

# Relative Importance of Environmental Stress and Herbivory in Reducing Litter Fall in a Semiarid Woodland

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## ABSTRACT

We examined the impact of soil stress (low water and nutrient availabilities) and two keystone insect herbivores on pinyon pine (*Pinus edulis*) needle litterfall. We compared trees growing on two distinct soil types: volcanic cinders, which exhibit pronounced water and nutrient limitation, and sandy-loam soils, which have higher water-storage capacity and nutrient availability. Using two long-term herbivore removal experiments (15 and 18 years, respectively), we also examined the effects of the pinyon needle scale (*Matsucoccus acalyptus*, which attacks juvenile trees) and the stem-boring moth (*Dioryctria albobittella*, which attacks mature trees) on pinyon litterfall. These herbivores reach high densities on cinder soils but are absent or occur at much lower levels on sandy-loam soils. Four years of litterfall measurements showed four major patterns. First, independent of herbivory, needle litterfall was 20% lower under trees on high-stress cinder soils than on sandy-loam soils. Second, in agreement with the negative impact of scales on tree growth (that is, a 30% decline in stem growth), trees with scale infestations had 25% lower litterfall rates than trees resistant to scale;

however, 15 years of scale-insect removal did not significantly increase needle litterfall. This implies possible intrinsic differences in litter production between scale-resistant and scale-susceptible trees. Third, in contrast with significant negative effects of moth herbivory on tree growth (that is, a 27% decline in stem growth), moth herbivory had no effect on needle litterfall. This, along with increased stem density in moth-susceptible trees, may be evidence of compensatory production. Fourth, there were strong year by soil type and year by scale herbivory interactions, such that in some years the effect on litterfall can be obscured or reversed by some other factor. In summary, soil stress has a strong and predictable effect on needle litterfall, whereas the relationship between insect herbivory and needle litterfall is weaker and depends on the individual herbivore. These effects, however, are mediated by other environmental factors that have considerable annual variation.

**Key words:** litterfall; pinyon pine; soil stress; herbivory; productivity; compensation; *Pinus edulis*; *Matsucoccus acalyptus*; *Dioryctria albobittella*.

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## INTRODUCTION

Litterfall is an important determinant of forest nutrient cycling. Nutrients in litterfall are made

available for uptake by plants through the processes of decomposition and nutrient mineralization, and the rates of nutrient release from organic materials may regulate the rate of forest growth (Attiwill and Adams 1993). In many temperate ecosystems, higher litterfall rates lead to greater amounts of litter present on the forest floor and increased rates of nutrient mineralization (Knutson 1997). Observations and experiments show that (a) litterfall is generally greater on more fertile soils (Boerner 1984; Madiera and others 1995; Vitousek and others 1995); (b) litterfall on more fertile soils has a higher concentration of nutrients than on less fertile soils (Madiera and others 1995; Vitousek and others 1995); (c) litterfall with higher concentration of nutrients decomposes faster than litter with lower nutrient concentration (Boerner 1984); and (d) nutrient release to the soil is higher in more fertile soils (Boerner 1984; Madiera and others 1995; Herbohn and Congdon 1998; Kavvadias and others 2001). Thus, more fertile soils tend to have higher litterfall rates and accelerated nutrient cycling.

In pinyon pine (*Pinus edulis*), soil stress (that is, low water and nutrient availability relative to plant demand) and chronic insect herbivory both adversely affect tree growth and reproduction (Whitham and Mopper 1985; DelVecchio and others 1993; Gehring and Whitham 1995; Cobb and others 1997, 2002; Trotter and others 2002). At Sunset Crater National Monument in Arizona, a 200-year long series of volcanic eruptions ending in about 1240 AD denuded 2000 km<sup>2</sup> of the surrounding landscape (Krutch 1974) and produced deep cinder fields that are coarse textured. These cinder soils have lower water content than nearby sandy-loam soils despite receiving similar amounts of rainfall (Mopper and others 1991b; Cobb and others 1997; Swaty and others 1998). They also have significantly lower levels of macronutrients and micronutrients (Cobb and others 1997) and lower rates of net nitrogen (N) mineralization (Gehring and Whitham 1994). Pinyons growing in cinders have a higher incidence of mutualistic mycorrhizae than those growing in sandy-loam soils (Gehring and Whitham 1994; Swaty and others 1998), which is consistent with the hypothesis that plants growing in water and nutrient poor environments invest more in mutualists.

Pinyons growing in cinder soils also suffer from higher infestations of two major insect herbivores (Mopper and others 1991a; Cobb and others 1997), a pattern consistent with the *plant stress hypothesis* (White 1993). The pinyon needle scale (*Matsucoccus acalyptus*, Margarodidae) feeds primarily on juvenile trees that have not reached the age of repro-

duction or produce just male strobili (pinyons are monocious, and older trees produce both male and female structures). The scale is a sessile insect that begins feeding on needle mesophyll prior to the emergence of the current year's needles, causing chlorosis and early senescence (DelVecchio and others 1993; Cobb and Whitham 1998). Scale-susceptible trees are chronically attacked, supporting millions of scale insects while maintaining only 2 years of needle cohorts. In contrast, scale-resistant trees support few or no scales and retain up to 7 years of needle cohorts. When scales are experimentally transferred to resistant trees, only 20% of the scale insects survive, whereas 70% survive when transferred to susceptible trees with scales or susceptible trees that have had scales removed for 8 years and appear to have recovered fully (Cobb and Whitham 1993). Chronic herbivory decreases stem biomass by fourfold, standing needle biomass by sixfold, female cone production by 10- to 29-fold, and male strobili production by tenfold (N. S. Cobb and others unpublished data).

