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Increased moth herbivory associated with environmental stress of pinyon pine at local and regional levels

Abstract Using 6 years of observational and experimental data, we examined the hypothesis that water and nutrient stress increase the susceptibility of pinyon pine (*Pinus edulis*) to the stem- and cone-boring moth (*Dioryctria albovittella*). At two geographic levels, a local scale of 550 km^2 and a regional scale of 10,000 km^2, moth herbivory was strongly correlated with an edaphic stress gradient. At a local scale, from the cinder soils of Sunset Crater to nearby sandy-loam soils, nine of ten soil macro- and micronutrients, and soil water content were lowest in cinder-dominated soils. Herbivore damage was six times greater on trees growing in the most water and nutrient deficient site at Sunset Crater compared to sites with well-developed soils. Percentage silt-clay content of soil, which was highly positively correlated with soil nutrient and soil moisture at a local scale, accounted for 56% of the variation in herbivory at a regional scale among 22 sites. Within and across sites, increased stem resin flow was positively associated with reduced moth attack. On the basis of moth distribution across a stress gradient, we predicted that pinyons growing in highly stressful environments would show increased resistance to herbivores if supplemented with water and/or nutrients. We conducted a 6-year experiment at a high-stress site where individual trees received water only, fertilizer only, and water + fertilizer. Relative to control trees, stem growth and resin flow increased in all three treatments, but only significantly in the water + fertilizer treatment. Although there was no significant difference in herbivore damage among these three treatments, there was an overall reduction in herbivore damage on all treatment trees combined, compared to control trees. This experiment suggests that release from stress leads to increased resistance to insect attack and is consistent with our observational data. While other studies have predicted that short-term stress will result in herbivore outbreaks, our studies extend this prediction to chronically stressed host populations. Finally, while flush-feeders are not predicted to respond positively to stressed host plants, we found a positive association between herbivore attack and stressed pinyon populations.

Key words *Dioryctria albovittella* · Herbivory · *Pinus edulis* · Stress · Vigor

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Introduction

The effect of water and nutrient stress on plant resistance to insect herbivory has been examined extensively (see review by Waring and Cobb 1992). There are two major and somewhat contradictory hypotheses that predict how plant stress should affect herbivores. White (1969, 1974, 1976, 1984, 1993) developed a hypothesis which predicted that herbivores, especially those that feed on senescing tissue, will increase on stressed plants. White reasoned that senescing tissues will be higher in soluble nitrogen, which will have a positive effect on the survival of young herbivores. Others have proposed additional mechanisms to account for increased susceptibility of stressed plants to herbivores, including reductions in defensive secondary compounds (Rhoades 1979, 1983, 1985), increased plant temperature, and reduced water content (Mattson and Haack 1987a,b). To avoid confusion among these different mechanisms we follow Price (1991) in referring to the "plant stress hypothesis" as the prediction that herbivore performance increases on stressed host plants, regardless of the mechanism.

The "vigor hypothesis" predicts that herbivores will prefer either the most vigorous host populations, the most vigorous plants within a population, and/or the most vigorously growing parts within a plant (Price et al. 1987a,b, 1990; Price 1991). The "vigor hypothesis" does not invoke any one mechanism to account for the positive rela-

tionship between increased herbivore performance and plant vigor, but recognizes a number of possible factors (e.g., increased resources, higher food quality, lack of induced defensive compounds) (Price 1991). Price (1991) noted that these two hypotheses are not mutually exclusive; herbivores may perform better on stressed plants or populations, but within an individual plant, they may still prefer to feed on the most vigorously growing plant tissues. These two hypotheses are also similar in that White (1993) predicts that herbivores feeding on senescent plant parts (i.e., senescence-feeders) are the most likely to respond positively to plant stress because during senescence, nitrogen is broken down into forms more nutritious for young herbivores. Herbivores that feed on growing plant parts (i.e., flush-feeders) are more likely to attack vigorous plants (Price 1991; White, 1993).

Waring and Cobb (1992) reviewed the results of over 450 studies that examined how herbivores respond to plant stress and found that observational and experimental studies generally showed opposite patterns. Many observational studies on water stress support White's prediction that herbivores perform significantly better (i.e., increased growth rate, fecundity, survival, and population density) on water-stressed plants. In contrast, experimental studies on water stress, and observational and experimental studies on nutrient stress, support the vigor hypothesis (Service 1984; Price et al. 1990; references in Waring and Cobb 1992). There are also cases where both hypotheses are supported. For the galling fly, *Aciurina trixa*, even though performance was greater on stressed rabbitbrush, *Chrysothamnus nauseosus*, females preferentially oviposited on more vigorously growing stems within a plant (Fernandes 1992). Similarly, while outbreaks of the pinyon sawfly (*Neodiprion edulicolis*) occur in highly stressed pinyon populations (Cobb 1993), within a population, sawflies have greater fecundity when grown on the least stressed pinyons (Mopper and Whitham 1992).

