Perpetuating old ponderosa pine

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Review

Perpetuating old ponderosa pine

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Abstract

We review current knowledge about the use of management treatments to reduce human-induced threats to old ponderosa pine (*Pinus ponderosa*) trees. We address the following questions: Are fire-induced damage and mortality greater in old than younger trees? Can management treatments ameliorate the detrimental effects of fire, competition-induced stress, and drought on old trees? Can management increase resistance of old trees to bark beetles? We offer the following recommendations for the use of thinning and burning treatments in old-growth ponderosa pine forests. Treatments should be focused on high-value stands where fire exclusion has increased fuels and competition and where detrimental effects of disturbance during harvesting can be minimized. Fuels should be reduced in the vicinity of old trees prior to prescribed burns to reduce fire intensity, as old trees are often more prone to dying after burning than younger trees. Raking the forest floor beneath old trees prior to burning may not only reduce damage from smoldering combustion under certain conditions but also increase fine-root mortality. Thinning of neighboring trees often increases water and carbon uptake of old trees within 1 year of treatment, and increases radial growth within several years to two decades after treatment. However, stimulation of growth of old trees by thinning can be negated by severe drought. Evidence from young trees suggests that management treatments that cause large increases in carbon allocation to radial xylem growth also increase carbon allocation to constitutive resin defenses against bark beetle attacks, but evidence for old trees is scarce. Prescribed, low-intensity burning may attract bark beetles and increase mortality of old trees from beetle attacks despite a stimulation of bole resin production.

Keywords: Bark beetle; Forest management; Fire; *Pinus ponderosa*; Prescribed burn; Restoration; Thinning

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1. Introduction

Much of past forestry research has focused on obtaining information to increase the efficiency of wood commodity production. Consequently, the majority of past silvicultural research has been directed at treatments to hasten regeneration and improve the growth and wood properties of young trees (Smith et al., 1997; Nyland, 2002). Large, old trees were rarely included in this research agenda.

Interest in using silviculture to perpetuate the vigor and longevity of existing old trees is growing. This interest has arisen from the recognition that old trees are rare on the landscape (Bailey and Ide, 2001; Sesnie and Bailey, 2003), are a living testimony of past disturbance and climate change (e.g., Speer et al., 2001; Soulé and Knapp, 2006), provide unique wildlife habitat (Reynolds et al., 1992; Kelly et al., 1993; Humes et al., 1999; Mazurek and Zielinski, 2004; Molina et al., 2006), sequester carbon over centuries (Harmon et al., 1990), and provide spiritual inspiration to many people (Ostlund et al., 2005). In, dry, fire-prone, forests of the western U.S., Fiedler (2000) recommended that stands containing old trees receive priority for fuel-reduction treatments because of their rarity and ecological importance, and because they are currently threatened by fire, competition stress, drought, and associated bark beetle attacks. This review focuses on old ponderosa pine (*Pinus ponderosa*), the dominant species of these forests (Hardin et al., 2001).

Definitions of old-growth ponderosa pine forests vary among authors and agencies, yet all emphasize the existence of old trees (Kaufmann et al., 1992). For example, attributes of old-growth ponderosa pine forests include containing trees with a diameter at breast height (DBH) greater than 41 cm and at least 200 years old in the Front Range of the Rocky Mountains, DBH greater than 41 cm and at least 160 years old in the Black Hills, South Dakota, and DBH greater than 46 cm and at least 160 years old in Arizona and New Mexico (Mehl, 1992). The mean age of ponderosa pines in old-growth stands in Arizona and New Mexico is about 279 years, with the oldest known tree 742 years old (Swetnam and Brown, 1992). In southern Oregon, mean age of ponderosa pine in two mixed confer stands ranged from 230 to 315 years, with the oldest tree over 400 years (Agee, 2003; Perrakis and Agee, 2006). In Montana, mean age of ponderosa pine in old-growth mixed conifer stands ranged from 179 to 374 years with the oldest tree over 450 years (Arno et al., 1995, 1997; Keeling and Sala, unpublished data). Trees older than about 400 years in remote unlogged areas are rare, perhaps because of extensive mortality from severe drought in the late 1500s (Swetnam and Brown, 1992). In addition to age, crown characteristics differ between old and younger, but mature trees. Height growth is slow in old trees producing a flattened crown top compared to the more conical crown top of younger trees with more rapid height growth (Keen, 1936; Bond, 2000). In this review, we use the term ‘‘old’’ to refer to ponderosa pines that are at least 160 years old or have a DBH greater than 40 cm, and the terms ‘‘young’’ or ‘‘younger’’ to refer to trees that are less than 160 years of age or have a DBH less than 40 cm.

