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PLANT PHENOTYPE AND INTERSPECIFIC COMPETITION BETWEEN INSECTS DETERMINE SAWFLY PERFORMANCE AND DENSITY[1]

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Abstract. Host plants not only influence herbivore performance, they can also mediate interactions between herbivores. We conducted a 5-yr field study to test the effects of pinyon pine (*Pinus edulis*) phenotype and competitive interactions on the colonization success, mortality, fecundity, and sex ratios of a foliage-feeding sawfly, *Neodiprion edulicolis*. Our experiments revealed four major patterns. (1) Sawfly survival was significantly higher on susceptible trees than on resistant trees. (2) In contrast, sawfly fecundity was significantly lower on susceptible trees than on resistant trees. (3) Interactions with a stem moth, *Dioryctria albovitella,* caused significantly reduced sawfly fecundity on susceptible trees. (4) Sawfly mortality, rather than sawfly fecundity, was the dominant factor influencing population growth rates: after four generations, sawflies transferred to susceptible trees reached significantly greater densities than sawflies transferred to resistant trees. A model developed with performance information from our field experiments accurately described patterns of population increase in the field: sawflies rapidly attain high densities on susceptible trees, and accumulate slowly on resistant trees. Trees displaying a susceptible phenotype are therefore better hosts than resistant phenotypes, despite the negative competitive interactions that occur between sawflies and moths on heavily infested susceptible trees.

Key words: Dioryctria albovitella; *extinction; fecundity; herbivore performance; interspecific competition; mortality;* Neodiprion edulicolis; *phenotype;* Pinus edulis; *resistant; sex ratios; susceptible.*

INTRODUCTION

Intrapopulation variation in infestation of host plants by herbivorous insects is a pattern observed by many insect ecologists (Edmunds and Alstad 1978, Moran 1981, Denno and McClure 1983, Wainhouse and Howell 1983, Service 1984, Whitham and Mopper 1985, Karban 1987, Maddox and Root 1987, Clancy and Price 1989, Moran and Whitham 1990*b*). Variable infestation levels are often related to host genotype or clonal identity (Moran 1981, Service 1984, Karban 1987, Maddox and Root 1987, Fritz and Price 1988), although genotype by environment interactions (Tingey and Singh 1980, Maddox and Cappuccino 1986, Maddox and Root 1987, Preszler and Price 1988), and even plant sex (Danell et al. 1985, Elmqvist et al. 1988, Boecklen et al. 1990) can strongly influence the phenotypic expression of plant resistance or susceptibility to insect attack.

Although many studies have documented variable infestation levels, few have comprehensively examined the host plant effects on insect life cycles that give rise to such patterns. Variation in insect density among host plants may result from preferential host selection by ovipositing females, or, differential mortality, fecundity, or sex ratios. Extremes in host suitability may influence insect performance differentially and ultimately result in conflicting population patterns. Plants can affect performance in myriad ways that may or may not be consistent with observed densities. For example, the larval stage may benefit and the cocoon stage may be negatively influenced by traits of the same host individual. For these reasons it is essential to evaluate insect performance comprehensively in each life stage on individual host plants to understand fully the variable patterns of infestation and avoidance so frequently observed in nature.

When plants are susceptible to attack by several insect species, interactions between them are likely to occur. Interspecific interactions may potentially affect insect populations and recent evidence suggests that they are more common than previously thought (Stiling and Strong 1983, 1984, Stamp 1984, West 1985, Faeth 1986, Fritz et al. 1986, Harrison and Karban 1986, Karban 1986, Crawley and Pattrasudhi 1988, Moran and Whitham 1990*b*). Both direct and temporally separated competitive interaction may be host mediated and must be studied to further our understanding of the relative importance of factors determining insect abundance.

Our goal was to ascertain the insect life stages most influenced by extremes in host phenotype, and to assess the importance of insect competitive interactions to sawflies (*Neodiprion edulicolis*) in the Sunset Crater

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FIG. 1. Second- and third-instar sawfly larvae attacking pinyon needle tissue. Late-instar larvae will devour entire needles. Larvae feed in groups throughout the larval period and each group defoliates several shoots.

pinyon pine (*Pinus edulis*) population. For five field seasons we evaluated sawfly performance on resistant and susceptible pinyon phenotypes by measuring egg, larval, and cocoon mortality, cocoon masses, fecundity, and sex ratios. Using the performance data provided by these field experiments, we developed a model that evaluates the relative importance of the different life stages by predicting patterns of sawfly population increase on resistant and susceptible trees. Our research provides data upon which hypotheses can be formulated that explain the variable patterns of host infestation prevalent in natural systems.

NATURAL HISTORY

We conducted our experiments at Sunset Crater National Monument in northern Arizona, USA. The study site (elevation 2000 m) is a pinyon–juniper woodland with a diverse mixture of plant species. The pinyon pine (*Pinus edulis* Englm.) population grows in a lava and cinder soil and is heavily infested by several insect herbivores. Our main study organism is a foliage-feeding sawfly, *Neodiprion edulicolis* Ross (Fig. 1) that feeds in March and April and reaches high densities on many pinyons.

