FAST-GROWING JUVENILE PINYONS SUFFER GREATER HERBIVORY WHEN MATURE

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Abstract. We examined the hypothesis that tree-ring analyses of juvenile growth traits could be used to predict herbivory during mature years. At Sunset Crater National Monument, Arizona, USA, some pinyon pines (*Pinus edulis*) are highly susceptible to the stem-boring moth, *Dioryctria albovittella*, and suffer chronic attack, while other adjacent trees are resistant and have remained relatively moth-free for years. Five major patterns emerged: (1) Susceptible trees suffer from 11 times more shoots killed per tree and produce <0.05 times as many cones as resistant trees. (2) This herbivore is largely restricted to reproductively mature trees that, at this site, are generally older than 46 yr. (3) Analysis of tree-ring data from resistant and susceptible trees shows that trees that eventually became susceptible grew more vigorously during their attack-free juvenile years than resistant trees (growth rings were 29% wider). However, when they matured and suffered chronic herbivory, susceptible trees produced growth rings 13% smaller than resistant trees. (4) Although previous studies showed that resistance was associated with higher oleoresin flow, we did not observe this pattern. Instead, we found that resistance was best correlated with slower juvenile growth rates. Current-year shoots of susceptible mature trees averaged 50% larger than those on resistant mature trees. (5) Tree-ring analyses supported the hypothesis of a trade-off between growth and resistance. This study shows that dendrochronology can be used as a tool to predict future herbivory and demonstrates that the fastest growing juvenile trees suffer the poorest performance decades later when they become moth-susceptible mature trees. Furthermore, it illustrates that traits associated with plant development can greatly affect herbivore distributions, and that herbivore selection pressures on juvenile trees can be very different than on mature trees.

Key words: dendrochronology; Dioryctria albovittella; *herbivory; pine;* Pinus edulis; *pinyon; plant–herbivore interactions; plant vigor; Sunset Crater National Monument, Arizona, USA; tree rings.*

INTRODUCTION

Plant–herbivore interactions link two major trophic levels (e.g., Hunter et al. 1992) that can have community and ecosystem-level consequences (e.g., Naiman et al. 1986, Dickson and Whitham 1996, Ritchie et al. 1998), and are of great economic concern in forestry and agriculture (e.g., Maxwell and Jennings 1980). The study of plant–herbivore interactions has spawned numerous hypotheses to explain patterns in host-plant susceptibility and resistance. These hypotheses often include important roles for nutrients (e.g., carbon and nitrogen, Bryant et al. 1983), environmental factors (e.g., plant stress, White 1969), or plant growth characteristics (e.g., plant vigor, Price 1991; adaptation to resource availability, Coley et al. 1985). Several of these hypotheses assume that there is a physiological trade-off between growth and defense in plants (e.g., Coley et al. 1985, Herms and Mattson 1992). However, empirical evidence of such a trade-off or cost of resistance in natural plant–herbivore systems is scarce

(Han and Lincoln 1995, Bergelson and Purrington 1996). Most studies have been restricted to measurements during a single season or, at most, a few seasons. The details of interactions in any given year may, however, be the result of long-term processes (e.g., delayed inducible resistance, Haukioja et al. 1985; transgenerational induction, Agrawal et al. 1999). This is especially true for trees because of their long life-spans.

The use of tree rings (dendrochronology) allows the incorporation of a broader temporal view of plant–herbivore interactions. Previous work with dendrochronology has used tree rings to reconstruct past climate, date events (fires and insect outbreaks), and estimate timber yield (e.g., LaMarche 1974, Morin et al. 1993, Swetnam and Lynch 1993, Mason et al. 1997). Recently, researchers have begun using dendrochronology to examine a range of topics in ecology, including community interactions (McLaren and Peterson 1994) and mortality patterns during severe drought (Ogle et al. 2000). In this study, we used dendrochronology to investigate differences among trees in susceptibility to an herbivore (see Craighead 1925), and to explore the potential for using tree rings in predicting future herbivory. Recent studies in other systems, including a wood-mining agromyzid fly (*Phytobia betulae*) and a

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shoot-boring moth (*Dioryctria sylvestrella*), suggest that these herbivores perform best on the trees with the largest growth rings (Ylioja et al. 1999, Sarajishvili 1997).

The interaction of pinyon pine (*Pinus edulis*) and the stem-boring moth (*Dioryctria albovittella* [Lepidoptera: Pyralidae]) at Sunset Crater National Monument, Arizona, USA, provides a model system for testing hypotheses about the role of plant growth in plant–herbivore interactions. In the southwestern U.S., this univoltine moth typically feeds only on reproductively mature *Pinus edulis* and *Pinus monophylla* (Stevens et al. 1988, Mopper et al. 1991, Cobb et al. 1997). Such development-based herbivory is common and frequently results in mature trees supporting different arthropod communities than juvenile trees (e.g., Waltz and Whitham 1997). Changes in herbivory with maturity can be due to physiological aging and/or changes in gene expression associated with maturity (e.g., Kearsley and Whitham 1997). In the fall, eggs are laid near the bud at the tip of the shoot. The following spring, larvae enter the current year's shoot growth and consume the tissue during shoot elongation, resulting in a hollow and dead shoot.

This study was conducted in an area that was denuded of vegetation by the 200-yr eruption of Sunset Crater that began in AD 1064 (Krutch 1974). On these young cinder soils, some pinyon trees are highly susceptible to moth herbivory, suffer chronic attack, and have a shrub-like growth form, whereas resistant trees are lightly attacked and have a normal upright growth form (Whitham and Mopper 1985). Susceptible trees also have reduced cone crops relative to resistant trees (Whitham and Mopper 1985), and support lower levels of mycorrhizal mutualists (Gehring and Whitham 1991). Resistant and susceptible trees grow intermixed, and allozyme analyses show that they are genetically differentiated (Mopper et al. 1991). Experimental removal of the moth results in a release effect on mycorrhizae, stem growth, and reproduction, confirming that the moth larval herbivory is responsible for depressing these traits (Whitham and Mopper 1985, Gehring and Whitham 1995).

