001$; 1982–1982, $F = 28.58$, df = 8,80, $P < .001$).

Hydrolyzable tannin content (Fig. 2) also did not differ significantly between experimental and control trees (1981–1982, $F = 0.37$, df = 1,10, $P > .50$; 1982–1983, $F = 0.11$, df = 1,10, $P > .50$). Within experimental and control trees, there was a significant effect of damage in 1982–1983 ($F = 20.21$, df = 1,10, $P < .001$), but not in 1981–1982 ($F = 1.59$, df = 1,10, $P > .20$). The effect of time (date of sample) in each season is only significant (1981–1982, $F = 3.96$, df = 6,60, $P < .01$; 1982–1983, $F = 28.67$, df = 8,80, $P < .001$) when the first sample date is included (Fig. 2).

Condensed tannin content (Fig. 3) did not differ significantly between control and treatment trees in either 1981–1982 ($F = 0.47$, df = 1,10, $P > .50$) or 1982–1983 ($F = 1.02$, df = 1,10, $P > .30$). Again, damage to experimental trees did not alter overall levels of tannins in experimental trees relative to control trees. However, damaged leaves of both types within control and experimental trees had significantly greater condensed tannin content than intact leaves (1981–1982, $F = 10.19$, df = 1,10, $P < .01$; 1982–1983, $F = 24.30$, df = 1,10, $P < .001$) (Fig. 3). Levels of these compounds also varied significantly with time in both growing seasons (1981–1982, $F = 24.42$, df = 6,60, $P < .001$; 1982–1983, $F = 38.06$, df = 8,80, $P < .001$) (Fig. 3).

I also tested for differences in phytochemistry between insect- and manually damaged leaves within ex-

TABLE 8. Survivorship and mortality of leaf miners analyzed separately for damaged and intact leaves within control and experimental trees. N = number of mines observed.

	Successful emergence		Nonemergence		Parasitism*		Death (not parasitized)†	
Treatment	%	N	%	N	%	N	%	N
1981–1982 damaged leaves								
Control	29.6	8	70.4	19	42.1	8	57.9	11
Experimental	26.7	12	73.3	33	45.4	15	54.6	18
		χ^2 = 0.07, df = 1, NS				χ^2 = 0.05, df = 1, NS		
1982–1983 damaged leaves								
Control	4.2	1	95.8	23	78.3	18	21.7	5
Experimental	29.3	22	70.7	53	46.2	25	53.8	28
		χ^2 = 6.46, df = 1, $P < .01$				χ^2 = 6.31, df = 1, $P < .05$		
1981–1982 intact leaves								
Control	45.7	79	54.3	94	21.3	20	78.7	74
Experimental	51.2	21	48.8	20	20.0	4	80.0	16
		χ^2 = 0.41, df = 1, NS				χ^2 = 1.19, df = 1, NS		
1982–1983 intact leaves								
Control	36.4	75	63.6	131	21.4	28	78.6	103
Experimental	37.8	14	62.2	23	13.0	3	87.0	20
		χ^2 = 2.76, df = 1, NS				χ^2 = 0.84, df = 1, NS		

* Proportion of total number of nonemerged leaf miners.

† Includes all other categories of mortality (predation, abscission, death from other causes).