Another important pinyon herbivore is a stem- and cone-boring moth (*Dioryctria albovitella* Hust.) that feeds within stems and cones in May and June. Whitham and Mopper (1985) and Mopper and Whitham (1986) described the moth's severe impact on the architecture and reproduction of susceptible trees (Fig. 2). Unlike the moth, which is widely dispersed throughout the Sunset Crater pinyon population, sawflies are patchily distributed. When their distributions overlap, the moth and sawfly co-occur on the same trees; trees heavily infested with sawflies also have high moth densities.

The sawfly is sexually dimorphic and has a haplodiploid mating system (McGregor and Sandin 1968, 1969). In late fall, adult females emerge from cocoons beneath the host with 15–60 fully developed eggs ready for fertilization (Coppel and Benjamin 1965). Because of the full complement of eggs they carry, females are poor dispersers (Knerer and Atwood 1973). This species is probably one of the many hymenopterans in which egg sex is parentally controlled and determined at the time of oviposition (Flanders 1965). After overwintering in the needles, eggs hatch in late March or early April. Sibling larvae aggregate into a feeding group that cooperates in breaking through the tough needle tissue and eventually defoliates 3–4 shoots. Female sawflies require six larval instars to mature, one more

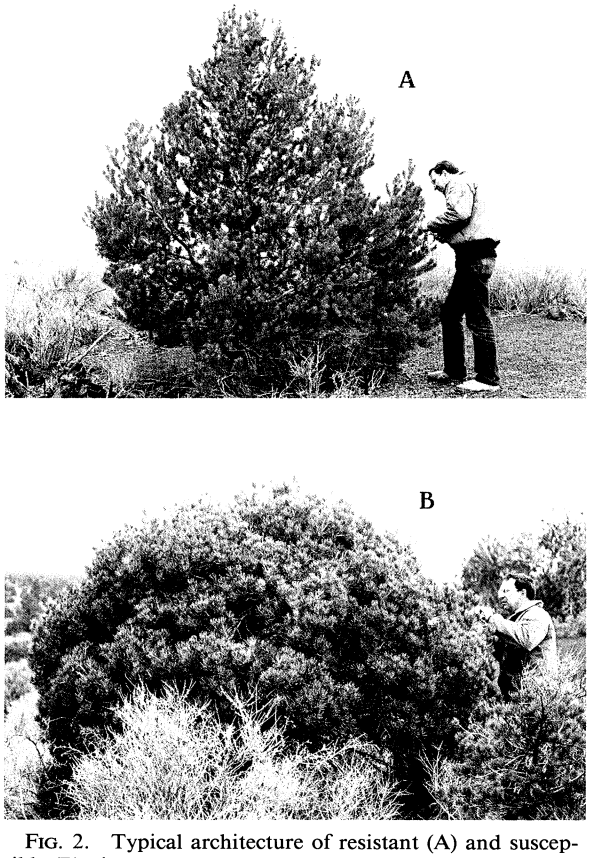

FIG. 2. Typical architecture of resistant (A) and susceptible (B) pinyons at Sunset Crater. (Resistance and susceptibility refer to damage by the moth *Dioryctria albovitella*.) Shrubby canopy and elimination of female cone production of (B) results from moth (*Dioryctria albovitella*) destruction of the terminal stems, and subsequent lateral bud initiation.

than males (McGregor and Sandin 1968). When larvae finish feeding, they drop to the cinders and spin cocoons beneath the tree. Little is known about sawfly impact on infested trees.

Methods

Transfer experiments

We transferred early instar larvae to resistant and susceptible trees to determine how host plants and the stem moth influenced sawfly performance. First we haphazardly selected medium-sized reproductively mature trees that were either resistant or susceptible to moth attack, but free of sawflies. Because sawflies are patchily distributed, trees that are potentially susceptible to their attack are often colonized by the moth, but not by sawflies. We distinguished resistant from susceptible phenotypes by the following criteria: (1) resistant trees displayed an open canopy architecture and had <15% of their shoots destroyed by the moth (Fig. 2A), (2) susceptible trees had a shrubby canopy architecture and at least 50% of their shoots were destroyed by moths (Fig. 2B). The susceptible (*S*) trees averaged 66.84 ± 8.36% shoot destruction (mean ± 1 SE) and the resistant (*R*) trees averaged 9.88 ± 3.88% shoot destruction. Resistant and susceptible phenotypes are also characterized by significant differences in resin production, needle morphology, and stem morphology (S. Mopper, *personal observation*). The *R* and *S* trees grew interspersed in a 1-ha subsection of the Sunset Crater pinyon population with a minimum distance of 50 m between trees. There were no differences in moisture, particle size, or nutrient content between the soils beneath resistant and susceptible trees (S. Mopper et al., *personal observations*).

We selected four trees within the same area that were heavily infested by both the moth and sawfly to act as donor trees for the sawfly transfers. These susceptible donor trees (*SD*) averaged 58.01 ± 6.87% total moth-caused stem destruction and 2090 ± 671 sawflies per tree. In April of 1984, we collected second-instar sawfly larvae from the four *SD* trees and transferred 20 larvae to each of 20 *R* and 15 *S* trees. We clipped shoots with larvae from the *SD* trees and tied the shoots to the *R* and *S* receptor trees. Transferred larvae moved from the old shoots to the new host within 24 h. After approximately 4 wk they completed the larval stage and dropped to the cinders beneath their new hosts to spin cocoons.

