

Regulation of ponderosa pine foliar physiology and insect resistance mechanisms by basal area treatments

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Received April 25, 1997

Summary We compared foliar physiology and several measures of tree resistance to insect attack among ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.) trees growing in thinned stands. Measurements were made in a second-growth ponderosa pine forest in northern Arizona where the basal area treatments (6.9, 18.4, 27.6, 78.2 m² ha⁻¹) have been experimentally maintained by frequent thinnings for 32 years before our measurements began in 1994. Most of the physiological characteristics measured were affected by the basal area treatments. As stand basal area increased from 6.9 to 78.2 m² ha⁻¹, predawn water potential, midday water potential, net photosynthetic rate, resin production, phloem thickness, and foliar toughness decreased. Foliar nitrogen concentration was greatest in trees in the intermediate basal area treatments. Our results show that the physiological condition of second-growth ponderosa pine can be manipulated by silvicultural control of stand basal area, and support the hypothesis that high stand basal area increases tree stress and decreases tree resistance to insect attack.

Keywords: Arizona, foliar toughness, herbivory, phloem thickness, photosynthesis, *Pinus ponderosa*, resin, thinning, water relations.

Introduction

Numerous silvicultural experiments on ponderosa pine have shown that reduction of stand basal area by thinning increases individual tree growth (Schubert 1971, Oliver 1979, Ronco et al. 1985, Cochran and Barrett 1993), and reduces the risk of attack by some insects, especially pine bark beetles (Sartwell and Stevens 1975, Larsson et al. 1983, Schmid et al. 1994, Olsen et al. 1996). However, our understanding of why dense ponderosa pine stands are more susceptible to insect attack is incomplete. The tree resistance hypothesis (Berryman 1976, Berryman 1978, Mitchell et al. 1983) assumes that trees in dense stands are more susceptible because intense resource competition among trees limits resource allocation to resistance mechanisms, such as resin production. If this hypothesis is correct, then trees in high basal area stands should have lower rates of resource capture and weaker defensive capability against insect attack than trees in low basal area stands. To date, the tree resistance hypothesis has not been rigorously tested for ponderosa pine in the southwestern United States,

and few studies have addressed whether and how stand density affects the physiological condition of ponderosa pine (Schmid et al. 1991, Covington et al. 1997).

The effects of stand density, basal area, and thinning on tree water and carbon relations have been studied for several conifers (e.g., Wambolt 1973, Sucoff and Hong 1974, Whitehead et al. 1984, Donner and Running 1986, Aussenac and Granier 1988, Cregg et al. 1990, Ginn et al. 1991, Schmid et al. 1991). However, the results have been inconsistent. For example, previous studies of the effects of thinning on water relations of conifers have indicated little or no effect of thinning on leaf water potential (Cregg et al. 1990, Schmid et al. 1991), a decrease in leaf water potential in thinned versus unthinned stands (Whitehead et al. 1984, Ginn et al. 1991), and an increase in leaf water potential in thinned versus unthinned stands (Sucoff and Hong 1974, Donner and Running 1986, Aussenac and Granier 1988). In the only study on the effect of stand thinning on the physiological condition of ponderosa pine trees, Schmid et al. (1991) found that predawn and midday water potentials did not differ among stand basal area treatments one to three years following treatment.

We compared the effects of four stand basal area treatments on several measures of tree physiological condition and resistance against insect attack in a second-growth ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.) forest in northern Arizona. Our study site is unique because the same basal areas have been maintained by frequent thinnings for 32 years prior to our measurements in 1994 (Ronco et al. 1985). We hypothesized that trees in high basal area stands would be more stressed and would have lower defensive capability against insect attack than trees in low basal area stands.

Methods and materials

Study site

The study site is Taylor Woods, a portion of the Fort Valley Experimental Station (35°16'11" N, 111°44'30" W) located within the Coconino National Forest approximately 15 km northwest of Flagstaff, Arizona. Topography of the area is gentle (slopes less than 5%) with a southwest aspect and an elevation of 2,266 m. Soils at Taylor Woods are derived from basalt and volcanic cinders and are classified in the montmoril-

lonitic complex of frigid Typic Argiborolls and Argiboralfs (Wollum and Schubert 1975, Ronco et al. 1985). Vegetation at Taylor Woods consists of a forest overstory of the Rocky Mountain variety of ponderosa pine (*Pinus ponderosa* var. *scopulorum*) and an understory dominated by grasses and a variety of forbs.