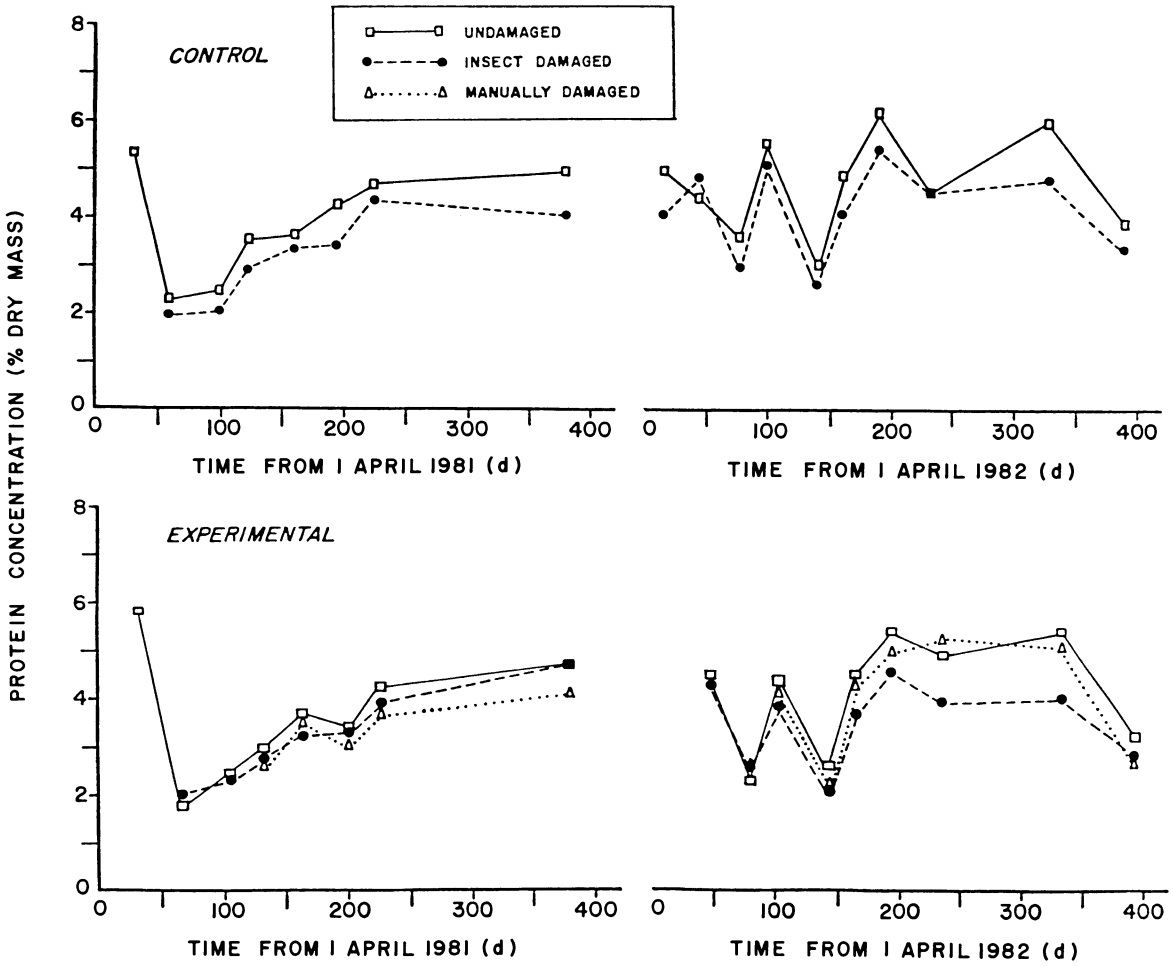

FIG. 1. Seasonal changes in protein content of undamaged and damaged leaves on control and experimental trees in 1981–1982 and 1982–1983. Each point is the mean of six trees. Standard errors for individual points are in Appendix I and II.

perimental trees, since induction of some phytochemical parameters appeared greater in manually damaged leaves relative to insect-damaged leaves (Figs. 1–3). In both seasons, manually damaged leaves contain significantly greater amounts of condensed tannin than insect-damaged leaves (damage effect 1981–1982, $F = 7.27$, df = 1,5, $P < .05$; 1982–1983, $F = 8.25$, df = 1,5, $P < .05$). Neither hydrolyzable tannin nor protein content differed significantly between manually and insect-damaged leaves in either growing season.

DISCUSSION

Price et al. (1980) suggested that communities of phytophagous insects may be structured by interactions between three trophic levels: the plant, herbivores, and natural enemies of herbivores. These interactions may be subtle and indirect. For example, changes in host plant quality may directly affect survivorship of phytophagous insects through increases in plant toxins or decreases in nutrition, but may also indirectly increase vulnerability of insect hosts to predators or parasites (Vinson 1976, Price et al. 1980, Schultz 1983).

Price et al. (1980) adumbrated that guilds of phytophagous insects may interact via chemical or physical alterations in the host plant, even though the guilds do not feed simultaneously. However, there has so far been little evidence that temporally separated guilds of phytophagous insects interact and affect organization of insect guilds on host plants (Strong et al. 1984). My results show early leaf-chewing herbivory affects distribution and survivorship and mortality of the late-feeding, leaf-mining guild. These interguild effects are mediated by physical and chemical alterations in the shared host plant, *Q. emoryi*.