In contrast to scales that attack juvenile trees, the stem-boring moth (*Dioryctria albovittella*, Pyralidae) feeds mainly on older, reproductively mature trees that produce both male strobili and female cones. Moths oviposit eggs on stem buds, and the feeding larvae bore through the stems and kill them. This results in a more compact, shrubby architecture rather than the upright growth of resistant trees (Whitham and Mopper 1985). Relative to moth-resistant trees, susceptible trees suffer a 30% loss of their mycorrhizal mutualists (Gehring and Whitham 1995). Cone production is often eliminated in moth-susceptible trees (Cobb and others 2002), and the seed-dispersing pinyon jays, scrub jays, and Clark's nutcrackers abandon sites of high susceptibility because foraging is unprofitable (Christensen and Whitham 1991, 1993). The negative impacts of moths and scales on susceptible pinyons also affect other community members, such as sawflies (Mopper and others 1990) and mycorrhizal mutualists (DelVecchio and others 1993; Gehring and Whitham 1994, 1995; Gehring and others 1997). These two insects have such a disproportionate impact on individual tree performance and the pinyon ecosystem that they are appropriately viewed as keystone herbivores [for example, see Hunter (1992)].

Given these abiotic and biotic stresses to pinyon, we made the following two predictions. First, we predicted that needle litterfall would be lower on high-stress cinder soils than on nearby lower-stress sandy-loam soils. Second, we predicted that reduced litterfall on cinders would be compounded by insect herbivory, such that scale-susceptible and

moth-susceptible trees would have lower needle litterfall than herbivore resistant trees. Our study is unique in that it includes both observational data from across a natural soil stress gradient, and data from the long-term experimental removal of two chronic herbivores (18 years of moth removal and 15 years of scale removal). The presence of naturally resistant scale and moth trees also allows us to quantify how resistant and susceptible trees might have different patterns of litterfall and, ultimately, different pathways of nutrient cycling. Our study is also based on 4 years of litterfall collection, whereas most litterfall studies have taken place over a span of 1 or 2 years.

## METHODS

### Sites and Weather

The study area is located in Northern Arizona. Soils at our six "cinder" study sites are classified as Vitrandic Ustochrepts, with some inclusions of Typic Ustorthents (Miller and others 1995). These cinder sites span 14 km near Sunset Crater National Monument. Soils at three of our six noncinder sites are a complex of Lithic and Calcic Ustochrepts and Typic and Lithic Haplustals (Miller and others 1995). These soils are derived from limestone parent materials, are located 17 km south of Sunset Crater, and span a distance of about 5.5 km. Soils at the other three noncinder sites are a complex of Typic Argiustolls, Typic and Vertic Haplustals, and Typic and Vitrandic Ustochrepts, derived from basaltic parent materials (Miller and others 1995). These sites are located 27 km to the northwest of Sunset Crater and span about 4 km. All six of these sites generally have a sandy-loam texture; hence, hereafter, we refer to them collectively as *sandy-loam* sites, in contrast to the six *cinder* sites.

Precipitation during the 4-year study was highly variable. Precipitation records were obtained from the Flagstaff municipal airport, which is located within 48 km of all the study sites. Based on the water year from September to August, the 100-year mean for Flagstaff annual precipitation is 52.8 cm. Precipitation in 1995–96 was 18.1 cm, and increased to 36.8 cm during 1996–97. Precipitation continued to increase in 1997–98 (63.6 cm) and 1998–99 (53.1 cm); both years were higher than the 100-year mean. Precipitation then decreased again in 1999–2000 to 36.7 cm.

### Study Trees

On the cinders near Sunset Crater, two long-term experiments are in place where moth and scale

herbivores have been removed since 1983 and 1985, respectively. Moth herbivory is prevented by spraying susceptible trees with the insecticide Cygon, which kills moth larvae without otherwise affecting tree growth or reproduction (Whitham and Mopper 1985). Scale herbivory is prevented by manually removing egg masses from the base of trees prior to the emergence of the insect each spring (Cobb and Whitham 1993). In both removal experiments, herbivore-resistant, susceptible, and removed trees were spatially intermixed. The effect of herbivory on tree litterfall rates can be assessed unequivocally by comparing rates of litter production under herbivore-susceptible and herbivore-removed trees. The use of resistant trees enabled us to determine whether differences in susceptible trees were due completely to herbivore impact, or whether there may be intrinsic differences between susceptible and resistant trees. Mopper and colleagues (1991b) found significant differences in allelic and genotypic frequency in three allozymes, indicating there are genetic differences between resistant and susceptible trees.

To test for soil stress effects (Gehring and Whitham 1994; Cobb and others 1997), we randomly selected 60 juvenile trees and 60 intermediate (which have both male and female function) aged trees on each of the two soil types (ten trees of each age class per site) for litterfall collection. We presumed that soil stress levels were higher on cinder soils versus sandy-loam soils, based on previous studies at the same or nearby locations with the current study (Gehring and Whitham 1994; Cobb and others 1997, 2002; Swaty and others 1998). To test for herbivore effects, we collected litter from 60 trees in the scale-removal experiment and 60 trees in the moth-removal experiment. In each herbivore-removal experiment, we collected litterfall from 20 resistant trees, 20 susceptible trees, and 20 susceptible trees from which herbivores had been removed. A number of trees (particularly in the soil comparison group) had to be removed from the study due to cutting or destruction of the litter traps by cattle or destruction/vandalism by people. Therefore, the actual sample sizes used were slightly lower than in the experimental design (Table 1).