Mean annual temperature from 1909 to 1990 near the study site was 6.0 °C and mean annual precipitation was 56.4 cm with about half of this amount typically occurring as snow (Schubert 1974, NOAA 1990). Monthly precipitation at the study site is typically lowest in May and June, averaging 1.8 and 1.0 cm, respectively. The average frost-free growing season is 94 days (Schubert 1974). In the year of our study (1994), total precipitation between January and September near the study site was about 6% above the long-term average.

Stand history

In 1962, an experiment designed to determine the effects of thinning on ponderosa pine growth was initiated by the USDA Forest Service at Taylor Woods (Myers 1967, Ronco et al. 1985). Before 1962, Taylor Woods contained a variable-aged overstory of sawtimber-sized trees and an even-aged understory of ponderosa pine saplings, most of which established in 1919 (Ronco et al. 1985, Savage et al. 1996). All sawtimber was harvested in 1962, leaving the saplings.

The experiment consisted of six basal area treatments (6.9, 13.8, 18.4, 23.0, 27.6, 34.4 m² ha⁻¹) and an unthinned control applied to the stand in a completely random design with three replications of each treatment. The treatments were established by thinning each plot to leave an evenly spaced population of saplings with large, healthy crowns. The first thinning took place in 1962, and subsequent thinnings were performed in 1972, 1982, and 1992 to maintain the specified basal areas.

In all treatments, tree growth increased after thinning (Schubert 1971, Ronco et al. 1985). Trees in the 6.9 m² ha⁻¹ basal area treatment increased in growth in the first year after thinning, whereas trees in the 27.6 and 34.4 m² ha⁻¹ basal area treatments did not respond until the third year after thinning. Twenty years after the original thinning, periodic annual diameter growth and average diameter were negatively related to basal area, with a two- to threefold difference in periodic annual diameter growth and a two-thirds difference in average diameter between the highest and lowest basal area treatments. In contrast, plot volume increment was positively related to basal area because of greater tree densities in the high basal area treatments than in the low basal area treatments.

For our study, we selected two replications of each of four treatments, representing a range of current basal areas: 6.9, 18.4, 27.6 m² ha⁻¹, and the unthinned control (78.2 m² ha⁻¹). Measurements of basal areas of these plots in 1994 confirmed that the specified basal areas had been closely maintained by the thinning treatments.

Tree water relations

Every two weeks between late May and early September 1994, we measured needle water potentials at predawn and midday with a pressure chamber (Model 1000, PMS Instruments,

Corvallis, OR) of trees growing in each basal area treatment. We used a total of ten trees located in the middle of each replication of each basal area treatment (Table 1) for the water potential measurements; two of these trees were randomly selected for measurement on each date. For the predawn measurements, we collected needles between 0400 and 0530 h at every measurement period and measured the water potential of both replications of all basal area treatments on the same day. For the midday measurements, we measured one replication of each basal area treatment on one day, and measured the other replication of each basal area treatment on the next day. On each day, we collected needles for the midday measurements from all treatments from the most sunlit branches in the canopy within one hour; this 1-hour interval occurred between 1000 and 1300 h, depending on the day. In May, June, and July, all measurement dates had clear skies so that needles for the midday measurements were sampled from branches exposed to full sun. After the onset of regular thundershowers in August and September, skies were frequently cloudy so that the tree crowns were typically shaded by clouds during at least some of the day.

For each tree, we measured water potential on needles sampled from one twig from the lower third of the crown, and on needles sampled from one twig from the upper third of the crown. Immediately following excision of a twig from the crown with pole pruners, one-year-old needles (elongated in 1993) were cut from the twig with a razor blade and sealed in a plastic bag containing a damp towel and stored under dark, cool conditions for up to 4 h before measurement. This procedure of sampling and storage yielded water potential measurements that were similar to those made immediately after excision of needles from the tree (Kaufmann and Thor 1982, J.E. Stone and T.E. Kolb, unpublished data). We measured water potential on needles from each twig until three values were within 0.1 MPa of each other. The mean of these three values was used as the water potential of the twig.

