

THE PLANT STRESS PARADOX: EFFECTS ON PINYON SAWFLY SEX RATIOS AND FECUNDITY¹

SUSAN MOPPER² AND THOMAS G. WHITHAM

Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA

Abstract. Plant stress theory predicts and many observational studies support the notion that abiotic stress can increase plant quality and benefit the performance of phytophagous insects. Paradoxically, numerous experiments contradict this assumption. To test the theory, we conducted experiments to determine the influence of pinyon pine (*Pinus edulis*) stress on pinyon sawfly (*Neodiprion edulicolis*) performance. In a natural pinyon population, we transferred first-instar sawfly larvae to 41 trees divided into four groups of 11; each group received either water, fertilizer, water and fertilizer, or no supplements. Upon completion of their penultimate larval instar, we collected sawflies and determined their fecundity and sex ratios. Although sex ratios are rarely used to estimate insect performance in natural systems, we believe that their sensitivity to changes in plant quality may play an overlooked role in insect–plant interactions.

Most of our results refuted theoretical predictions, because sawflies performed better on trees receiving both water and fertilizer. However, in some cases, sawflies did benefit from pinyon stress. We contend that “simultaneous plant stress,” such as low precipitation while the insect is feeding or ovipositing, can reduce performance. In contrast, “sustained plant stress,” such as chronically poor soil conditions or prolonged drought, can benefit insect performance. These different effects on herbivores may parsimoniously explain some discrepancies between theoretical and empirical plant stress studies.

Key words: differential larval mortality of sexes; Diprionidae; fecundity; field experiment; herbivory; *Neodiprion edulicolis*; *Pinus edulis*; plant quality; precipitation; sex ratios; simultaneous plant stress; sustained plant stress.

INTRODUCTION

Phytophagous insects often reach outbreak densities on plants suffering moisture and nutrient stress (White 1969, 1976, Mattson 1980, Landsberg and Wylie 1983, Larsson and Tenow 1984, Waring and Pitman 1985, Mattson and Haack 1987). The plant stress theory states that stressed plants are a higher-quality food for insects than nonstressed plants, probably because of greater availability of soluble nitrogen and carbohydrates and reduced defensive compounds (White 1969, 1974, 1976, Rhoades 1979, 1983). However, experiments testing the effects of stress on the performance of tissue-feeding insects on woody plants report conflicting results (Miles et al. 1982, Wagner 1986, Watt 1986, Bultman and Faeth 1987, McCullough and Wagner 1987, Kimberling et al. 1990, Wagner and Frantz 1990, Craig et al. 1991).

Because of inconsistencies between empirical studies and plant stress theory, we conducted field observations and experiments to test the effects of plant stress on the performance of a leaf-chewing insect. Outbreaks of diprionid sawflies are often associated with plant stress (McLeod 1970, Knerer and Atwood 1973, Mattson and Addy 1975, Larsson and Tenow 1984). Pinyon

pinus (*Pinus edulis* Englm.) growing in the cinder fields of Arizona's Sunset Crater experience greater water and nutrient stress (Mopper et al. 1991) and are heavily infested by the diprionid pinyon sawfly, *Neodiprion edulicolis* Ross (Mopper et al. 1990). Plant stress theory predicts that, in this already-stressful environment, plant stress will increase with low precipitation, and sawfly performance should improve. In contrast, providing pinyons with water and fertilizer should reduce plant stress, and sawfly performance ought to decline.

At Sunset Crater, sawflies display wide annual variation in sex ratios (Mopper et al. 1990), which we contend may be influenced by changes in plant quality resulting from environmental stress. Many studies document biased sex ratios of hymenopteran parasitoids in response to insect-host quality (Clausen 1939, Sandlan 1979, Vinson and Iwantsch 1980, Charnov 1982, Werren 1982, Wellings et al. 1986), but few studies have investigated the influence of plant quality on herbivore sex ratios. This lack of interest is puzzling not only because plant quality may strongly influence sex ratios, but because facultative manipulation of offspring sex represents a means by which haplodiploid herbivores can adapt rapidly to changes in food quality (Burley 1982, Alstad and Edmunds 1989; T. P. Craig, J. K. Itami, and P. W. Price, *unpublished manuscript*).

PINYONS AND PINYON SAWFLIES

We conducted this study at Sunset Crater in Coconino County, northern Arizona (elevation: 2000 m). Sun-

¹ Manuscript received 9 July 1990; revised 30 April 1991; accepted 15 May 1991.

² Present address: Department of Biological Science B-142, Florida State University, Tallahassee, Florida 32306–2043, USA.

set Crater volcano ceased activity in 1265 after blanketing vast areas with thick layers of lava, cinders, and ash. The pinyons that colonized the cinder fields from bordering sandy-loam soils have had only a few generations to adapt to the new environment. Comparison of cinder soils with neighboring sandy-loam soils indicates that cinders are much lower in moisture and nutrient content (Mopper et al. 1991). Further evidence that cinder-soil pinyons are stressed is their significantly greater xylem pressure relative to pinyons growing in the sandy-loam soils (Mopper et al. 1991). Consistent with the plant stress–insect performance hypothesis, cinder-soil pinyons are much more heavily infested by several insect species than are trees growing at the neighboring sandy-loam soil sites (Whitham and Mopper 1985, Mopper and Whitham 1986, Christensen and Whitham 1991).

Many pinyons within the Sunset Crater population are perpetually and heavily infested by the pinyon sawfly (Mopper et al. 1990). This foliage feeder is univoltine and has a haplodiploid mating system: fertilized eggs become diploid females; unfertilized eggs become haploid males (McGregor and Sandin 1968, 1969). In March, prior to bud elongation, eggs hatch and larvae feed gregariously for about a month, then drop to the ground, spin cocoons, and spend the summer in a prepupal diapause beneath the tree. In the fall, adult females emerge with 15 to 60 fully developed eggs, which they lay within the newest foliage of pinyon shoots. As in other haplodiploid hymenopterans, egg fertilization is optional and occurs during oviposition, probably in response to environmental cues (Clausen 1939, Flanders 1965). This sex-determining mechanism potentially allows the insects to manipulate offspring sex in response to plant quality.

MATERIALS AND METHODS

The relationship between cocoon mass and fecundity

If cocoon mass reflects female fecundity, it can be used in lieu of fecundity to measure performance. We collected one group of late-instar sawfly larvae from each of four sawfly-infested trees and placed them in paper lunch bags with fresh pinyon foliage. After larvae spun cocoons, we weighed and stored them in separate vials until their emergence in the fall. We dissected 48 females and counted the eggs they carried. We used a simple regression to determine the relationship between fecundity and cocoon mass (Zar 1984).

Estimating sawfly performance

Fecundity.—We weighed all cocoons and used the equation obtained from the linear regression of cocoon mass on fecundity to calculate the number of eggs each sawfly contained.

Sex ratios.—Female cocoons have at least twice the mass of male cocoons and are easily and nondestructively recognized by weighing (Mopper et al. 1990). All

sex-ratio data were obtained from cocoon masses, which were used to estimate the sex ratio of each sawfly colony. To stabilize the variance and normalize the data, we used arcsine square-root transformation before analysis. All sex-ratio figures and regression equations are of nontransformed data, but statistical tests were conducted on transformed data.

Reproductive potential.—Reproductive potential is a measure of the combined effects of a colony's sex ratio and its average female fecundity. For example, in colonies with a high proportion of males and low female fecundity, average individual reproductive potential would be low. To estimate reproductive potential, we multiplied the proportion of females in each colony by their average fecundity. In a colony with 60% females whose average lifetime fecundity is 47 eggs, individual reproductive potential = (0.60) (47), or 28 eggs per individual in the colony.