The first objective of this study was to use dendrochronology to test whether moth herbivory also had a negative impact on the radial growth of susceptible trees. Other studies have found that chronic herbivory can depress radial growth (e.g., LaMarche and Morrow 1978). If susceptible and resistant trees have similar ring widths during the juvenile period (i.e., approximately the first 43 yr) when moth herbivory is absent, but susceptible trees have smaller ring widths than resistant trees during the mature period when moth herbivory is present, we would conclude that moth herbivory affects radial growth negatively. However, it is possible that susceptible and resistant trees will have different growth patterns during the juvenile period (when moth herbivory is absent) that indicate inherent growth differences between the groups. If susceptible trees grew less than resistant trees in juvenile years, moths would appear to prefer slow-growing hosts. If, on the other hand, susceptible trees grew more than resistant trees in juvenile years, moths would appear to prefer fast-growing hosts. In fact, a congeneric moth, *Dioryctria zimmermani*, has higher attack densities and inflicts more damage on faster growing genotypes of *Pinus sylvestris* (Wright et al. 1975). Shoot moths may prefer trees that grow faster because they invest less in defense, or have larger modules or resource sinks available for larval feeding.

Our second objective was to evaluate potential proximate causes for the differences in herbivory between susceptible and resistant trees. All conifers produce an oleoresin (a mixture of monoterpenes, resin acids, and neutral compounds) that can confer defense against herbivores. Resin production varies among conifer species, populations, and individuals within a stand (Hodges et al. 1977, 1979, Barbosa and Wagner 1989). Herbivores from squirrels to bark beetles prefer and/or attain higher reproductive success on trees with less resin (Snyder 1992, Reeve et al. 1995). In other species of *Dioryctria*, it appears that particular terpenes can serve as oviposition cues, although the evidence suggests that these cues are more important in aiding female choice of a suitable pine species than in host selection among trees within a species (Jactel et al. 1996, Dormont et al. 1997, Sadof and Grant 1997, Shu et al. 1997). Studies with pinyon pine and the stem-boring moth have found that susceptible trees had lower or similar amounts of resin exuded by cut shoots when compared to resistant trees (Mopper et al. 1991, Cobb et al. 1997). If the shoots of susceptible trees contain less resin, this could explain their relative susceptibility.

Alternatively, differences in susceptibility could be related to resource availability for the feeding larvae. Because the moth larvae bore into and mine the shoots as they elongate, females may prefer to oviposit in the largest shoots, which presumably provide the most food resources for larvae. The fact that moths attack large terminal shoots eight times more frequently than smaller lateral shoots (Whitham and Mopper 1985) also suggests that shoot size is an important factor in resource quality. Shoot size could also explain why juvenile trees are not attacked if these trees have smaller shoots than trees that have reached reproductive maturity. Many other insects, including another shoot moth, have been found to have higher attack rates and/or performance on more vigorous tissue, such as large leaves and long shoots (e.g., Whitham 1978, Craig et al. 1989, Price et al. 1990, Spiegel and Price 1996). This pattern is the foundation of the plant vigor hypothesis (Price 1991). Answers to these questions are also important to issues concerning the potential role of tree-ring analyses in reconstructing past herbivore events.

METHODS AND MATERIALS

Mature tree selection and performance

This study was conducted during 1997–1999 within the Sunset Crater National Monument, Coconino County, Arizona, USA (35°22′ N, 111°32′ W). We chose groups of mature moth-susceptible and resistant trees based on architecture that indicated past herbivory (n = 16 per group; see Whitham and Mopper 1985). Susceptible and resistant trees were intermixed within ~2 km² of woodland. We only included trees that appeared to be 60–90 yr old. Treatment groupings were validated by counting the number of current-year shoots killed by moths on each tree on 29 July 1999 and comparing groups with a Wilcoxon rank sum test. Data from similar trees nearby showed that resistant and susceptible trees do not differ in the total number of shoots. On 1 October 1999, we counted the number of current-year female conelets on each tree to quantify the suppression of female reproduction. These data were also compared with a Wilcoxon rank sum test.

Juvenile trees

We determined the typical age of first reproduction at this site by randomly selecting 60 young trees that spanned the range from prereproductive trees to trees that were entering the first one to two years of reproductive maturity, which we define as the production of female cones. All trees were cored at 20 cm height and/or sacrificed for cross sections. We could not core the trees at ground level because we needed space to turn the handle of the increment borer. Therefore, to estimate the age of each tree, we counted the number of rings present and added eight years (our estimate of the years required to reach 20 cm). The eight years at the 20-cm estimate was derived by aging the limited number of young seedlings found at our study site (n = 4). Trees under 30 cm are extremely rare at this site because already low recruitment rates have been further hampered by a long-term drought. The age estimates were integral to the design of the following dendrochronology methods so they are reported here. The average age of trees initiating female cone production was 46.9 ± 3.0 yr (mean ± 1 SE, n = 23), which was very similar to the age of trees showing the first signs of moth attack (46.3 ± 2.6 yr, n = 19). To confirm that moth attack coincides with reproductive maturity, we ran a chi-square test of independence on all 60 young trees to determine whether trees exhibiting the first signs of reproduction were more likely to be attacked by moths than trees with no evidence of reproduction.

Dendrochronology

In 1998, we extracted two cores at 20 cm height from each of the 32 mature trees. Subsequent analyses were based on the average ring width of each tree in each year. Using aging methods described above, susceptible and resistant trees did not differ in age (82.6 ± 2.4 vs.