Foliar nitrogen concentration

We measured total foliar nitrogen concentration on one-year-old needles from the same twigs that were sampled for water potential in late May and early September. Leaf tissue was ground (< 0.85 mm) and digested by a micro-Kjeldahl method (Issac and Johnson 1976). Nitrogen concentration was measured with a Lachat flow-injection analyzer (QuikChem Systems 1992) and expressed on a mass per mass basis.

Table 1. Mean and range of diameters at breast height of ponderosa pine trees growing at four basal area treatments ($n = 10$).

	Basal area (m ² ha ⁻¹)			
	6.9	18.4	27.6	78.2
Mean (cm)	40.9	30.5	26.7	10.7
Range (cm)	35.3–44.7	26.4–35.6	22.8–31.2	9.1–11.7

Foliar gas exchange

We measured net photosynthetic rate and stomatal conductance to water vapor on one-year-old needles attached to the same twigs sampled for midday water potential measurements. Immediately following excision of the twig from the crown, two fascicles (six needles) were placed in a 250-ml cuvette attached to an LI-6200 portable photosynthesis system (Li-Cor Inc., Lincoln, NE) and water and CO₂ fluxes were measured over 30 s. Photosynthetic light-saturating conditions (>1000 μmol m⁻² s⁻¹; Kolb and Robberecht 1996) were created by natural sunlight (May, June, and July) or by illumination with a projector lamp (approximately 15% of all measurements in August and September). During measurement, water vapor pressure and temperature in the cuvette were generally within 10% and 3 °C of ambient values, respectively. Preliminary studies showed that the net photosynthetic rates of ponderosa pine needles on detached twigs do not differ from those of needles attached to the tree under our experimental conditions (J.E. Stone and T.E. Kolb, unpublished data). We calculated net photosynthetic rate and stomatal conductance on the basis of total needle surface area. Total needle surface area was estimated by measuring the length and diameter of the needle portions contained in the gas exchange cuvette and by assuming that each fascicle approximated a cylinder (Svenson and Davies 1992).

Insect resistance mechanisms

We measured two mechanisms of tree resistance to insect attack in each basal area treatment. The first mechanism is resin production in response to wounding. On June 20, 1994, we wounded five trees in each of two replications per basal area treatment. We created the wounds by hammering a 2.54-cm diameter Osborne arch punch (Model 149, King Bearing Co., Flagstaff, AZ) through the bark, phloem, and cambium to the outside of the xylem. Each tree was wounded twice (north and south sides) 1 m above the soil surface. We collected the resin with funnels attached to test tubes over two measurement times: the first 24 h after wounding, and until all resin flow had stopped. All trees were monitored frequently and test tubes were changed to prevent over filling. We also measured phloem thickness with a digital micrometer on the phloem extracted by the wounding procedure.

We measured the second resistance mechanism, foliage toughness, with a penetrometer (TA-XT2 Texture Analyzer, Texture Technologies Corp., Scarsdale, NY) on one-year-old needles sampled from the same twigs used for the water potential measurements, except for twigs collected on June 28 when toughness was not measured. Following excision from the tree, the twig was immediately sealed in a plastic bag, placed in a dark cooler containing ice, and transported to the laboratory where toughness was measured within 6 h of field collection. The penetrometer measures the amount of pressure (mass per area) required to penetrate the surface of the needle. A constant needle tip surface area was used for all measurements, thus differences in toughness are expressed in units of mass (g). We measured toughness at three locations in the middle of each of five representative needles on each twig.