All trees that were directly compared were of similar age. We measured age of trees that were more than 10 cm in basal trunk diameter by coring and counting tree rings. Trees less than 10 cm were too small to core without damaging them for future study, so we estimated their age according to the following formula

**Table 1.** Comparison of Annual Stem Growth, Crown Volume, Number of Stems, and Stem Density Among Stress Groups

Tree Group	N	Annual Stem Length (mm)	Canopy Height Above Litter Trap (m)	Stems Above Litter Trap	Stems per m <sup>3</sup> of Canopy
Soil comparison (juvenile)					
Cinder	53	27.5 ± 1.6 <sup>a**</sup>	0.84 ± 0.05 <sup>b</sup>	140.1 ± 8.7 <sup>b</sup>	3800.5 ± 256.1 <sup>a</sup>
Sandy loam	41	31.8 ± 1.4 <sup>a**</sup>	0.99 ± 0.05 <sup>a</sup>	173.0 ± 11.6 <sup>a</sup>	3657.6 ± 228.1 <sup>a</sup>
Soil comparison (intermediate)					
Cinder	46	35.1 ± 1.4 <sup>b</sup>	1.70 ± 0.09 <sup>b</sup>	175.8 ± 11.3 <sup>b</sup>	2282.5 ± 176.7 <sup>a</sup>
Sandy loam	40	43.0 ± 1.7 <sup>a</sup>	1.99 ± 0.09 <sup>a</sup>	244.9 ± 16.4 <sup>a</sup>	2717.0 ± 224.3 <sup>a</sup>
Scale removal experiment					
Resistant	18	36.2 ± 1.9 <sup>a</sup>	1.20 ± 0.07 <sup>a</sup>	199.5 ± 21.4 <sup>a</sup>	3436.4 ± 328.7 <sup>a</sup>
Susceptible	19	22.8 ± 0.8 <sup>b</sup>	0.68 ± 0.06 <sup>b</sup>	131.5 ± 9.3 <sup>b</sup>	4421.8 ± 471.5 <sup>a</sup>
Removed	20	32.3 ± 1.5 <sup>a</sup>	1.00 ± 0.61 <sup>a</sup>	175.2 ± 10.9 <sup>a</sup>	3675.5 ± 215.1 <sup>a</sup>
Moth removal experiment					
Resistant	16	45.0 ± 3.6 <sup>a,b</sup>	2.61 ± 0.10 <sup>a</sup>	183.1 ± 14.8 <sup>a</sup>	1443.8 ± 103.8 <sup>b</sup>
Susceptible	16	36.8 ± 1.3 <sup>b</sup>	1.26 ± 0.13 <sup>b</sup>	127.5 ± 13.4 <sup>b</sup>	2335.4 ± 285.5 <sup>a</sup>
Removed	17	50.7 ± 2.9 <sup>a</sup>	1.69 ± 0.14 <sup>b</sup>	139.4 ± 9.7 <sup>b</sup>	1812.1 ± 145.8 <sup>a,b</sup>

All tree groups that were directly compared are of statistically similar age. Shaded values indicate that statistics were performed on natural log-transformed data. Different superscripts are statistically significant at  $P < 0.05$ . Values are means ± 1 SE. \*Stem growth data for juvenile trees in the soil comparison group are available only from 1989 to 2000. \*\* $P = 0.052$ , so a strong trend is indicated, although the difference it is not significant at  $P < 0.05$ .

$$A_e = H_t / (H_n / -n) + \delta \quad (1)$$

where  $A_e$  is the estimated age of the tree,  $H_t$  is the total height of the tree,  $H_n$  is the height of the tree where nodes from individual years of growth are still discernible,  $n$  is the number of nodes discernible, and  $\delta$  is a correction factor. To determine the correction factor, we estimated age and counted tree rings on 48 small trees, and then subtracted the age estimate from the ring count and took the mean difference for each group. This age-estimation method assumes constant growth throughout the lifetime of the tree, and the correction factor accounts for changes in the growth rates through time among the various tree groups. The correction factor was 4.0 years for scale-susceptible trees, 3.2 years for scale-resistant trees on cinders, and 12.7 years for trees on sandy loam.

### Litterfall Sampling

A single litter-collection bucket (with a 491-cm<sup>2</sup> opening and 17 or 24 cm in height, depending on tree size) was placed at the midpoint of the crown radius at a random directional bearing for each tree. We secured the litter traps with rebar, cut several small holes in the base and covered them with 1-mm mesh to allow water to escape, and suspended 1.5-mm wire mesh above the base to trap litter above any remaining moisture present at

the bottom of the trap. Trees were far enough apart (and the traps were sheltered enough by the canopies) that it can be safely assumed that litterfall collected was from the study tree only. Litter was collected from the litter traps three times each year: in April, July, and November. Litter was air-dried (if necessary), sorted by type (needle, cone, seed, strobili, woody debris, and nonpinyon litter), and weighed in the laboratory. At the end of the first year of collection, we quantified the proportions of the total litterfall mass comprised by each of these different litter types. We found that needles comprised an average of 81% of the litter collected. The next highest input was woody debris, which comprised 17% of litterfall and was distributed equally across tree groups. Male and female reproductive inputs totaled only 2% of pinyon litterfall (seeds were less than 1%). Therefore, we decided to consider only needle litterfall in our subsequent analyses.

### Crown Architecture, Stem Density, and Annual Stem Growth

As mentioned previously, herbivory can alter crown architecture. We wanted to determine whether any differences in litterfall might be explained by differences in architecture. For all study trees, we estimated crown height above the bucket and foliated stem density as potential correlates to

litterfall. Four times above each bucket (90° apart), we inserted vertically a 3.3-cm diameter PVC pipe. We measured crown height (from lowest foliage to highest) and counted the number of times a foliated stem contacted the pipe. We then divided the number of stems counted by the volume of the pipe to estimate number of stems per cubic meter. We multiplied stems per cubic meter by volume above the litter trap to estimate the total number of stems in the cylinder above the trap.

As another potential predictor of litterfall and aboveground productivity, we measured average annual stem growth on each tree from 1986 to 2000 by using the easily recognizable bud scars at the beginning of each year's new growth (Gehring and Whitham 1994). In 1996 and 2000, we haphazardly chose eight terminal stems throughout the entire crown and measured the length of the growth increment between scars.

### Landscape Patterns in Litterfall

To assist in assessing the landscape-level effects of abiotic and biotic stress on litterfall, we estimated the relative crown coverage of each tree type by using line transects (Ludwig and others 1999). We established a 20-m line transect at a random distance (between 1 and 10 m) and direction from each litter bucket. We then recorded the length of pinyon crown that intersected the transect. For transects on cinder soils, we noted whether the tree was subject to scale or moth herbivory comparable to that experienced by susceptible trees in the removal experiments. This enabled us to account for possible differences in pinyon cover across soil types, and to assess the relative cover of herbivore-infested and herbivore-free trees, in order to determine whether differences in litterfall at the individual tree level might translate into differences in litterfall at the landscape level.