77.6 ± 2.8 yr, respectively, $F_{1,19}$ = 1.8, P = 0.19). Thus, an average tree began growing in 1922, and became reproductive and susceptible to moth herbivory in 1965 (mean age = 46). Achieving balanced analyses required that we had data for all trees in all years, so we were forced to reduce the years examined as well as the number of trees (n = 12 susceptible and 9 resistant trees). In the juvenile years (1940–1964), when moth herbivory was absent, we were testing for evidence of inherent differences in growth between susceptible and resistant trees. In the mature years (1965–1997), we were testing for depression of radial growth (due to herbivory) in susceptible trees relative to resistant trees. Ring widths were analyzed with an ANOVA model that included susceptibility class (susceptible or resistant), year, tree-nested-within-susceptibility, and susceptibility class × year interaction. Analyses were based on raw ring widths rather than de-trended indices because these provided the most direct measure of growth, and because de-trending would have removed some of the variation among trees in which we were interested (see LaMarche 1974).

Shoot resin and size

We randomly selected three shoots from each tree and used pruning shears to remove the current year's growth (n = 16 susceptible and 16 resistant trees). Sampling was performed in the upper third of the crown, where moth herbivory is concentrated; susceptible and resistant trees do not differ in herbivory of the lower crown. After 15 min, resin beaded on the surface of the cut stem was collected in capped vials and weighed. Resin was collected on 12 May, 5 June, 18 June, and 17 September 1998. Data were analyzed with an ANOVA that included susceptibility class, tree-within-susceptibility-class, and date × susceptibility class.

We measured the size of the current-year shoots on susceptible and resistant trees to compare the food modules available to feeding larvae. We randomly chose 10 shoots in the upper crown of each tree (n = 16 susceptible and 16 resistant trees), and used calipers to measure the length of the current year's growth four times during the 1999 season. Log-transformed shoot lengths were analyzed with an ANOVA model that included susceptibility class, date, tree-within-susceptibility, and susceptibility × date.

We also examined the hypothesis that the pruning effect of herbivory alters source/sink relations such that previous attack makes trees more suitable to subsequent attack (e.g., Danell et al. 1997). We measured shoots at an adjacent site, where 33 susceptible trees had had moths experimentally removed (through controlled use of chemical pesticide) over the past 17 yr; we measured 12 shoots per tree on 17–18 May 1999 on each of 26 susceptible, 33 moth-removal, and 25 resistant trees. Square-root transformed shoot lengths were analyzed with an ANOVA model that included
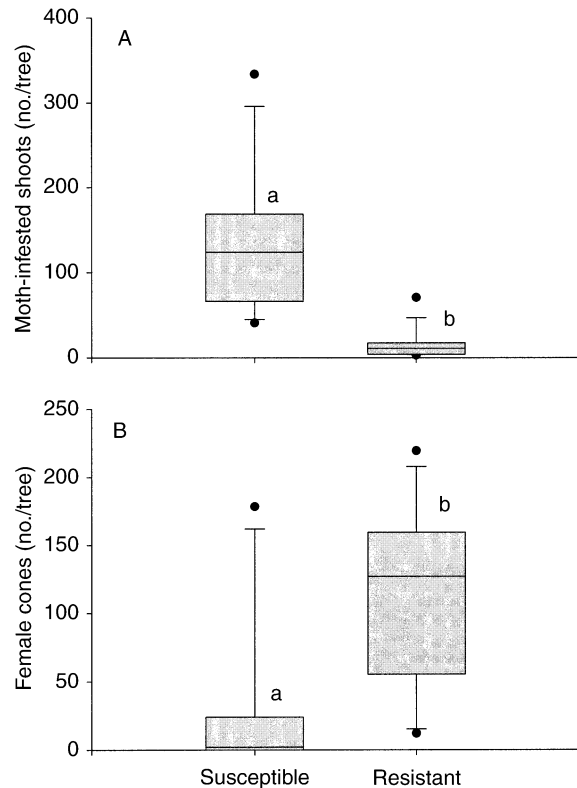
FIG. 1. (A) Relative to moth-resistant trees, susceptible trees suffered nearly 11 times the number of moth-killed shoots ($P < 0.0001$), and (B) a severe reduction in female cone production ($P < 0.001$). The ends of the boxes represent the 25th and 75th quartiles, and the line across the middle of the box identifies the median sample value. The whiskers extend to the 10th and 90th percentiles, and the solid circles represent the outliers. Significant differences between groups are indicated by different letters above each box.

treatment (susceptible vs. resistant vs. removal) and tree-nested-within-treatment.

To test if shoot size could explain why moths did not attack juvenile trees, we measured 10 shoots in the upper crown of each of the 60 young trees on 24–25 May 1999. We used a Wilcoxon rank sum test to compare shoot lengths between juvenile trees and trees in their first one to two years of reproduction.

RESULTS

Herbivory coincides with reproductive maturity

Data from young trees confirmed that moth herbivory begins during the transition to female cone production. Among the 60 young trees, those in the first one to two years of reproduction were much more likely to be attacked by moths than trees that were not yet reproductive (16 of 31 reproductive trees attacked vs. 5 of 29 nonreproductive trees; $\chi^2 = 8.1$, df = 1, $P < 0.01$). The 50% attack rate in mature trees were consistent with the normal proportion of susceptible vs. resistant trees at this site. The five nonreproductive

trees that were attacked averaged 44.4 ± 5.0 yr of age (mean $\pm$ 1 SE), suggesting that they were approaching maturity.

Impacts of herbivory on tree performance

Mature susceptible trees suffered nearly 11 times more moth-killed shoots per tree than resistant trees (Fig. 1A; median 124 vs. 11, respectively; Wilcoxson $\chi^2 = 21.8$, df = 1, $P < 0.0001$). Other studies in the same system have demonstrated similar patterns of chronic shoot mortality over a 19-yr period and experimentally shown that the removal of moths results in a release effect on tree architecture (Whitham and Mopper 1985).