Modifying plant stress and quality

To examine how plant stress influences sawfly sex ratios, female fecundity, and reproductive potential, we transferred sawflies to trees in the field that received supplemental water and nutrients. In 1985 we selected 44 small (1.5–2.5 m in height), sexually mature pinyons at Sunset Crater. We randomly assigned them to four groups of 11 trees each: a watered group, a fertilized group, a watered-and-fertilized group, and a control group that received no supplements (N. S. Cobb, *personal communication*).

In 1985–1988 during the dry season from May through July, we provided supplemental water and nutrients to the treatment trees. The fertilized and watered-and-fertilized groups received 340 g per 2.54 cm of trunk diameter of a water-soluble tree fertilizer composed of 19% nitrogen, 8% phosphorus, and 10% potassium in a water base. This was the only time throughout the entire experiment that we applied water to the fertilized trees. In 1986–1988 we applied a balanced, slow-releasing 10:10:10 NPK dry fertilizer to the fertilized and watered-and-fertilized trees in the amount of 100 g/m² of soil beneath the canopy.

To evaluate the effects of each treatment, we measured pinyon foliage nitrogen content at the end of the growing season in 1987. We determined total foliage nitrogen by collecting 10 needles from each tree and placing them on ice in the field. We stored the needles at –80°C then freeze-dried them prior to analysis. We used a modified micro-Kjeldahl digestion method to prepare the foliage for analysis (Parkinson and Allen 1975) and determined total foliage nitrogen colorimetrically with a Technicon Auto Analyzer.

In addition to foliage nitrogen, we used stem growth to assess plant response to treatment. In 1987 after shoots had elongated, we measured the lengths of 10 shoots per tree in each treatment group and calculated their average growth. We compared foliage nitrogen

contents and shoot growths of the four treatment groups with a one-way analysis of variance (ANOVA) test. When the ANOVA indicated differences between groups we employed Tukey tests for multiple comparisons. Multiple comparisons were considered significantly different when P was $\leq .05$.

Transfer experiments

In March 1988, after the trees had received 3 yr of water and/or nutrient supplementals, we transferred one colony of first-instar sawflies to the southwestern side of each tree. All trees were initially devoid of sawflies. We collected sawflies for transfer from four infested trees (see Mopper et al. [1990] for detailed methods). Each colony contained from 20 to 40 larvae. Larvae remained gregarious after transfer and fed freely in a group until the end of the larval cycle. We collected each colony in a paper bag containing fresh foliage from its respective tree. Because of predation and unknown mortality, some colonies either disappeared or were substantially reduced in the field. When this was the case, we could not collect data for the tree. Therefore, each group is represented by a different number of trees, ranging from 6 to 11. Larvae spun cocoons, which we weighed and sexed. After weighing we returned cocoons to the soil beneath trees in two of the four treatment groups (control and watered-and-fertilized) for colonization the following spring. In 1989 six control and six watered-and-fertilized trees were successfully colonized by sawflies.

In 1988 we collected data from four groups, and in 1989 we collected data from two groups. We employed one-way ANOVAs to compare the four groups in 1988 and the two groups in 1989. Because of unequal cell sizes between years, we used a two-way analysis of variance rather than a repeated-measures design to test the effects of treatment, year, and year \times treatment interactions on sawfly fecundity, sex ratios, and reproductive potential for control and watered-and-fertilized groups in 1988 and 1989.

Performance of field and laboratory sawflies

In this experiment we determined how foliage water content influenced sawfly cocoon mass, sex ratios, and reproductive potential. We also investigated the roles played by differential mortality (secondary sex determination) and parental sex allocation (primary sex determination) in determining sawfly sex ratios in the field.

In March 1987 we collected two to three pinyon shoots bearing sawfly eggs from each of 10 trees and placed each shoot in a vial of water in the laboratory. When eggs hatched and larvae began feeding, we regularly replaced old with fresh foliage collected from the same trees from which we collected eggs. Therefore, each sawfly group in the lab was only fed foliage col-

lected from their original tree. Sawflies completed the larval stages within a month and entered the cocoon prepupal stage. In April 1987 we collected two to three late-instar larval colonies from each of the same 10 trees in the field and allowed them to spin cocoons. We weighed and sexed all field and laboratory cocoons.

We measured the water content of field and laboratory foliage. Field samples were placed in airtight bags on ice, then returned to the laboratory. Field and laboratory samples were weighed, oven-dried for 3 d, and weighed again. We compared foliage water content, cocoon sex ratios, adult fecundity, and reproductive potential of our laboratory and field groups with paired t tests.

Maintaining sawflies in the laboratory from egg hatch until pupation virtually eliminated mortality and enabled us to estimate primary sex ratios. We could then compare parentally determined (primary) sex ratios with sex ratios of adult sawflies (secondary sex ratios). To test whether primary (laboratory-reared) or secondary (field-reared) sawfly sex ratios differed from equality, we used a chi-squared analysis.

The relationship between precipitation and sawfly performance

Because of the moisture stress experienced by pinyons at Sunset Crater, we hypothesized that increased precipitation might reduce plant stress and food quality, thereby negatively affecting sawfly fecundity and sex ratios. We compared Sunset Crater precipitation patterns with female cocoon mass, sex ratios, and reproductive potential over a 7-yr period. From 1984 to 1990 we collected from one to three late-instar sawfly colonies from the same four trees each year and weighed and sexed cocoons. We used precipitation data collected by the Sunset Crater National Monument staff.

We compared sawfly performance with March and with April precipitation because that is when sawflies hatch and feed. We also compared sawfly performance with the total amount of precipitation received the year prior to egg hatch. Sawflies oviposit in late fall and feed in early spring, prior to bud elongation; thus precipitation in the year of oviposition may influence food quality. If females allocate egg sex on the basis of plant quality, sex ratios may be affected by precipitation in the year leading up to oviposition. To compare performance with precipitation, we used both simple- and multiple-regression models with cocoon mass, reproductive potential, and arcsine-square-root-transformed cocoon sex ratios as dependent variables. Because we had three predictor variables (March and April precipitation and precipitation the previous year), we conducted stepwise regression from simple to multiple-factor models. None of the independent variables were correlated. In comparisons between precipitation in March, April, and the previous year, all $r^2 \cong 0.0\%$. Figures presented are the simple linear regressions.

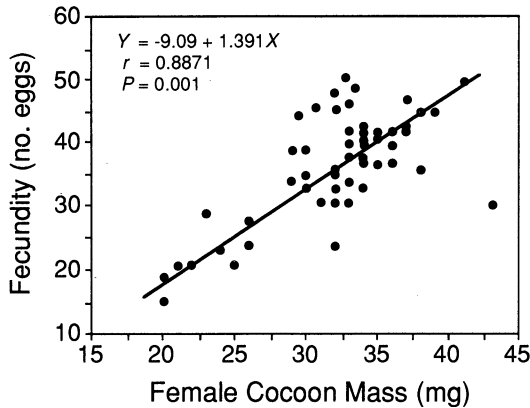


FIG. 1. The relationship between number of eggs and cocoon mass of adult female sawflies ($n = 48$ individuals, $F = 174.7$).