### Data Analysis

We calculated the total needle litterfall for each year from 1997 to 2000 for each tree. Because the litterfall was weighed air-dried, we multiplied the mass by 0.952, the established ratio of oven-dried pinyon needle mass to air-dried pinyon needle mass (S. Chapman, Northern Arizona University, personal communication). To assess soil effects, we used repeated-measures analysis of covariance (ANCOVA) analyses, with scale density as a covariate for juvenile trees and moth density as a covariate for intermediate-aged trees. Scale density (insects per centimeter of needle length) and moth density (number of moth-killed stems per cubic

meter of crown) have been measured annually on these trees since 1997. For these ANCOVA analyses, the site was nested within soil type (cinder or sandy loam) as the between-subjects factor. To assess herbivore effects in the removal experiments and annual stem growth for all data sets, we used repeated-measures analyses of variance (ANOVAs) with Games–Howell post hoc tests. We used one-way ANOVAs with Games–Howell post hoc tests to assess crown height and stem numbers and densities. When necessary, we performed natural log transformations on the raw data to comply with the assumptions of the ANOVA model, and we noted which tests were performed on transformed data in the results. We used a *P* value of less than 0.05 to denote statistical significance. Statistical analyses were performed using SPSS version 10.0 for Windows.

## RESULTS

### Soil Stress Effect

We predicted that abiotic stress caused by water- and nutrient-limited cinder soils would reduce needle litterfall rates, and our data supported this prediction for three of the four years assessed (Figure 1). Over a 4-year period, juvenile and intermediate-aged trees on cinder soils produced 20% less needle litterfall per square meter than did juvenile and intermediate-aged trees on sandy-loam soils ( $F = 8.3$ ,  $P = 0.005$ ; and  $F = 10.8$ ,  $P = 0.002$ , respectively). There was significant annual variation (juvenile  $F = 80.0$ ,  $P < 0.0005$ ; and intermediate  $F = 50.4$ ,  $P < 0.0005$ ) and a significant year by soil type interaction (juvenile  $F = 11.5$ ,  $P < 0.0005$ ; and intermediate  $F = 12.9$ ,  $P < 0.0005$ ) where cinder soil litterfall was higher in 1997 for both tree age classes.

Stem and crown measurements showed that pinyons grow poorly on cinder soils relative to sandy-loam soils. Intermediate-aged trees on cinders had 18% lower annual stem growth from 1986 to 2000 ( $F = 10.1$ ,  $P = 0.002$ ), and juvenile trees grew 14% less from 1989 to 2000, a marginally significant change [ $F = 3.9$ ,  $P = 0.052$  (Table 1)]. This reduced annual growth on cinders eventually leads to smaller trees. Intermediate-aged trees on cinders were 14% shorter ( $F = 4.9$ ,  $P = 0.029$ ) and had 28% fewer stems ( $F = 12.5$ ,  $P = 0.001$ ) than did trees on sandy loam (Table 1). Juvenile trees on cinders were 15% shorter ( $F = 4.2$ ,  $P = 0.043$ ) and had 19% fewer stems ( $F = 5.4$ ,  $P = 0.022$ ) than trees on sandy loam. Neither age class differed in stem density or litterfall on a crown volume basis

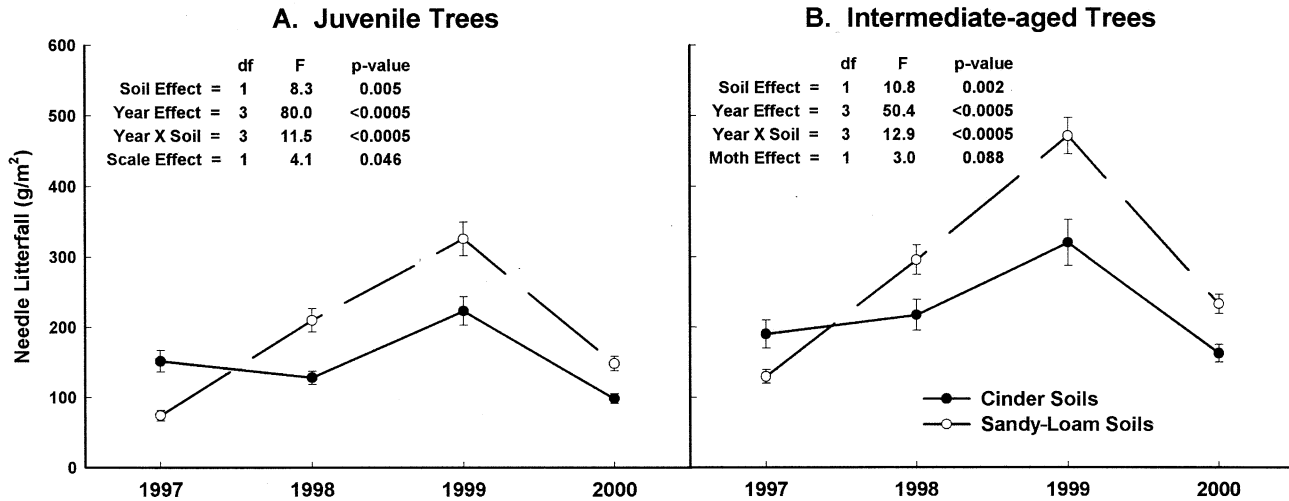


Figure 1. Juvenile trees (A) and mature intermediate-aged trees (B) on high-stress cinder soils had lower annual needle litterfall than did trees of similar age on low-stress sandy-loam soils. There was significant annual variation and significant year by soil-type interaction for both groups. Statistics were performed on natural log-transformed data. A repeated-measures ANCOVA was used, with scale density as a covariate in juvenile trees and moth density as a covariate in intermediate-aged trees. Values are mean needle litterfall in  $\text{g/m}^2 \pm 1$  SE.

across soil types. There were no significant site effects within each soil type.

