

Insect Infestations Linked to Shifts in Microclimate: Important Climate Change Implications

A. T. Classen, S. C. Hart, T. G. Whitman, N. S. Cobb, and G. W. Koch

ABSTRACT

Changes in vegetation due to drought-influenced herbivory may influence microclimate in ecosystems. In combination with studies of insect resistant and susceptible trees, we used long-term herbivore removal experiments with two herbivores of piñon (*Pinus edulis* Endelm.) to test the general hypothesis that herbivore alteration of plant architecture affects soil microclimate, a major driver of ecosystem-level processes. The piñon needle scale (*Matsucoccus acalyptus*, Herbert) attacks needles of juvenile trees causing them to develop an open crown. In contrast, the stem-boring moth (*Dioryctria albiovittella* Hulst.) kills the terminal shoots of mature trees, causing the crown to develop a dense form. Our studies focused on how the microclimate effects of these architectural changes are likely to accumulate over time. Three patterns emerged: (i) scale herbivory reduced leaf area index (LAI) of susceptible trees by 39%, whereas moths had no effect on LAI; (ii) scale herbivory increased soil moisture and temperature beneath susceptible trees by 35 and 26%, respectively, whereas moths had no effect; and (iii) scale and moth herbivory decreased crown interception of precipitation by 51 and 29%, respectively. From these results, we conclude: (1) the magnitude of scale effects on soil moisture and temperature is large, similar to global change scenarios, and sufficient to drive changes in ecosystem processes. (2) The larger sizes of moth-susceptible trees apparently buffered them from most microclimate effects of herbivory, despite marked changes in crown architecture. (3) The phenotypic expression of susceptibility or resistance to scale insects extends beyond plant-herbivore interactions to the physical environment.

CLIMATE CHANGE assessments and models have traditionally focused on how large meso-scale alterations in climate may alter vegetation. However, one of the major challenges in dealing with climate change effects is trying to anticipate and predict the secondary and cascading effects in ecosystems. Vegetation not only responds to climate change but also creates distinct microclimate patterns; and ecosystem processes are affected by both the general climate and by these microclimate patterns. Insect infestations are predicted to increase with climate change and can cause rapid changes in vege-

tation with concomitant changes in microclimate (Lindroth, 1996; Dale et al., 2001; Logan et al., 2003). Despite the potential importance of the insect infestation, vegetation canopy change, microclimate change, ecosystem processes response chain, studies are lacking on this connection. This connection may be particularly important in heterogeneous dryland ecosystems, where near-ground energy budget is strongly affected by canopy coverage (Martens et al., 2000).

Soil temperature and moisture are controlled in the coarse sense by regional macroclimate, but these abiotic drivers are also highly sensitive to the influence of local vegetation on radiation, precipitation interception, wind speed, and evapotranspiration. To the extent that herbivory alters plant growth form and LAI (Fahnestock and Knapp, 1994; Kielland and Bryant, 1998; Ritchie et al., 1998), herbivory has the potential to affect both soil moisture and temperature and the biotic processes driven by these abiotic factors, including decomposition and nutrient mineralization (Whicker and Detling, 1988; Morecroft et al., 1998). We expect these indirect effects of herbivory on ecosystems to be particularly important where moisture and temperature are strong regulators of nutrient cycling rates, and where chronic herbivory maintains the architectural changes in vegetation that could give rise to altered soil microclimate.

The influence of herbivory on nutrient cycling can occur along various pathways. Among the more studied pathways are those related to changes in biotic factors, including: direct alteration of litter quantity (e.g., Grace, 1986; Chapman et al., 2003), induced or disruptive changes in litter chemical quality (e.g., McInnes et al., 1992; Findlay et al. 1996; Grime et al., 1996), changes in litter quality arising from shifts in plant species composition (e.g., Pastor and Naiman, 1992; Kielland and Bryant, 1998; Maron and Jefferies, 1999; Olofsson and Oksanen, 2002; Olofsson et al., 2004), and the deposition of herbivore by-products (e.g., Hollinger, 1986; Frank and Evans, 1997; Christenson et al., 2002). Despite the fact that in many ecosystems abiotic conditions, including soil moisture and temperature, are the dominant regulators of decomposition and nutrient mineralization (Meentemeyer, 1978; Aerts, 1997; Hart and Perry, 1999), only a few studies have examined indirect effects of herbivory on these important drivers of ecosystem processes. For instance, vertebrate herbivory has been shown to decrease soil moisture (Holland and Detling, 1990; Frank and Groffman, 1998) and increase soil temperature (Fahnestock and Knapp, 1994) in grasslands. Further, Brown (1994) found that beetle folivory significantly increased light penetration and soil moisture in monocultures of goldenrod,

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Abbreviations: LAI, leaf area index; MANOVA, multivariate analysis of variance.

which led to an increase in net N mineralization rates. Insects are important herbivores in coniferous forests (Schowalter, 2000), yet we are aware of no studies that have examined how they affect the abiotic soil environment in forests. Here, we focus on how two insect herbivores indirectly influence soil moisture and temperature in a semiarid coniferous woodland via their effects on tree architecture.