Old ponderosa pine in areas historically subjected to frequent low-severity fire regimes is currently threatened by several factors that are distinct from the logging that reduced their abundance over the past 150 years. The first of these factors is wildfire. Recent increases in wildfire activity and severity in the western U.S. that often kill old pines have been linked to temperature increases since the mid 1980s (Westerling et al., 2006) and fuel accumulation resulting from a century of fire exclusion (Habeck, 1994; Arno et al., 1995, 1997; Covington et al., 2001; Keane et al., 2002; Fulé et al., 2004; Moore et al., 2004). The increase in fuels due to fire exclusion, however, appears to be less predictable in old-growth forests of the northern Rocky Mountains relative to drier forests of the southwestern U.S. (Keeling et al., 2006). Increasing evidence also suggests that historic logging disturbance may also promote regeneration and increase fuel accumulation in the long-term beyond that caused by fire exclusion (Minnich et al., 1995; Kaufmann et al., 2000). In ponderosa pine forests where current fire regimes are clearly outside the historic range of variability, wildfire severity and frequency are expected to increase in the future in the western U.S. as temperatures rise and relative humidity decreases (Brown et al., 2004). Restoration treatments, consisting of thinning or prescribed burning to reduce fuels and modify fuel structure, have been recommended to reverse the current trend of large, stand-replacing wildfires (e.g., Covington, 2000; Fiedler, 2000; Fulé et al., 2001; Allen et al., 2002; Fitzgerald, 2005).

A second threat to old ponderosa pine is competition with mid- or under-story trees. This threat may be natural, or non-anthropogenic, in some mixed-species higher elevation forests containing ponderosa pine whose fire regime does not deviate much from historic variability (Brown et al., 1999; Schoennagel et al., 2004), but is of anthropogenic origin in regions where fire exclusion has increased tree density beyond its natural range of variability. For instance, increased tree density in the understory and in former openings and meadows over the last century of fire exclusion has increased competition between old and younger trees in some areas (Biondi, 1996; Feeney et al., 1998; Stone et al., 1999; McDowell et al., 2003). The use of silvicultural treatments to reduce competition stress on old trees is a relatively new idea (Harrington and Sackett, 1992;

Kaufmann et al., 1992; Fiedler, 2000). Several experiments have been started recently to address impacts of thinning and prescribed burning on old ponderosa pine (Covington et al., 1997; Oliver, 2000; Ritchie, 2005), yet only a few conclusive results have been published and synthesis of these results is currently lacking. Information on the growth rate of old trees in low-competition environments is scarce for all tree species (Bond, 2000).

The last significant threats to old ponderosa pine are drought and bark beetle attacks. Mortality of ponderosa pine attributed to drought and associated bark beetle attacks has increased recently (e.g., Macomber and Woodcock, 1994; Savage, 1994; Agee, 2003; Guarin and Taylor, 2005). Bark beetle attacks interact with fire damage and increase the probability of post-fire tree mortality (McHugh et al., 2003; Parker et al., 2006). Climate change forecasts include an increase in the frequency and severity of drought in the western U.S. (Houghton et al., 2001; Coquard et al., 2004), which may increase bark beetle attacks (Breshears et al., 2005). Partial cutting has been recommended to increase resistance of ponderosa pine to bark beetles (Schmid and Amman, 1992; Fettig et al., 2007), yet information to support this recommendation for old trees is scarce.

Our objectives are to review current knowledge about the use of management treatments to reduce human-induced threats to old ponderosa pine in the western U.S. Specifically, we address the following questions: Are fire-induced damage and mortality greater in old trees than younger trees? Can management treatments ameliorate the detrimental effects of fire, competition-induced stress, and drought on old trees? Can management increase resistance of old trees to bark beetles?