Moth-susceptible trees also suffered a pronounced decline in relative fitness (Fig. 1B). During the 1999 mast cone-producing year, resistant trees produced a median of 127 cones per tree, whereas the median for susceptible trees was only two cones (Wilcoxson $\chi^2 = 11.6$, df = 1, $P < 0.001$). Other work shows that cone production rebounds when moths are experimentally removed (Whitham and Mopper 1985).

Dendrochronology reflects and predicts herbivory

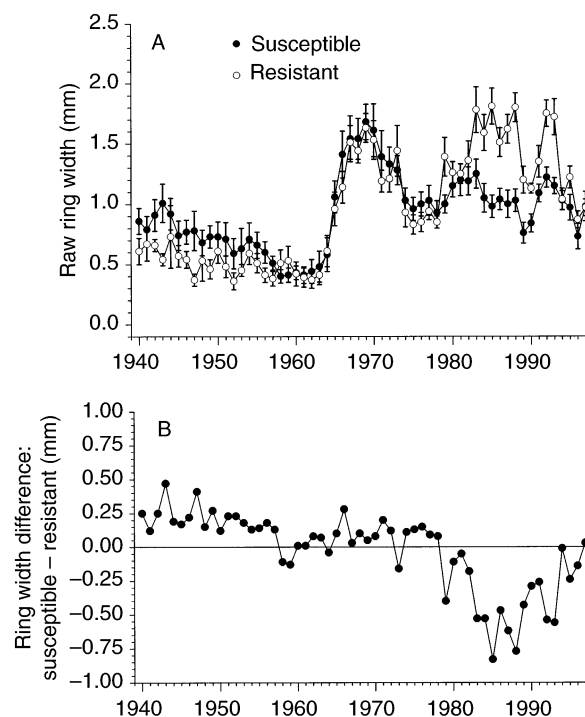Susceptible and resistant trees did not differ in average radial growth throughout their life-span (Fig. 2A;

FIG. 2. (A) Annual ring widths of moth-susceptible and resistant trees suggest that moths have negatively impacted radial growth in recent years, but during early years when herbivory was absent, susceptible trees actually grew more than resistant trees. (B) This pattern is also evident looking at the difference in ring width between susceptible and resistant groups over time.
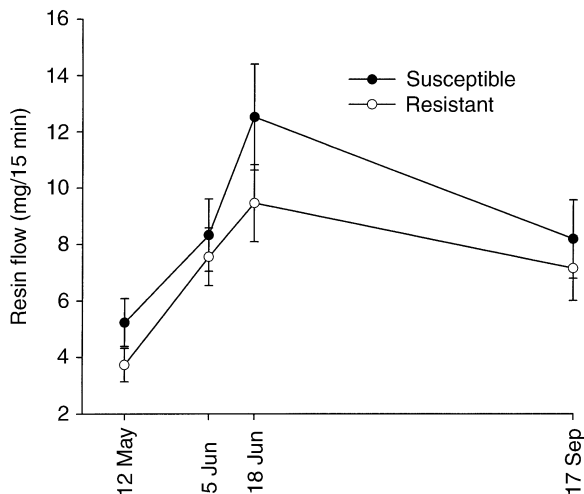
FIG. 3. Moth-susceptible and resistant trees did not differ in stem resin flow ($P = 0.25$). The early season increase is probably related to increasing temperature and stem elongation ($P < 0.0001$).

0.93 ± 0.06 vs. 0.96 ± 0.05 mm, respectively; $F_{1, 317} = 16.3$, $P = 0.17$). However, a significant susceptibility $\times$ year interaction reflected a reversal over time in the difference between groups (Fig. 2B; $F_{1, 1083} = 3.4$, $P < 0.0001$). In the absence of moth herbivory (1940–1964), ring widths on trees that would later become susceptible averaged 29% greater than resistant trees (Fig. 2B; 0.66 ± 0.03 vs. 0.51 ± 0.02 mm), but once they were exposed to moth herbivory (1965–1998), ring widths on susceptible trees averaged 13% smaller than the ring widths of resistant trees (Fig. 2B; 1.13 ± 0.04 vs. 1.30 ± 0.05 mm). For both resistant and susceptible trees, a pronounced increase in growth began in the early 1960s (Fig. 2A; effect of year: $F_{1, 1102} = 237.4$, $P < 0.0001$). Because the same increase in growth was also observed in adjacent, much older pinyon trees, as well as older ponderosa pines (*Pinus ponderosa*; J. Ruel and T. Whitham, *unpublished data*), this change was apparently due to an environmental effect and unrelated to tree age.

Potential mechanisms

The amount of oleoresin exuded by shoots did not appear to be the proximate cause of differences in herbivory. Shoot resin flow did not differ between susceptible and resistant trees (Fig. 3; $F_{1,30} = 1.4$, $P = 0.25$), although trees varied significantly within groups ($F_{30, 337} = 6.2$, $P < 0.0001$). Resin flow increased through the early summer, presumably reflecting the combined effects of warmer temperatures and elongating stems (Fig. 3; date effect, $F_{30, 337} = 20.3$, $P < 0.0001$).

Although oleoresin failed to predict susceptibility to moths, we found that susceptible trees offer greater food resources for moth larvae in the form of larger shoots (Fig. 4; $F_{1,30} = 14.6$, $P < 0.001$). In early spring,

when buds were just beginning to elongate, the current-year shoots of susceptible trees were 33% larger than resistant trees. These differences persisted and increased throughout the spring and early summer. The pattern was not a consequence of chronic herbivory, because susceptible trees that had been protected from moths for 17 yr still had larger shoots than resistant trees (Fig. 5; $F_{2,81} = 6.7$, $P < 0.01$; $P < 0.05$ for contrast between resistant trees vs. susceptible removal treatment). Mean values for susceptible, moth-removal, and resistant were 18.4 mm, 16.6 mm, and 14.1 mm, respectively.