The interaction of piñon (*Pinus edulis*, Endelm.) with herbivores in semiarid woodlands of the Southwestern USA provides an exceptional opportunity to quantify how plant resistance affects microclimate. Piñon-juniper woodlands of this region are characterized by a cool, montane climate and low soil moisture for much of the year. Conant et al. (1998) reported that soil respiration, an index of soil catabolic activity, was highly correlated with temperature but constrained by moisture in these woodlands. Previous studies have documented striking impacts of herbivory by two insects, the piñon needle scale (*Matsucoccus acalyptus*, Herbert) and the stem-boring moth (*Dioryctria albovittella*, Hulst.), in piñon populations under conditions of low water availability (Christensen and Whitham, 1991, 1993; Del Vecchio et al., 1993; Mopper et al., 1991a; Gehring and Whitham, 1991, 1994; Gehring et al., 1997; Cobb et al., 1997, 2002). Chronic herbivory by the scale insect, which primarily attacks juvenile trees, removes all but the youngest cohort of needles of susceptible trees, and results in a tree with a sparse and open crown (Mopper et al., 1991a; Cobb and Whitham, 1993). In contrast, the stem-boring moth attacks mature piñons >46 yr old that produce female cones (Ruel and Whitham, 2002), and slows growth and alters crown architecture of susceptible trees (Whitham and Mopper, 1985; Mopper et al., 1991a; Brown et al., 2001). Preferential attack of terminal shoots causes moth-susceptible trees to develop a dense, shrub-like architecture (Whitham and Mopper, 1985).

Long-term studies in northern Arizona have identified trees that are resistant and susceptible to each herbivore, and trees of each type are found intermixed within the woodland. At this site, herbivore-removal experiments have been in place for nearly 20 yr, providing the opportunity to demonstrate how chronic herbivory influence soil microclimate and dependent ecosystem processes. Finally, because piñon resistance to moths has a genetic component (Mopper et al., 1991b), the potential exists for linking population-level variation in plant genetics to key abiotic regulators of ecosystem processes.

Based on the documented impacts of the needle scale and stem-boring moth on crown architecture of piñons, we tested three predictions: (1) both herbivores will change the leaf area index (LAI) of susceptible trees, thus reducing (scale) or increasing (moth) crown interception of precipitation and light; (2) soil moisture will be higher and soil temperature lower beneath moth-susceptible trees than beneath moth-resistant or moth-removal trees; and (3) soil moisture and temperature will be higher beneath scale-susceptible trees than beneath scale-resistant or scale-removal trees because lower LAI will increase precipitation throughfall and decrease transpiration, and increase soil surface temper-

atures. Tests of the predictions demonstrate how plant resistance traits and herbivory potentially interact to affect microclimate.

MATERIALS AND METHODS

Site Description

Our study site covers 5 ha in Northern Arizona, adjacent to Sunset Crater National Monument (35°22' N lat., 111°33' W long.) at an elevation of approximately 2100 m. Thirty-year means of annual precipitation and air temperature at the Monument Visitor Center (about 12 km west and 300 m higher than our site) are 423 mm and 8.6°C, respectively (Chapman et al., 2003). Sunset Crater soils are classified as cindery, mesic Typic Ustorthents. This site has approximately 40% woody cover and 80% of the trees are piñons. One-seed juniper (*Juniperus monosperma* Engelm.), Apache plume (*Fallugia paradoxa* Endelm.), Mormon tea (*Ephedra viridis* Coville), and squawbush (*Rhus trilobata* Nutt.) are the other dominant woody species. Trees are often isolated by large inter-crown spaces that consist of vegetation free soil.

Moth insects have been eliminated from a subset of susceptible trees since 1982 with a commercially available systemic spray insecticide (Cygon [C₅H₁₂NO₃PS₂, BASF Corp., Agricultural Product Group, Research Triangle, NC]) that has no apparent fertilizer effect (Whitham and Mopper, 1985). Scale insects have been removed yearly since 1985 from a subset of susceptible trees by physically removing egg sacs located at the base of the trunk (Trotter et al., 2002). The long-term removal of these two herbivores results in a “release effect,” where tree productivity increases to resemble resistant trees (Gehring et al., 1997; Brown et al., 2001). This experiment allows us to evaluate herbivore effects on soil abiotic processes through time.