2. Response of old ponderosa pine to fire

Impacts of prescribed fire on growth of ponderosa pine have been addressed in several studies of trees that were mature but younger than our definition of an old tree. Studies on old trees are rare. In Oregon, height, basal area, and volume growth of young ponderosa pine were reduced over an 8-year period after prescribed fire, and the effect was more pronounced in burned areas with higher duff consumption (Landsberg et al., 1984). In northern Arizona, prescribed fire reduced radial growth of young, mature ponderosa pine for several years after burning even in the absence of obvious crown damage from fire, after which growth recovered to pre-burn rates (Sutherland et al., 1991). Prescribed fire with and without prior thinning had little effect on radial growth of young ponderosa pine in Montana (Sala et al., 2005). Prescribed fire intervals of 4 or 6 years have been reported to stimulate radial growth of young trees slightly, whereas intervals of 1, 2, 8 and 10 years decreased growth relative to no burning (Peterson et al., 1994). Prescribed, low-intensity fire rarely kills young ponderosa pine unless fire intensity is severe enough to girdle the tree by killing cambium or removing much of the canopy by scorch or consumption (Ryan, 1982, 1990; McHugh and Kolb, 2003; Sieg et al., 2006).

Whereas impacts of low-intensity fires are expressed in young ponderosa pine primarily in growth responses, the effects of such fires on old pine are often expressed by increased tree mortality. In Oregon, mortality of ponderosa pine over 70 cm diameter, 4 years after a prescribed fire, significantly exceeded that in adjacent unburned areas (Thomas and Agee, 1986). In the same areas, Agee (2003) measured mortality of ponderosa pine for 13 years. The average size and age of ponderosa pines that died in the first 4 years after burning were 10–20 cm and less than 100 years old. Between the 4th and 13th post-fire years, those averages increased to 45–100 cm and 100–400 years. Precipitation was below average in every year but one between post-fire years 4 and 13, suggesting a role of drought in the delayed mortality of the old trees.

Prescribed burning at Crater Lake National Park in Oregon between 1976 and 1986 increased mortality of old ponderosa pine compared with control, unburned stands (Swezy and Agee, 1991). In burned stands, mortality was moderately high for the smaller diameter classes, declined as diameter increased, and then increased sharply for the largest diameter trees. Mortality of trees with diameters greater than 100 cm in burned stands varied between 21 and 50%, and trees in the oldest class with moderate to low vigor class had mortality of 71–100% (Swezy and Agee, 1991). A majority (68%) of dead trees after a fire in 2002 had evidence of western pine beetle (*Dendroctonus brevicomis*) attacks (Perrakis and Agee, 2006). Crown vigor, measured with Keen's crown vigor classes, was significantly related to mortality after burning—mortality was highest for low vigor trees.

Similar to experiences in Oregon, prescribed fire also can increase the mortality of old ponderosa pine in northern Arizona. Prescribed fire applied to a stand in northern Arizona after 100 years of fire exclusion resulted in 39% mortality of old trees compared with 16% in a control, unburned stand, within 20 post-fire years (Sackett et al., 1996). This mortality was associated with complete consumption of the forest floor from the bole to the dripline. Mortality of the old trees started 1.5 years after the fire and continued for 20 years after fire. Prescribed fire at Grand Canyon National Park, Arizona, increased mortality of old ponderosa pine (10–23% depending on stand) compared with control, unburned stands (1–3%) (Kaufmann and Covington, 2001). Following thinning and prescribed burning on shallow, lava-derived soils in northern Arizona, Fulé et al. (2002) reported 67% mortality of large (>50 cm diameter) ponderosa pine compared with 19% mortality for small (<50 cm diameter) pine within 2 years of burning.

Old ponderosa pines are often more susceptible to mortality after fire than younger, mature trees. For example, a "U-shaped" relationship between post-fire mortality and diameter at breast height (Fig. 1) was reported for ponderosa pine in both southern Oregon (Agee, 2003) and northern Arizona (McHugh and Kolb, 2003). In Arizona, mortality 3 years after fire was highest for trees with the smallest diameter (<20 cm) as would be expected because of their thin bark. Mortality decreased as diameter increased between 20 and 50 cm as would be expected due to increasing bark thickness. However, mortality increased as diameter increased between 50 cm and the largest trees at 80 cm. A very similar relationship was found in the Oregon data which included larger diameter trees (Fig. 1). While Harrington (1993) reported decreasing mortality with increasing diameter