Statistical analysis

Differences in all measured variables among basal area treatments on each date were tested by ANOVA calculated with the SAS software package (SAS Institute, Cary, NC). For resin and phloem characteristics, basal area was the only factor in the ANOVA. For foliar gas exchange variables, nitrogen concentration, water potential, and foliar toughness, factors in the ANOVA were basal area, crown position, and their interaction. Day was an additional factor in the ANOVA on midday water potential and foliar gas exchange characteristics to account for variation between the two days used for measurements during each two-week sampling interval. All ANOVAs of tree variables were performed on averages for the two to five trees sampled in each replication. Resin production data were log-transformed before analysis to stabilize variances; however, means of the non-transformed data are presented to facilitate interpretation. Differences among basal area treatment means were tested by the Student-Newman-Kuels' Test. Because of limited replication of plots ($n = 2$ per basal area treatment), the threshold for rejection of the null hypothesis was $\alpha = 0.1$.

Results

Tree crown position

The interaction between crown position and basal area was not significant for any tree physiological variable on any date, indicating that the basal area treatments had similar effects on the physiological variables measured in the upper and lower crowns. Consequently, we present all subsequent data for each basal area treatment as the mean of the measurements for the two crown positions. Upper and lower crown positions differed significantly for predawn and midday water potentials and foliar toughness on some dates. In general, water potentials were slightly lower and foliage toughness was higher in the upper crown compared with the lower crown (data not shown).

Tree water relations

Predawn water potential of the needles differed significantly among basal area treatments on all dates in June, July and August, but not in May and September (Figure 1). Predawn water potential was consistently lowest in trees in the 78.2 m² ha⁻¹ basal area treatment, intermediate in trees in the 27.6 and 18.4 m² ha⁻¹ basal area treatments, and generally greatest in trees in the 6.9 m² ha⁻¹ basal area treatment. Midday water potential differed significantly among basal area treatments on June 28, and July 6 and 22, when the water potential was greatest in trees in the 6.9 m² ha⁻¹ basal area treatment (Figure 1).

Foliar nitrogen concentration

Foliar nitrogen concentration differed significantly among basal area treatments in both May and September (Figure 2). On both dates, nitrogen concentration was greater in trees in the intermediate basal area treatments (either 18.4 or 27.6 m² ha⁻¹) than in trees in the high (78.2 m² ha⁻¹) or low (6.9 m² ha⁻¹) basal area treatments.

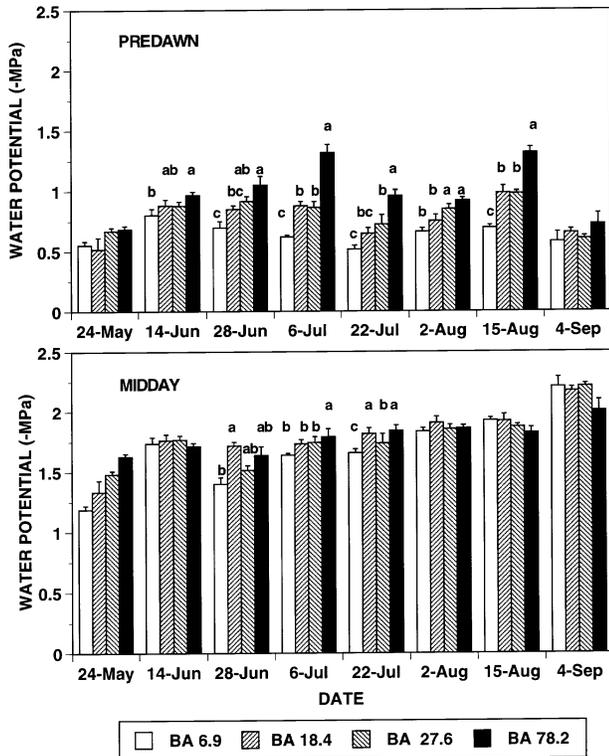


Figure 1. Mean predawn and midday water potentials of ponderosa pines growing at four basal area treatments (BA, $\text{m}^2 \text{ha}^{-1}$) on eight dates in 1994. Bars indicate one standard error of the mean. For each date, basal area means labeled with different letters differ significantly ($P \leq 0.10$; Student-Newman-Keuls' Test).