Not all trees were successfully colonized the following year (1985). From those that were, we haphazardly selected eight *R* and eight *S* trees to evaluate sawfly performance for five field seasons. Because of low sawfly densities on individual trees, we could not collect sawflies from all eight *R* and eight *S* receptor trees for all performance estimates each year. We did not cage the *R* and *S* receptor trees and subsequent natural sawfly colonization was possible but unlikely. Female sawflies are relatively poor dispersers because they emerge from cocoons heavy with fully developed eggs, and usually fly immediately to the canopy to search for oviposition sites (Kapler and Benjamin 1960, Coppel and Benjamin 1965, S. Mopper, *personal observation*). This behavior and low pinyon density are probably responsible for their patchy distribution patterns at Sunset Crater.

Sawfly extinction and densities on resistant and susceptible hosts

In 1985 we determined the proportion of trees that had been successfully colonized by offspring of the 1984 transferred sawflies. Of these, we allowed sawflies on three *R* and four *S* trees to reproduce for four generations without further disturbance. In 1988 we censused sawfly densities on these seven trees.

Egg mortality

We estimated egg mortality on *R* and *SD* trees in 1985 and *R* and *S* trees 1986. In 1985 we collected foliage containing hatched sawfly eggs from four *SD* and three *R* hosts (samples from *S* trees were destroyed by a fungus before we could analyze them), and in 1986 we collected foliage from three *S*, and four *R* trees. We examined the egg chambers with a dissecting microscope to determine egg fate. We could not always identify the cause of death: some eggs were parasitized but most seemed to die from unknown causes. We calculated the proportion of dead eggs from each tree. We compared the arcsine square-root transformed egg mortality data for the *R*, *S*, and *SD* trees with a one-way analysis of variance using trees as experimental units (Zar 1984).

Larval mortality

In 1984 and 1986 we compared larval mortality on *R* and *S* trees. In 1984 we estimated mortality of transferred larvae on eight *R* and eight *S* trees, and in 1986 we estimated mortality of the descendents of the 1984 transfers on four *R* and three *S* trees. To determine larval mortality, we selected feeding groups low in the canopy that we could observe without disturbing. We counted larvae as they hatched and allowed them to complete the larval stage. We surrounded late-instar feeding groups with mesh bags that we collected after larvae had formed cocoons.

Mortality in the larval stage is caused by ant and bird predators and unknown factors. Because parasitized larvae survive to the cocoon stage, our estimate of mortality is conservative. We calculated the proportion of dead larvae for each tree. We compared the arcsine square-root transformed larval mortality data for the *R* and *S* trees with a one-way analysis of variance using trees as experimental units.

Cocoon mortality

In 1987 we estimated cocoon mortality beneath resistant and susceptible trees. We collected 500 cocoons

from the four *SD* trees and placed 50 beneath each of five *R* and five *S* trees. The cocoons were contained in a large gauze-bottomed embroidery hoop. They remained partially submerged in the cinders from May until November, when adults emerged. We then retrieved the hoops and examined the cocoons to estimate mortality.

Cocoons are exposed to a variety of predators and parasites that create unique cocoon scars. These characteristic scars enabled us to differentiate between successfully emerged and killed sawflies. Parasitized larvae can survive to spin cocoons so our estimate of mortality during the cocoon stage may include sawflies that were parasitized as larvae. We compared the arcsine square-root transformed cocoon mortality data for the *R* and *S* trees with a one-way analysis of variance using trees as experimental units.

Cocoon mass and fecundity

Establishing a correlation between cocoon mass and female fecundity is important because a strong relationship allows the use of mass to estimate fecundity. To evaluate the strength of the relationship we dissected females and compared the number of eggs they contained with their cocoon mass. We conducted a regression analysis on data from the four *SD* trees in 1984 and from four *R* and four *S* trees in 1987. We employed an analysis of covariance test to determine if the slopes of the relationship between cocoon mass and fecundity, and the cocoon mass-adjusted means, were equal for *R* and *S* trees (Zar 1984).

Host plant influence on cocoon mass and fecundity

To evaluate host influence on cocoon mass we collected cocoons of sawflies reared on *R* and *S* trees from 1984 to 1988. When larval groups approached the final instars we surrounded them with gauze bags that we later collected after cocoon formation. We weighed cocoons on an electronic balance and calculated a mean cocoon mass for males and females from each tree. We analyzed the data with one-way analysis of variance with trees as experimental units.

Moth removal experiment

Because moths and sawflies often co-occur at high densities on susceptible trees, we conducted this experiment to examine potential competitive interactions. On 1 d in August of 1983 and 1984 we sprayed an application of Cygon, a systemic dimethoate insecticide, on three pinyons with high moth densities. In 1983, 35.57 ± 6.66% of the stems on these trees were killed by the moth. In 1985, after 2 yr of Cygon application, the average proportion of stems destroyed by moths had dropped to <1% ($\bar{X}$ = 0.98 ± 0.36%). We did not apply insecticide in 1985 (see Whitham and Mopper 1985 for description of insecticide control). In April of 1986 we transferred 45 second-instar sawflies to each of these trees. We enclosed the late-instar feeding groups in mesh bags and later collected and weighed the cocoons. We compared the mean average cocoon mass of sawflies reared on moth-removed trees with those reared on the *R* and *S* trees with a one-way analysis of variance and Student-Newman-Keuls (SNK) multiple comparison tests.