Distribution of leaf miners

In general, leaf miners occurred significantly more often on intact leaves than damaged leaves in both growing seasons (Tables 3 and 4). I conclude that females selected intact leaves (or conversely, avoided damaged leaves) for oviposition because adult females

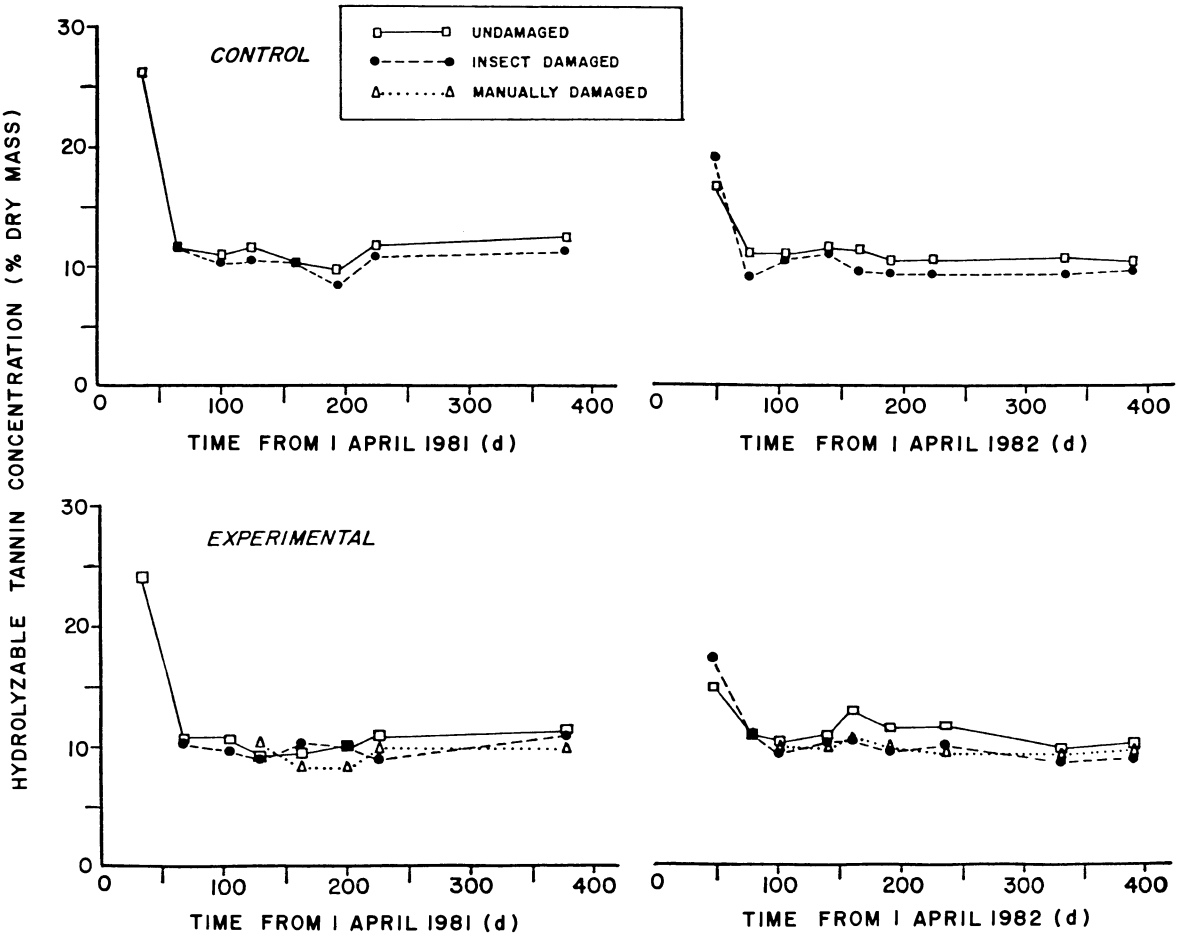

FIG. 2. Seasonal changes in hydrolyzable tannin content of undamaged and damaged leaves on control and experimental trees in 1981–1982 and 1982–1983. Each point is the mean of six trees. Standard errors for individual points are in Appendix I and II.

solely determine egg and larval distribution of leaf miners on leaves. Furthermore, differential egg mortality on various leaves that might partially determine larval distribution did not occur in this system (Faeth 1985*a*). This selection of intact leaves occurred both at endemic levels of herbivory by leaf chewers (control trees; Tables 3 and 4) and at experimentally increased levels of herbivory (treatment trees; Tables 3 and 4).