RESULTS

The relationship between cocoon mass and fecundity

There was a strong positive linear relationship between cocoon mass and sawfly fecundity (Fig. 1). Cocoon mass accounted for almost 80% of the variation in a female sawfly's egg yield ($F_{1,46} = 174.4$, $P < .0001$).

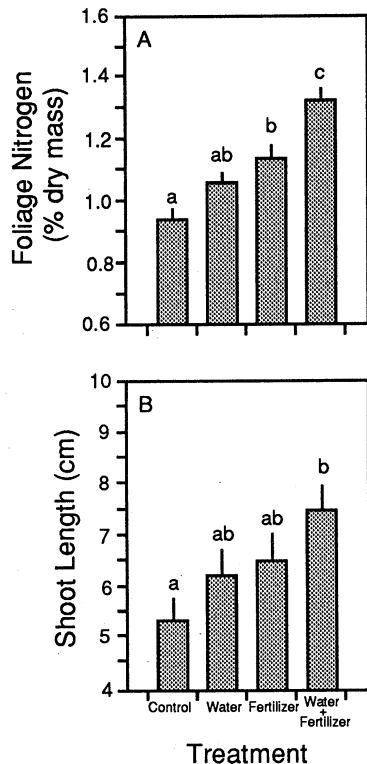


FIG. 2. Foliage nitrogen content (A) and stem lengths (B) of control, watered, fertilized, and watered-and-fertilized pinyon pine trees. Bars are means plus 1 SE; different letters above bars indicate differences between groups at $P \leq .05$.

TABLE 1. Analysis of variance of foliage nitrogen content and stem lengths of pinyons provided either with no supplements or with water, fertilizer, or water-plus-fertilizer.

Source of variation	ss	df	F	P
Total foliage nitrogen				
Treatment	0.6680	3	10.57	$\ll .0001$
Error	0.6317	30		
Stem lengths				
Treatment	25.22	3	2.51	.073
Error	127.32	38		

Because of this strong relationship, we used the linear regression equation, (number of eggs) = $-9.09 + 1.391$ (cocoon mass), to estimate sawfly fecundity.

Modifying plant stress and quality

Watering and fertilizing pinyons significantly influenced stem lengths and foliage nitrogen (Table 1, Fig. 2). Both foliage nitrogen and stem lengths were lowest in the control group ($n = 8$ and 10 trees), highest in the watered-and-fertilized group ($n = 9$ and 11), and intermediate in the watered ($n = 9$ and 11) and the fertilized ($n = 8$ and 10) groups. Female cone and resin production also increased significantly on trees that were watered and fertilized (N. S. Cobb, *personal communication*).

Plant stress and sawfly performance

Fecundity.—In 1988 sawfly fecundity increased on plants with greater stem growth and foliage nitrogen because larvae reared on watered-and-fertilized pinyons had significantly heavier mean cocoon mass than did larvae reared on control trees (Table 2, Fig. 3A). Sawflies reared on watered and on fertilized trees were intermediate in mass and did not differ significantly from each other. A similar pattern emerged in 1989; sawfly cocoons from watered-and-fertilized trees weighed more than controls, but the differences were not significant (Table 2, Fig. 3B).

Sex ratios.—It appears that water and water-plus-fertilizer have opposing effects on sawfly sex ratios. In 1988 sawflies reared on trees provided with water-plus-fertilizer had significantly higher proportions of adult females than the water-only treatment (Table 2, Fig. 3C). Although lower than the watered-and-fertilized group, the control and the fertilized groups did not differ significantly. Consistent with the 1988 results, there was a higher proportion of females from watered-and-fertilized trees than from controls, but the differences were not significant (Table 2, Fig. 3D).

Reproductive potential.—In 1988, reproductive potential, an estimate of the combined effects of fecundity and sex ratio, increased substantially on watered-and-fertilized trees compared with all other groups (Table 2, Fig. 3E). A similar pattern emerged in 1989 but it was not significant (Table 2, Fig. 3F).

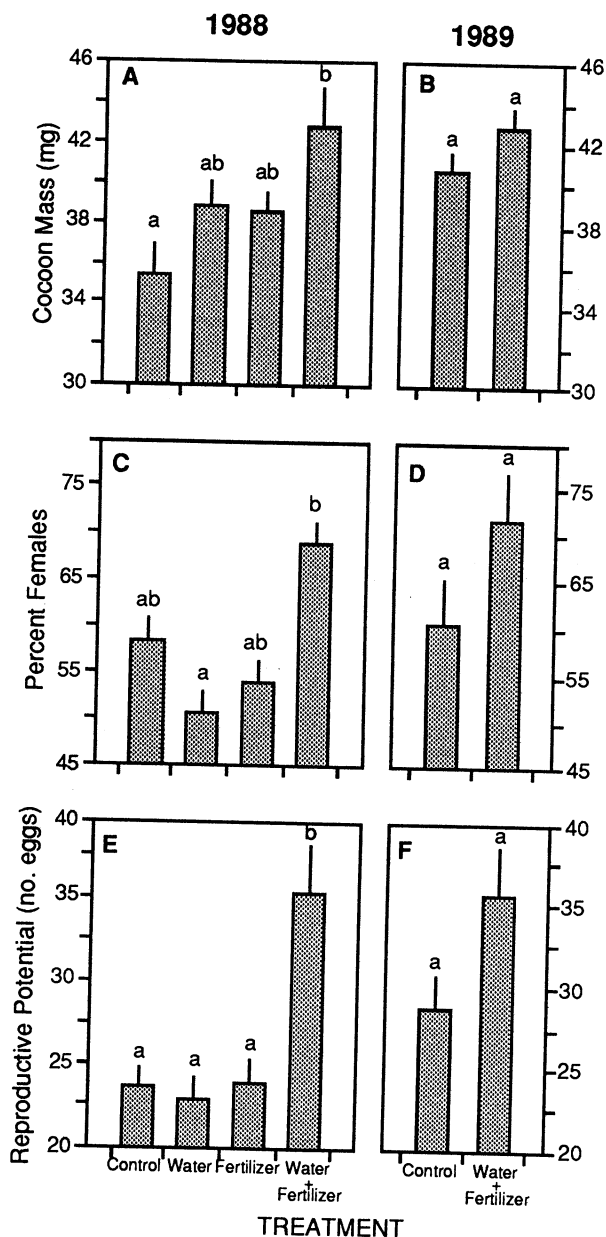


FIG. 3. Female cocoon mass (A, B), percentage of adult females (C, D), and estimated reproductive potential (E, F) on control ($n = 6$), watered ($n = 11$), fertilized ($n = 8$), and watered-and-fertilized ($n = 9$) pinyon pine trees in 1988 and on control ($n = 6$) and watered-and-fertilized ($n = 7$) trees in 1989. Bars are means plus 1 SE; different letters above bars indicate differences between groups at $P \leq .05$.

Year effects on sawfly performance.—The two-way ANOVAs comparing cocoon mass, sex ratios, and reproductive potential on the control and watered-and-fertilized trees in 1988 and 1989 indicate significant overall treatment effects despite the weaker (but consistent) patterns in 1989 (Table 2). Thus, sawfly performance rises significantly on plants with reduced water and nutrient stress. We detected no significant year or year \times treatment interaction effects on the cocoon

mass, sex ratios, or reproductive potential of sawflies in any treatment group (Table 2).

The weaker treatment effect and overall better performance of sawflies in 1989 were probably affected by the 10-fold difference in March rainfall between years. In 1988, rainfall in the month of March (when eggs hatch and larvae begin to feed) was only 0.30 cm, but it was 3.15 cm in 1989.