Shoot size may explain why moths mainly attack reproductively mature trees. Among 60 young trees, those that were beginning to reproduce had current-year shoots 31% larger than those on nonreproductive trees (median 15.5 vs. 11.8 mm, respectively; Wilcoxson $\chi^2 = 15.8$, df $= 1$, $P < 0.0001$). Thus, we found an increase in shoot lengths associated with the shift from the juvenile to the mature phase that coincides with the timing of the onset of moth herbivory.

DISCUSSION

Juvenile and mature trees face different selection pressures

The trees that grew fastest as juveniles grew the slowest as adults and had the lowest reproductive success (Figs. 1 and 2). This switch in performance may reflect changing selection pressures. The xeric cinder environment is probably a major source of seedling and juvenile mortality. Temperatures 10 cm below the soil surface can be as high as 55°C. We postulate that there is strong selection for trees able to grow rapidly during
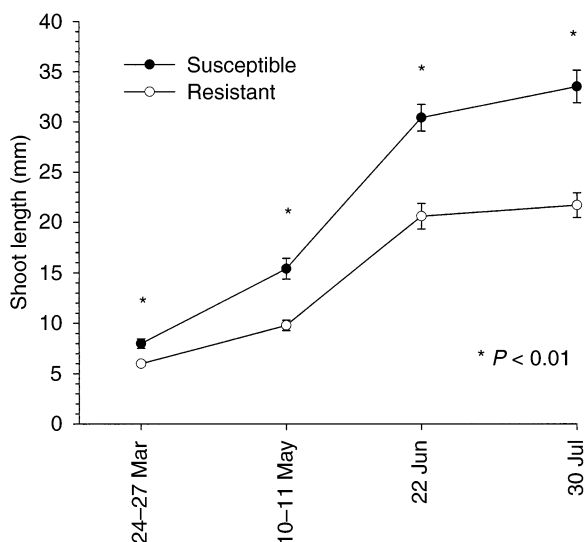

FIG. 4. Moth-susceptible trees had consistently larger shoots than resistant trees (50% longer on average; $P < 0.001$; significant differences [$P < 0.05$] within dates marked with *). The increase over time reflects shoot elongation during the growing season.
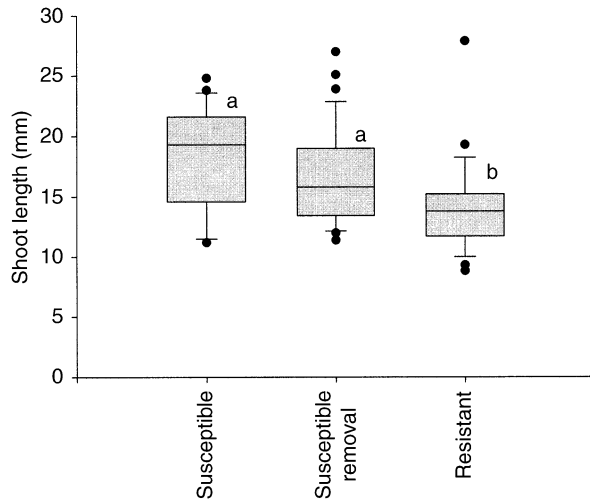
FIG. 5. Using another set of trees at an adjacent site, moth-susceptible trees had longer shoots than resistant trees ($P < 0.01$). Even after 17 yr of moth removal, susceptible trees still had shoots that were larger than resistant trees ($P < 0.05$). The ends of the boxes represent the 25th and 75th quartiles, and the line across the middle of the box identifies the median sample value. The whiskers extend to the 10th and 90th percentiles, and the solid circles represent the outliers. Significant differences between groups are indicated by different letters above each box.

juvenile years to escape the high temperatures of the surface and upper soil. Growing the shoot taller, the roots deeper, and the bole thicker would all help buffer the seedling against extreme temperatures.

The onset of female cone production coincides with the introduction of another selection pressure: herbivory by the stem-boring moth. Herbivory appears to coincide with the age of first reproduction because of a concurrent increase in shoot size, the food module for the larvae. When surviving trees reach maturity, those with intrinsically rapid growth encounter the most extreme herbivory from moths (Figs. 1 and 2). The result of these conflicting selection pressures is that, by suppressing growth and reproduction, moth herbivory turns the most vigorous juvenile trees into the slowest growing and poorest reproducing mature trees. The differences in cone counts probably underestimate the negative impact of herbivory on reproduction because susceptible trees also suffer a decline in seed size and viability (B. Wade and T. G. Whitman, *unpublished data*), and because Clark's Nutcrackers, which are important dispersal agents, preferentially visit trees with large cone crops (Christensen et al. 1991). Thus, the advantages of rapid early growth at this arid site are opposed by increased herbivory during maturity.

The ecological and evolutionary implications of a shift in selection pressures with tree age will be most important if the differences between susceptible and resistant trees are genetically based. In a similar system, genotypes of *Pinus sylvestris* that grew more

quickly suffered more damage from *Dioryctria zimmermani* (Wright et al. 1975). Several lines of evidence indicate that differences between susceptible and resistant pinyons in our study are also genetically based. First, allozyme analyses revealed significant differences in allelic frequencies and heterozygosity between susceptible and resistant trees (Mopper et al. 1991). Second, 19 yr of study on individual trees shows that trees do not switch groups; susceptible trees suffer higher rates of attack year after year (Whitham and Mopper 1985, Cobb et al. 1997). Third, microsite environmental factors are unlikely because susceptible and resistant trees often grow side by side, emerging from the ground only inches apart, and soils under the two tree types do not differ in nutrient or water availability (Gehring and Whitham 1991).