Although leaf miners selected intact leaves, densities of leaf miners were not significantly different between control and experimental trees (Table 2), despite experimental trees having ≈50% more damaged leaves than control trees. Therefore, I conclude that selection of intact leaves by leaf miners occurred within trees, rather than between trees. This suggests adult females locate the correct host plant, then choose leaves for oviposition within each tree.

Distributions of leaf miners on intact and damaged leaves were significantly different within experimental trees and control trees. In other words, leaf miners selected intact or avoid damaged leaves to a greater extent on experimental trees where proportions of manually damaged leaves were greatly increased. This suggests that the physical and chemical cues associated with avoidance of damaged leaves were more exaggerated in manually damaged leaves than insect-damaged leaves (see Phytochemical Changes in Damaged vs. Intact Leaves).

Survivorship and mortality of leaf miners

Mortality of leaf miners in damaged leaves was increased through enhanced parasitism, but the mortality due to other causes was decreased (Tables 5a and 6b). These results suggest that trade-offs occurred for leaf miners in damaged leaves. However, negative effects of feeding on damaged leaves outweighed beneficial effects, since overall survivorship was significantly less on damaged than intact leaves (Tables 5b and 6b). These positive and negative effects of feeding on damaged leaves are discussed in conjunction with chemical and physical changes in damaged leaves below (see Phytochemical Changes in Damaged vs. Intact Leaves).

Damaged leaves were less suitable for leaf miner survival when relatively few leaves within a tree were damaged. When large fractions of leaves were damaged (experimental trees), parasitism was less and survivorship was greater on damaged leaves within experimental trees than control trees, at least in 1982–1983 (Table 8). However, it was still advantageous for leaf miners to occur in intact leaves within experimental trees because leaf miners experience greater survivorship (37.8%) and less parasitism (13.0%) than leaf miners in damaged leaves (Table 8, successful emergence = 29.3%, parasitism = 78.3%).

When leaf miners on intact leaves are considered separately, survivorship and parasitism did not differ for miners on these leaves between experimental and control leaves (Table 8). Thus, differences in survivorship and parasitism between leaf miners on intact and damaged leaves were caused by changes in these factors associated with damaged leaves rather with intact leaves. If proximal selection of leaves by adult leaf miners is ultimately linked with survivorship, then the observed distributions of leaf miners on leaves should be a consequence of avoidance of damaged leaves rather than preference for intact leaves.

Phytochemical changes in damaged vs. intact leaves

Damaged leaves within experimental and control trees differed significantly in protein and condensed tannin content compared to intact leaves in 1981–1982 and 1982–1983 (Figs. 1 and 3). Hydrolyzable tannin content was not significantly different between damaged and intact leaves in 1981–1982, but was different in 1982–1983 (Fig. 2). However, the apparent decrease in hydrolyzable tannin content in damaged leaves was probably attributable to relative increases in condensed tannin in these leaves, rather than a true decline in hydrolyzable tannin production, since hydrolyzable tannin content did not vary with time once leaves expanded (Fig. 2). This phenomenon could also account