It is difficult to determine why contradictory patterns exist between experimental and observational studies because few studies have collected both types of data for the same system (Waring and Cobb 1992). Based upon both experimental and observational data, three different studies support the vigor hypothesis: *Pemphigus betae* on *Chenopodium album* (Moran and Whitham 1988); *Euura lasiolepis* on *Salix lasiolepis* (Price and Clancy 1986; Preszler and Price 1988; Waring and Price 1988); *Daktulopsphaira vitifolia* on *Vitis arizonica* (Kimberling et al. 1990). All showed increased performance on more vigorously growing plants in the field and in water supplementation experiments. On the basis of both observational and experimental data, only two studies support the "plant stress hypothesis": *N. sertifer* on *Pinus sylvestris* (Larsson and Tenow 1984; but see Bjorkman et al. 1991), and *A. trixa* on *C. nauseosus* (Fernandes 1992). Two other studies have not found agreement between observational and experimental data: a leaf miner (*Cameraria* sp.) on *Quercus emoryi* (Bultman and Faeth 1987), and spruce budworm (*Choristoneura fumiferana*) on several host plants. With spruce budworm, observational data supported the "plant stress hypothesis" (Shepard 1959;

Kemp and Moody 1984; Thomson et al. 1984; Hix et al. 1987), but experimental data showed no differences (Mattson et al. 1983).

Due to these discrepancies, we conducted both observational and experimental studies to determine the effect of plant stress on herbivory by the stem- and cone-boring moth, *Dioryctria albovittella*. We asked the following questions: (1) In northern Arizona, does an edaphic stress gradient exist for pinyon pines growing in recently derived volcanic soils and older soils derived from limestone and sandstone? (2) Do herbivores track host plants along this edaphic stress gradient at both a local and regional level? (3) Can we experimentally alleviate host plant stress and reduce herbivory?

Materials and methods

Observational tests of the "plant stress hypothesis"

Soil characteristics

We initially selected six sites that appeared to represent three levels of herbivory and three distinct soil types. We measured soil nutrient and moisture levels to determine if these sites also represented three levels of edaphic stress (i.e., reduced soil moisture and nutrients). All sites were located within 60 km of Flagstaff, Ariz.

We collected five soil samples per site in late September 1987 to examine soil chemistry and soil particle size composition. Sample locations were selected along a transect at approximately 10-m intervals. The sampling was stratified in that we only sampled in the open to avoid litter effects from individual plants (see Mopper et al., 1991b for analysis of soils sampled under canopies). Each sample contained approximately 200 cm^3 of soil collected 10–15 cm below the soil surface, where fine roots were most abundant. Using standard soil sieves, soil particles were categorized into four size groups, less than 0.0625 mm, between 0.0625 and 1 mm, between 1 and 2 mm, and greater than 2 mm in diameter. For this data set and all other statistical tests, percentage data were arcsine transformed to reduce variance (Zar 1984), although raw means and standard errors (Ses) are presented in graphs and tables. Levels of ten soil micro- and macronutrients in soil samples were determined at I.A.S. Laboratories, Phoenix, Ariz. Sites within a soil type were grouped for these statistical analyses because we were interested solely in differences in soil type and constrained by the expense of the nutrient analyses. To test for differences among the soil types with regard to both particle sizes and nutrients, we performed separate MANOVAs followed by individual ANOVAs for each variable using the SAS GLM procedure (SAS Institute 1990). Overall significance of individual variables was determined on the basis of the sequential Bonferroni adjustment (Rice 1989). We classified soil types on their composition of four classes of particle size (Donahue et al. 1983).

To quantify soil water content, we collected ten soil samples per site at three sites that were a subset of the sites initially selected. Following the same method used in obtaining soil nutrient samples, samples for soil moisture analysis were collected on 7 June 1988, near the end of the dry season. Percentage soil water was gravimetrically determined and differences among sites were analyzed by an ANOVA followed by a Tukey LSD test to compare individual means using BMDP 7D (BMDP Statistical Software 1992).

Resin production

Although other studies have provided evidence that pinyons respond to edaphic stress (Christensen and Whitham 1991; Mopper et al. 1991b; Gehring and Whitham 1994, 1995), here we examined the production of plant resin as another response variable. Additionally, resin flow in pinyon pine has previously been implicated as a resistance mechanism against moth herbivory, resistant

trees producing more resin than susceptible trees (Mopper et al. 1991b). If resin flow is an important determinant of pinyon resistance to herbivory, levels of resin flow should exhibit two patterns. First, in a comparison of trees growing side by side in the same substrate, trees resistant to moth attack should produce more resin than trees susceptible to moths. Second, resin production should decline along a gradient from sandy-loam (low stress) to loamy-sand (intermediate stress) and cinder soil (high stress). To test these predictions, we measured the flow of stem resin (i.e., oleoresin) from trees growing in three soil types. Fifteen trees were randomly selected from a loamy-sand site, 15 from a sandy-loam site, and 30 growing in cinder soils. Of this latter group, 15 trees suffered high levels of damage by moths and 15 trees suffered little or no damage. Because the mortality of moth larvae on uninfested trees is 70%, while only 39% on infested trees (T.G. Whitham, unpublished data), we designated these trees as susceptible and resistant, respectively.