As a result of these combined impacts, moths may be exerting a pressure that selects against high growth in pinyons at this site. Susceptible trees (1) had higher radial growth when young, (2) have larger shoots today, but greatly altered architectures, (3) are genetically differentiated from resistant trees, and (4) suffer from severely reduced female cone production. Other evidence for insects playing a role in the evolution of plants mostly concerns the evolution of plant defensive compounds and the potential for coevolution in pollination scenarios (Ehrlich and Raven 1964, Price 1997). Many other studies assume or offer evidence that radial growth in woody tree species is a good correlate of fitness (e.g., Coyea and Margolis 1994). In this case, however, the trees that, for the first 43 yr, would appear most fit suffer from reduced growth and limited cone production as adults. Herbivores may be stronger agents of natural selection than previously appreciated.

Given the selective pressure exerted by moths, why do susceptible genotypes persist in the population? The population is young; pinyons are colonizing very recent volcanic soil (≤ 800 yr old) on which primary succession is still taking place. In combination with a long-lived tree species, we would not expect dramatic changes in just a few tree generations. Furthermore, changes in gene frequencies will be limited if there is significant gene flow from other nearby sites where susceptible genotypes grow in older soils and do not suffer from the negative effects of herbivory. It is also possible that increased male function may compensate for the loss of female function (Cobb et al. 2002). Yet another possible scenario is that the genotypes persist because, except in the wettest years, recruitment is much higher in susceptible trees because of their higher juvenile growth rates.

Support for plant vigor hypothesis

Three different lines of evidence all indicate that the proximate cause for susceptibility to moth attack is large shoots that provide large food modules for feeding larvae: (1) susceptible mature trees have larger shoots than resistant trees (Fig. 4), (2) terminal shoots,

which are larger than lateral shoots, are attacked preferentially, and (3) the development of susceptibility is linked to an increase in shoot size as trees age. A congeneric species, *Dioryctria sylvestrella*, also seems to track the vigor of its host (Sarajishvili 1997). Large shoots may be important to larvae for several reasons. First, large modules are less physically constraining. Small shoots may not provide viable habitat for late instar larvae, because the inside diameter of the shoots is less than the head capsule width of the larvae of *Dioryctria albovittella*. Second, larger modules may offer better protection from predators and parasites (e.g., Weis et al. 1985, Price and Pschorn-Walcher 1988). Individual larvae kill one to three shoots during development. During transit from one shoot to the next, the larvae probably experience a high risk of predation, as well as exposure to the environment. Survival could be higher on trees with larger shoots if larvae have to travel less often and less far to new shoots. Third, larger modules may afford better nutrition and/or be less well defended.

Plant growth and defense

Numerous studies indicate lower constitutive defenses in plants or plant modules that are dominated by growth processes as opposed to differentiation (Herms and Mattson 1992, Han and Lincoln 1995, Lombardero et al. 2000). In fact, our dendrochronology and shoot size results alone would be consistent with an optimal allocation hypothesis involving a trade-off between growth and defense (e.g., Coley et al. 1985; Herms and Mattson 1992). It might appear that the susceptible trees suffer increased herbivory because they invest more in growth and less in defense. However, susceptible and resistant trees did not differ in resin flow (Fig. 3), suggesting that differences in constitutive plant defenses probably cannot explain observed differences in herbivory. Similarly, Latta and Linhart (1997) found that differences in herbivory by *Dioryctria auranticella* on *Pinus ponderosa* did not relate to tree-to-tree differences in resin flow or monoterpene composition. Perhaps for these trees, the real cost of investment in growth is not the opportunity cost (diverting resources away from defense), but instead, the simple cost that larger modules suffer an increased probability of attack by the moth.

Neonate larvae are not very mobile, so the selection of host trees (and shoots) is largely a function of oviposition behavior. However, the extent to which female adults preferentially oviposit in large shoots or the proximate cues that they employ remain unknown. In some shoot-galling sawflies, ovipositing females appear to use chemoreception to pick the largest shoots (Kolehmainen et al. 1994, Roininen et al. 1999).

Predicting present and future conditions

Several general issues arise from these studies that are relevant in using the past to predict present and future conditions. Understanding chronic and current levels of herbivory required examination of dendrochronological data going back 60 yr. During juvenile years, when moth herbivory was absent, trees that later became susceptible grew more vigorously than trees that would be resistant when they matured (Fig. 2). Another recent study that stresses the need to examine the past to understand current interactions involves induced progeny that resulted from herbivore-attacked mother plants (Agrawal et al. 1999). Many dendrochronology studies have sought to date past events, including insect outbreaks, or reconstruct climate history. Our study shows that growth in the juvenile phase can predict herbivory in the mature phase.

Our study also suggests that genetic variation in resistance to herbivores can be an important factor affecting the interpretation of tree rings. The fact that moth-resistant and susceptible trees exhibit different lifetime growth patterns suggests that the interaction of herbivory and plant genetics can be important in interpreting the dendrochronological signal. Although other studies have demonstrated that herbivores can impact tree rings (e.g., LaMarche 1974, Morin et al. 1993, Swetnam and Lynch 1993, Mason et al. 1997), the different impacts of resistant and susceptible genotypes has not been previously been considered.

Lastly, global change is predicted to result in increasingly arid continental interiors that experience more frequent and intense droughts, with semi-arid ecosystems among the most sensitive (Risser 1995, Allen and Breshears 1998). Because Sunset Crater already suffers from chronic environmental stress and herbivory, trees here are likely to be especially sensitive to further global changes, and may serve as barometers in revealing how natural and anthropogenic perturbations affect population, community, and ecosystem-level processes (Brown et al. 2001). In such marginal or ecotonal environments, tree rings may be especially sensitive to perturbations, and allow us to integrate diverse factors that would be harder to interpret in more benign habitats where tree rings might be more complacent. For example, Ogle et al. (2000) found that during a recent drought, pinyons at Sunset Crater were 2.5 times more likely to die, and exhibited greater variation in ring widths relative to pinyons growing in nearby, more favorable sandy-loam soils. Other examples of how marginal or ecotonal populations are barometers of climate change and can result in major habitat shifts have been developed by Betancourt et al. (1993), Allen and Breshears (1998), and Swetnam and Betancourt (1998).