Sawfly sex ratios

We ascertained the sex of sawflies collected from the newly colonized *R* and *S* trees from 1985 through 1989. In 1984 we determined the sex of sawflies collected from an independent group of eight moth-susceptible and three moth-resistant trees that had low sawfly densities. From 1984 to 1989 we also collected sawflies from the four high sawfly density *SD* trees. Because females grow to double the size of males, we used cocoon mass to identify sawfly sex. We also reared out a subsample of cocoons each year to ensure that mass did accurately predict sex. Because the proportions were normally distributed we did not transform them prior to the two-way analysis of variance test, using years as a blocking factor (Zar 1984).

Predicting sawfly densities on resistant and susceptible hosts

We developed a model that incorporates field data to predict population densities on resistant and susceptible trees (see Table 5). The model begins with 20 larvae on each host to emulate our field transfers. For larval mortality we used the average of the 1984 and 1986 data for *R* and *S* trees. Because we did not have data in 1985 for egg mortality on *S* trees we used only the 1986 data for *R* and *S* trees. We averaged the 1984–1989 sex ratios from *R* and *S* trees, and calculated the number of eggs per female, using the regression equation of cocoon mass and fecundity for *R* and *S* hosts. We compared the model predictions of sawfly density after four generations, with actual sawfly densities after four generations on the three resistant and four susceptible trees that were successfully colonized by sawflies in 1984, and left undisturbed until 1988.

Results

Sawfly extinction and densities on resistant and susceptible hosts

Sawfly extinction was more than twice as likely to occur on resistant hosts as on susceptible hosts, but the differences were not significant with a chi-square analysis. By the second field season, sawflies were extinct on 9 of the 20 (45%) *R* trees and on 3 of 15 (20%) *S* trees. The estimated 95% confidence intervals (based on arcsine transformations) of the probability of sawfly extinction on resistant and susceptible trees are $25\% < \bar{X} < 88\%$, and, $0\% < \bar{X} < 35\%$, respectively.

By 1988, sawfly densities were significantly different on the successfully colonized *R* and *S* trees (Fig. 3). The 20 sawflies transferred to each of the four *S* trees

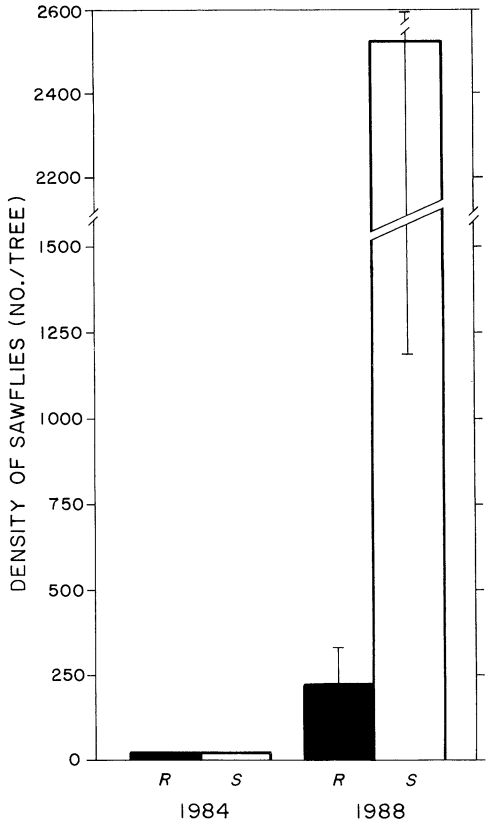

FIG. 3. Increase in sawfly densities from 1984 to 1988 on the three undisturbed resistant (*R*) and four undisturbed susceptible (*S*) pinyons. (Resistance and susceptibility refer to damage by the moth *Dioryctria albovitella*.) Bars are means ± 1 SE.

in 1984 had increased to an average of 2527 sawflies in 1988, but sawflies transferred to the three *R* trees had increased to only 246 in 1988 (two-sample *t* test, $t = 3.25$, df = 5, $P < .02$).

Densities on the four *SD* trees averaged 2635 ± 844 sawflies per tree in 1984, and 3114 ± 1312 per tree in 1988 (two-sample *t* test, $t = 0.31$, df = 6, $P = .77$). This nonsignificant increase suggests that sawflies had reached their carrying capacity; however, we collected sawflies from the *SD* trees throughout the study and may have artificially lowered densities on those trees. In 1988, sawfly densities on *S* trees had reached the same level as those on *SD* trees (2527 and 3114 individuals per tree, respectively, two-sample *t* test, $t = 0.10$, df = 6, $P > .90$). The rapid attainment of sawfly

TABLE 1. Analysis of variance of sawfly (*Neodiprion edulicolis*) mortality on host pinyon pines resistant and susceptible to damage by the moth *Dioryctria albovitella*.