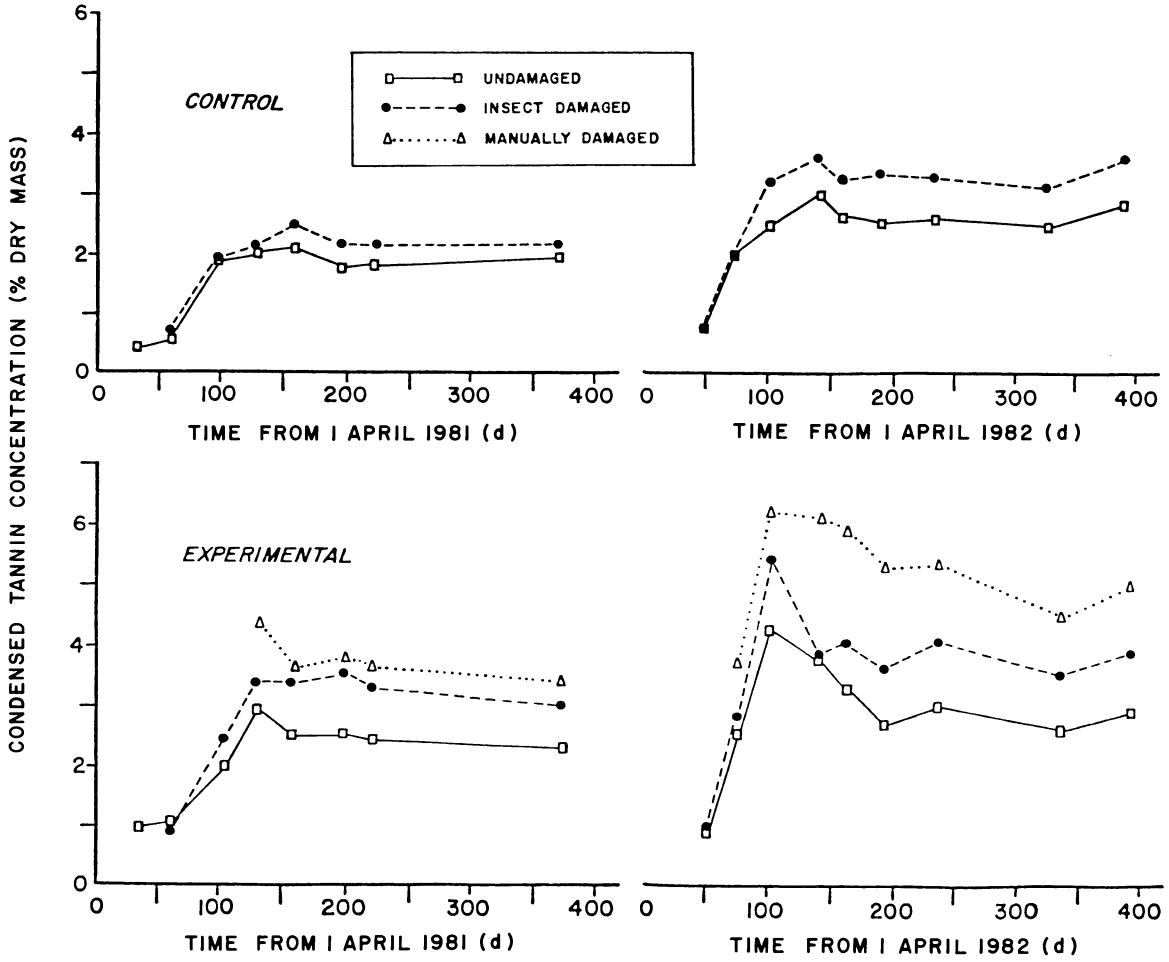

FIG. 3. Seasonal changes in condensed tannin content of undamaged and damaged leaves on control and experimental trees in 1981–1982 and 1982–1983. Each point is the mean of six trees. Standard errors for individual points are in Appendix I and II.

for apparent declines in protein content in leaves (Fig. 1). However, protein levels, unlike hydrolyzable tannin content, did vary seasonally (Fig. 1) and it is possible protein synthesis or mobilization actually decreased in damaged leaves. Nevertheless, it is clear that condensed tannins were induced in response to both insect and manual damage (Fig. 3).

Induction of phenolic compounds in response to complete defoliation or severe mechanical or insect damage is well known (Haukioja and Niemelä 1979, Ryan 1979, Bryant 1981, Schultz and Baldwin 1982, Baldwin and Schultz 1983), but has not been reported for relatively small amounts of damage per leaf (average damage per leaf in this study was 16%).

The effect of damage on phytochemistry was localized within trees on damaged leaves. Although intact and damaged leaves within trees differed significantly in protein and condensed tannin content, these phytochemical parameters did not differ significantly between control and experimental trees. Therefore, experimentally increasing proportions of damaged leaves from 25% to 75% in 1981–1982 and from 19% to 72% in 1982–1983 did not alter overall levels of at least the phytochemical parameters in question.

Chemical and physical changes and leaf-miner selection of leaves

It is not known precisely what cues adult leaf miners used in discriminating intact from damaged leaves. Certainly, selection may simply be based upon physical damage. However, gravid dipteran leaf miners are known to pierce leaf tissues repeatedly with their ovipositor before depositing an egg (Hering 1951). These leaf miners sample the exudate from oviposition holes with their mouthparts and apparently can discriminate subtle chemical differences between and within leaves (Hering 1951, M. Parrella, *personal communication*). Leaf miners on *Q. emoryi* do not have piercing ovipositors. However, like most lepidopterous insects, leaf miners likely possess tarsal chemoreceptors (Feeny et al. 1983). Whether leaf miners can detect increased tannins or decreased protein content in damaged leaves via these chemoreceptors is currently unknown. Other cues in damaged leaves that may have been used by leaf miners are structural changes in leaves, decreased surface area, reduced water content, or volatile compounds that covaried with changes in tannin and protein content. However, it is interesting that selection of leaves by leaf miners occurred within but not between trees, much as did changes in protein and tannin content.