A total of 120 piñons and 10 inter-crown spaces were randomly selected in June of 1999. Study plots were centered on individual trees chosen to represent six different herbivore conditions: scale-susceptible, scale-resistant, scale-susceptible trees with scales removed (hereafter “scale-removed trees”), moth-susceptible, moth-resistant, and moth-susceptible trees with moths removed (hereafter “moth-removed trees”; $n = 20$ in each of the six treatment groups). The 10 vegetation-free inter-crown spaces were randomly distributed throughout the site.

Leaf Area Index

Crown LAI was measured with a Sunfleck Ceptometer PAR sensor (Decagon Devices, Pullman, WA) in March of 2002 on 26 scale study trees (6 resistant, 10 susceptible, 10 removed), and in May of 2002 on 60 moth study trees (20 resistant, 20 susceptible, and 20 removed). Measurements for scale trees were taken in two ways: (1) A 90 by 300 cm grid of PVC pipe (1.27-cm diam.) was placed against the tree trunk and aligned with the long axis parallel with the tree shadow. Measurements were recorded every 10 cm along the grid and then averaged for each tree crown. (2) A single measurement was taken beneath the crown midway between the crown dripline and the tree trunk. Leaf area indices were calculated as outlined in the Sunfleck operator's manual (Decagon Devices, Pullman, WA). Leaf area indices estimated by the grid and single measurement approaches were well correlated ($r^2 = 0.8$, $p < 0.0001$); therefore, the single measurement approach was used for the remaining scale and all of the moth treatment trees.

Crown Interception of Precipitation

We estimated crown interception of precipitation to understand how changes in LAI and crown architecture might alter water inputs to the soil. Precipitation collectors were placed in 10 inter-crown spaces and mid-way between the dripline and tree bole beneath the crown of 10 trees in each of the six treatment groups. Collectors were 1-L Nalgene small mouth bottles with 14 cm diam. powder funnels attached to the top. A piece of 2-mm metal mesh screening and four marbles were inserted into the funnel flute to reduce evaporation. Two collectors were placed beneath each moth treatment tree, and one collector was placed beneath each scale tree and in each inter-crown location. Collectors were emptied weekly during the monsoon season (August–September 2001) and within a day of precipitation during the rest of the year (October 2001–August 2002). Collected water was weighed and converted to centimeters of precipitation assuming a water density of 1 Mg m⁻³. Fraction of crown interception was calculated for each study tree as: (mean inter-crown precipitation - crown throughfall)/mean inter-crown precipitation.

Soil Moisture

Beneath eight trees in each of the six study groups and eight inter-crown spaces, volumetric soil moisture was measured by time domain reflectometry (Trase System 1, Soil Moisture Corporation, Goleta, CA) at three mineral soil depths (0–15, 0–30, and 0–60 cm). Depths were chosen to represent the soil surface (0–15 cm), the rooting zone (15–30 cm), and below the rooting zone (30–60 cm). Probes were buried midway between the crown dripline and the tree trunk at random compass bearings. Inter-crown probes were inserted away (at least one crown-height) from any vegetation, randomly throughout the study area. Measurements were taken every 2 wk throughout the growing season (July–November 1999; March–October 2000; February–October 2001; February–April 2002) and once a month during winter (November 2000–January 2001; November 2001–January 2002). Measurements were not taken during the winter of 1999. Inter-crown measurement locations were increased from one to eight in May of 2000. Soil moisture content of the 15- to 30-cm layer was calculated using soil moisture values from the 0- to 15- and 0- to 30-cm probes, while soil moisture content of the 30- to 60-cm layer was calculated using soil moisture values from the 0- to 30- and 0- to 60-cm probes (Kolb et al., 1997).

Soil Temperature

Soil temperature was monitored using calibrated Stowaway XTI temperature thermistor probes (Onset Computer Corp., Bourne, MA). Probes were buried at 5- and 15-cm mineral soil depths beneath eight trees in each of the six study groups and two inter-crown spaces. Probes were placed adjacent to soil moisture probes. Temperature measurements were logged every 15 min in 1999 and every hour from 2000 to 2002; these data were summarized to daily means, minima and maxima.

Statistics

Soil moisture data were analyzed by repeated measures multivariate analysis of variance (MANOVA). Contrasts were used to test for differences among treatment means. Inter-crown measurement locations were added to the study 9 mo after the experiment was initiated, thus they were not included in the repeated measures design. Instead, measurements were averaged by year to compare values between treatments and inter-crown spaces. A one-way analysis of variance (ANOVA)

was used to test if LAI, crown throughfall, and soil temperature differed among treatments within each tree size-class. Leaf area index data for both moth and scale trees were log transformed because they violated the normality assumption of ANOVA. Least significance difference multiple comparison tests were used to determine differences among sample means. All statistical analyses were performed using JMP 4 statistical software (SAS Institute, 2001); the *p* level to denote statistical significance was set at 0.05 for all analyses.