	Source of variation	SS	df	MS	*F*	*P*
		Egg mortality				
1985	Host plant	456.4	1	456.4	21.58	.006
	Error	105.7	5	21.1		
1986	Host plant	443.7	1	443.7	6.91	.047
	Error	321.0	5	64.2		
		Larval mortality				
1984	Host plant	590	1	590	1.28	.271
	Error	9212	20	461		
1986	Host plant	3124	1	3124	10.42	.023
	Error	1499	5	300		
		Cocoon mortality (incl. missing)				
1987	Host plant	72.4	1	72.4	0.96	.359
	Error	525.7	7	75.1		

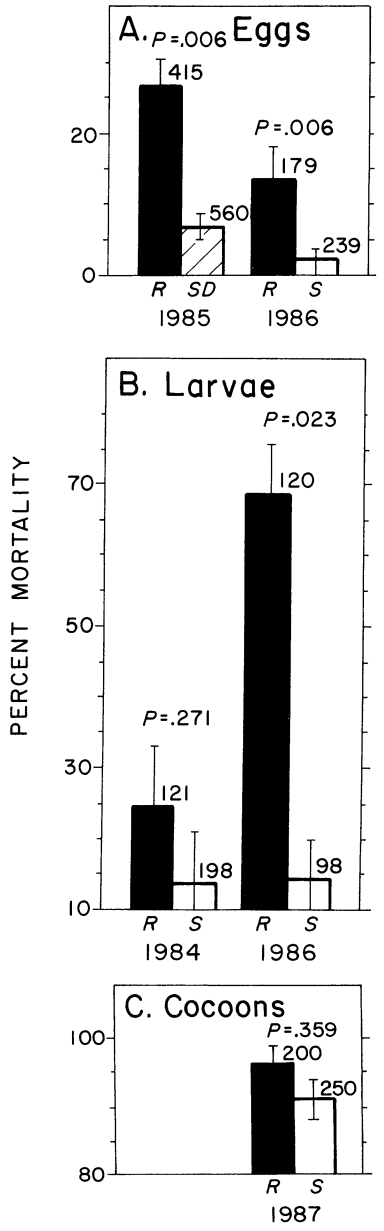

FIG. 4. Egg (A), larval (B), and cocoon (C) mortality on resistant (*R*, ■), susceptible (*S*, □), and susceptible donor (*SD*, ▨) pinyons. (Resistance and susceptibility refer to damage by the moth *Dioryctria albovitella*.) Bars are means ± 1 SE, with total number of sawflies above. We used trees as experimental units in the statistical analysis.

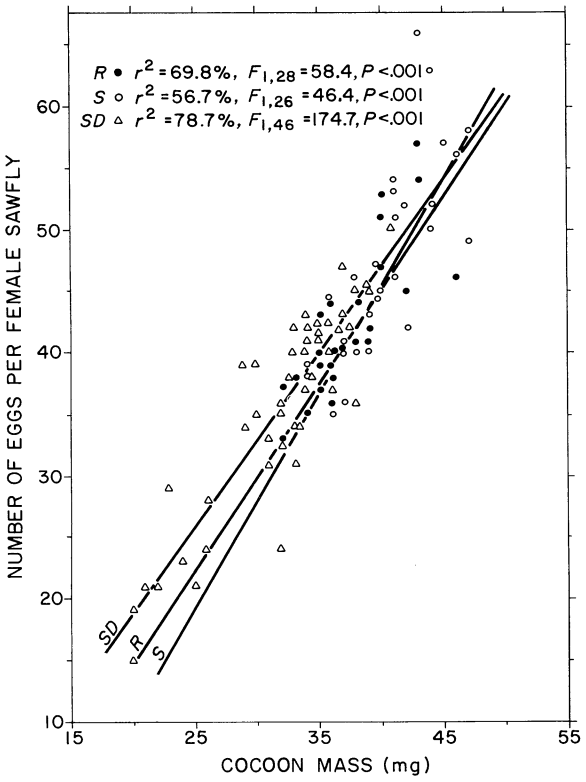

FIG. 5. Relation between sawfly fecundity and cocoon mass on resistant (*R*, ●), susceptible (*S*, ○), and susceptible donor (*SD*, △) trees. (Resistance and susceptibility refer to damage by the moth *Dioryctria albovitella*.) Regression equation for *R*: $Y = -15.4 + 1.501(X)$, *S*: $Y = -24.8 + 1.741(X)$, and *SD*: $Y = -9.09 + 1.391(X)$.

densities on *S* trees comparable to the heavily infested *SD* trees suggests that sawflies colonizing susceptible trees may quickly reach carrying capacity.

Egg mortality

Sawfly eggs suffered significantly greater mortality on *R* trees than on *S* or *SD* trees (Table 1, Fig. 4A). In 1985, egg mortality was roughly four times as great on *R* trees as on *SD* trees (26.3 and 6.7%, respectively). Similarly, 1986 egg mortality was six times as great on *R* trees as on *S* trees (13.5 and 1.9%, respectively).

Larval mortality

Larval mortality was greater on *R* trees than on *S* trees in both years studied, but in 1984 the data were not significantly different (Table 1, Fig. 4B). In 1984, larvae transferred to *R* trees suffered almost twice the mortality of larvae transferred to *S* trees (24.8 and 13.3%, respectively), and in 1986, larvae on *R* trees suffered more than four times the mortality of larvae on *S* trees (68.6 and 14.9%, respectively).

Cocoon mortality

In 1987 cocoon mortality was high for both *R* and *S* hosts and the differences were not significant (Table 1, Fig. 4C). We could not locate the hoop beneath one of the *R* trees so we compared four *R* trees with five *S* trees. Cocoons beneath *R* trees suffered 50.5% mortality, and cocoons beneath *S* trees suffered 66.0% mortality. Many cocoons were missing from the hoops, perhaps because of predators. Other studies on diprionid sawflies have shown that small mammals remove cocoons from beneath trees (McLeod 1972), and missing cocoons are commonly scored as preyed upon (Hanski and Parviainen 1985). With missing cocoons included in our analysis mortality rises to 96.0% for *R* trees and 91.2% for *S* trees, a nonsignificant difference.