Avoidance of insect- and manually damaged leaves was not equivalent within experimental and control trees (i.e., leaf miners occurred more frequently in intact leaves of experimental than control trees). This result conflicts with the expectation that lower proportions of leaf miners should occur in intact leaves when such leaves become scarcer relative to damaged leaves on experimental trees and, therefore, more difficult to locate. However, manually damaged leaves differed in inducible chemistry and also probably in structural aspects. The directional increases in condensed tannins for insect- and manually damaged leaves were similar throughout the growing seasons, but increases were much greater for manually damaged leaves (Fig. 3). I attempted to approximate insect damage closely by hole-punching, but it was not possible to mimic insect damage exactly. Manual damage differed from insect damage in (1) timing (insects damage leaves more slowly than abrupt hole punching), (2) pattern of damage within a leaf (e.g., some insects selectively feed on edges or interiors of leaves), (3) saliva secretions of chewing insects that may affect plant growth (Dyer and Bokhari 1976), and (4) between-leaf variability in damage. Manually damaged leaves were consistently damaged (three to four holes per leaf), while leaf-chewing damage between leaves was much more variable (10–50% of leaf area consumed). Leaf miners showed greater avoidance of manually damaged than insect-damaged leaves, either as a consequence of greater inducible increases in condensed tannins or one or more of the aforementioned differences between insect- and manually damaged leaves.

Chemical and physical changes in leaves and leaf miner survival

Although it remains uncertain what cues adult female leaf miners used for discriminating intact and damaged leaves, consequences for larval leaf miners on damaged leaves are clear. In both seasons, survival of leaf miners was lower on damaged leaves (Tables 5b and 6b). Decreases in survival on damaged leaves are attributable to parasitism by hymenopterans that more than doubled in both seasons (Tables 5a and 6a). It is unclear how damage and increased parasitism interacted, although parasites may have used physical and chemical changes in these leaves to facilitate search. Vinson (1975) showed that parasites increase search for *Heliothis virescens* on damaged tobacco leaves. On *Q. emoryi,* parasites may also have used changes in physical or chemical aspects of damaged leaves to enhance or prolong search for leaf miners. It is unlikely that parasites use the reported increases in condensed tannins as long-range attractants because tannins are nonvolatile. However, degradation products of tannins may be volatile, or increased tannins in damaged leaves could have covaried with other volatile compounds. Increases in condensed tannins may also slow larval development (Chan et al. 1978, Reese 1981, Reese et al. 1982) so that leaf miners are exposed longer to parasitoids. Finally, condensed tannins may be used by parasitoids as contact attractants (sensu Vinson 1976) that cause parasitoids to remain longer on damaged leaves.

The relationship of intensified parasitism, and consequently, lowered survivorship, with increasing frac-

tion of damaged leaves was inversely density dependent in 1982–1983. Leaf miners on damaged leaves within experimental trees actually experienced higher survivorship and lower parasitism than leaf miners in damaged leaves within control trees (Table 8), although damaged leaves were still less suitable for survival than intact leaves within experimental trees (Table 8). I suggest that as the fraction of damaged leaves increased, parasitoid search for leaf miners on damaged leaves became less effective because parasites were swamped with physical and chemical cues associated with large numbers of damaged leaves. Leaf miners were relatively rare and densities were not different on experimental and control trees (Table 2). Therefore, the probability of locating a rare leaf miner on a damaged leaf decreased on experimental trees because parasitoids must search a greater number of damaged leaves. I suggest that the negative effect of leaf chewers through increased parasitism may be more severe at low, endemic levels of herbivory and ameliorated at higher, epidemic levels. Other workers have reported that parasitism on phytophagous insects operates in an inverse density-dependent fashion (Varley et al. 1973, Morrison and Strong 1980, 1981, Hassell 1982, Strong et al. 1984). Experiments involving intermediate levels of herbivory are necessary to determine if changes in parasitism are a monotonically declining function of increasing fractions of damaged leaves, or if some threshold is reached.