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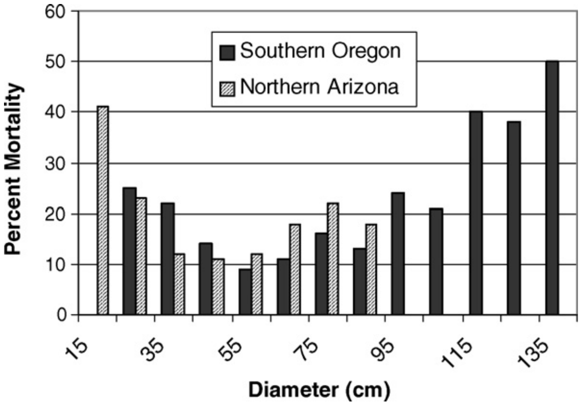

Fig. 1. The U-shaped mortality trend in Southern Oregon (Agee, 2003) and Northern Arizona (McHugh and Kolb, 2003), showing highest post-fire mortality in the smallest and largest size classes of ponderosa pine. Missing columns indicate no data for that size class. A three-class running mean was used for the Arizona data to express it in the same classes as the Oregon data.

for ponderosa pine, the largest size class of trees he studied was 30 cm, which is consistent with Fig. 1. This ‘‘U-shaped’’ distribution between post-fire mortality and diameter has also been reported in another study of ponderosa pine (Finney, 1999), and for Scots pine (*Pinus sylvestris*) in Sweden (Linder et al., 1998). Relationships between the probability of post-fire mortality and total crown damage from fire for stands in northern Arizona suggest that fire can increase mortality of large-diameter, old trees more than smaller, younger trees even when crown damage from fire is standardized over tree size classes (Fig. 2).

What reasons may account for high levels of mortality in old ponderosa pine after fire? First, old, large trees may have previous fire and lightning scars, and damage from insects and fungi, that enable fire to extend deeper into the cambium and higher up the bole causing higher levels of crown damage (Weaver, 1943; Linder et al., 1998). Second, ponderosa pine sheds bark pieces annually, in contrast to the persistent bark of Douglas-fir (*Pseudotsuga menziesii*) or true firs (*Abies* spp.), and over decades the shed bark mixed with leaf litter can build up to 20 cm in thickness or more (Fig. 3). A single prescribed fire can consume much of this material, and these old trees can therefore experience greater root or cambial temperatures than younger trees (Sackett and Haase, 1998; Finney, 1999). Third, old trees may have low amounts of carbohydrate available to replace or repair damaged tissues because of low net photosynthetic rate (Yoder et al., 1994; Bond, 2000; Kolb and Stone, 2000), low leaf area relative to carbon sink demands (Ryan et al., 1997), and large carbon allocation to roots and mycorrhizae (Ryan et al., 1997). Fourth, large trees have thicker phloem than small trees (Kolb et al., 1998, 2006) and thus may be a better food source for phloem-feeding insects, such as the western pine beetle that can cause tree mortality after fire (Miller and Keen, 1960; McHugh et al., 2003; Breece, 2006).

Other factors may predispose old ponderosa pine to accelerated mortality after fire. Old trees with substantial fire scars can burn through to the cambium and die more easily than younger trees with fewer scars (Perrakis and Agee, 2006). Depending on the timing of drought (before or after the fire), stress may be exacerbated by a low-intensity fire that would have less effect during non-drought periods (Agee, 2003). Interception of precipitation prior to burning by the thick forest floor beneath old-growth ponderosa pine (Fig. 3) may cause additional water stress that exacerbates effects of fire. Older

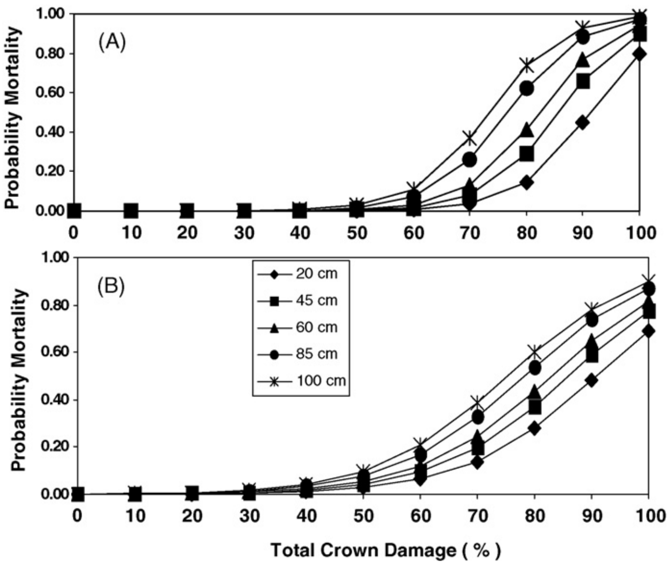

Fig. 2. Distribution of predicted probability of ponderosa pine mortality for logistic regression models using total crown damage (percent of crown scorched + consumed) and diameter at breast height for two wildfires (A, side wildfire; B, Bridger Knoll Wildfire) that burned in late spring, 1996, in northern Arizona shows that large-diameter trees had a higher probability of mortality than small-diameter trees. Derived from McHugh and Kolb (2003).