Sawfly cocoon mass and fecundity

Cocoon mass was an accurate predictor of sawfly fecundity (Fig. 5). In 1984 there was a strong positive correlation between cocoon mass and fecundity of sawflies collected from the four *SD* trees. Similarly, in 1987 the fecundity of sawflies reared on both *R* and *S* hosts was significantly correlated with cocoon mass. An analysis of covariance test detected no significant differences between the slopes of *R* and *S* regression lines ($F_{1,54} = 0.50$, $P = .48$), or the adjusted means of cocoon mass ($F_{1,55} = 0.003$, $P = .959$).

Host plant influence on cocoon mass and fecundity

Surprisingly, average female cocoon mass, and therefore fecundity, was significantly greater on *R* hosts than *S* hosts in 1984, 1986, and 1988 (Table 2, Fig. 6A). In 1985 and 1987 there were no significant differences in

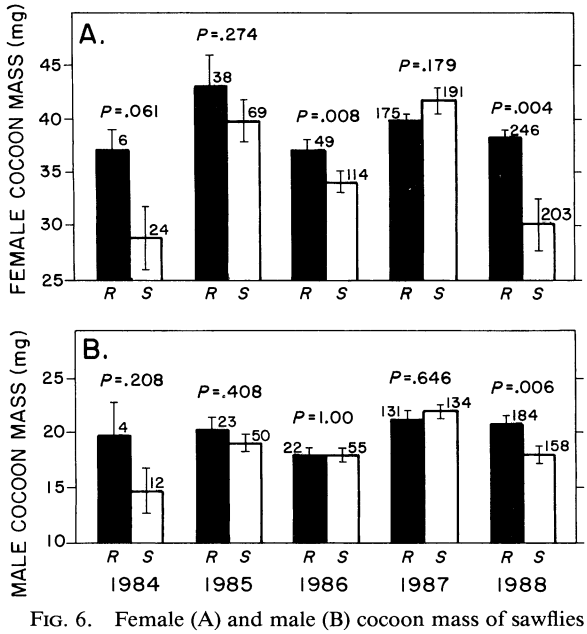

FIG. 6. Female (A) and male (B) cocoon mass of sawflies transferred to and colonizing resistant (*R*, ■) and susceptible (*S*, □) trees in 1984. (Resistance and susceptibility refer to damage by the moth *Dioryctria albovitella*.) Bars are means ± 1 SE, with total number of sawflies above. We used trees as experimental units in the statistical analysis.

TABLE 2. Analysis of variance of sawfly (*Neodiprion edulicolis*) cocoon mass on host pinyon pines resistant and susceptible to damage by the moth *Dioryctria albovitella*.

	Source of variation	SS	df	MS	*F*	*P*
		Female cocoon mass				
1984	Host plant	158.7	1	158.7	4.97	.061
	Error	223.6	7	31.9		
1985	Host plant	36.6	1	36.6	1.32	.274
	Error	304.3	11	27.7		
1986	Host plant	19.27	1	19.27	12.50	.008
	Error	12.33	8	1.54		
1987	Host plant	8.12	1	8.12	2.12	.179
	Error	34.43	9	3.83		
1988	Host plant	145.00	1	145.00	13.73	.004
	Error	105.6	10	10.56		
		Male cocoon mass				
1984	Host plant	51.50	1	51.50	1.87	.208
	Error	220.10	8	27.5		
1985	Host plant	3.26	1	3.26	0.75	.408
	Error	43.66	10	4.37		
1986	Host plant	0.00	1	0.00	0.00	1.000
	Error	4.00	5	0.80		
1987	Host plant	0.26	1	0.26	0.23	.646
	Error	10.46	9	1.16		
1988	Host plant	22.04	1	22.04	11.83	.006
	Error	18.63	10	1.86		

female cocoon mass between *R* and *S* groups. In 1988 the cocoon mass of male sawflies differed significantly between *R* and *S* trees (Table 2, Fig. 6B), and the same pattern emerged: sawflies reared on resistant trees were heavier. There were no significant differences in male cocoon mass of *R* and *S* sawflies from 1984 through 1987.

Stem moth impact on sawfly cocoon mass and fecundity

Co-occurrence with the moth had a significant negative influence on sawfly fecundity. Sawflies reared on moth-removed susceptible trees had significantly greater cocoon mass than sawflies reared on moth-infested susceptible trees. Their mass was equal to that of sawflies reared on resistant trees with no moths (Table 3, Fig. 7). There were no significant differences in male cocoon mass among groups. Because sawfly fecundity was highly correlated with cocoon mass (Fig. 5), we conclude that moths negatively affect sawfly fecundity. We do not know what impact the moth may have on sawfly mortality.

Sawfly sex ratios

From 1984 through 1989 sawfly sex ratios were highly variable among hosts and years, but a consistent pattern did emerge: on most trees in most years, sex ratios were female biased (Fig. 8). The average proportions of females over 6 yr for the *R*, *S*, and *SD* hosts were not statistically different (Table 4), and there was wide, but nonsignificant among-year variation.