Mortality from other causes was significantly less for leaf miners on damaged than intact leaves (Tables 5b and 6b), although this positive effect did not compensate for the negative effects of increased parasitism. This category of mortality includes death from bacterial, fungal, and viral attack, noxious effects of plant chemistry, and abiotic factors. Larval leaf miners are buffered from abiotic factors such as temperature and desiccation, because larvae are enclosed within leaf tissues, and constantly experience 100% humidity (Hering 1951). Seven of nine species feed through winter months (Table 1), when temperature frequently drops below 0°C. However, the high humidity within mines apparently renders larvae highly susceptible to bacterial and fungal attack in the first instars (Faeth and Bultman 1986). Feeding on damaged leaves with increased tannins may protect larvae from bacteria and fungi, since tannins have well-known bactericidal and fungicidal properties (Swain 1979).

Interactions between guilds

Early season herbivory by the leaf-chewing guild clearly affected organization and dynamics of the late-feeding, leaf-mining guild, even though these guilds are generally separated in time. Endemic (control trees) and experimentally increased levels of early season herbivory resulted in a skewed distribution of leaf miners on intact leaves. This effect occurred at the within-tree but not among-tree scale of organization. Early season herbivory negatively affected overall survivorship of leaf miners, but may have had both positive and negative effects in terms of individual sources of mortality. The negative effects of early season herbivory on leaf miners were more severe at low endemic levels than at high levels of leaf damage. These effects on distribution and survivorship of leaf miners were mediated by physical and chemical changes in damaged leaves.

West (1985) also showed that leaf chewers reduce larval survivorship and pupal mass of leaf miners on *Q. robur*. He concluded that chemical defenses induced by leaf chewers were responsible, although these defenses were not identified. Parasitism was not positively related to increased levels of damage. C. West (*personal communication*) also found that leaf miners avoid damaged leaves within trees. The differences between West's results and those presented here may be explained by the large amount of leaf damage (40–50% of leaf area removed) on *Q. robur* compared to *Q. emoryi* (<5%). If changes in rates of parasitism are inversely density dependent with leaf damage, then parasitism should decrease at higher damage levels. In fact, West (1985) showed parasitism on second-generation leaf miners decreases when mean levels of leaf-chewer damage are greater.

These results contradict conventional ideas regarding probability of interactions within and between guilds. Pianka (1983) suggested interactions within guilds should be more likely than between guilds because guild members use a common resource in a similar fashion (Root 1967). In this study, interactions within at least the leaf-mining guild should be rare, since densities of leaf miners are very low (Table 2) and individual leaf miners rarely co-occur on the same leaf. The potential for interaction between leaf chewers is less clear. Certainly, leaf chewers do affect leaf miners. This effect was probably unidirectional; leaf miners were unlikely to affect leaf chewers because of very low densities of miners, small amounts of miner damage to leaves, and the fact that leaf chewers feed on newly emerged leaves before leaf miners feed. Therefore, the negative interaction between leaf chewers and miners was so asymmetric that it approaches an amensalistic relationship commonly found between interacting insects (Lawton and Hassell 1981, Strong et al. 1984).

The effects of early-season herbivory on the leaf-mining guild occurred at relatively low levels of herbivory. Endemic leaf chewers damaged at least 25% (1981–1982) and 19% (1982–1983) of leaves, but removed <5% of total leaf area on control trees. Experimental trees had higher fractions of damaged leaves (75%, 1981–1982; 72%, 1982–1983), but still <15% of leaf area of trees was removed. Temporally separated leaf chewers and leaf miners can interact at low levels of herbivory, and intensity of interactions may actually decline at higher levels. However, these interactions are different from classical competition for a resource (Janzen 1973, Lawton and Strong 1981). Instead, ef-

fects of early feeders are inversely density-dependent, indirect, and mediated by physical and chemical changes in the host plant. Host plant alterations, in turn, affect natural enemies of the leaf-mining guild.