To measure stem resin flow, we cut three healthy terminal stems per tree, at 120° intervals around the mid-height of the tree canopy. Stems were cut just below the growth of the current year and the resin that had accumulated after 5 min was collected. We weighed the resin within 6 h of collection and tabulated a mean for each tree. All resin flow samples were collected in the morning, within a 3-day span in June 1989, when moth larvae were feeding. To assess differences in stem resin flow among soil types we performed an ANOVA followed by a Tukey LSD test to compare individual means using BMDP 7D (BMDP Statistical Software 1992).

Herbivore distribution

Two levels of comparisons were made, at a local scale where different soil types existed in relatively close proximity, and at a regional scale. At the local level, which encompassed a total area of 550 km², we compared moth herbivory on trees growing in three soil types (two sites per type) based on 30 trees at each of six sites. We selected the first 30 mature trees encountered that were taller than 3 m. In 1986, we cut one 50-cm-long branch per tree and counted the percentage of all stems killed by moth larvae (old damage as well as current-year damage). The actual collection of branches was conducted by someone naive to the purpose of the project. To test whether there was differential herbivory among soil types we performed a nested ANOVA using the SAS nested procedure (SAS Institute 1990), followed by contrast comparisons among soil types. In this analysis, sites within a soil type were nested within soil types because sample sizes were large enough to test for site effects.

At a broader geographical scale, we selected 22 additional sites in northern Arizona that covered approximately 10,000 km² and crossed a wide range of soil conditions. We collected two soil samples per site using the same methods for examining of soils at the local level, except that the two samples were mixed together and we only measured percentage silt-clay content. Our analysis of soils from a local scale showed that percentage silt-clay (<0.0626 mm diameter) was positively correlated with nutrient levels ($R^2 = 0.94$). We therefore chose percentage silt-clay content as an easily measured variable which would reflect environmental stress and serve as a predictor of herbivore abundance over a broader geographical level. Herbivore damage (percentage stems killed) was determined as described above. Linear regression using the SAS REG procedure (SAS Institute 1990) was performed with percentage stems killed as the dependent variable and percentage silt-clay content as the predictor. Because the dependent variable was percentage data, we performed an arcsine-square root transformation (Zar 1984) prior to the analysis. We then transformed predicted values from this analysis back to raw values to develop a curve plotted with original raw values.

Experimental manipulation of environmental stress

In 1985, we selected 44 trees with high herbivore loads at a cinder site, and randomly assigned individual trees to one of four treat-ments: control, watered, fertilized, and watered + fertilized. To control for potential size and age effects, we stratified our sample by selecting trees that were approximately 60 years old. For all trees, including controls, we dug a shallow trench around the dripline of the tree canopy and filled it with pinyon pine duff from adjacent trees to act as a mulch to retain water. We applied water to the trench and the base of the tree. Trees were watered approximately every 5th day during the dry season, from mid-April to early July. Trees received water in proportion to trunk diameter. Watered + fertilized trees received an average of 40 (± 3.65 SE) l/tree and watered-only trees received an average of 39 (± 4.1 SE) l/tree. This amount of water allowed the soil to be fully saturated down to the root level, comparable to what we observed after rains. In the first year, we applied a water-soluble fertilizer (19% nitrogen, 8% phosphorus, and 10% potassium) once in May at the rate of 340 g/2.54 cm of trunk diameter. To avoid potential problems with supplemental water used in water-soluble fertilizer, from 1986 to 1989, we applied a dry fertilizer (10:10:10 NPK) at a rate of 100 g/m² under the canopy of each tree once each year in April.

Plant responses to watering and/or fertilization that we measured included stem resin flow, stem growth rates (i.e., centimeters of stem elongation per year), and percentage stems killed by moth larvae. Resin (oleoresin) flow was determined in 1989 by the method described above for among-site sampling. We quantified stem growth by measuring total stem elongation between 1986 and 1990 (i.e., bud scale scars that form each year allowed us to measure 5 years of growth). Stem growth was measured on eight randomly selected terminal stems per tree so that all parts of the canopy were sampled. Herbivore damage on treatment and control trees were estimated annually by counting the percentage of current-year stems killed by moth larvae on eight small branches per tree. Branches were selected in the same manner as for stem growth. We initially performed individual ANOVAs using BMDP 7D (BMDP Statistical Software 1992) to determine if treatment groups differed in response variables. Because we did not find significant differences among treatment groups with regard to herbivory, data for all treatments were pooled. Due to our small sample sizes in this analysis, the possibility for a type II error was high, so we also conducted an analysis using Sigma-Stat to determine the sample size needed to detect a significant difference among the three treatment groups. We performed a repeated-measures ANOVA using BMDP 7D (BMDP Statistical Software 1992) to test for differences in herbivore damage between control and treatment groups, and to determine the effects of time and treatment on herbivory. In the first year of the experiment before treatment groups received water and/or fertilizer, there were no significant differences in moth damage between treatment and control plants ($t = 1.20$, $P = 0.25$).