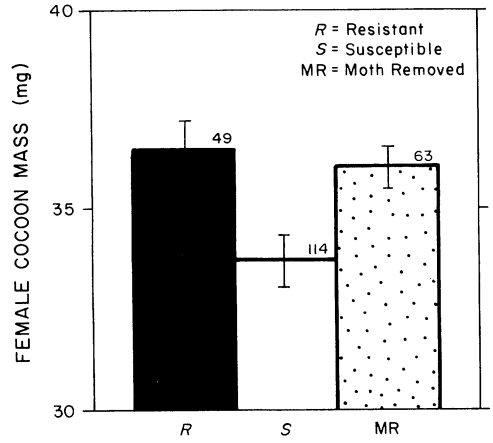

FIG. 7. Female cocoon mass of sawflies reared on resistant (*R*, ■), susceptible (*S*, □), and moth-removed (MR, ⊡) trees in 1986. (Resistance and susceptibility refer to damage by the moth *Dioryctria albovitella*.) Bars are means ± 1 SE, with total number of sawflies above. We used trees as experimental units in the statistical analysis.

Predicting sawfly densities on resistant and susceptible trees

Our model consolidates the field performance data and predicts that sawfly survival overcompensates for reduced fecundity on susceptible trees. After four generations, larval density increases from 20 to 3969 on susceptible hosts, and from 20 to 785 on resistant hosts (Table 5, Fig. 9). The factors of the greatest relative importance to these density patterns were egg and larval mortality. Whereas cocoon mortality was much greater than egg or larval mortality, it did not differ between resistant and susceptible trees. Although sawfly fecundity was significantly greater on resistant hosts, the difference was too impuissant to compensate for the effects of mortality.

DISCUSSION

Effects of host phenotype on sawfly performance

In general, sawfly performance on resistant and susceptible pinyons corresponded to their abundance on these hosts. Sawfly egg and larval survival was significantly greater, and they attained the highest densities

TABLE 3. Analysis of variance of sawfly (*Neodiprion edulicolis*) cocoon mass on host pinyon pines moth-removed, resistant, and susceptible to damage by the moth *Dioryctria albovitella*.

Source of variation	SS	df	MS	*F*	*P*
	Female cocoon mass				
Host plant	24.69	2	12.35	9.50	.005
Error	13.00	10	1.3		
	Male cocoon mass				
Host plant	3.73	2	1.87	1.96	.211
Error	6.67	7	0.95		

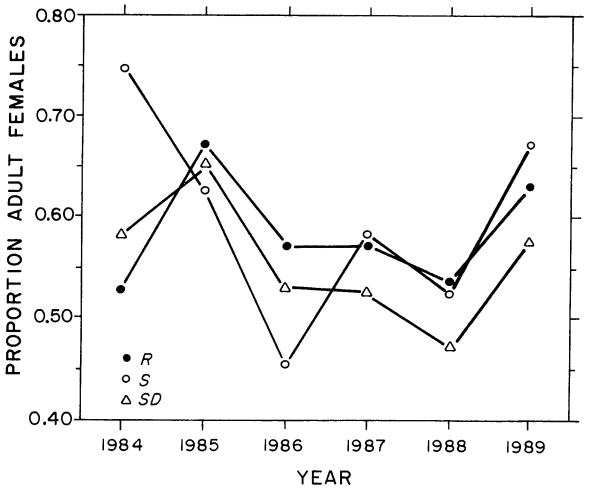

FIG. 8. Proportion adult females on resistant (*R*, ●), susceptible (*S*, ○), and susceptible donor (*SD*, △) trees from 1984 to 1988. (Resistance and susceptibility refer to damage by the moth *Dioryctria albovitella*.)

on susceptible trees (Figs. 4 and 9). In contrast, sawfly fecundity as estimated by cocoon mass was significantly greater on resistant trees (Fig. 6). This unexpected result is a caveat for reductionist population studies that focus on only one life stage. For sawflies in the Sunset Crater system, realization of the greatest fecundity and highest survival were disjunct, and occurred on hosts with extremely different phenotypes.

Adult sex ratios were virtually always female biased (Fig. 8). Several studies have documented male- and female-biased sex ratios in natural populations of diprionid sawflies (Benjamin 1955, Dahlsten 1967, McGregor and Sandin 1968, McLeod 1972, Geri et al. 1985). Patterns of male bias in haplodiploid scale insects have been attributed to pest adaptation to host plants (Edmunds and Alstad 1978, Alstad and Edmunds 1983), and female-biased sex ratios of parasitic hymenoptera have been ascribed to differential mortality of haploid males relative to diploid females (Smith and Shaw 1980). With few exceptions (e.g., Alstad et al. 1980, Alstad and Edmunds 1983), sex ratio allocation patterns of herbivorous insects have been ignored, despite the fact that they have important practical and theoretical implications for local adaptation to host plants, measures of herbivore performance, and population trends.

TABLE 4. Two-way analysis of variance of sawfly (*Neodiprion edulicolis*) sex ratios on resistant, susceptible, and susceptible donor host pinyon pines. Resistance and susceptibility refer to damage by the moth *Dioryctria albovitella*.

Source of variation	SS	df	MS	*F*	*P*
Host	374.3	2	187.2	1.1	.341
Year	1592.0	5	318.4	1.9	.113
Year × host	1664.2	10	166.4	1.0	.475
Error	10939.8	64	170.9		

TABLE 5. Model predictions of sawfly (*Neodiprion edulicolis*) abundance on host pinyon pines resistant and susceptible to damage by the moth *Dioryctria albovitella*.