Performance of field and laboratory sawflies

Although the leaves were collected from the same trees, the water content of foliage consumed by sawflies in the laboratory exceeded that of foliage eaten by field-reared sawflies by 5% (paired t test, $t = 8.99$, $P \ll .0001$, Fig. 4A). Therefore, by keeping shoots in vials of water in the lab, we could increase foliage moisture and examine its effect on sawfly performance. The protected laboratory environment may also have had a beneficial effect on sawfly performance.

Cocoon mass.—The cocoon mass of laboratory-reared sawflies significantly exceeded that of field-reared sawflies (paired t test, $t = 3.41$, $P = .0077$, Fig. 4B). Furthermore, because fecundity is highly correlated with

TABLE 2. One-way analyses of variance of female cocoon mass, adult sex ratios, and reproductive output of sawflies reared on control, watered, fertilized, or watered-and-fertilized pinyons in 1988 and control and watered-and-fertilized pinyons in 1989, plus two-way analyses of variance of overall treatment effect, year effect, and treatment \times year interactions for control and watered-and-fertilized trees in 1988 and 1989.

Source of variation	ss	df	F	P
Cocoon mass				
1988 Treatment	201.7	3	4.24	.013
Error	475.5	30		
1989 Treatment	14.3	1	1.46	.252
Error	07.6	11		
Two-way ANOVA				
Treatment	152.3	1	8.18	.009
Year	51.7	1	2.78	.109
Treatment \times Year	45.2	1	2.43	.132
Sex ratios				
1988 Treatment	0.2613	3	2.88	.052
Error	0.9073	30		
1989 Treatment	0.0606	1	1.90	.195
Error	0.3503	11		
Two-way ANOVA				
Treatment	0.08	1	3.625	.069
Year	0.005	1	0.204	.655
Treatment \times Year	0.000	1	0.005	.947
Reproductive output				
1988 Treatment	956.0	3	3.73	.022
Error	2562.0	30		
1989 Treatment	128.2	1	2.44	.147
Error	578.9	11		
Two-way ANOVA				
Treatment	556.0	1	5.8	.024
Year	22.2	1	0.2	.634
Treatment \times Year	50.9	1	0.532	.473

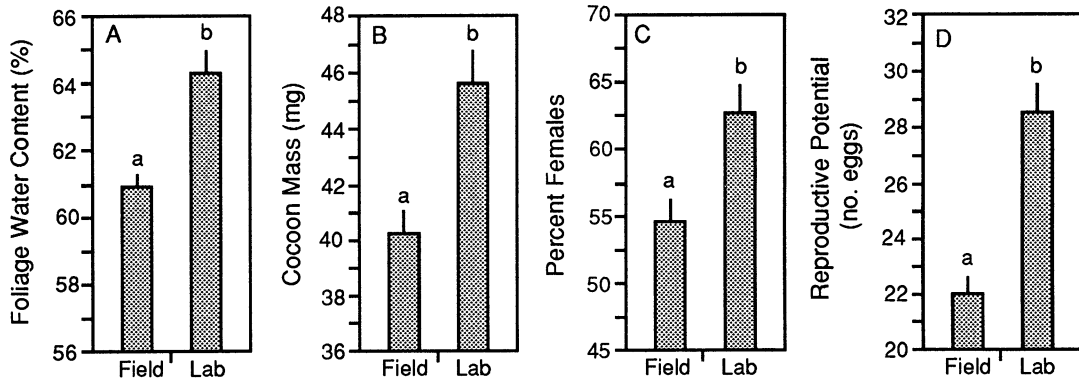


FIG. 4. Foliage water content (A), female cocoon mass (B), percentage of adult females (C), and estimated reproductive potential (D) of field-reared and laboratory-reared sawflies. Bars are means of 10 trees each plus 1 SE; different letters above bars indicate differences between groups at $P \leq .05$.

cocoon mass (Fig. 1), increased foliage water should increase egg production.

Sex ratios.—There were three important patterns in sawfly sex allocation (Fig. 4C). First, primary sex ratios (the sex ratios of eggs laid on trees in the field) were female biased. Cocoon sex ratios of laboratory-reared sawflies averaged $63.5 \pm 0.04\%$ females (mean ± 1 SE) and deviated significantly from equality ($\chi^2 = 23.0$, $P < .001$). Because field-collected laboratory-reared sawflies suffered negligible egg-to-cocoon mortality (0.9%), cocoon sex ratios accurately estimate the sex ratios of sawfly eggs.

Second, the sex ratios of field and laboratory sawflies differed significantly, indicating that differential female mortality occurred in the field (Fig. 4C). There were proportionately more females among laboratory-reared sawflies (63.5%) than among field-reared sawflies (55.1%), a significant difference of 13% (paired t test, $t = 2.75$, $P = .023$).

Third, despite differential female larval mortality, cocoon sex ratios of field-reared sawflies were nevertheless slightly female biased (55%) and deviated significantly from equality ($\chi^2 = 5.3$, $P < .025$). Apparently ovipositing females laid more female than male eggs, perhaps to compensate for subsequent higher female larval mortality.

Reproductive potential.—Reproductive potential was significantly greater for sawflies reared in the laboratory, exceeding that of field sawflies by 20% (paired t test, $t = 4.91$, $P \ll .0001$, Fig. 4D). Thus, the benign effects of increased foliage water and laboratory rearing increased cocoon mass and female survival and caused a substantial rise in individual reproductive potential.

Precipitation and sawfly performance

Cocoon mass.—There was a positive, nonsignificant trend ($P = .115$) between sawfly cocoon mass and precipitation in March, when eggs hatch and early-instar larvae begin to feed (Table 3, Fig. 5A). There was no significant relationship between cocoon mass and precipitation in the year prior to egg hatch (Fig. 5B).

Sex ratios.—The proportion of females in a sawfly colony was not significantly associated with March precipitation but it was strongly negatively ($P = .004$) correlated with precipitation the previous year (Table 3, Figs. 5C and 5D).

Reproductive potential.—Reproductive potential, an estimate of the combined effects of fecundity and sex ratio on sawfly performance, responded positively and significantly (at the $P < .06$ level) to precipitation in March (Table 3, Fig. 5E). There was also a nonsignificant ($P = .102$) negative relationship with the previous year's total precipitation (Fig. 5F).

Although only some of these comparisons were significant (perhaps owing to only seven data points), all performance measures exhibited consistent trends: positive associations with precipitation in March when larvae feed, and negative associations with total precipitation the previous year (Table 3). April precipitation accounted for none of the variation in cocoon

TABLE 3. Simple and multiple regressions using March, April, and previous year's total precipitation as predictor variables, and female cocoon mass, arcsine-square-root-transformed adult sex ratios, and individual reproductive potential as response variables.