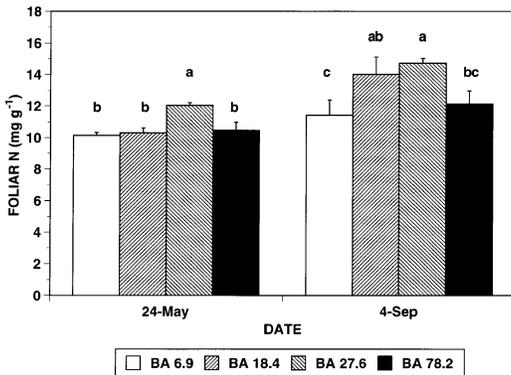


Figure 2. Mean foliar nitrogen concentration of ponderosa pines growing at four basal area treatments (BA) on two dates in 1994. Bars indicate one standard error of the mean. For each date, basal area means labeled with different letters differ significantly ($P \leq 0.10$; Student-Newman-Keuls' Test).

Foliar gas exchange

Net photosynthetic rate differed significantly among basal area treatments in June, August, and September (Figure 3). Except for the first measurement date in May, net photosynthetic rate on all dates was typically highest in trees in the $6.9 \text{ m}^2 \text{ha}^{-1}$

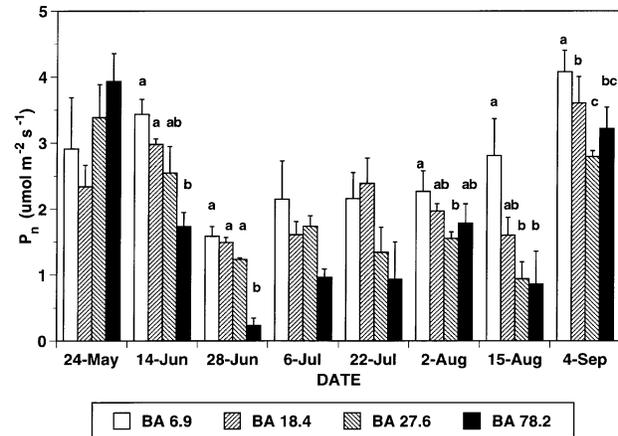


Figure 3. Mean net photosynthetic rate (P_n) of ponderosa pines growing at four basal area treatments (BA) on eight dates in 1994. Bars indicate one standard error of the mean. For each date, basal area means labeled with different letters differ significantly ($P \leq 0.10$; Student-Newman-Keuls' Test).

basal area treatment and lowest in trees in the $78.2 \text{ m}^2 \text{ha}^{-1}$ basal area treatment. Stomatal conductance was positively and significantly correlated with net photosynthetic rate over all measurements ($r = 0.75$, $P < 0.0001$, $n = 331$). Furthermore, the pattern of differences in stomatal conductance among basal area treatments (data not shown) was similar to the treatment-induced differences in net photosynthetic rate.

Insect resistance mechanisms

Trees growing at $6.9 \text{ m}^2 \text{ha}^{-1}$ had significantly thicker phloem, higher resin production, and a longer number of days of resin production compared with trees growing in the higher basal area treatments (Table 2). Trees growing at 18.4 and $27.6 \text{ m}^2 \text{ha}^{-1}$ did not differ significantly in resin characteristics, but phloem was significantly thicker in trees growing at 18.4 than at $27.6 \text{ m}^2 \text{ha}^{-1}$. Among treatments, trees growing at $78.2 \text{ m}^2 \text{ha}^{-1}$ had the thinnest phloem and lowest resin production and duration of flow.

Foliar toughness (Figure 4) differed significantly among basal area treatments on May 24, August 2, and September 4. On these dates, toughness was greatest in trees in the $6.9 \text{ m}^2 \text{ha}^{-1}$ basal area treatment and least in trees growing in the $78.2 \text{ m}^2 \text{ha}^{-1}$ basal area treatment.

Discussion

Control of stand basal area by frequent thinnings over 32 years influenced the water relations of second-growth ponderosa pines in northern Arizona. Water availability to the trees, as measured by predawn water potential, increased as stand basal area decreased from 78.2 to $6.9 \text{ m}^2 \text{ha}^{-1}$. On several dates, differences in predawn water potential between the highest and lowest basal area treatments (0.5 to 0.7 MPa) were probably large enough to affect physiological processes that are sensitive to water availability, such as stomatal conductance, photosynthesis, and cell turgor. Although differences in midday

Table 2. Mean (and standard error of the mean) phloem thickness, 24-h resin flow, total resin flow, and duration of resin flow in late June 1994 for ponderosa pines growing at four basal area treatments. Means followed by different letters are significantly different ($P \leq 0.10$; Student-Newman-Keuls' Test).