### Scale-insect Effect

We predicted that stress caused by chronic scale herbivory would reduce needle litterfall rates, and our data offer some support for this prediction [ $F = 4.3$  (Figure 2)]. Scale-susceptible trees produced 25% less needle litterfall per square meter than did scale-resistant trees ( $P = 0.029$ ), while scale-removed trees dropped an intermediate amount statistically similar to the other two groups. There was significant annual variation and a significant year by scale herbivory interaction ( $F = 26.6$ ,  $P < 0.0005$ ; and  $F = 8.5$ ,  $P < 0.0005$ , respectively).

Scale-susceptible trees had 37% and 29% lower annual stem growth over the last 15 years than did scale-resistant and scale-removed trees, respectively [ $F = 34.5$ ,  $P < 0.0005$  (Table 1)]. This reduced growth of susceptible trees led to trees that were 44% and 33% shorter ( $F = 15.6$ ,  $P < 0.0005$ ) and had 35% and 25% fewer stems ( $F = 4.9$ ,  $P = 0.011$ ) than did scale-resistant and scale-removed trees, respectively (Table 1). There was no difference in stem density or litterfall on a per-crown-volume basis across herbivory categories.

### Moth Effect

We predicted that chronic stem-boring moth herbivory would reduce needle litterfall as well, but

our results did not support this prediction. There was no significant difference in the amount of annual needle litterfall collected from moth-resistant, moth-susceptible, and moth-removed trees [ $F = 0.7$ ,  $P = 0.526$  (Figure 3)]. There was a strong annual variation ( $F = 28.0$ ,  $P < 0.0005$ ), but no year by moth-herbivory interaction ( $F = 1.0$ ,  $P = 0.408$ ).

Moth-removed trees had 27% greater stem growth than did moth-susceptible trees ( $F = 9.2$ ,  $P = 0.001$ ), while growth of moth-resistant trees was statistically similar to both other groups (Table 1). Moth-susceptible trees and moth-removed trees were shorter than resistant trees ( $F = 29.1$ ,  $P < 0.0005$ ), but susceptible trees had 38% higher stem density than did moth-resistant trees ( $F = 4.4$ ,  $P = 0.018$ ), while moth-removed trees were intermediate (Table 1). Crown volume of moth-susceptible trees was 50% less than that of moth-resistant or moth-removed trees ( $F = 6.5$ ,  $P = 0.003$ ). Hence, moth-susceptible trees produced greater litter per unit of crown volume than did moth-resistant or moth-removed trees ( $F = 10.8$ ,  $P < 0.0005$ ).

### Pinyon Crown Cover

Total pinyon crown cover (all sizes and herbivore categories) was 14.7% on cinders and 17.1% on sandy loam, but these values were statistically similar ( $F = 1.3$ ,  $P = 0.252$ ). On the cinder soils, trees with scale infestations comparable to trees

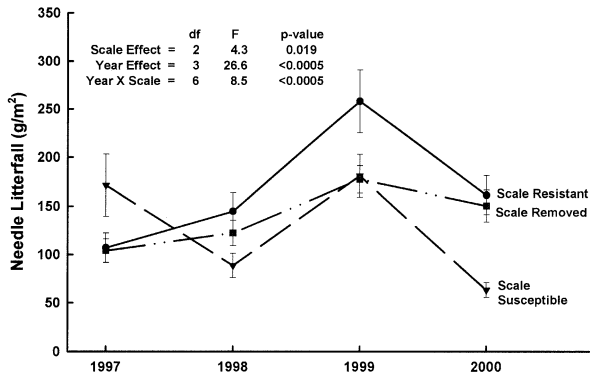


Figure 2. Scale-susceptible trees produced significantly less litterfall than resistant trees, whereas scale-removed trees produced an intermediate amount that was statistically similar to both resistant and susceptible trees. There was significant annual variation and year by herbivory interaction. Statistics were performed on natural log-transformed data. Values are mean needle litterfall in  $\text{g/m}^2 \pm 1 \text{ SE}$ .

used in the scale-removal experiment covered only 1.3% of the ground, less than 10% of the total pinyon cover. Moth-susceptible trees with infestations comparable to trees used in the moth-removal experiment covered 3.8% of the ground, or about 25% of the total pinyon coverage.

## DISCUSSION

### Soil Stress Effect

Elevated plant stress due to low soil resource availability clearly affects needle litterfall in these semiarid woodlands. Trees growing on high-stress cinder soils that have relatively low water (Mopper and others 1991b; Cobb and others 1997; Swaty and others 1998) and nutrient availabilities (Gehring and Whitham 1994; Cobb and others 1997) produced less needle litterfall than did trees growing on low-stress, sandy-loam soils with higher soil resource availabilities (Table 2). Because herbivory occurs to a much greater degree on cinder than on sandy-loam soils, herbivory, not soil stress, might have been partially driving this decrease in litterfall. However, when herbivory was controlled for by including the level of herbivory as a covariate, there was still a strong soil effect. Furthermore, the moth-removal experiment showed that moths had no effect on litterfall. Because juvenile trees (some of which are scale susceptible) and intermediate trees (some of which are moth susceptible) showed an almost identical litterfall pattern (Figure 1), it is very likely that the effect of reduced litter produc-

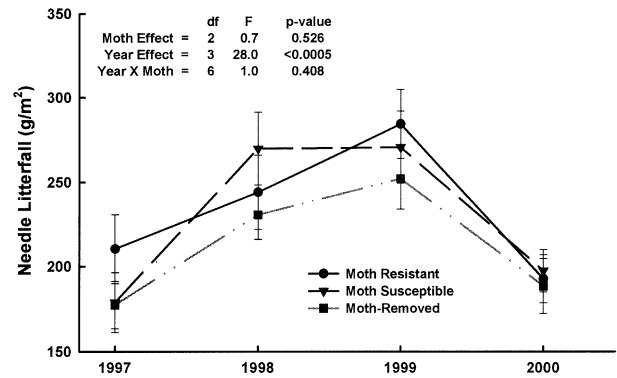


Figure 3. Moths did not affect the amount of needle litterfall produced on a per square meter of crown cover. However, because moth-susceptible trees have architecturally different and smaller crown volumes than do moth-resistant and moth-removed trees, they produced a greater amount of litterfall *per unit of crown volume*. There was statistically significant annual variation, but no significant year by herbivory interaction. Values are mean needle litterfall in  $\text{g/m}^2 \pm 1 \text{ SE}$ .

tion of pinyons on cinder soils is a direct result of soil stress.