Performance measure	r	F	P
Cocoon mass			
March	0.5523	3.63	.115
April	≈ 0.0	0.24	.648
Previous year	≈ 0.0	0.26	.635
March \times Previous year	≈ 0.0	0.77	.583
Sex ratios			
March	0.4123	2.23	.196
April	≈ 0.0	0.59	.475
Previous year	-0.8967	25.57	.004
March \times Previous year	0.9592	35.40	.003
Reproductive potential			
March	0.6782	6.11	.056
April	≈ 0.0	0.75	.427
Previous year	-0.5779	4.01	.102
March \times Previous year	0.8307	7.67	.043

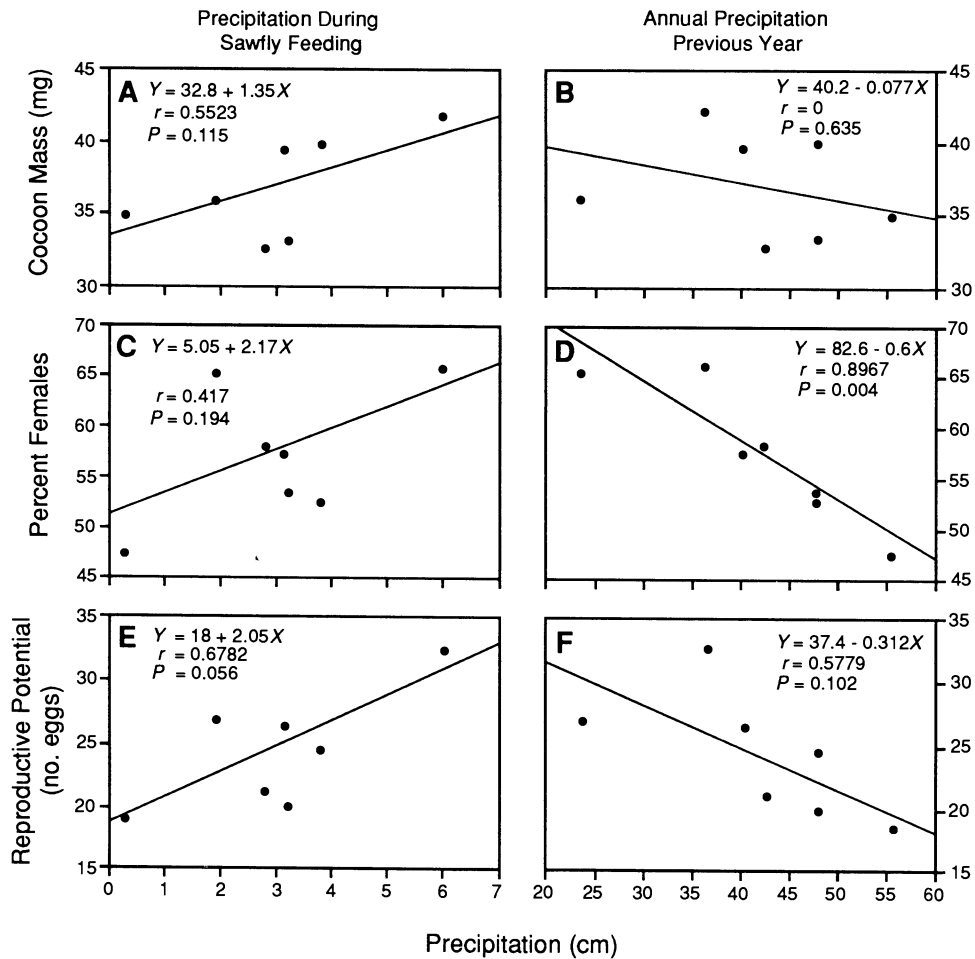


FIG. 5. Correlations between female cocoon mass (A, B), percentage of adult females (C, D), reproductive potential (E, F), and precipitation in March and in the previous year. Each point represents the mean value of sawflies collected from four trees. Regression equation, *r*, and *P* values in figures are calculated from non-transformed data.

mass, sex ratios, or reproductive potential (all *rs* \approx 0.0, all *Ps* > .40).

Multiple-regression model.—Although the multiple-regression model explained none of the variation in cocoon mass (*P* = .583), the model best fitting the sex-ratio data included precipitation in March and in the previous year and explained 92.0% of the variation ($Y = 1.05 + 0.0136[\text{March}] - 0.00554[\text{previous year}]$, *P* = .003; Table 3). The same variable best predicted reproductive potential and explained 69% of the variation ($Y = 29.2 + 1.69[\text{March}] - 0.239[\text{previous year}]$, *P* = .043).

DISCUSSION

Sawfly sex ratios and plant quality

We contend that sex ratios of haplodiploid insects can be highly sensitive to plant quality. Apparently, both primary and secondary sex-determining mechanisms operate in pinyon-sawfly interactions. In this study we found that primary (egg) sawfly sex ratios were female biased (Fig. 4C). Surprisingly, secondary

(cocoon) sex ratios are female biased as well, despite the greater mortality among female larvae than among males. In fact, at Sunset Crater sawfly cocoons are consistently female biased year after year (Mopper et al. 1990). Perhaps this biased pattern in sex allocation represents a compensating mechanism for subsequent differential female mortality.

The strong negative correlation between sawfly sex ratios and total precipitation in the year of oviposition (Fig. 5D) suggests that females make sex-allocation decisions as they oviposit, perhaps in response to plant quality. If so, recent work on the sex-allocation behavior of a distantly related gall-forming sawfly (T. P. Craig, J. K. Itami, and P. W. Price, *unpublished manuscript*) is corroborated. Some studies have demonstrated patterns of secondary sex-ratio variation in herbivorous insects caused by differential mortality or behavior in response to plant characteristics (Alstad and Edmunds 1983, 1989, Starzyk and Witkowski 1986, Haack et al. 1987, Lawrence 1987). These facultative and secondary sex-ratio shifts of haplodiploid phy-

tophagous insects in response to plant quality may play an overlooked role in pest outbreaks.

Sawfly sex ratios and fecundity in response to plant stress

In support of plant stress theory.—Some of our results and field observations support the prediction that plant stress benefits insects. For example, the proportion of females contained in a sawfly colony was strongly negatively correlated with total precipitation occurring the year prior to egg hatch (Fig. 5D). That is, many more sawfly females reached the cocoon stage following dry years than did so after wet years. In addition, more females (but not significantly more) were found on control trees than on watered-only or fertilized-only trees (Fig. 3C). We have also observed that densities of the pinyon shoot moth, *Dioryctria albovitella*, are strongly negatively correlated with annual precipitation ($r^2 = 91\%$, $P < .001$, S. Mopper and T. G. Whitham, unpublished data).

These results confirm the predictions of plant stress theory and corroborate observations that pinyons in the relatively xeric and nutrient-poor cinder soils of Sunset Crater are much more heavily infested by several insect species than are pinyons in moister and more nutrient-rich neighboring soils (Mopper and Whitham 1986, Christensen and Whitham 1991, Mopper et al. 1991).

In opposition to plant stress theory.—Most of our experimental results refute plant stress theory and demonstrate that plant stress can be detrimental to insect performance. First, cocoon mass, proportion of females, and individual reproductive potential were all significantly greater for sawflies field-reared on watered-and-fertilized plants than for those on controls (Table 2, Fig. 3). Second, cocoon mass, proportion of females, and reproductive potential were significantly higher in laboratory-reared colonies that consumed foliage high in water (Fig. 4). Third, sawfly reproductive potential was significantly positively correlated with precipitation in March (Fig. 5E).

The plant stress paradox

Although it has achieved paradigm status, the plant stress–herbivory theory remains highly controversial. On the one hand, many studies document a strong positive relationship between insect outbreaks and plant stress (White 1969, 1976, McLeod 1970, Knerer and Atwood 1973, Mattson and Addy 1975, Averill et al. 1982, Landsberg and Wylie 1983, Larsson and Tenow 1984, Munster-Swendsen 1984, Mattson and Haack 1987, Larsson 1989, Waring and Cobb 1992). On the other hand, numerous experimental studies document negative insect responses to plant stress (Miles et al. 1982, Hargrove et al. 1984, Redak and Cates 1984, Wagner 1986, Watt 1986, Bultman and Faeth 1987, Clancy and Price 1987, Lightfoot and Whitford 1987, McCullough and Wagner 1987, Wilcox and Crawley

1988, Larsson 1989, Kimberling et al. 1990, Wagner and Frantz 1990, Waring and Cobb 1992).