LITERATURE CITED

Agrawal, A. A., C. LaForsch, and R. Tollrian. 1999. Transgenerational induction of defences in animals and plants. Nature (London) **401**:60–63.

Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proceedings of the National Academy of Sciences (USA) **95**:14839–14842.

Barbosa, P., and M. R. Wagner. 1989. Introduction to forest and shade tree insects. Academic Press, San Diego, California, USA.

Bergelson, J., and C. B. Purrington. 1996. Surveying patterns in the cost of resistance in plants. American Naturalist **148**:536–558.

Betancourt, J. L., E. A. Pierson, K. A. Rylander, J. A. Fairchild-Parks, and J. S. Dean. 1993. Influence of history and climate on New Mexico piñon–juniper woodlands. Pages 42–62 *in* E. F. Aldon and D. W. Shaw, editors. Managing piñon–juniper ecosystems for sustainability and social needs. USDA Forest Service Technical Report RM-236.

Brown, J. H., T. G. Whitham, S. K. Morgan Ernest, and C. A. Gehring. 2001. Complex species interactions and the dynamics of ecological systems: long-term experiments. Science **293**:643–650.

Bryant, J. P., F. S. Chapin, III, and D. R. Klein. 1983. Carbon/nutrient balance in boreal plants in relation to vertebrate herbivory. Oikos **40**:357–368.

Christensen, K. M., T. G. Whitham, and R. P. Balda. 1991. Discrimination among pinyon pine trees by Clark's Nutcrackers: effects of cone crop size and cone characters. Oecologia **86**:402–407.

Cobb, N. S., S. Mopper, C. A. Gehring, M. Caouette, K. M. Christensen, and T. G. Whitham. 1997. Increased moth herbivory associated with environmental stress of pinyon pine at local and regional levels. Oecologia **109**:389–397.

Cobb, N. S., R. T. Trotter, III, and T. G. Whitham. 2002. Long-term sexual allocation in herbivore-resistant and susceptible pinyon pine (*Pinus edulis*). Oecologia **130**:78–87.

Coley, P. D., J. P. Bryant, and F. S. Chapin, III. 1985. Resource availability and plant antiherbivore defense. Science **230**:895–899.

Coyea, M. R., and H. A. Margolis. 1994. The historical reconstruction of growth efficiency and its relationship to tree mortality in balsam fir ecosystems affected by spruce budworm. Canadian Journal of Forest Research **24**:2208–2221.

Craig, T. P., J. K. Itami, and P. W. Price. 1989. A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. Ecology **70**:1691–1699.

Craighead, F. C. 1925. Relation between mortality of trees attacked by the spruce budworm (*Cacoecia fumiferana* Clem.) and previous growth. Journal of Agricultural Research **XXX**:541–555.

Danell, K., E. Haukioja, and K. Huss-Danell. 1997. Morphological and chemical responses of mountain birch leaves and shoots to winter browsing along a gradient of plant productivity. Ecoscience **4**:296–303.

Dickson, L. L., and T. G. Whitham. 1996. Genetically-based plant resistance traits affect arthropods, fungi, and birds. Oecologia **106**:400–406.

Dormont, L., A. Roques, and C. Malosse. 1997. Efficiency of spraying mountain pine cones with oleoresin of Swiss stone pine cones to prevent insect attack. Journal of Chemical Ecology **23**:2261–2274.

Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution **18**:586–608.

Gehring, C. A., and T. G. Whitham. 1991. Herbivore-driven mutualism in insect-susceptible pinyon pine. Nature (London) **353**:556–557.

Gehring, C. A., and T. G. Whitham. 1995. Duration of herbivore removal and environmental stress affect the ectomycorrhizae of pinyon pines. Ecology **76**:2118–2123.

Han, K., and D. E. Lincoln. 1995. The evolution of carbon allocation to plant secondary metabolites: a genetic analysis of cost in *Diplacus aurantiacus*. Evolution **48**:1550–1563.

Haukioja, E., J. Suomela, and S. Neuvonen. 1985. Long-term inducible resistance in birch foliage: triggering cues and efficacy on a defoliator. Oecologia **65**:363–369.

Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. Quarterly Review of Biology **67**:283–335.

Hodges, J. D., W. W. Elam, and W. F. Watson. 1977. Physical properties of the oleoresin system of the four major southern pines. Canadian Journal of Forest Research **7**:520–525.

Hodges, J. D., W. W. Elam, W. F. Watson, and T. E. Nebeker. 1979. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera: Scolytidae) attacks. Canadian Entomologist **111**:889–896.

Hunter, M. D., T. Ohgushi, and P. W. Price. 1992. Effects of resource distribution on animal–plant interactions. Academic Press, San Diego, California, USA.

Jactel, H., M. Kleinhentz, A. Marpeau-Bezard, F. Marion-Poll, P. Menassieu, and C. Burban. 1996. Terpene variations in maritime pine constitutive oleoresin related to host tree selection by *Dioryctria sylvestrella* Ratz. Journal of Chemical Ecology **22**:1037–1050.

Kearsley, M. J. C., and T. G. Whitham. 1997. The developmental stream of cottonwoods affects ramet growth and resistance to herbivory by galling aphids. Ecology **79**:178–191.

Kolehmainen, J., H. Roininen, R. Julkunen-Tiitto, and J. Tahvanainen. 1994. Importance of phenolic glucosides in host selection of shoot galling sawfly, *Euura amerinae*, on *Salix pentandra*. Journal of Chemical Ecology **20**:2455–2466.

Krutch, J. W. 1974. The paradox of lava flow. Southwest Parks and Monuments Association. Phoenix, Arizona, USA.

LaMarche, V. C., Jr. 1974. Paleoclimatic inferences from long tree-ring records. Science **183**:1043–1048.

LaMarche, V. C., Jr., and P. A. Morrow. 1978. Tree ring evidence for chronic insect suppression of productivity in subalpine *Eucalyptus*. Science **201**:1244–1246.