The mechanism for reduced litter production on cinders compared with sandy-loam soils is most likely decreased aboveground net primary productivity (ANPP) in trees growing on cinders. Cobb and colleagues (1997) demonstrated experimentally that pinyon trees growing on these cinder soils experience greater water and nutrient limitation than do trees growing on sandy-loam soils, which should reduce ANPP. In general, there is a reasonably strong correlation between litterfall and ANPP in forests over the long term [for example, see Runyon and others (1994), Megonigal and others (1997), and DeLucia and others (1999)]. The lower stem growth in trees on cinders lends support to this conclusion. The effect of soil stress to reduce litterfall is clearer than either herbivore stress effect.

### Scale-insect Effect

Scale herbivory does seem to lower annual needle litterfall. In the scale removal experiment, scale-susceptible trees produced less litterfall per square meter than did resistant trees. Because scale-susceptible trees are shorter, have fewer stems, and show lower annual stem growth (Table 2) than scale-resistant and scale-removed trees, it would appear that scale herbivory reduces ANPP in a similar manner as soil stress. However, if scales were the cause of this reduction in productivity, then their removal should cause formerly suscep-

**Table 2.** Summary of the Relative Effects of Abiotic and Biotic Stress

	Abiotic (Soil) Stress			Scale Herbivory		Moth Herbivory	
	Juvenile Trees	Intermed. Trees	Scale Susceptible (vs Scale Resistant)	Effect of Scale Removal	Moth Susceptible (vs Moth Resistant)	Effect of Moth Removal	
	Cinder (vs s.l.)	Cinder (vs s.l.)					
Stem length	↓ 13.5%	▼ 18.4%	▼ 37.0%	▲ 29.4%	↓ 18.2%	▲ 27.4%	
Height above trap	▼ 14.6%	▼ 14.3%	▼ 44.1%	▲ 32.7%	▼ 51.6%	↑ 25.3%	
Number of stems	▼ 19.0%	▼ 28.2%	▼ 34.1%	▲ 24.9%	▼ 30.4%	↑ 8.5%	
Stem density	↑ 3.8%	↓ 16.0%	↑ 22.3%	↓ 16.9%	▲ 38.2%	↓ 22.4%	
Litterfall rate	▼ 20.6%	▼ 19.6%	▼ 24.9%	↑ 9.0%	↓ 1.6%	↓ 7.5%	

Arrows indicate direction of change; block arrows indicate change is significant at  $P = 0.05$ . Soil stress columns show values for trees on cinders relative to trees on sandy loam (s.l. in the table). Herbivore-susceptible columns show values for susceptible trees relative to resistant trees. Herbivore-removed columns show values of formerly susceptible trees relative to currently susceptible trees.

tible trees to increase their production to a level comparable to scale-resistant trees. Fifteen years after scale removal, the trees have increased litterfall only marginally, to a level generally intermediate and statistically similar to resistant and susceptible trees. Hence, we have not established a causal link between scale herbivory and reduced annual needle litterfall. However, because of the relatively long retention time of pinyon needles (up to 7 years on scale-resistant trees), more time may be required for scale-removed trees to regain the annual litter production levels found in resistant trees despite their recovery of stem growth to scale-resistant tree levels. Alternatively, lower needle production might be an intrinsic property of scale-susceptible trees, and thus litter production in scale-removed trees may never equal that of resistant trees.

### Moth Effect

We could not find any evidence that stem-boring moths reduce litterfall, as there was no difference in litterfall per square meter among resistant, susceptible, and moth-removed trees overall or in any one year. By killing growing terminal stems, the moths reduce average annual stem length compared with moth-removed trees and crown volume compared with moth-resistant trees (Table 2). However, moth-susceptible trees have higher stem density than do moth-resistant trees, perhaps due to increased production of lateral stems in response to the death of terminal stems. As a result, moth-susceptible trees produce more needle litterfall per unit of crown volume.

The *plant compensatory growth hypothesis* suggests that plants subjected to moderate levels of herbivory often can replace lost tissue and therefore maintain or even increase NPP even though standing crop may be reduced [for example, see McNaughton (1983) and Trumble and others (1993)]. The relationship that was demonstrated between stem-boring moths and pinyon litterfall may support this hypothesis. Moths reduce annual stem growth and crown volume, but they increase needle-bearing stem density and litterfall per cubic meter. This may compensate for lower individual stem growth and crown volume, resulting in unchanged overall needle production per square meter (Table 2).

### Landscape Patterns of Herbivory

Soil stress should have landscape-level effects on litterfall and nutrient cycling. Pinyon coverage was statistically similar on cinder (14.7%) and sandy-



loam (17.1%) soils. Therefore, the lower litterfall rate per square meter on cinders multiplied by the similar pinyon coverage translates into less litter falling annually on less fertile cinder soils. This, in turn, should result in lower rates of nutrient cycling on these soils [for example, see Boerner (1984) and Madiera and others (1995)].

Herbivore stress may not affect litterfall quantity at the landscape level. Even though up to 80% of juvenile trees can be infested with scale in the highest infestation areas, scale trees account for less than 10% of pinyon canopy cover. This is because scale susceptibility decreases with age (DelVecchio and others 1993), and the majority of pinyon canopy cover consists of larger trees beyond the typical age of infestation. Therefore, even if scales do cause reduced litterfall, this effect is probably small at the landscape level. Because moth herbivory had no effect on individual litterfall rates, its effects on litterfall quantity at the landscape level are likely also negligible. However, both herbivores may have important nutrient-cycling effects at the individual tree level by altering litterfall quality [Chapman and others (2004); see also Schowalter and others (1991) and Risley and Crossley (1992)] and the microclimate underneath the tree crown (A. Classen and others, Northern Arizona University, personal communication).