Furthermore, water and nutrient stress are clearly very different, and, as our study demonstrates (Fig. 3), the interaction between water and nutrients can have a stronger effect than either alone. In many experimental studies, supplemental water or water plus fertilizer have positive effects on insect performance or attack rates (Price and Clancy 1986, Bultman and Faeth 1987, Clancy and Price 1987, Lightfoot and Whitford 1987, McCullough and Wagner 1987, Kimberling et al. 1990, Wagner and Frantz 1990), whereas fertilization alone has a range of effects from negative to positive (Smirnoff and Bernier 1973, Hargrove et al. 1984, Popp et al. 1986, Lightfoot and Whitford 1987, Strauss 1987, Wilcox and Crawley 1988).

Researchers have proposed several hypotheses to explain these inconsistencies, such as differential guild- and/or stage-specific responses to stress (see reviews by Mattson and Haack 1987, Larsson 1989, Wagner 1991, Waring and Cobb 1992). For example, species like stem-galling tenthredinid sawflies may require more vigorous, nonstressed plants with rapid stem growth to maximize their performance when feeding as larvae inside stem galls (Craig et al. 1986, Price and Clancy 1986, Kimberling et al. 1990). Although life history may account for some discrepancies between theory and field observations, many studies that refute theory predictions involve a variety of guilds, including gall formers, leaf miners, and leaf chewers (Miles et al. 1982, Hargrove et al. 1984, Redak and Cates 1984, Wagner 1986, Watt 1986, Bryant et al. 1987, Bultman and Faeth 1987, McCullough and Wagner 1987, Wilcox and Crawley 1988, Craig et al. 1991).

Another alternative is the “stress as a continuum” hypothesis, in which insects are most successful at levels intermediate between mild and severe plant stress (Hsiao 1973, White 1984, Bultman and Faeth 1987, Mattson and Haack 1987, Larsson 1989). This is an appealing theory that may explain why outbreaks do not occur in extremely low- or extremely high-stress conditions, but it does not satisfactorily address why so many experimental studies on intermediate levels of stress oppose theory predictions. A new approach that incorporates tree ontogeny, genotype, and stress level to generate a three-dimensional “response surface” in order to predict the performance of pine sawflies (Wagner 1991) is promising, but may prove unmanageably complex for some situations.

Simultaneous and sustained plant stress

Are complicated models required for understanding insect performance on stressed plants? We contend that, for perennial plants, many apparent discrepancies between experiments and field observations can be simply explained by the differences between temporary *simultaneous* and long-term *sustained* plant stress (Fig. 6).

Simultaneous stress.—We propose that simultaneous plant stress can often have detrimental effects on insects. Our model (Fig. 6) predicts that if plant stress is in the low range while insects are feeding, insect performance will be high. Once plant stress reaches some critical intermediate level, insect performance will drop rapidly. At the highest stress levels, the plant becomes an inadequate food source.

Two factors that virtually all experimental studies of woody plant stress have in common are (1) they are brief, limited to one or two seasons, and (2) treatments such as trenching, watering, and fertilizing are applied to plants *concurrent with insect feeding and oviposition* (Miles et al. 1982, Hargrove et al. 1984, Popp et al. 1986, Wagner 1986, Watt 1986, Bryant et al. 1987, Bultman and Faeth 1987, McCullough and Wagner 1987, Kimberling et al. 1990). Thus, many studies contesting plant stress–herbivory predictions apply stress treatments only during direct insect–plant interactions such as feeding or oviposition and discover that insects do better on plants with the least amount of stress, i.e., those that receive water and/or fertilizer. In our laboratory study, performance improved when sawflies consumed foliage with high water content (Fig. 4). In the field, we also detected a positive relationship ($P = .056$) between sawfly reproduction potential and March precipitation, when eggs hatch and larvae begin to feed (Fig. 5E). Other studies have demonstrated the immediately beneficial effects of foliage water content on insect performance (Scriber 1977, 1979, 1984, Scriber and Slansky 1981, Bultman and Faeth 1987). High stress (e.g., no precipitation) during insect feeding may temporarily reduce tissue water content, which can be an important factor limiting insect growth (Scriber and Slansky 1981).

Sustained plant stress.—In contrast to simultaneous plant stress, sustained stress is extended, prevailing while insects are both active and inactive. Sustained environmental stress (such as repeated drought or poor soil), by causing numerous plant metabolic changes such as hydrolysis, increased nitrogen availability, and reduced secondary compounds (Coley et al. 1985, Waring and Cobb 1992), can be beneficial to insects. Many insect outbreaks occur after several years of stressful conditions (Morris 1964, White 1969, Landsberg and Wylie 1983, Larsson and Tenow 1984, Munster-Swendsen 1984). Moreover, outbreaks are often associated with permanent environmental characteristics such as soils with low moisture and nutrients (Knerer and Atwood 1973, Averill et al. 1982, Kemp and Moody 1984, Larsson and Tenow 1984, Waring and Price 1990, Mopper et al. 1991).

The plant-stress continuum theory represents insect responses to *sustained*, not *simultaneous* stress (Fig. 6). Here, folivorous insects are relatively successful on plants of low stress. Their performance improves on plants experiencing intermediate stress, then declines when very high stress makes the host plant an inade-

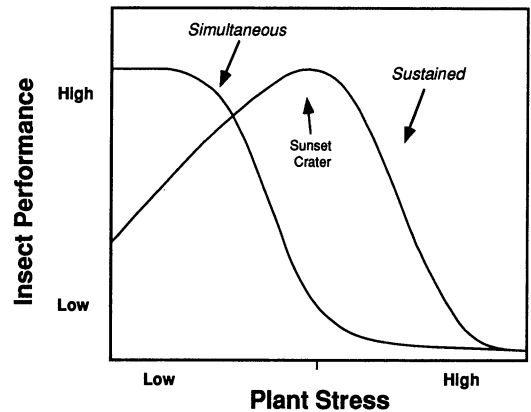


FIG. 6. Hypothetical relationship between insect performance and simultaneous and sustained plant stress. Conditions at Sunset Crater are indicated.

quate resource. We contend that the optimum host for a folivorous insect would be a plant that has experienced long-term intermediate stress, then is temporarily released from stress (e.g., by abundant precipitation) while the insect is feeding. At Sunset Crater the positive relationship between environmental stress and high insect densities is well documented (Whitham and Mopper 1985, Mopper and Whitham 1986, Mopper et al. 1990, 1991, Christensen and Whitham 1991, N. S. Cobb, *personal communication*). However, despite poor soil conditions, pinyons do grow and reproduce, and mortality is rare. This indicates that Sunset Crater falls near the center of the sustained stress curve (Fig. 6). Furthermore, sawfly performance (Fig. 5) and stem moth densities (S. Mopper and T. G. Whitham, *unpublished data*) rise when annual precipitation is low, an indication that Sunset Crater is an intermediate-not high-stress environment.