	Resistant host	Susceptible host
Mean prop. eggs surviving	0.80	0.98
Mean prop. larvae surviving	0.53	0.86
Mean prop. cocoons surviving	0.28	0.21
Mean prop. females	0.59	0.61
Mean no. eggs per female	43.22	36.1
Generation zero		
No. larvae	20.0	20.0
Generation one		
No. eggs	75.68	79.54
No. larvae	60.55	77.95
No. cocoons	32.09	67.04
No. adults	8.66	14.08
No. females	5.11	8.59
Generation two		
No. eggs	220.94	310.06
No. larvae	176.75	303.85
No. cocoons	93.68	261.31
No. adults	25.29	54.88
No. females	14.67	33.47
Generation three		
No. eggs	633.96	1208.43
No. larvae	507.17	1184.26
No. cocoons	268.80	1018.46
No. adults	72.58	213.88
No. females	42.82	130.47
Generation four		
No. eggs	1850.67	4709.79
No. larvae	1480.53	4615.59
Predicted no. larvae surviving in 1988	784.68	3969.41
Actual no. larvae in 1988	245.67	2526.75

Interspecific interactions between insects

Surprisingly, host-mediated negative interactions with the pinyon stem moth resulted in lower sawfly

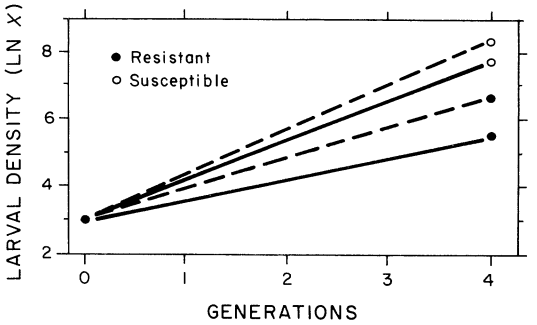

FIG. 9. Comparison of actual data (——) and model predictions (— — —) of sawfly densities after four generations of population growth on resistant (*R*, ●) and susceptible (*S*, ○) pinyon pines. (Resistance and susceptibility refer to damage by the moth *Dioryctria albovitella*.) Data are natural log transformed.

fecundity on susceptible trees than on resistant trees (Fig. 7). Stem moths indirectly affect sawflies by killing terminal shoots and eliminating current-year foliage. Sawfly larvae must then feed on sparse lateral shoot foliage, or on older needles that have significantly less water and nutrients (S. Mopper, *personal observation*). Consequently, cocoon mass and adult fecundity are reduced.

This may or may not be an asymmetrical interaction: sawfly impacts on moth performance are unknown. Our attempts to mimic sawfly damage on shoots bearing feeding moth larvae have failed because moths quickly leave artificially damaged shoots. This behavior may enable moth larvae to avoid interacting with sawflies. Nevertheless, on trees heavily infested by sawflies, the moth is likely to be affected. Despite the drawbacks of host-sharing, the benefits probably outweigh the disadvantages because susceptible trees supporting high moth and sawfly populations commonly occur adjacent to moth- and sawfly-free trees.

There are an increasing number of examples of interspecific competition between phytophagous insects (Stiling and Strong 1983, 1984, Harrison and Karban 1986, Karban 1986, Crawley and Pattrasudhi 1988, Moran and Whitham 1990*a*). Our findings support patterns commonly observed in these studies: interactions between phytophagous insects are often asymmetrical, indirect, and mediated by changes in plant quality caused by the phenologically advanced species (McClure 1980, Lawton and Hassell 1981, 1984, Stamp 1984, Strong et al. 1984, Faeth 1985, 1986, West 1985, Fritz et al. 1986, Harrison and Karban 1986, Karban 1986, Crawley and Pattrasudhi 1988, Moran and Whitham 1990*a*, Mopper et al., *in press*). The consistent patterns emerging from this and other recent field studies are vital to the construction of a general theory describing competitive interactions between phytophagous insects.

Predicting sawfly densities on resistant and susceptible hosts

The model qualitatively corroborates our field observations and demonstrates that the performance parameters measured in our experiments were the major factors influencing sawfly population growth (Fig. 9). It demonstrates that survival, which was higher on susceptible trees, rather than sawfly fecundity, which was higher on resistant trees, was the most important influence on population growth. Nevertheless, model predictions exceeded actual field densities by 57% for susceptible hosts and 219% for resistant trees (Table 5). This overestimation may have arisen from the model assumptions that all females mate, all females oviposit, and no immigration or emigration occurs.

This study demonstrates that insect performance and densities can vary widely within a host population and are influenced by extremes in host phenotype. The densities sawflies attained on trees with resistant and susceptible phenotypes were significantly different and most strongly influenced by mortality. However, host impacts on performance were not entirely predictable owing to interspecific interactions between insects. Here, pinyons highly susceptible to one insect species were also highly susceptible to another species with a very different feeding behavior and life history. Both affirmative and opposing examples of multiple susceptibility have been documented recently in other natural systems, generally for closely related species (Maddox and Root 1987, Fritz and Price 1988, Boecklen and Price 1989, Moran and Whitham 1990*b*). The issue of susceptibility to one or to all may not be resolved into one general paradigm, but its resolution will contribute mightily to our understanding of insect abundance patterns, to the continued development of theories of plant defense, and to our perception of competitive interactions among insect herbivores.

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