	Basal area ($\text{m}^2 \text{ha}^{-1}$)			
	6.9	18.4	27.6	78.2
Phloem thickness (mm)	4.69 (0.012) a	3.27 (0.246) b	2.65 (0.136) c	1.80 (0.086) d
24-h Resin flow (ml)	8.7 (2.17) a	3.9 (0.06) b	4.1 (0.19) b	0.7 (0.21) c
Total resin flow (ml)	29.8 (8.97) a	14.6 (1.94) a	14.8 (1.02) a	2.4 (0.46) b
Duration of resin flow (days)	7.2 (0.05) a	6.7 (0.08) b	6.9 (0.05) b	4.6 (0.08) c

water potential among basal area treatments were not as consistent or as large (maximum difference of about 0.3 MPa) as treatment-induced differences in predawn water potential, midday water potential was significantly increased in trees in the lowest basal area treatment on three dates in June and July.

In the only other study on the influence of basal area treatments on water relations of second-growth ponderosa pine, Schmid et al. (1991) found that basal area treatments ranging between 9.2 and 35.1 $\text{m}^2 \text{ha}^{-1}$ had no consistent effect on predawn or midday water potentials measured one to three years after thinning. Important differences between our study and the study of Schmid et al. (1991) include the duration of the thinning treatment (32 years versus 3 years) and the greater basal area of the untreated control in our study (78.2 $\text{m}^2 \text{ha}^{-1}$ versus 35.1 $\text{m}^2 \text{ha}^{-1}$). In our study, the largest differences in predawn water potential, and other measured physiological characteristics, occurred between the untreated control and the thinned treatments, especially between the control and the 6.9 $\text{m}^2 \text{ha}^{-1}$ treatment. Although we also detected significant differences in predawn water potential among the three thinned treatments (6.9, 18.4, and 27.6 $\text{m}^2 \text{ha}^{-1}$) on several dates, the magnitude of these differences was no more than 0.2 MPa.

There was a significant effect of basal area treatments on net photosynthetic rate that was consistent with the effect of the treatments on water potential: net photosynthetic rate generally increased as stand basal area decreased. Of the variables that we measured, the one most likely to explain differences in net photosynthetic rate among stand basal area treatments is predawn water potential, which was sufficiently low in the high basal area treatments to reduce carbon uptake as a result of stomatal closure. We conclude that differences in net photosynthetic rate among basal area treatments were not related to foliar nitrogen concentration, because the highest foliar nitrogen concentration in both May and September was measured in trees in the intermediate basal area treatments.

Although we do not fully understand the cause of the variation in foliar nitrogen concentration, we hypothesize that the most important limitation to nitrogen uptake by trees in the lowest basal area treatment (6.9 $\text{m}^2 \text{ha}^{-1}$) was competition with herbaceous plants and shrubs, whereas the most important limitation to nitrogen uptake by trees in the highest basal area treatment (78.2 $\text{m}^2 \text{ha}^{-1}$) was competition with trees. We did not measure understory growth; however, understory biomass increases as basal area typically decreases in ponderosa pine forests in northern Arizona (Moore and Deiter 1992). If our hypothesis is correct, tree nitrogen uptake was highest at intermediate basal areas because the total competition for nitrogen between a tree and the neighboring vegetation was less than the total competition for nitrogen at higher or lower basal areas.