Fig. 3. Substantial buildup of organic material, including leaf litter and bark flakes, at the base of an old ponderosa pine can create substantial temperature increases around the base of the tree when burned by a prescribed fire. Photo by J.K. Agee.

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stands may be severely infested with dwarf mistletoe (*Arceuthobium* spp.), which can cause localized torching and may be associated with higher mortality after fire (Kaufmann and Covington, 2001; Parker et al., 2006).

3. Management amelioration of detrimental fire effects

The previous section showed that prescribed- and wild-fire often increase mortality of old ponderosa pine. Here, we address management treatments that have been used to reduce such mortality. The results have not been universally successful, and monitoring of mortality from such treatments has usually been short-term, despite evidence that post-fire mortality of old trees can continue over a 10–20-year period after burning (Sackett and Haase, 1998; Agee, 2003).

3.1. Raking

Raking of debris around the base of old trees before burning has been the most-studied management technique to ameliorate the effect of burning. All the studies we review have evaluated a first prescribed fire after many decades of fire exclusion, as subsequent prescribed fires may not require manual fuel removal.

Several studies have suggested that raking is a successful technique. In the southwestern U.S., the mortality incurred at Chimney Springs, Arizona after prescribed fires without raking (Sackett and Haase, 1998) prompted a recommendation that organic material be raked to a distance of 0.5–1 m away from tree bases to avoid potential girdling effects (Sackett et al., 1996). Kolb et al. (2001) reported little mortality of old trees at the Gus Pearson Natural Area in northern Arizona up to 6 years after prescribed fire when the lower layers (“duff”) of the forest floor were removed entirely, not just raked away from tree boles, and dried grass (to simulate presettlement understory fuel loading) was added to litter around the bases of presettlement trees prior to the first prescribed burn. Cambial temperatures measured with thermocouples did not reach lethal levels on most trees (Covington et al., 1997). Only 3 of 49 trees died, two from windthrow and one from bark beetles.

Other studies indicated that within burned areas, trees that were raked had similar mortality to those not raked. Kaufmann and Covington (2001) reported low mortality after prescribed burning at Grand Canyon, Arizona, but cautioned that their study extended only 5 years after burning. Perrakis (2004) found no difference in mortality of old trees for either spring or fall burning between trees with fuels raked around their base and control trees in Oregon.

Yet other studies have found that mortality of old trees was high on certain soils even with a raking treatment. Two years after a prescribed fire, 35% of all trees growing on shallow, lava-derived soils at Mount Trumbull in northern Arizona died, and 67% of the trees above 50 cm diameter died (Fulé et al., 2002). They observed that on other soils burned in the same fire, unusual levels of mortality did not occur. In Oregon on soils developed from avalanche deposits of gravel and pumice, raking of the surface organic horizons allowed the lower horizons to dry, so that a higher proportion of the forest floor was consumed in spring burns (Swezy and Agee, 1991). Fine-root biomass was lower in the rake-burn treatment than a burn-only treatment. These studies were conducted on soils derived from volcanic deposits where many of the roots are concentrated in surface mineral and organic horizons, and this may negate the effect of an ameliorating treatment, such as raking. The results of these studies suggest that the effects of raking treatment may be site specific.

Because raking can directly affect roots by removing live roots in the surface organic horizons, it may be useful to delay prescribed burning after raking. Raking 1 year, and perhaps burning the next year or several years later, may ameliorate the immediate loss of fine roots due to the raking treatment before further fine-root loss is incurred by burning.

3.2. Understory removal and pruning

Understory trees have the potential to torch and increase crown scorch to old trees during prescribed burning. Swezy and Agee (1991) suggested that felling, girdling, or removing small trees in the vicinity of old trees before prescribed burning might result in less heat damage to the older trees. In Oregon, understory shrubs are mown before burning to compact fuels and reduce fireline intensity (Fitzgerald, 2005). Similarly, pruning of low-hanging mistletoe branches can reduce the probability of torching of old trees (Youngblood et al., 2004).