RESULTS

Leaf Area Index

Scale, but not moth, herbivory reduced LAI (Fig. 1A and 1B). Multiple comparison tests within the scale treatment trees showed significant differences between susceptible and resistant trees and between susceptible and removed trees (*p* < 0.001 for both). The scale removal experiment clearly separates cause and effect; when insects are removed, tree LAI recovers to resemble resistant trees.

Crown Interception of Precipitation

Scale herbivore effects on trees decreased crown interception of precipitation by 60 and 51% relative to resistant and removal trees, respectively (*p* = 0.006 for both, Fig. 1C), while moth herbivore effects on trees decreased precipitation interception over 26% relative to resistant and removed trees (*p* = 0.027 for both, Fig. 1D). Across all study trees, crown throughfall and LAI were negatively correlated (*r*² = 0.68, *p* < 0.001, data not shown). Throughfall measured in the inter-crown locations (i.e., precipitation) averaged 131 mm (±0.41) over the collection period (13 Aug. 2001–15 Aug. 2002). In comparison, a weather station (Campbell Scientific, Logan, UT) located at the site recorded 135 mm of cumulative precipitation over this same period (Tipping bucket rain gauge and snow adaptor #TE525, Texas Electronics, Dallas, TX).

Soil Moisture

Averaged over the entire study period (July 1999–April 2002), volumetric soil moisture within the 15- to 30-cm layer beneath scale-susceptible trees was significantly (*p* < 0.020) higher than beneath scale-removed and scale-resistant trees; however, soil moisture was similar among treatments within the 0- to 15- and 30- to 60-cm layers (Fig. 2A, Table 1). Soil moisture was similar among moth treatments at all depths (Table 1). Inter-crown spaces had consistently higher soil moisture than both the scale and moth treatments within the 15- to 30-cm layer (*p* < 0.001, 0.004, respectively), and the moth treatment trees within the 30- to 60-cm layer (*p* = 0.007; Table 1); however there were no differences within the 0- to 15-cm layer (Table 1).

Soil Temperature

Herbivore effects on crown architecture significantly increased daily maximum soil temperatures at 5 and 15 cm when compared with resistant trees (5 cm: *p* =

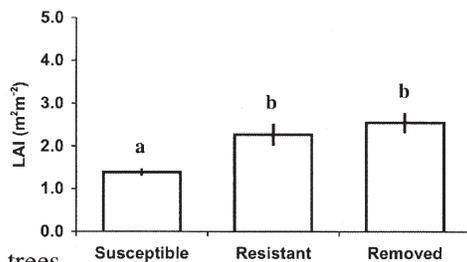
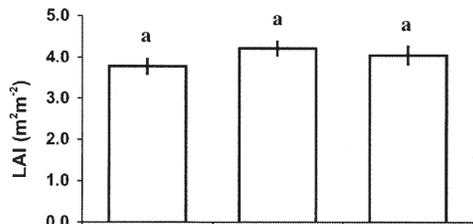
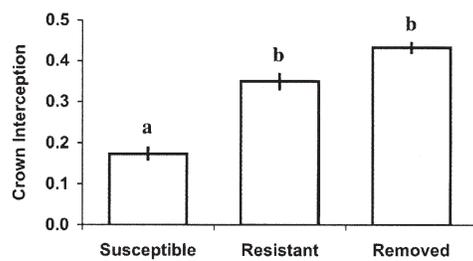
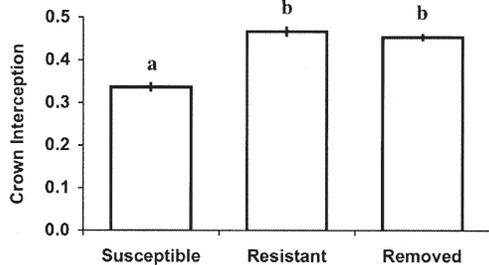
A Scale trees**B** Moth trees**C** Scale trees**D** Moth trees

Fig. 1. Insect herbivore (scale and moth) effects on tree leaf area index (LAI) and precipitation interception by the tree crown in a piñon-juniper woodland. Treatments include trees that were herbivore-susceptible, resistant, and susceptible but with the herbivore removed. (A) Scale herbivory significantly reduced piñon LAI. (B) Moth herbivory has no effect on piñon LAI. (C) Scale herbivory decreased crown interception of precipitation up to 60%. (D) Moth herbivory decreased crown interception at least 26%. Stars (*) indicate significant differences using a LSD test; error bars are \pm one standard error.