Dense, low-vigor stands of ponderosa pine are often prone to insect outbreaks, especially by pine bark beetles (Sartwell and Stevens 1975, Larsson et al. 1983, Schmid et al. 1994, Olsen et al. 1996). The tree resistance hypothesis (Berryman 1976, Berryman 1978, Mitchell et al. 1983) explains this relationship on the basis that tree resistance against insect attack is reduced in dense stands because intense resource competition limits resource allocation to resistance mechanisms. For ponderosa pine, important mechanisms of resistance against insect attack include development of tough foliage to resist defoliators (Wagner and Zhang 1993), and resin production to resist pine bark beetles (Wood 1962, Cates and Alexander 1982, Christiansen et al. 1987), both of which require carbohydrates (e.g., Christiansen et al. 1987, Dunn and Lorio 1992). Our data on the effects of stand basal area treatments on resin production and foliar toughness in ponderosa pine support the tree resistance hypothesis; both resin flow and

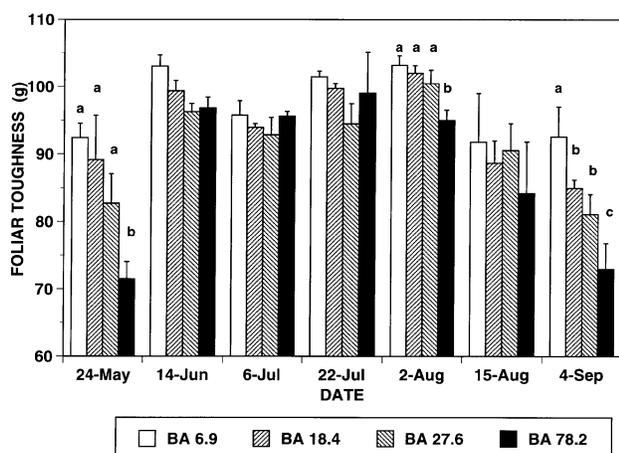


Figure 4. Mean foliar toughness of ponderosa pines growing at four basal area treatments (BA) on seven dates in 1994. Bars indicate one standard error of the mean. For each date, basal area means labeled with different letters differ significantly ($P \leq 0.10$; Student-Newman-Keuls' Test).

foliar toughness decreased as stand basal area increased, and this decrease was associated with a decrease in foliar water potential and net photosynthetic rate. Similar effects of thinning on resin production have been reported for loblolly pine (*Pinus taeda* L.) (Brown et al. 1987, Matson et al. 1987). Regardless of the mechanism, our data suggest that ponderosa pine trees have greater defensive capability against both stem-boring insects and foliage-feeding insects in stands of low basal area than in stands of high basal area.

Although ponderosa pines grown at high stand basal areas have reduced defensive capability against bark beetles because of low resin production, these stands are not considered to be at a high risk of attack by some bark beetle species (e.g., mountain pine beetle, *Dendroctonus ponderosae* Hopkins) until the mean stand diameter exceeds some threshold, estimated to range between 15 to 20 cm (Stevens et al. 1980, McCambridge et al. 1982). Brood production and adult growth of the mountain pine beetle are positively related to phloem thickness in ponderosa pine because thick phloem provides more food resources to the beetle (Amman and Pasek 1986). In our study, phloem thickness varied positively with tree diameter and negatively with stand basal area. We concluded, therefore, that the 78.2 m² ha⁻¹ basal area stand had a low risk of mountain pine beetle attack because the mean tree diameter (10.7 cm) was well below the usually cited threshold value, and more importantly because the phloem was thinner in this treatment than in the other basal area treatments. The 18.4 and 27.6 m² ha⁻¹ basal area stands probably have a higher risk of successful bark beetle attack than the 6.9 m² ha⁻¹ basal area stand because trees in these stands combine low resin production with moderately thick phloem and a mean stem diameter above the normal threshold.

In summary, 32 years of thinning treatments to maintain the same stand basal areas changed the physiological condition of second-growth ponderosa pines in northern Arizona. As stand basal area increased from 6.9 to 78.2 m² ha⁻¹, predawn water potential, midday water potential, net photosynthetic rate, resin production, phloem thickness, and foliar toughness decreased. We conclude that the physiological explanation for previously reported differences in the risk of bark beetle attack among stand basal area treatments is that trees in the high basal area stands are more stressed and therefore have a lower defensive capability against insect attack than trees in the low basal area stands.

Acknowledgments

We thank Dr. Stephen C. Hart (Northern Arizona University School of Forestry) for providing equipment and advice for the foliar nitrogen concentration analyses, Carl B. Edminster (USDA Forest Service) for facilitating our work at Taylor Woods, and John D. Bailey (Northern Arizona University School of Forestry) for constructive comments on an earlier version of the manuscript.

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