Results

Observational Test of the "plant stress hypothesis"

Soil characteristics

One of the most obvious differences among sites was in the composition of soil particle sizes (Fig. 1). Based on the composition of particle sizes, we resolved three soil textural classes: cinder, loamy-sand, and sandy-loam (Donahue et al. 1983). Results from a MANOVA showed significant differences among soil types ($F_{6,50} = 29.62$, $P<0.0001$, Wilks' lambda = 0.0482). Individual ANOVAs (Fig. 1) demonstrated that the differences among sites were due to the relative proportion of the cinder fraction (particles >2 mm diameter) and the silt-clay fraction (particles <0.0625 mm diameter). Sandy-loam sites had the highest percentage of silt-clay [mean = 42.9 ± 3.16% (SE)] and the lowest percentage

PARTICLE SIZE COMPOSITION
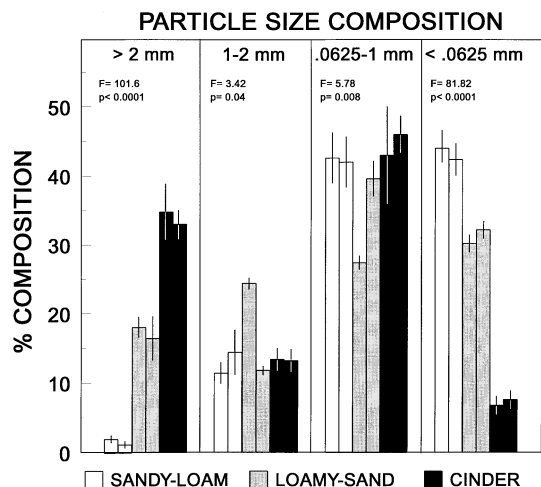
Fig. 1 Percentages of four particle size classes (means ± 1 SE) of soils from six sites (*n* = 5/site), show that cinder soils are much coarser than other soil types. Three soil types are represented: sandy-loam (low stress), loamy-sand (intermediate stress), and cinder (high stress). All *P* values are significant at table-wide *P*<0.05, based on sequential Bonferonni adjustment

Fig. 2 Percentages of soil nutrients (means ± 1 SE) in soils from six sites (*n* = 5/site) show that cinder soils are nutrient poor relative to loamy soils. Three soil types are represented: sandy-loam (low stress), loamy-sand (intermediate stress), and cinder (high stress). All *P* values are significant at table-wide *P*<0.05, based on sequential Bonferonni adjustment

cinders (mean = 5.1 ± 0.09%). In contrast, the silt-clay fraction of cinder soils was 6.5 times less than that of sandy-loam soils, and the cinder fraction was 30 times higher than in sandy-loam soils (Fig. 1). In loamy-sand soils, levels of silt-clay and cinder were intermediate between cinder and sandy-loam soils.

Nutrient levels were significantly different among the three soil types and generally lowest in cinder soils. When we examined all nutrients simultaneously in a MANOVA, we found significant differences ($F_{20,36}$ = 33.15, *P*<0.0001, Wilks' lambda = 0.0026). For all soil nutrients except sulfur, sandy-loam soils exhibited the highest values, cinder soils were lowest, and loamy-sand soils were intermediate (Fig. 2). Percentage soil water content mirrored the pattern of soil nutrients; the highest levels were found in sandy-loam soils, they were intermediate in loamy-sand, and lowest in cinder soils (Fig. 3).

Resin production

Resin flow in pinyon pine has previously been implicated as a resistance mechanism against moth herbivory, resistant trees producing more resin than susceptible trees (Mopper et al. 1991b). Consistent with these earlier findings, we found that for trees growing in cinder soils resin flow was almost threefold higher in moth-resistant than in moth-susceptible trees. Thus, within the cinder soil type, resin flow corresponds to the degree of susceptibility to moth attack (Fig. 4).