### Interactions and Annual Variation

We noted that there were frequently significant year by soil type and year by scale herbivory interactions. It is also interesting to note that annual variation in litterfall follows a similar pattern for both soil stress and scale herbivory. Litterfall peaks in 1999 for all groups and is significantly lower in trees on cinders (compared with trees on sandy-loam soils) and in scale-susceptible trees (compared with scale-resistant trees) for every year except 1997.

In 1995–96, Northern Arizona experienced a 100-year record drought, which reduced pinyon stem growth in 1996 and 1997 and caused higher than normal mortality in some regional sites (Ogle and others 2000), though not in these study sites. Despite the dry years, only seven of the 964 study trees died during the study period. We speculate that the litterfall from trees subject to chronic water and nutrient deficiencies or scale herbivory will be less affected by severe events such as the 1996 drought. Plants subject to environmental fluctuations can alter the partitioning of carbon between shoots and roots to offset the consequences of the change (Wilson 1988; Minchin and others 1994).

Trees under chronic water and nutrient stress (those on cinders) should have lower shoot–root ratios than do trees on more benign (sandy loam) soils, which should result in a lower standing crop of needles. Trees on more benign soils with more needles may react to drought by senescing needles 1 or more years early to prevent excess evapotranspiration. There would then be less litterfall produced by these trees growing on more benign soils in the years following a drought. However, the trees with lower shoot–root biomass ratio on higher-stress cinder soils would not adjust their foliar biomass to as large a degree. For scale-susceptible trees, on the other hand, because of their already reduced foliar biomass relative to their root system, water loss due to evapotranspiration is less detrimental than loss of photosynthetic material to herbivory. These trees would not be expected to senesce needles early as a result of drought, whereas their scale-resistant neighbors would do so because of higher shoot–root ratios.

Our results suggest that, although litterfall and ANPP are positively correlated in the long-term, they are not necessarily correlated in the short term. For example, in a 1-year study, Chapman and colleagues (2004) found that scale-susceptible trees produced more needle litterfall than did resistant trees without scales. In our study, this was true only in 1997 (Figure 2). This year by stress type interaction highlights the need for longer-term studies to fully understand trends in litter production across sites of contrasting productivity and herbivory levels.

### CONCLUSIONS

Soil stress has a compound effect on pinyon litterfall dynamics. First, it directly reduces needle litterfall regardless of insect herbivory. This reduction in litterfall rate translates into a landscape-level reduction in litter input and should slow nutrient-cycling processes on cinders. Second, stressed trees are more susceptible to scale and moth herbivory. Scale herbivory may further reduce needle litterfall, although the failure of scale-removed trees to show a statistically significant increase in litter production after 15 years casts some doubt on this conclusion. Although moth herbivory decreases stem growth and crown height, it has no effect on litterfall per square meter. However, moth herbivory increases stem density and litterfall rates per cubic meter of crown volume, which suggests compensatory growth. The difference between scale and moth effects on litterfall rates indicates that the type of herbivory is important to consider

when assessing the impacts of herbivores on ecosystem processes.

Both soil type and scale herbivory can influence needle litterfall dynamics over the long term, but other factors can obscure or reverse these trends in the short term. Our study does not conclusively identify any of these factors, but we do suggest that severe weather such as drought may be important. The region regularly experiences substantial variation in precipitation from year to year, as it did during our study. It is likely that this year-to-year variation strongly shapes these ecosystems. In our study, 2 years were below average, 1 about average, and 1 above average precipitation. The last part of the 20th century was particularly wet; we don't know whether we now are back on a drier track (Betancourt personal communication). However, it is likely that weather does interact with herbivores and soils to shape the structure and function of these woodlands, both today, in the past, and in the future. The potentially large effects of these short-term factors suggest that longer-term studies are necessary to better understand litterfall dynamics in semiarid forest ecosystems.