3.3. Slash compression

We know of only one study that has evaluated the effect of compressing slash prior to prescribed burning on post-fire mortality of old ponderosa pine (Jerman et al., 2004). The study was performed in northern Arizona and the slash was compressed with a bulldozer. Slash and forest floor were removed for a distance of 0.5–1 m around the base of the trees, and the remaining slash (about 60 Mg ha^{-1}) from a thinning operation was either compressed or left uncompressed before a prescribed fire was applied. Crown scorch volume was 14% in the uncompressed slash burn compared to less than 1% in the compressed slash burn. After 2 years, mortality of old trees in the uncompressed slash area was 14% compared to 0% in the compressed slash area. This study (Jerman et al., 2004) and others (e.g., Hummel and Agee, 2003) suggest that arrangement of fuels, as much as total mass, may affect fireline intensity and mortality of old ponderosa pine after prescribed burning.

Understory trees have the potential to torch and increase crown scorch to old trees during prescribed burning (Scott and Reinhardt, 2001). Swezy and Agee (1991) suggested that felling, girdling, or removing small trees in the vicinity of old trees before prescribed burning might result in less heat damage to the older trees, and this recommendation has been incorporated into broad perspectives for restoring southwestern ponderosa pine forests (Allen et al., 2002). Fulé et al. (2002) developed operational guidelines for two levels of understory thinning around old pines in the Southwest. The intensive treatment included removing nearly all young trees in the

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vicinity of old trees, while the less intensive treatment cleared most young trees within a radius of 12–18 m of each old trees, with a longer radius in the downslope/downwind direction.

4. Stimulation of old-growth ponderosa pine vigor by management

It is well known that resource uptake and growth of young ponderosa pine can be increased by management treatments, such as thinning that reduce inter-tree competition (Schubert, 1971; Cochran and Barrett, 1993; Kolb et al., 1998; Sala et al., 2005; McDowell et al., 2006). Accelerating the growth of young trees by thinning and prescribed burning treatments has been recommended to promote more rapid development of old-growth conditions in ponderosa pine forests (e.g., Sesnie and Bailey, 2003; Skov et al., 2005).

Growth of old trees appears to be more limited by competition than for younger trees. For example, basal area increment (BAI) of old ponderosa pine declined more than BAI of young pine during a 70-year period in which tree density and stand basal area increased at the G.A. Pearson Natural Area (GPNA) in northern Arizona (Biondi, 1996). In 1920–1930 old pine was growing faster than young pine, but by 1980–1990 old pine was growing slower than young pine (Biondi, 1996). Consequently, the application of management treatments to current old-growth stands to increase the vigor of old trees has been proposed (Harrington and Sackett, 1992; Kaufmann et al., 1992; Covington et al., 1997), but little information exists on the response of old trees to such treatments.

4.1. Ecophysiology of old tree response to management treatments

A number of physiological changes occur as trees become older and larger that likely influence their response to management treatments. As the path length of water transport from the roots to the foliage increases with tree size, both frictional and gravitational constraints on water movement increase (Ryan et al., 2006). These constraints result in reduced stomatal conductance to avoid cavitation, which subsequently limits photosynthesis due to limited CO_2 diffusion from the atmosphere to foliage mesophyll. Decreased stomatal conductance and photosynthesis with increased tree size has been consistently observed in ponderosa pine (Yoder et al., 1994; Hubbard et al., 1999; Kolb and Stone, 2000; Skov et al., 2004; Sala, 2006). Moreover, cell turgor can decrease with increased tree size because tissue water potential becomes more negative (Koch et al., 2004; Woodruff et al., 2004). These hydraulic constraints on photosynthesis and cell growth have been proposed as mechanisms of the commonly observed decrease in growth efficiency, defined as stemwood growth per unit leaf area, at the individual tree- and stand-levels, with increasing tree age and size (Ryan et al., 1997, 2006; Martinez-Vilalta et al., 2007).