0.026; 15 cm: $p = 0.019$; Fig. 2B, Table 2); however, daily minimum (Fig. 2B, Table 2) and daily mean soil temperatures were similar between these two treatments (Table 2). At both depths, daily minimum, maximum, and mean soil temperatures were similar among moth treatments (Table 2).

DISCUSSION

Many studies have addressed how herbivores alter both aboveground (i.e., Ritchie et al., 1998; Peinetti et al., 2001) and belowground plant biomass (i.e., McNaugh-

ton et al., 1998; Ruess et al., 1998; Guitian and Bardgett, 2000), but few have addressed how these changes may alter abiotic conditions of the soil environment. Our study is the first we know of to show a sustained, long-term change in soil microclimate due to an insect herbivore.

Herbivore Effects on Leaf Area Index and Crown Interception of Precipitation

As expected from their visual appearance and previous studies (Cobb and Whitham 1993; Del Vecchio et al., 1993; Chapman et al., 2003), scale-susceptible trees had significantly lower LAI than resistant trees. In contrast, there were no differences in LAI among moth-susceptible, resistant, or removed trees. This was surprising given previous research in this system demonstrating that long-term moth herbivory dramatically alters crown structure and significantly reduces radial trunk growth (Brown et al., 2001; Ruel and Whitham, 2002). It is possible that moth herbivory modified crown architecture in a way that did not change LAI. Our LAI measurements did not distinguish between leaves and stems and may therefore have failed to resolve relatively small reductions in leaf area if there were also co-occurring increases in stem area. If the LAI measurements accurately captured the leaf area of moth-susceptible trees, then it appears that a similar leaf area is compressed into a tree of shorter stature, which is consistent with the flat-topped visual appearance of the crown of moth-susceptible trees compared to the taller and more conical crown of resistant trees.

Scale and moth herbivory resulted in tree crowns that intercepted significantly less precipitation compared with trees resistant to or maintained free of these insects. Crowns of scale-susceptible trees intercepted only about half as much precipitation as scale-resistant or scale-removed trees. Moth-susceptible trees reduced crown interception by 30%, despite an apparent lack of reduction in LAI. We suspect that the dense, flat-topped crowns caused by moth herbivory increases the interception efficiency per unit of leaf and stem area compared with a similar LAI distributed across a taller, more open and conical crown. Our results indicate that insect-resistant and insect-removed trees did not differ in mean LAI and crown interception of precipitation and strongly suggest that these herbivores are the causal agents responsible for the observed differences in LAI and precipitation interception in the susceptible trees that did experience herbivory.

Herbivore Effects on Soil Microclimate

Chronic herbivory of piñons altered soil temperatures and moisture beneath scale-susceptible trees, but not moth-susceptible trees. These effects likely arose from scale herbivory significantly reducing LAI compared with insect-removed and resistant trees, while moth herbivory had no effect on LAI. Lower LAI in the scale-susceptible trees increased insolation at the soil surface, thereby warming soils. Lower LAI also led to greater precipitation throughfall in scale-susceptible trees, and