If such indirect and three-trophic-level interactions are common among host plants, phytophagous insects, and natural enemies, then theories of organization of phytophagous insect communities need to be re-evaluated. For example, Lawton and Strong (1981), as well as others (Root 1973, Simberloff 1978), suggested that "insect communities are often loosely structured on plants with species living more or less independently of most others in the same trophic level." While phytophagous insect communities may not be organized via classical resource-based competition, indirect interactions between species of the same trophic level can affect distribution and survivorship. These interactions, if of sufficient prevalence and magnitude, could result in insect communities that are considerably more structured than currently proposed. Indirect interactions can affect distribution and survivorship of insect species under conditions of low herbivory (i.e., total leaf area removed) provided that sufficient fractions of leaves are damaged, or the remaining intact leaves are less suitable for insect development.

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APPENDIX I

Standard errors of means for concentrations of components of leaves of control trees in Figs. 1–3. Standard errors are not shown on graphs because of some overlap of standard error bars.

	Protein		Hydrolyzable tannin		Condensed tannin	
Date	Intact	Damaged	Intact	Damaged	Intact	Damaged
30 Apr 81	0.75	...	2.57	...	0.26	...
31 May 81	0.42	0.78	1.30	1.41	0.43	0.36
9 Jul 81	0.93	1.01	2.36	2.03	1.32	1.24
2 Aug 81	0.65	0.63	2.31	1.74	1.37	1.39
5 Sep 81	0.52	0.59	0.98	1.47	1.42	1.63
10 Oct 81	0.62	0.70	1.37	2.57	1.19	1.45
7 Nov 81	0.71	0.87	2.40	1.84	1.25	1.48
11 Apr 82	0.24	0.31	1.21	3.01	1.23	1.43
30 Apr 82	0.62	0.38	...	...	...	...
19 May 82	0.86	0.73	4.37	6.30	0.40	0.45
16 Jun 82	1.36	0.74	1.85	1.76	0.75	0.54
14 Jul 82	0.82	0.50	1.95	1.59	0.75	0.86
18 Aug 82	0.77	0.96	1.67	2.43	0.81	1.76
11 Sep 82	0.59	0.51	1.38	1.56	0.86	1.42
7 Oct 82	1.05	0.83	1.73	1.57	0.57	0.98
19 Nov 82	0.76	0.96	1.83	1.99	0.87	0.59
26 Feb 82	1.05	1.44	1.31	1.31	0.66	1.11
26 Nov 83	0.56	0.37	1.49	2.00	0.76	1.51

APPENDIX II

Standard errors of means for concentrations of components of leaves of experimental trees in Figs. 1–3. Standard errors are not shown on graphs because of some overlap of standard error bars.

	Protein			Hydrolyzable tannin			Condensed tannin		
Date	Intact	Insect-damaged	Manually damaged	Intact	Insect-damaged	Manually damaged	Intact	Insect-damaged	Manually damaged
30 Apr 81	0.84	...	...	4.91	...	...	0.20	...	...
31 May 81	0.45	0.30	...	1.76	1.44	...	0.49	0.36	...
9 Jul 81	0.17	0.18	...	1.71	1.26	...	1.05	1.44	...
2 Aug 81	0.27	0.31	0.44	1.85	1.12	2.02	1.69	1.30	2.15
5 Sep 81	0.35	0.48	0.49	1.63	1.72	1.62	1.73	1.80	2.10
10 Oct 81	0.44	0.35	0.34	2.01	1.65	1.98	1.27	1.53	1.80
7 Nov 81	0.46	0.46	0.56	1.62	2.62	1.46	1.01	1.58	1.70
11 Apr 82	0.70	0.80	0.63	1.87	1.24	1.13	1.30	1.23	1.73
19 May 82	0.73	0.78	...	3.45	2.86	...	0.40	0.40	...
16 Jun 82	0.52	0.36	0.56	1.61	0.98	1.73	1.43	0.92	1.86
14 Jul 82	0.66	0.16	0.45	1.86	1.98	1.67	1.50	0.73	3.00
18 Aug 82	0.63	0.44	0.29	2.66	1.15	2.13	1.64	0.98	3.19
11 Sep 82	0.83	0.84	0.95	1.84	2.05	1.90	1.21	1.54	2.76
7 Oct 82	0.69	0.83	0.64	2.30	1.95	2.28	1.35	0.88	2.86
19 Nov 82	0.69	0.89	0.91	2.25	1.10	1.78	1.61	1.19	2.03
26 Feb 82	0.64	0.72	0.87	2.35	1.91	1.53	0.98	0.81	1.76
26 Nov 83	0.42	0.37	0.31	1.86	1.19	1.68	1.19	0.85	2.25