Resolving the plant stress paradox

Many factors influence how insects perform on stressed plants. Clearly, the effects of simultaneous and sustained stress must be separated in future plant stress–herbivory experiments. Furthermore, prevailing conditions may also affect the outcome of empirical field studies. For example, the abundant March 1989 precipitation (3.15 cm) may have weakened the treatment effects and improved overall sawfly performance compared to 1988 (Fig. 3), in which March precipitation (0.30) was scant. For these reasons, it is tempting to suggest that we limit ourselves to controlled laboratory tests of plant stress (Wagner 1991), but recent experimental studies demonstrate the dangers of extrapolating from the artificial to the natural (Baldwin 1988a, b, Letourneau and Fox 1989). Field studies in natural systems need not be hopelessly complex if properly designed, and will certainly shed light on the plant stress paradox.

Despite the complexity of plant stress–herbivore interactions, we contend that differences between simultaneous and sustained plant stress can parsimoniously explain many puzzling discrepancies. If sustained stress is a continuum in which insects perform best at intermediate levels, then simultaneous stress, occurring only while insects interact with the plant, may have more negative effects (Fig. 6). Their combined impacts on plants may play a key role in determining how insects perform and when outbreaks occur.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of Kehath S. Mopper. We thank the United States Forest Service for permission to work at the study site and the Sunset Crater National Monument staff for their generous support and access to the precipitation data. The chemists at the Bilby Research Center provided valuable assistance in conducting the foliage nitrogen analyses. We are grateful to W. Boecklen, N. Cobb, E. Jacobson, K. Mopper, D. Simberloff, and T. Wood for field assistance. N. Cobb, L. Fox, W. Lawrence, J. Maschinski, P. Price, D. Strong, A. Thistle, and an anonymous reviewer critically reviewed and significantly improved this manuscript. W. Boecklen provided statistical consultation. Special thanks are due to G. Waring, P. Price, K. Clancy, and D. Simberloff for helpful discussions of the plant stress paradox. This study was funded by NSF grants BSR-8501071, BSR-8604983, and BSR-8705347 and USDA grants 94-CRCR-1-1443 and GAM-8700709.

LITERATURE CITED

- Alstad, D. N., and G. F. Edmunds. 1983. Selection, outbreeding depression, and the sex ratio of scale insects. *Science* **220**:93–95.
- Alstad, D. N., and G. F. Edmunds. 1989. Haploid and diploid survival differences demonstrate selection in scale insect demes. *Evolutionary Ecology* **3**:253–263.
- Averill, R. D., L. R. Wilson, and R. F. Fowler. 1982. Impact of the red-headed pine sawfly (Hymenoptera: Diprionidae) on young red pine plantations. *Great Lakes Entomologist* **15**:65–91.
- Baldwin, I. T. 1988a. Short-term damage-induced increases in tobacco alkaloids protects plants. *Oecologia (Berlin)* **75**:367–370.
- . 1988b. The alkaloidal responses of wild tobacco to real and simulated herbivory. *Oecologia (Berlin)* **77**:378–381.
- Bryant, J. P., T. P. Clausen, P. B. Reichardt, M. C. McCarthy, and R. A. Werner. 1987. Effect of nitrogen fertilization upon the secondary chemistry and nutritional value of quaking aspen (*Populus tremuloides* Michx.) leaves for the large aspen tortrix (*Choristoneura conflictana* (Walker)). *Oecologia (Berlin)* **73**:513–517.
- Bultman, T. L., and S. H. Faeth. 1987. Impact of irrigation and experimental drought stress on leaf-mining insects of Emory oak. *Oikos* **48**:5–10.
- Burley, N. 1982. Facultative sex ratio manipulation. *American Naturalist* **120**:81–107.
- Charnov, E. L. 1982. *The theory of sex allocation*. Princeton University Press, Chicago, Illinois, USA.
- Christensen, K. M., and T. G. Whitham. 1991. Indirect herbivore mediation of avian seed dispersal in pinyon pine. *Ecology* **72**:534–542.
- Clancy, K. M., and P. W. Price. 1987. Rapid herbivore growth enhances enemy attack: sublethal plant defenses remain a paradox. *Ecology* **68**:733–737.
- Clausen, C. P. 1939. The effect of host size upon the sex ratio of hymenopterous parasites and its relation to methods of rearing and colonization. *New York Entomological Society* **47**:1–9.
- Coley, P. D., J. P. Bryant, and F. S. I. Chapin. 1985. Resource availability and plant anti-herbivore defense. *Science* **230**:895–899.
- Craig, T. P., J. K. Itami, and P. W. Price. 1986. Resource regulation by a stem-galling sawfly on arroyo willow. *Ecology* **67**:419–425.
- Craig, T. P., M. R. Wagner, D. G. McCullough, and D. P. Frantz. 1991. Effects of experimentally altered plant moisture stress on the performance of *Neodiprion* sawflies. *Forest Ecology and Management*, special issue: XVIII International Congress of Entomology Symposium Towards Integrated Pest Management of Forest Defoliators, *in press*.
- Flanders, S. E. 1965. On the sexuality and sex ratios of hymenopterous populations. *American Naturalist* **99**:489–494.
- Haack, R. A., R. C. Wilkinson, and J. L. Foltz. 1987. Plasticity in life-history traits of the bark beetle *Ips calligraphus* as influenced by phloem thickness. *Oecologia (Berlin)* **72**:32–38.
- Hargrove, W. W., D. A. Crossley, Jr., and T. R. Seastedt. 1984. Shifts in insect herbivory in the canopy of black locust, *Robinia pseudoacacia*, after fertilization. *Oikos* **43**:322–328.
- Hsiao, T. C. 1973. Plant responses to water stress. *Annual Review of Plant Physiology* **24**:519–570.
- Kemp, W. P., and U. L. Moody. 1984. Relationship between regional soils and foliage characteristics and western spruce budworm (Lepidoptera: Tortricidae) outbreak frequency. *Environmental Entomology* **13**:1291–1297.
- Kimberling, D. N., E. R. Scott, and P. W. Price. 1990. Testing a new hypothesis: plant vigor and phylloxera distribution on wild grape in Arizona. *Oecologia (Berlin)* **84**:1–8.
- Knerer, G., and C. E. Atwood. 1973. Diprionid sawflies: polymorphism and speciation. *Science* **179**:1090–1099.
- Landsberg, J., and F. R. Wylie. 1983. Water stress, leaf nutrients and defoliation: a model of dieback of rural eucalyptus. *Australian Journal of Ecology* **8**:27–41.
- Larsson, S. 1989. Stressful times for the plant stress–insect performance hypothesis. *Oikos* **56**:277–282.
- Larsson, S., and O. Tenow. 1984. Areal distribution of a *Neodiprion sertifer* (Hym., Diprionidae) outbreak on Scots pine as related to stand condition. *Holarctic Ecology* **7**:81–90.
- Lawrence, W. S. 1987. Effects of sex ratio on milkweed beetle emigration from host plant patches. *Ecology* **68**:539–546.
- Letourneau, D. K., and L. R. Fox. 1989. Effects of experimental design and nitrogen on cabbage butterfly oviposition. *Oecologia (Berlin)* **80**:211–214.
- Lightfoot, D. C., and W. G. Whitford. 1987. Variation in insect densities on desert creosote bush: is nitrogen a factor? *Ecology* **68**:547–557.
- McCullough, D. G., and M. R. Wagner. 1987. Influence of watering and trenching ponderosa pine on a pine sawfly. *Oecologia (Berlin)* **71**:382–387.
- McGregor, M. D., and L. O. Sandin. 1968. Observations on the pinyon pine sawfly, *Neodiprion edulicolis*, in eastern Nevada (Hymenoptera: Diprionidae). *Canadian Entomologist* **100**:51–57.
- McGregor, M. D., and L. O. Sandin. 1969. Pinyon sawfly, *Neodiprion edulicolis* Ross. *Forest Pest Leaflet* **117**:1–4.
- McLeod, J. M. 1970. The epidemiology of the Swaine jack-pine sawfly, *Neodiprion swainei* Middleton. *Forestry Chronicle* **46**:125–133.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics* **11**:119–161.
- Mattson, W. J., and N. D. Addy. 1975. Phytophagous in-