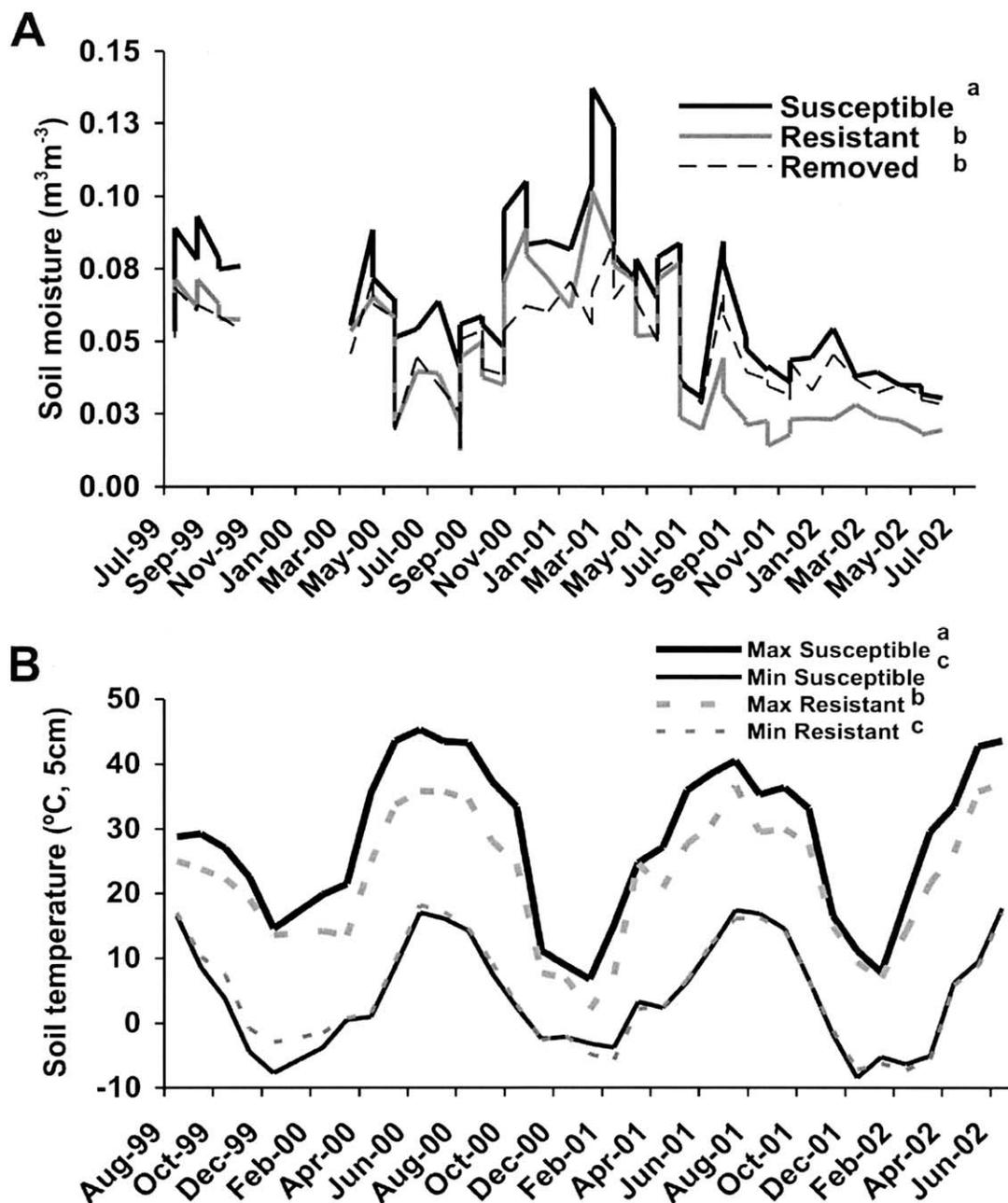


Fig. 2. The effect of scale herbivory on soil moisture and daily maximum and minimum soil temperatures measured from August 1999–June 2002 in a piñon-juniper woodland. Treatments include trees that were scale-susceptible, scale-resistant, and susceptible but with the scale removed. (A) Soil moisture was up to 35% higher in the primary piñon rooting depth beneath trees with scale herbivory (15–30 cm). (B) Daily maximum soil temperatures were on average 5°C higher at 5 cm beneath scale-susceptible trees, but herbivory had no effect on daily minimum soil temperatures (or mean temperatures, data not shown). Different letters indicate significant differences using contrasts.

likely decreased transpirational water uptake from the primary rooting zone (15- to 30-cm depth; Hedlund, 2002; Haskins, 2003); we speculate that both of these mechanisms were responsible for the higher soil moisture concentrations observed beneath the scale-susceptible trees. Although the evaporation rate from the soil surface was probably enhanced somewhat beneath scale-susceptible trees due to the greater insolation and higher soil temperatures, we expect the magnitude of this enhancement was relatively small for these coarse-textured, cindery soils (Brady and Weil, 1999). These results for insect herbivory

of a conifer are qualitatively similar to the increase in soil moisture resulting from mammalian grazing in grasslands (Fahnestock and Knapp, 1993; McNaughton, 1983). Furthermore, soil microclimatic impacts of this degree may be common and long-lasting in coniferous forests that experience chronic or severe defoliation by insects. For instance, Veblen et al. (1991) found that a spruce beetle outbreak in the 1940s altered forest structure and productivity for 50 yr after infestation.

The greater soil water availability we observed beneath scale-susceptible trees may account for the higher

Table 1. Insect herbivore (scale and moth) effects on mean volumetric soil moisture content measured in surface soils (0–15 cm), in the rooting zone (15–30 cm), and below the rooting zone (30–60 cm) from July 1999 to June 2002 in a piñon-juniper woodland. Treatments included trees that were herbivore-susceptible, herbivore-resistant, herbivore-susceptible but with the herbivore removed, and vegetation-free inter-crown areas. Standard errors are shown in parentheses below the average values.