SOIL MOISTURE
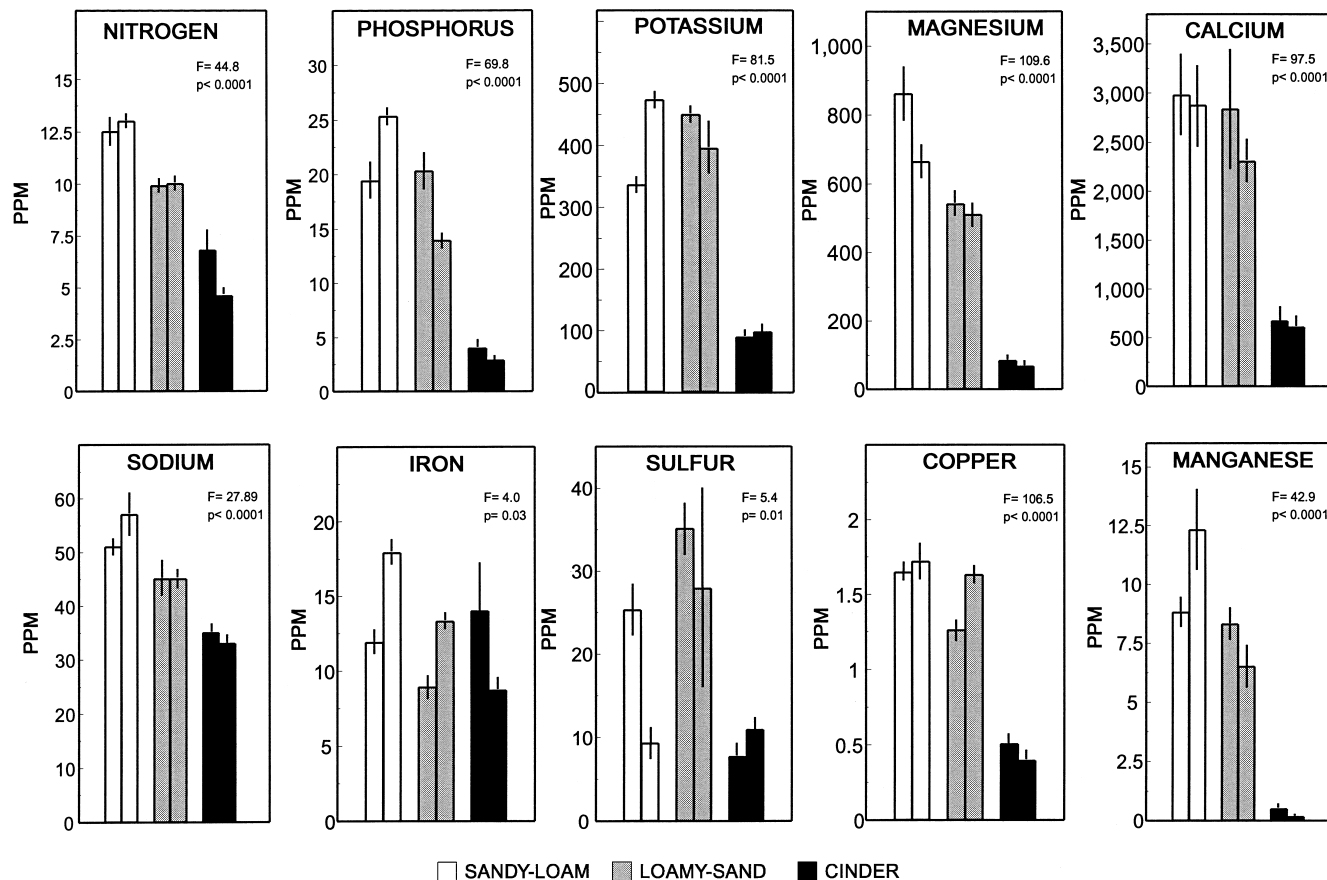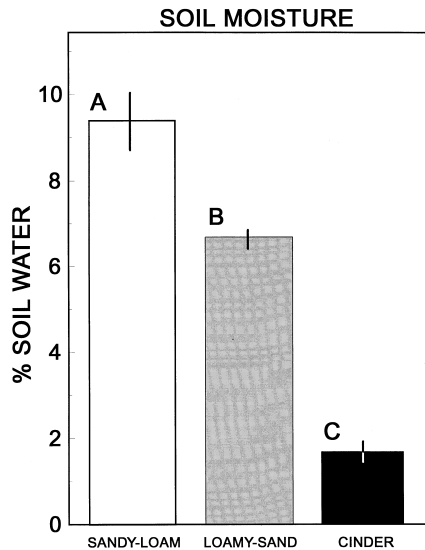
Fig. 3 Percentage soil water (means ± 1 SE) in soil from six sites (*n* = 10/site) shows that soil water was lowest in cinder soils. Three soil types are represented: sandy-loam (low stress), loamy-sand (intermediate stress), and cinder (high stress). Different *letters above the bars* represent significant differences between soil types at *P*<0.05

RESIN PRODUCTION
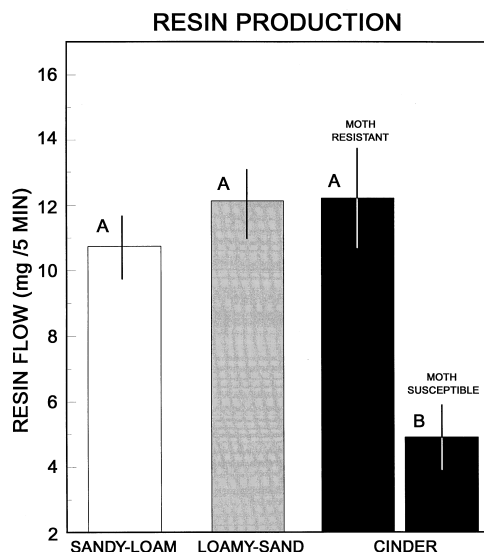
Fig. 4 Stem resin flow (means ± 1 SE) from trees at a low-stress, intermediate-stress, and a high-stress site (*n* = 15/site). Trees at the high-stress site represent moth-resistant and moth-susceptible trees. Different *letters above the bars* represent significant differences between groups at *P*<0.05

A similar pattern emerged in resin production among sites. Trees growing in all soil types produced similar levels of resin, except moth-susceptible trees growing in cinder soils, which produced only 30% of the resin typically produced by all other tree categories (Fig. 4). This indicates that trees growing in cinder soils are less able to produce resin. However, conclusions from the among-site comparison should be regarded with some caution, because we did not obtain a random sample of resin production by trees growing on cinder soils. However, be-