There are a number of changes in tree morphology and physiology that may compensate for the hydraulic constraints that occur in large, old trees (Mencuccini and Magnani, 2000; McDowell et al., 2002a; Mencuccini, 2003; Ryan et al., 2006). Examples include changes in carbon allocation that increase the ratio of root absorbing area to leaf area (Ewers et al., 2000; Hacke et al., 2000; Magnani et al., 2000), and increase the ratio of sapwood area to leaf area (Mencuccini and Bonosi, 2001; Fischer et al., 2002; McDowell et al., 2002b, 2006; Barnard and Ryan, 2003; Sala, 2006). Other potentially compensating changes include an increase in sapwood capacitance (Waring and Running, 1978; Goldstein et al., 1998; Phillips et al., 2003), sapwood conductivity (Pothier et al., 1989), and increased water potential gradient from soil to leaf (Hacke et al., 2000; McDowell et al., 2002a; Barnard and Ryan, 2003).

Decreased hydraulic conductance with increased tree size results in a more limited range of stomatal conductance for tall trees than short trees (McDowell et al., 2005). This can be demonstrated using a hydraulic corollary to Darcy's Law applied to trees, as originally developed by Whitehead et al. (1984):

$$g_s = \frac{k_l(\Psi_s - \Psi_l)}{\text{VPD}}, \tag{1}$$

in which k_l is whole plant hydraulic conductance, Ψ_s the soil water potential (MPa), Ψ_l the daytime leaf water potential, and VPD is vapor pressure deficit (kPa). From the framework in Eq. (1) we made generalized predictions of how different size trees may respond to changes Ψ_s associated with thinning. We applied Eq. (1) in a similar fashion to McDowell et al. (2005). We assumed that Ψ_l is constant (isohydric) regardless of site water availability (Maherali and DeLucia, 2001; McDowell et al., 2006) and that hydraulic conductance of old, tall trees is half that of young, short trees. Young, short trees with high hydraulic conductance are predicted to have a broader range of stomatal conductance and a steep response of stomatal conductance to Ψ_s, whereas old, tall, trees are predicted to be less responsive (Fig. 4).

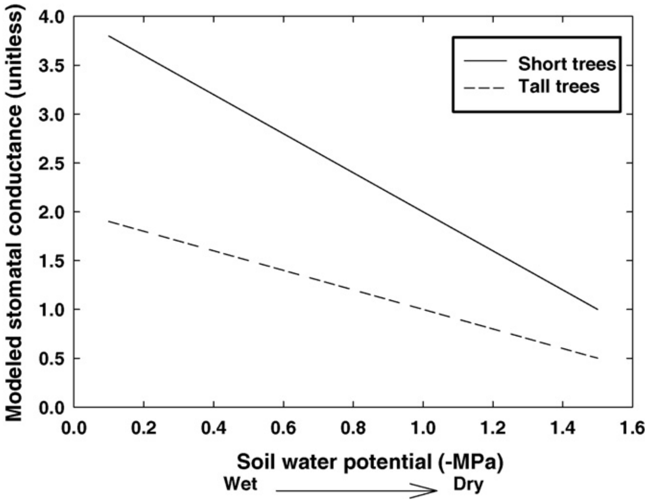

Fig. 4. Predictions of stomatal conductance verses soil water potential using the Whitehead et al. (1984) modeling approach shows that conductance of old, tall trees is less sensitive to drying soil than young, short trees. Hydraulic conductance of tall trees was set to 50% of that of short trees. Model adapted from McDowell et al. (2005).

The model results from Eq. (1) suggest that management actions in ponderosa pine forests that increase availability of soil water, such as thinning (Feeney et al., 1998; Kolb et al., 1998; Sala et al., 2005; McDowell et al., 2006), stimulate stomatal conductance of young, short trees more than old, tall trees. Stomatal response of old, tall trees to increased soil water content is constrained by lower hydraulic conductance from soil to leaf as a consequence of a longer path length compared with young, short trees. Because stomatal conductance is strongly related to photosythesis in ponderosa pine (Feeney et al., 1998; Skov et al., 2004), we should expect larger and faster stimulation of photosynthesis and growth in young, short trees than old, tall trees. This theoretical expectation is consistent with results of an experiment in northern Arizona where thinning stimulated stomatal conductance and net photosynthetic rate (Skov et al., 2004) and bole radial increment (Skov et al., 2005) of small, mature ponderosa pine more than for old pine in the same stand.