Soil depth	Volumetric soil moisture, m ³ m ⁻³						Inter-crown area
	Scale			Moth			
	Susceptible	Resistant	Removed	Susceptible	Resistant	Removed	
	cm						
0–15	0.062 ^{a†} (0.002) [‡]	0.064 ^a (0.003)	0.063 ^a (0.004)	0.058 ^a (0.002)	0.058 ^a (0.002)	0.057 ^a (0.005)	0.060 ^{a*} (0.003)
15–30	0.064 ^{a**} (0.005)	0.047 ^b (0.005)	0.049 ^b (0.003)	0.041 ^a (0.007)	0.054 ^a (0.006)	0.047 ^a (0.004)	0.070 ^{a***} (0.004)
30–60	0.053 ^a (0.004)	0.047 ^a (0.005)	0.050 ^a (0.004)	0.042 ^a (0.004)	0.045 ^a (0.003)	0.037 ^a (0.006)	0.060 ^{a***} (0.003)

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† Within rows, different letters denote significant differences within scale and moth treatment trees and compared with inter-crown areas.

‡ Standard errors are shown in parentheses below the average values.

leaf-level rates of photosynthesis and transpiration found in scale-susceptible compared with scale-resistant trees (Giovannini, 1997). It also suggests that scale herbivory may confer a degree of drought tolerance to piñon, as suggested by studies showing a smaller relative reduction in annual radial trunk growth for scale-susceptible trees compared with scale-resistant piñons during drought conditions (Trotter et al., 2002). Although scale and moth herbivory significantly reduce radial growth in most years (Ruel and Whitham, 2002; Trotter et al., 2002), such reductions may be smaller during periods of extreme moisture stress.

Scale herbivory increased maximum soil temperatures as much as 5°C compared with trees resistant to scale. This is a large effect when considering typical Q_{10} values of 2 to 3 for many plant and microbial metabolic processes (Chapin et al., 2002). It is also of similar magnitude to temperature increases expected at mid-latitudes for the next hundred years due to global warming (Houghton et al., 2002). In this ecosystem, higher soil temperature may promote the activity of soil microorganisms during winter, but reduce their activity during the sum-

mer months (A.T. Classen, S.C. Hart, T.G. Whitham, N.S. Cobb, and G.W. Koch, unpublished data, 2004). when soil surface maximum temperatures at a 5-cm mineral soil depth reached 50°C beneath scale-susceptible trees and 60°C in the inter-crown spaces (data not shown).

The similarity of soil temperatures beneath scale-susceptible and scale-removed treatments may reflect the importance of a surface litter layer in moderating the underlying mineral soil temperature. Although the scale removal treatments have been in place for 17 yr, it is likely that the accumulation of needle litter has not yet recovered to the level found beneath trees resistant to scales. For example, we estimate that needles take ~13 yr to decompose (Classen, 2004), so that even our long-term removals may not be long enough for the litter layer of susceptible scale removal trees to resemble scale resistant trees. A thinner surface litter layer would result in a lower surface albedo (noticeably higher for needle litter compared with the underlying black cinder soils) and greater thermal diffusivity of soil beneath scale-removed trees than found beneath scale-resistant trees.

Table 2. Herbivore (scale and moth) effects on average daily maximum, minimum, and mean soil temperatures measured from August 1999–June 2002 in a piñon-juniper woodland. Treatments included trees that were herbivore-susceptible, herbivore-resistant, and herbivore-susceptible but with the herbivore removed. The range of temperatures over the period measured is shown in parentheses below the mean values.

Soil depth/ temp. variable	Soil temperature (°C)						Inter-crown area
	Scale			Moth			
	Susceptible	Resistant	Removed	Susceptible	Resistant	Removed	
	5 cm						
Maximum	27.9 ^{a**} (2.5–50.4)	22.2 ^b (1.6–42.5)	29.4 ^a (5.2–52.5)	21.4 ^a (2.4–40.0)	22.4 ^a (1.7–43.8)	21.1 ^a (2.0–49.9)	37.9 [†] (5.5–60.2)
Minimum	4.0 ^a (–10.4–21.5)	4.6 ^a (–9.4–19.5)	4.9 ^a (–11.4–20.9)	6.2 ^a (–10.4–20.5)	6.7 ^a (–12.0–23.0)	7.4 ^a (–7.0–23.7)	1.5 (–10.4–14.9)
Mean	14.4 ^a (–2.0–32.4)	12.7 ^a (–2.1–27.7)	15.5 ^a (–1.2–30.7)	13.2 ^a (0.0–26.9)	13.8 ^a (–0.4–28.9)	13.5 ^a (0.2–29.2)	16.2 (–2.1–33.0)
	15 cm						
Maximum	22.2 ^{a**} (1.2–51.5)	19.7 ^b (1.6–43.8)	21.0 ^a (20.5–36.6)	19.4 ^a (2.8–41.2)	19.1 ^a (2.1–41.9)	18.7 ^a (2.1–37.9)	26.4 (6.3–48.9)
Minimum	7.4 ^a (–6.9–27.6)	8.6 ^a (–5.6–22.2)	8.5 ^a (–6.9–23.9)	8.9 ^a (–5.1–23.6)	8.4 ^a (–3.3–22.6)	9.1 ^a (–2.9–22.6)	8.3 (–6.4–22.2)
Mean	14.8 ^a (–1.6–31.1)	13.8 ^a (–0.8–28.1)	14.5 ^a (–1.0–28.8)	13.5 ^a (–1.4–26.8)	13.1 ^a (0.0–27.0)	12.8 ^a (0.9–24.5)	16.5 (–1.0–31.2)