Latta, R. G., and Y. B. Linhart. 1997. Path analysis of natural selection on plant chemistry: the xylem resin of ponderosa pine. Oecologia **109**:251–258.

Lombardero, M. J., M. P. Ayres, P. L. Lorio, Jr., and J. J. Ruel. 2000. Environmental effects on constitutive and inducible resin defenses of loblolly pine. Ecology Letters **3**:329–339.

Mason, R. R., B. E. Wickman, and H. G. Paul. 1997. Radial growth response of Douglas-fir and grand fir to larval densities of the Douglas-fir tussock moth and the western spruce budworm. Forest Science **43**:194–205.

Maxwell, F. G., and P. R. Jennings. 1980. Breeding plants resistant to insects. John Wiley and Sons, New York, New York, USA.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose and tree rings on Isle Royale. Science **266**:1555–1558.

Mopper, S., J. B. Mitton, T. G. Whitham, N. S. Cobb, and K. M. Christensen. 1991. Genetic differentiation and heterozygosity in pinyon pine associated with resistance to herbivory and environmental stress. Evolution **45**:989–999.

Morin, H., D. Laprise, and Y. Bergeron. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Canadian Journal of Forest Research **23**:1497–1506.

Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Eco-system alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology **67**:1254–1269.

Ogle, K., T. G. Whitham, and N. S. Cobb. 2000. Tree-ring variation in pinyon predicts likelihood of death following severe drought. Ecology **81**:3237–3243.

Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. Oikos **62**:244–251.

Price, P. W. 1997. Insect ecology. John Wiley and Sons, New York, New York, USA.

Price, P. W., N. Cobb, T. P. Craig, G. Wilson Fernandes, J. K. Itami, S. Mopper, and R. W. Preszler. 1990. Insect herbivore population dynamics on trees and shrubs: new approaches relevant to latent and eruptive species and life table development. Pages 2–38 *in* E. A. Bernays, editor. Insect-plant interactions. CRC Press, Boca Raton, Florida, USA.

Price, P. W., and H. Pschorn-Walcher. 1988. Are galling insects better protected against parasitoids than exposed feeders? A test using tenthredinid sawflies. Ecological Entomology **13**:195–205.

Reeve, J. D., M. P. Ayres, and P. L. Lorio, Jr. 1995. Host suitability, predation, and bark beetle population dynamics. *In* Population dynamics: new approaches and synthesis. Pages 339–357 *in* N. Cappuccino and P. W. Price, editors. Academic Press, San Diego, California, USA.

Risser, P. G. 1995. The status of the science of examining ecotones. Bioscience **45**:318–325.

Ritchie, M. E., D. Tilman, and J. M. H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology **79**:165–177.

Roininen, H., P. W. Price, R. Julkunen-Tiitto, J. Tahvanainen, and A. Ikonen. 1999. Oviposition stimulant for a gall-inducing sawfly, *Euura lasiolepis*, on willow is a phenolic glucoside. Journal of Chemical Ecology **25**:943–953.

Sadof, C. S., and G. G. Grant. 1997. Monoterpene composition of Pinus sylvestris varieties resistant and susceptible to *Dioryctria zimmermani*. Journal of Chemical Ecology **23**:1917–1927.

Sarajishvili, K. G. 1997. Dendrochronological indication of entomoresistance in *Pinus eldarica* against *Dioryctria sylvestrella* Ratz (Lepidoptera, Pyralidae) in Georgia. Acta Phytopathologica et Entomologica Hungarica **32**:245–250.

Shu, S., G. G. Grant, D. Langevin, D. A. Lombardo, and L. MacDonald. 1997. Oviposition and electroantennogram responses of *Dioryctria abietivorella* (Lepidoptera: Pyralidae) elicited by monoterpenes and enantiomers from eastern white pine. Journal of Chemical Ecology **23**:35–50.

Snyder, M. A. 1992. Selective herbivory by Abert's squirrel mediated by chemical variability in ponderosa pine. Ecology **73**:1730–1741.

Spiegel, L. H., and P. W. Price. 1996. Plant aging and the distribution of *Rhyacionia neomexicana* (Lepidoptera: Tortricidae). Environmental Entomology **25**:359–365.

Stevens, R. E., L. D. Merrill, and J. W. Brewer. 1988. *Dioryctria albovittella* (Hulst) (Lep., Pyralidae) in shoots and cones of pinyon (*Pinues edulis* Engelm.) in Colorado. Journal of Applied Entomology **105**:387–392.

Swetnam, T. W., and J. L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climate variability in the American Southwest. Journal of Climate **11**:3128–3147.

Swetnam, T. W., and A. M. Lynch. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. Ecological monographs **63**:399–424.

Waltz, A. M., and T. G. Whitham. 1997. Plant development affects arthropod communities: opposing impacts of species removal. Ecology **78**:2133–2144.

Weis, A. E., W. G. Abrahamson, and K. D. McCrea. 1985. Host gall size and oviposition success by the parasitoid *Eurytoma gigantea*. Ecological Entomology **10**:341–348.

White, T. C. R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. Ecology **50**:905–909.

Whitham, T. G. 1978. Habitat selection by *Pemphigus* gall aphids in response to resource limitation and competition. Ecology **59**:1164–1176.

Whitham, T. G., and S. Mopper. 1985. Chronic herbivory: impacts on architecture and sex expression of pinyon pine. Science **228**:1089–1091.

Wright, J. W., L. F. Wilson, and J. N. Bright. 1975. Genetic variation in resistance of Scotch pine to Zimmerman pine moth. Gt. Lakes Entomol. **8**:231–236.

Ylioja, T., H. Roininen, M. P. Ayres, M. Rousi, and P. W. Price. 1999. Host-driven population dynamics in an herbivorous insect. Proceedings of the National Academy of Science **96**:10735–10740.