- sects as regulators of forest primary production. *Science* **190**:515-522.
- Mattson, W. J., and R. A. Haack. 1987. The role of drought stress in provoking outbreaks of phytophagous insects. Pages 365-407 in P. Barbosa and J. C. Schultz, editors. *Insect outbreaks*. Academic Press, San Diego, California, USA.
- Miles, P. W., D. Aspinall, and A. T. Correll. 1982. The performance of two chewing insects on water-stressed food plants in relation to changes in their chemical composition. *Australian Journal of Ecology* **30**:347-355.
- Mopper, S., J. B. Mitton, T. G. Whitham, N. S. Cobb, and K. M. Christensen. 1991. Allozyme variation and heterozygosity in pinyon pine associated with resistance to herbivory and environmental stress. *Evolution* **45**:989-999.
- Mopper, S., and T. G. Whitham. 1986. Natural bonsai of Sunset Crater. *Natural History* **95**:42-47.
- Mopper, S., T. G. Whitham, and P. W. Price. 1990. Plant phenotype and interspecific competition between insects determine sawfly performance and density. *Ecology* **71**: 2135-2144.
- Morris, R. F. 1964. The value of historical data in population research with particular reference to *Hyphantria ucu-nea* Drury. *Canadian Entomologist* **96**:356-368.
- Munster-Swendsen, M. 1984. The effect of precipitation on radial increment in Norway spruce (*Picea abies* Karst.) and on the dynamics of a lepidopteran pest insect. *Journal of Applied Ecology* **24**:563-571.
- Parkinson, J. A., and S. E. Allen. 1975. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. *Communications in Soil Science and Plant Analysis* **6**:1-11.
- Popp, M. P., H. M. Kulman, and E. H. White. 1986. The effect of nitrogen fertilization of white spruce (*Picea glauca*) on the yellow-headed spruce sawfly (*Pikonema alaskensis*). *Canadian Journal of Forest Research* **16**:832-835.
- Price, P. W., and K. M. Clancy. 1986. Multiple effects of precipitation on *Salix lasiolepis* and populations of the stem-galling sawfly, *Euura lasiolepis*. *Ecological Research* **1**:1-14.
- Redak, R. A., and R. G. Cates. 1984. Douglas-fir (*Pseudotsuga menziesii*)-spruce budworm (*Choristoneura occidentalis*) interactions: the effect of nutrition, chemical defenses, tissue phenology, and tree physical parameters on budworm success. *Oecologia* (Berlin) **62**:61-67.
- Rhoades, D. F. 1979. Evolution of plant chemical defense against herbivores. Pages 3-54 in G. A. Rosenthal and D. H. Janzen, editors. *Herbivores: their interactions with secondary plant metabolites*. Academic Press, London, England.
- . 1983. Herbivore population dynamics and plant chemistry. Pages 155-220 in R. F. Denno and M. S. McClure, editors. *Variable plants in natural and managed systems*. Academic Press, New York, New York, USA.
- Sandlan, K. 1979. Sex ratio regulation in *Coccygomimus turionella* Linnaeus (Hymenoptera: Ichneumonidae) and its ecological implications. *Ecological Entomology* **4**:365-378.
- Scriber, J. M. 1977. Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae). *Oecologia* (Berlin) **28**:269-287.
- . 1979. Effects of leaf-water supplementation upon post-ingestive nutritional indices of forb-, shrub-, vine-, and tree-feeding Lepidoptera. *Entomologia Experimentalis et Applicata* **25**:240-252.
- . 1984. Host plant suitability. Pages 159-180 in Bell and Carde, editors. *Chemical ecology of insects*. Chapman and Hall, London, England.
- Scriber, J. M., and F. Slansky, Jr. 1981. The nutritional ecology of immature insects. *Annual Review of Entomology* **26**:183-211.
- Smirnoff, W. A., and B. Bernier. 1973. Increased mortality of the Swaine jack-pine sawfly, and foliar nitrogen concentrations after urea fertilization. *Canadian Journal of Forest Research* **3**:112-121.
- Starzyk, J. R., and Z. Witkowski. 1986. Dependence of the sex ratio of cerambycid beetles (Col., Cerambycidae) on the size of their host trees. *Journal of Applied Entomology* **101**: 140-146.
- Strauss, S. Y. 1987. Direct and indirect effects of host-plant fertilization on an insect community. *Ecology* **68**:1670-1678.
- Vinson, B. S., and G. F. Iwantsch. 1980. Host suitability for insect parasitoids. *Annual Review of Entomology* **25**: 397-419.
- Wagner, M. R. 1986. Influence of moisture stress and induced resistance in ponderosa pine, *Pinus ponderosa* Dougl. ex Laws, on the pine sawfly, *Neodiprion autumnalis* Smith. *Forest Ecology and Management* **15**:43-53.
- . 1991. Sawflies and ponderosa pine: hypothetical response surfaces for pine genotype, ontogenetic stage, and stress level. Pages 21-34 in Y. N. Baranchikov, W. J. Mattson, F. Hain, and T. L. Payne, editors. *Forest insect guilds: patterns of interaction with host trees*. United States Forest Service General Technical Report NE-153.
- Wagner, M. R., and D. P. Frantz. 1990. Influence of induced water stress in ponderosa pine on pine sawflies. *Oecologia* (Berlin) **83**:452-457.
- Waring, G. L., and N. S. Cobb. 1992. The impact of plant quality on herbivore population dynamics: the case of plant stress. In E. A. Bernays, editor. *Insect-plant interactions*. CRC Press, Boca Raton, Florida, USA, *in press*.
- Waring, G. L., and P. W. Price. 1990. Plant water stress and gall formation (Cecidomyiidae: *Asphondylia* spp.) on creosote bush. *Ecological Entomology* **15**:87-95.
- Waring, R. H., and G. B. Pitman. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* **66**:889-897.
- Watt, A. D. 1986. The performance of the pine beauty moth on water-stressed lodgepole pine plants: a laboratory experiment. *Oecologia* (Berlin) **70**:578-579.
- Wellings, P. W., R. Morton, and P. J. Hart. 1986. Primary sex ratio and differential progeny survivorship in solitary haplo-diploid parasitoids. *Ecological Entomology* **11**:341-348.
- Werren, J. H. 1982. Sex ratio adaptations to local mate competition in a parasitic wasp. *Science* **208**:1157-1159.
- White, T. C. R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* **50**:905-909.
- . 1974. A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* of New Zealand. *Oecologia* (Berlin) **16**:279-301.
- . 1976. Weather, food and plagues of locusts. *Oecologia* (Berlin) **22**:119-134.
- . 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* (Berlin) **63**:90-105.
- Whitham, T. G., and S. Mopper. 1985. Chronic herbivory: impacts on architecture and sex expression of pinyon pine. *Science* **228**:1089-1091.
- Wilcox, A., and M. J. Crawley. 1988. The effects of host plant defoliation and fertilizer application on larval growth and oviposition behavior in cinnabar moth. *Oecologia* (Berlin) **76**:283-287.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.