* Within rows, different letters denote significant differences within scale and moth treatments ($P \leq 0.05$).

† Vegetation-free inter-crown areas were not included in the statistical analyses because the sample size was too low.

These putative differences in surface characteristics beneath scale-removed and scale-resistant trees may, in turn, have led to a soil temperature regime beneath scale-removed trees that was more similar to that found beneath scale-susceptible trees than beneath the scale-resistant trees.

Interestingly, we found no effect of moth herbivory on soil moisture or temperature. The relatively dense and large crowns of moth trees and low thermal diffusivity of a thick O-horizon may ameliorate herbivore effects on soil temperature and moisture.

Possible Implications of Herbivore-Caused Changes in Microclimate for Soil Processes

The magnitude and direction of herbivory impacts on rates of decomposition and nutrient cycling vary among ecosystems (e.g., Holland and Detling, 1990; Pastor et al., 1998; Tracy and Frank, 1998; van Wijnjen et al., 1999; Hunter, 2001; Lovett et al., 2002). This variation is likely due to differences in how herbivory impacts the physical (moisture and temperature) and biotic (litter quality and quantity, decomposer organisms) factors that regulate these processes. Previous research in this ecosystem demonstrated that needle litter decomposition rates were higher beneath herbivore-susceptible trees, and this was attributed in part to the increase in litter nutrient concentration that results when needles senesce rapidly after scale or moth attack (Chapman et al., 2003).

Our observation of increased precipitation throughfall beneath susceptible trees may augment this explanation. Surface litter presumably is wetted more frequently and for longer periods beneath the herbivore-susceptible trees, and this would tend to stimulate decomposition given the strong moisture-limitation of microbial processes in piñon woodlands (Conant et al., 1998). The warmer maximum temperatures observed beneath scale-susceptible trees may also stimulate decomposition during the cooler periods of the year, particularly if combined with increased litter moisture. Establishing an unequivocal link between microclimate and decomposition rates in this ecosystem would require direct measurement of moisture and temperature of the litter layer, as well as experimental manipulations of these abiotic factors to assess the sensitivity of decomposition changes in moisture and temperature. Nonetheless, in this relatively cool, semiarid ecosystem, both moisture and temperature should be strong drivers of decomposition and nutrient cycling, and we would expect to see an acceleration of these processes beneath scale-susceptible trees.

What Role Does Herbivore Resistance and Susceptibility Play in Nutrient Cycling?

Insect herbivores at this site have a dramatic effect on crown architecture, however only the juvenile, scale-susceptible trees had altered soil microclimate. The soil environment beneath the older moth trees appears to be buffered against herbivore-driven changes in soil microclimate. Furthermore, older, moth-susceptible sized trees produce more litterfall and the quality of this litter is less

influenced by herbivory than in younger, scale-susceptible sized trees (Chapman et al., 2003). Hence, as the woodland develops through time, insect herbivores may have a decreasing influence on ecosystem processes.

Driebe and Whitham (2000) and Treseder and Vitousek (2001) postulated that genetic differentiation within plant groups could influence aspects of decomposition and nutrient cycling. Our data support their findings. Experimental removal of scale insects from piñons reversed the effect of the herbivory on crown leaf area and soil microclimate. Previous research in this ecosystem has demonstrated that there is a significant plant genetic component to susceptibility and resistance to insect herbivory (Mopper et al., 1991b), which affects the quantity and quality of aboveground litter inputs (Chapman et al., 2003). In the present study, we have now demonstrated that insect herbivory also alters the soil abiotic conditions. All of these herbivore-driven changes likely interact to alter nutrient cycling rates in this ecosystem. In addition, if climate change increases insect outbreaks in forest ecosystems (Lindroth, 1996; Dale et al., 2001; Logan et al., 2003), then we may see a shift in the genetic population of trees within piñon woodlands, with concomitant changes in rates of ecosystem processes.

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