MOTH HERBIVORY (LOCALIZED)
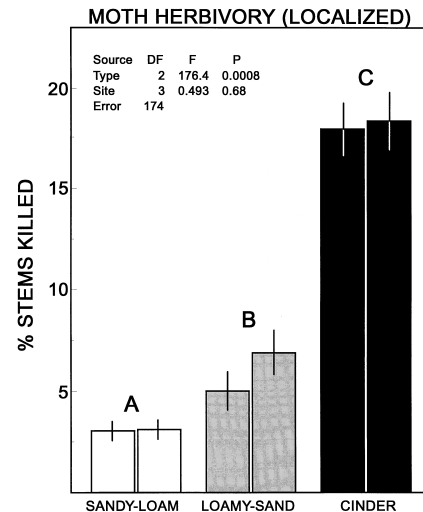
Fig. 5 Percentage of stems killed by moth larvae (means ± 1 SE) shows that damage caused by moths is highest on trees growing in cinder soils. Data from six sites representing the three soil types that cover a 550-km² area are presented. *Adjacent bars* denote individual sites within a soil type. Different *letters above the bars* represent significant differences between soil types at *P*< 0.05. Statistics from nested ANOVA are presented in the upper-left-hand corner

cause approximately 70% of the trees at Sunset Crater are susceptible to moths and suffer chronic, high levels of insect attack (T.G. Whitham and N.S. Cobb, unpublished data), moth-susceptible trees are likely to be representative of the population.

Herbivore distribution

At a local level where different soil types are relatively close (i.e., covering approximately 550 km²), herbivore damage on trees from cinder sites was six times higher than in sandy-loam sites, and three times higher than on trees from loamy-sand sites (Fig. 5). In contrast, herbivory was comparable between sites within each soil type, suggesting that variation in herbivore susceptibility between sites within a soil type is low. Consistent with the prediction from the "plant stress hypothesis", these results suggest that moths track host plants along a stress gradient and select stressed populations.

Over a broader geographical area covering approximately 10,000 km², we found a similar distribution of moth damage associated with pinyons growing in water- and nutrient-poor soils. We used the silt-clay fraction to predict herbivore damage because it was the most highly correlated with all the nutrient variables; i.e., 94% of the variation in the silt-clay content was explained by nutrient concentrations in a multiple regression analysis (*R²* = 0.941, *P*<0.0001). We found that herbivore damage across 22 sites was significantly correlated with the silt-clay fraction (Fig. 6). This relationship was not linear; the degree to which trees were attacked decreased exponentially as the silt-clay content of the soil increased. This suggests a threshold effect in which herbivory rises

MOTH HERBIVORY (REGIONAL)
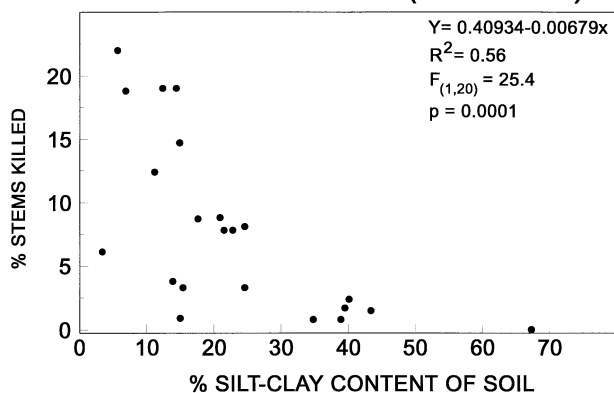
Fig. 6 The negative relationship between mean percentage stems killed by moth larvae and mean percentage silt-clay fraction found at 22 sites. Sites were located in an area covering 10,000 km². Silt-clay fraction was the best overall predictor of soil nutrient levels. Regression statistics based on arcsine-square root transformation (Zar 1984)
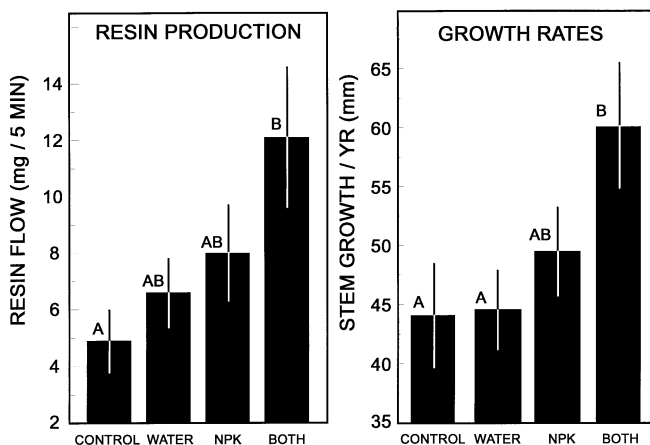
Fig. 7 Stem resin flow and growth rate (means ± 1 SE) on control, water-only, fertilizer-only, and water + fertilizer groups. Different *letters above the bars* represent significant differences between groups at $P<0.05$

sharply once the silt-clay fraction of the soil falls below 30%.

Experimental manipulation of water and nutrient stress

If water and nutrient stress result in increased herbivory via a decrease in plant defenses as our observations suggest, the experimental addition of water and nutrients to susceptible trees should make them more resistant. The results of a 6-year experiment largely agree with field observations and support predictions from the "plant stress hypothesis."