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#### REFERENCES

- Attiwill PM, Adams MA. 1993. Tansley review no. 50: nutrient cycling in forests. *New Phytol* 124:561–82.
- Boerner REJ. 1984. Nutrient fluxes in litterfall and decomposition in four forests along a gradient of soil fertility in southern Ohio. *Can J For Res* 14:794–802.
- Chapman S, Cobb NS, Hart SC, Whitham TG, Koch GW. 2004. Insect herbivory increases litter quality and decomposition rates: an extension of the acceleration hypothesis. *Ecology*. Forthcoming. 11:22–23.
- Christensen KM, Whitham TG. 1991. Indirect herbivore mediation of avian seed dispersal in pinyon pine. *Ecology* 72:534–42.
- Christensen KM, Whitham TG. 1993. Herbivore impact on competition between birds and mammals for pinyon pine seeds. *Ecology* 74:2270–8.
- Cobb NS, Mopper S, Gehring CA, Caouette M, Christensen KM, Whitham TG. 1997. Increased moth herbivory associated with environmental stress of pinyon pine at local and regional levels. *Oecologia (Berl)* 109:389–97.
- Cobb NS, Trotter RT, Whitham TG. 2002. Long-term sexual allocation in herbivore resistant and susceptible pinyon pine (*Pinus edulis*). *Oecologia (Berl)* 130:78–87.
- Cobb NS, Whitham TG. 1993. Herbivore deme formation on individual trees: a test case. *Oecologia (Berl)* 94:496–502.
- Cobb NS, Whitham TG. 1998. Prevention of deme formation by the pinyon needle scale: problems of specializing in a dynamic system. In: Mopper S, Strauss S, editors. *Genetic structure in natural insect populations of herbivorous insects*. New York: Chapman and Hall. p 37–63.
- DeLucia EH, Hamilton JG, Naidu SL, Thomas RB, Andrews JA, Finzi A, Lavine M, Matamala R, Mohan JE, Hendrey GR, Schlesinger WH. 1999. Net primary production of a forest ecosystem with experimental CO<sub>2</sub> enrichment. *Science* 284:1177–9.
- DelVecchio T, Gehring CA, Cobb NS, Whitham TG. 1993. Negative effects of scale insect (*Matsucoccus acalyptus*) herbivory on the ectomycorrhizae of pinyon pine. *Ecology* 74:2297–302.
- Gehring CA, Cobb NS, Whitham TG. 1997. Three-way interactions among ectomycorrhizal mutualists, scale insects and resistant and susceptible pinyon pines. *Am Nat* 149:824–41.
- Gehring CA, Whitham TG. 1994. Comparisons of ectomycorrhizae on pinyon pines (*Pinus edulis*; Pinaceae) across extremes of soil type and herbivory. *Am J Bot* 81:1509–16.
- Gehring CA, Whitham TG. 1995. Duration of herbivore removal and environmental stress affect the ectomycorrhizae of pinyon pines. *Ecology* 76:2118–23.
- Herbohn JL, Congdon RA. 1998. Ecosystem dynamics at disturbed and undisturbed sites in North Queensland wet tropical rain forest. III. Nutrient returns to the forest floor through litterfall. *J Trop Ecol* 14:217–29.
- Hunter MD. 1992. Interactions within herbivore communities mediated by the host plant: the keystone herbivore concept. In: Hunter MD, Price PW, Ohgushi T, editors. *Effects of resource distribution on animal-plant interactions*. San Diego: Academic. p 287–325.
- Kavvadias VA, Alifragis D, Tsiontsis A, Brofas G, Stamatelos G. 2001. Litterfall, litter accumulation, and litter decomposition rates in four forest ecosystems in Northern Greece. *For Ecol Manage* 144:113–27.
- Knutson RM. 1997. An 18-year study of litterfall and litter decomposition in a northeast Iowa deciduous forest. *Am Midl Nat* 138:77–83.
- Krutch JW.. 1974. *Thearadox of a lava flow Globe (AZ): Southwest Parks and Monuments Association*.
- Ludwig JA, Tongway DJ, Eager RW, Williams RJ, Cook GD. 1999. Fine-scale vegetation patches decline in size and cover with increasing rainfall in Australian savannas. *Landscape Ecol* 14:557–66.
- Madiera M, Araujo MC, Pereira JS. 1995. Effects of water and nutrient supply on amount and on nutrient concentration of litterfall and forest floor litter in *Eucalyptus globulus* plantations. *Plant Soil* 168–9:287–95.
- McNaughton SJ. 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40:329–36.
- Megonigal JP, Conner WH, Kroeger S, Sharitz RR. 1997. Aboveground production in southeastern floodplain forests: a test of the subsidy-stress hypothesis. *Ecology* 78:370–84.
- Miller G, Ambos N, Boness P, Reyner D, Robertson G, Scalzone K, Steinke R, Subirge T. 1995. *Terrestrial ecosystem survey of the Coconino National Forest*. Portland (OR): USDA Forest Service Southwestern Region.

- Minchin PEH, Thorpe MR, Farrar JF. 1994. Short-term control of root:shoot partitioning. *J Exp Bot* 45:615–22.
- Mopper S, Maschinski J, Cobb NS, Whitham TG. 1991a. A new look at habitat structure: consequences of herbivore-modified plant architecture. In: Bell SS, McCoy ED, Mushinsky HR, editors. *Habitat structure: the physical arrangement of objects in space*. London: Chapman and Hall. p 260–80.
- Mopper S, Mitton JB, Whitham TG, Cobb NS, Christensen KM. 1991b. Allozyme variation and heterozygosity in pinyon pine associated with resistance to herbivory and environmental stress. *Evolution* 45:989–99.
- Mopper S, Whitham TG, Price PW. 1990. Plant phenotype and interspecific competition between insects determine sawfly performance and density. *Ecology* 71:2135–44.
- Ogle K, Whitham TG, Cobb NS. 2000. Tree-ring variation in pinyon pine predicts likelihood of death following record drought. *Ecology* 81:3237–43.
- Risley LS, Crossley DA Jr. 1992. Contribution of herbivore-caused greenfall to litterfall nitrogen flux in several southern Appalachian forested watersheds. *Am Midl Nat* 129:67–74.
- Runyon J, Waring RH, Goward SN, Wells JM. 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. *Ecol Appl* 4:226–37.
- Schowalter TD, Sabin TE, Stafford SG, Sexton JM. 1991. Phytophage effects on primary production, nutrient turnover, and litter decomposition of young Douglas-fir in western Oregon. *For Ecol Manage* 42:229–43.
- Swaty RL, Gehring CA, Van Ert M, Theimer TC, Keim P, Whitham TG. 1998. Temporal variation in temperature and rainfall predicts ectomycorrhizal colonization. *New Phytol* 139:733–9.
- Trotter TR, Cobb NS, Whitham TG. 2002. Herbivory, plant resistance, and climate in the tree ring record: interactions distort climatic reconstructions. *Proc Natl Acad Sci* 99:10–197–202.
- Trumble JT, Kolodny-Hirsch DM, Ting IP. 1993. Plant compensation for arthropod herbivory. *Annu Rev Entomol* 38:93–119.
- Vitousek PM, Gerrish G, Turner DR, Walker LR, Mueller-Dombois D. 1995. Litterfall and nutrient cycling in four Hawaiian montane rainforests. *J Trop Ecol* 11:189–203.
- White TCR. 1993. *The inadequate environment* New York: Academic.
- Whitham TG, Mopper S. 1985. Chronic herbivory: impacts on tree architecture and sex expression of pinyon pine. *Science* 227:1089–91.
- Wilson JB. 1988. A review of evidence on the control of shoot:root ratio, in relation to models. *Ann Bot* 61:433–49.