Plant performance

There was an overall increase in growth rate and resin flow in response to watering and/or fertilization (Wilks'

Table 1 Moth damage [mean % stems killed (±1 SE) for four treatments from 1986 to 1990

Year	Control	Water	Fertilizer	Water and Fertilizer
1986	20.37 (2.47)	15.34 (3.92)	22.20 (2.20)	17.74 (1.99)
1987	33.02 (4.20)	21.60 (3.42)	23.00 (3.93)	20.45 (2.78)
1988	29.63 (5.48)	25.10 (5.38)	21.58 (4.66)	24.90 (3.51)
1989	20.16 (3.59)	12.07 (1.97)	17.56 (4.06)	14.5 (2.03)
1990	12.52 (2.86)	5.07 (1.11)	11.57 (3.68)	6.98 (1.35)

lambda = 0.692, $F_{6,64}$ = 2.15, P = 0.05). However, only watered + fertilized plants showed a significant increase in both growth and resin production relative to controls (Fig. 7).

Herbivore response among treatments

Consistent with the general lack of significant differences in plant growth and resin responses among the three treatments (water only, fertilizer only, or water + fertilizer), we also found no significant differences in herbivore damage among the three treatments ($F_{2,27}$ = 0.37, P = 0.69; Table 1). For the subsequent comparison of moth damage, we pooled data from the three treatments to compare them with control trees. A power analysis indicated that the minimal sample required to detect a significant difference among the three groups would be 47 trees/group (power = 0.4, α = 0.05). This is a relatively large sample size to detect a significant difference with low power, and therefore we believe we are justified in pooling the treatment groups.

Herbivore response in pooled treatments versus the control

In agreement with observational data that herbivory is greatest on stressed plants, when we experimentally reduced water and nutrient stress, herbivory significantly declined relative to control plants (i.e., an average of 9% less herbivory per year). While a repeated-measures analysis of variance showed a significant treatment effect (P = 0.050), a much stronger year-to-year effect was also detected ($P<0.001$). There was no significant interaction term between time and treatment type (P = 0.62), indicating that among-year variation in moth attack between treatment and control trees was comparable.

Discussion

Observational confirmation of the "plant stress hypothesis"

Several lines of observational data support the "plant stress hypothesis," which predicts increased herbivore performance on stressed plants (White 1969, 1974, 1976, 1984, 1993; Mattson and Haack 1987a,b).

Soil characteristics

At adjacent sites, we demonstrated that a stress gradient exists where volcanic-derived cinder soils have the lowest macro- and micronutrients, and soil moisture (Figs. 2, 3). These findings complement the nitrogen mineralization studies of Gehring and Whitham (1994), who found that nearly all of the nitrogen made available through decomposition was immobilized by decomposers in the cinder soils, while noncinder soils showed a net gain. These results also agree with ammonium and nitrate concentrations under tree canopies, where sandy-loam soils exhibited over threefold higher levels than cinder soils (Mopper et al. 1991b).

Resin production

We found that trees responded to increased stress with reduced plant resin production (Fig. 4), which was also consistent with moth damage (Fig. 5) for cinder and sandy-loam sites. However, while there was no difference in resin production by trees growing in sandy-loam and loamy-sand sites, they still differed in moth herbivory. This suggests that resin flow alone does not fully account for differences in resistance to moth larvae. It may also reflect a susceptibility threshold, with herbivores only responding dramatically to greatly reduced resin levels (Fig. 5).

In contrast to our among-site findings in resin flow, Mopper et al. (1991b) found lower resin levels in trees at a sandy-loam site compared to resistant and susceptible trees at a cinder site. However, the resin measurements taken by Mopper et al. (1991b) were obtained after moth larvae had already completed feeding. Because resin flow can vary fivefold within a season (Blanche et al. 1992), we feel that our measurements taken during the time of feeding better represent what moth larvae experience. Because our studies also indicate that there is considerable annual variation in resin production, the discrepancy between our data and those of Mopper et al. (1991b) may further reflect that variation.

Our resin production results are consistent with other studies that have measured plant performance in this system. Trees in the cinder soils exhibited reduced growth rates (Gehring and Whitham 1994), reduced cone production (Christensen and Whitham 1991), and decreased xylem water potentials (Mopper et al. 1991b) relative to pinyons growing in sandy-loam soils. Furthermore, Gehring and Whitham (1994) found higher levels of ectomycorrhiza on *Pinus edulis* growing in cinder soils compared to sandy-loam soils, which is consistent with the hypothesis that plants living in nutrient-poor environments invest more in mycorrhizal mutualists than those living in nutrient-rich environments (Meyer 1973). Taken together, these diverse data argue that pinyons respond to differences in edaphic stress between sandy-loam and cinder soils.

Herbivore distribution

We also show that moths respond positively to pinyons growing in water- and nutrient-poor soils both at a local (Fig. 5) and regional (Fig. 6) level, indicating a positive relationship between edaphic stress and pinyon susceptibility to moth herbivory. These results agree with most observational studies that have tested the importance of drought and chronic stress in affecting insect outbreaks (Waring and Cobb 1992), and are consistent with the other studies of this specific system (Christensen and Whitham 1991; Mopper and Whitham 1992; Cobb 1993). Infestation of pinyon by *D. albovittella* has important implications for plant performance, because feeding by moth larvae dramatically reduces tree growth, and cone production, and alters canopy architecture (Whitham and Mopper 1985; Mopper et al. 1991a).

Experimental release of water and nutrient stress in susceptible trees

In general, the results of the 6-year watering and fertilizer experiment support the "plant stress hypothesis." First, trees responded positively to the addition of water and fertilizer. Plant foliar nitrogen levels (Mopper and Whitham 1992), plant growth, and plant resin flow all increased in response to these supplements (Fig. 7).

Second, moth herbivory significantly decreased in response to watering and fertilization, although there was no difference among treatment groups in moth herbivory even though water + fertilizer produced the greatest overall increase in plant performance. We also found a much stronger year-to-year than treatment effect on moth damage. This suggests that factors other than water and nutrient availability had a significant impact on moth damage, and may include direct effects of annual weather variation on moth survivorship (Mattson and Haack 1987a,b) or annual variation in moth predation and/or parasitism. However, parasitism of larval *D. albovittella* is very low and not likely to be important in this system (O. Sholes, personal communication).

While our water and fertilization supplementations of susceptible trees growing in cinder soils succeeded in reducing moth damage, they did not reduce damage to levels observed on resistant trees or trees growing in sandy-loam soils, where the percentage of stems killed is typically less than 5%. This may have been an artifact of our experimental protocol. First, we did not allow these trees to recover from chronic herbivory before the experiment began, which may have affected their ability to respond to the treatments. Second, we only watered a small portion of the root system, covering the drip zone under the canopy. Third, determining the rate and form of fertilizer that will replicate natural situations is inherently problematic (Hargrove et al. 1984). Carrow and Betts (1973) found opposite effects of fertilizer on herbivory depending on the form of the nitrogenous fertilizer applied. Washburn et al. (1987) using six different fertilizer re-

gimes found significant differences in the performance of two scale species feeding on ice-plants (*Carpobrotus* spp.). Given the constraints of the experimental design, we feel it is impressive that we found a significant, albeit small, reduction in herbivory.

Why does a flush-feeder respond positively to plant stress?

Both White (1993) and Price (1991) predict that flush-feeders, herbivores that feed on growing plant tissues, are unlikely to respond positively to plant stress. This is because growing plant tissues are typically smaller when stressed, thus providing less resources for flush-feeders. Increased soluble nitrogen resulting from plant stress is probably not as important to flush-feeders as it is to senescence-feeders because new growth already contains levels of soluble nitrogen above the minimum requirements for herbivores (T.C.R. White, personal communication). *D. albovittella*, however, is a flush-feeder that bores out newly emerging terminal stems and exhibits the opposite pattern predicted by both White (1993) and Price (1991). We suggest an alternative to increased soluble nitrogen that may account for this pattern. Reduced resin production resulting from plant stress may be more important than nitrogen in mediating moth-pinyon interactions. This is supported by several lines of evidence. First, moth-resistant trees growing in cinder soils and trees growing in less stressful sandy-loam soils produce three times more stem resin than moth-susceptible trees growing in cinder soils (Fig. 4). Second, larval mortality is significantly greater on resistant than on susceptible trees (Whitham et al., unpublished data). Third, moth larvae exhibit specialized behavior to avoid resin. From the time moth larvae begin feeding, they always maintain a drainage hole in the stem so that resin drains from the feeding site. Thus, reduced resin defenses in susceptible pinyons may partially explain why this flush-feeder positively responds to host populations growing in stressful environments. Also, under conditions of stress, pinyons may invest proportionately more into growth and less into resin defenses making them highly susceptible to moth attack. Therefore, plant defensive compounds and not the nutritional quality of elongating shoots could be the critical factor determining moth attack as well as infestation levels of other insects (Rhoades 1979, 1983, 1985; Cates et al. 1983). However, we have not examined soluble nitrogen in pinyons across this stress gradient and we cannot rule out the potential role of increased soluble nitrogen in promoting moth outbreaks. Further experiments are needed to determine the relative roles of nitrogen and defensive compounds (e.g., resin production) in determining susceptibility of pinyon to *D. albovittella*.

In conclusion, this is one of the few studies to document a consistent pattern between experimental and observational results in support of the "plant stress hypothesis" (Waring and Cobb 1992) and show consistent geographic patterns at both local and regional scales. Additionally, although the "plant stress hypothesis" was developed to explain herbivore responses to short-term plant stress that encompasses one to a few seasons, we have also shown that chronic plant stress can produce a similar response from herbivores (Stoszek et al. 1981; Kemp and Moody 1984; Hix et al. 1987). Because these patterns have been observed since 1982, chronic stress and moth herbivory have now been associated for 14 years (Whitham and Mopper 1985). We have observed similar patterns for other parasites and herbivores that attack the dominant trees growing in the cinder soils of Sunset Crater [i.e., the mistletoe on juniper (Gehring and Whitham 1992); sap-feeding scales on pinyon (Cobb and Whitham 1996); needle-feeding sawflies on pinyon (N.S. Cobb and Whitham, unpublished data); hymenopteran seed parasites on ponderosa pine (T.G. Whitham, unpublished data)]. Thus our observations with moths appear to represent a general pattern. Because these interactions cross diverse taxa with different modes of feeding and phenologies, multiple mechanisms could be involved. In exploring these differences, future studies need to concentrate on the unifying mechanisms which may be common to these interactions.

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