4.2. *Empirical studies of response of old ponderosa pine to management*

The theoretical prediction (Fig. 4) that old, tall trees should be less responsive to management treatments that increase availability of soil water than younger, shorter trees raises the question as to whether resource uptake and growth of old ponderosa pine are responsive to management treatments that reduce competition. In this section, we summarize results from recent experiments in Arizona, Oregon, and Montana that have evaluated the response of old ponderosa pine to thinning and prescribed burning treatments.

4.2.1. *Arizona*

Growth and physiological responses of old ponderosa pine to management treatments have been studied for 10 years after initial treatment at the Gus Pearson Natural Area (GPNA) in northern Arizona. The GPNA is managed as a Research Natural Area by the U.S. Forest Service because it contains a stand of large, old ponderosa pine (current average age 438 years, diameter at breast height about 75 cm) and it had received no silvicultural management or harvests prior to the recent experiment. The treatments, described in detail in Covington et al. (1997), consisted of thinned, thinned and prescribed burned, and control (untreated) portions of the same 4.7 ha stand.

The goal of the thinned treatment was to recreate as closely as possible the tree size class distribution and spatial pattern that occurred on the site before the start of Euro-American settlement of the region in 1876. The thinning removed most post-settlement trees, defined as trees that established after Euro-American settlement of the region in 1876. A small number of post-settlement trees were left on site to replace dead presettlement trees that were identified by old logs and stumps. In addition, no trees with diameter at breast height greater than 40 cm were cut. The thinning occurred in November 1993 and reduced tree basal area by about 62% (34.5–13.0 m^2 ha^{-1}) and tree density by 95% (3100–151 trees ha^{-1}).

The goal of the thinned + burned treatment was to recreate both the presettlement structure and fire disturbance regime. The treatment consisted of application of low-intensity prescribed burns to a portion of the thinned stand. The first burn occurred in October 1994, about 1 year after thinning. Fuels were manipulated in the first burn in order to keep fire intensity low and minimize damage to old trees. All thinning slash was removed from the site, and the forest floor (i.e., duff and bark flakes) was raked from the entire area to be burned in order to simulate forest floor conditions hypothesized to occur prior to before disruption of the frequent fire regime. Next, dried foliage of native grasses and forbs (672 kg ha^{-1}) was put on the raked forest floor in addition to the litter layer prior to burning to simulate forest floor fuels of presettlement forests which often contained a dense, herbaceous understory. These herbaceous fine fuels were ignited and produced a low-intensity fire with average flame length of 15 cm and a maximum length of 60 cm. The initial burn in 1994 was followed by three additional prescribed burns at a 4-year interval (1998, 2002, 2006). All of the subsequent burns were conducted in the fall and were low-intensity. Fire was applied directly to fine fuels produced by herbaceous growth (Moore et al., 2006). Most of the combustion in these subsequent burns occurred in fine herbaceous fuels, leaf litter, and coarse woody debris on the forest floor.

In the first growing season after treatment, thinning increased soil water content which led to greater water uptake by old trees as indicated by higher predawn water potential (Stone et al., 1999). Thinning also increased leaf nitrogen content (mass $area^{-1}$) of the old trees, which combined with greater water availability, increased stomatal conductance and net photosynthetic rate. Tree canopy growth also responded positively to thinning after one growing season; thinning increased length of current-year leaves by 12% and mass of terminal buds by 53% (Stone et al., 1999).

Old trees in the thinned alone and thinned + burned treatments at GPNA had similar water relations and rates of leaf gas exchange, but burning affected leaf nitrogen concentration. One and 2 years after the first prescribed burn, leaf nitrogen concentration (mass $mass^{-1}$) was higher for trees in the thinned + burned treatment compared with the thinned alone treatment (Feeney et al., 1998). However, the opposite result occurred after the second prescribed burn; leaf nitrogen concentration was greater for trees in the thinned alone treatment than the thinned + burned treatment (Wallin et al., 2004). The first prescribed burn was the first fire at the GPNA since 1876, and it likely caused a pulse of plant-available nitrogen from mineralization associated with fire (Covington and Sackett, 1986, 1992; Kaye et al., 1999). Trees at the GPNA may have been especially responsive to the pulse of mineralized nitrogen considering the slow rate of nitrogen mineralization at the GPNA in the absence of restoration treatments (Kaye and Hart, 1998). The negative impact of the second prescribed burn on tree leaf nitrogen concentration compared with the thinned only treatment may reflect losses of nitrogen from the site due to volatilization that exceeded nitrogen mineralization (e.g., Wright and Hart, 1997).

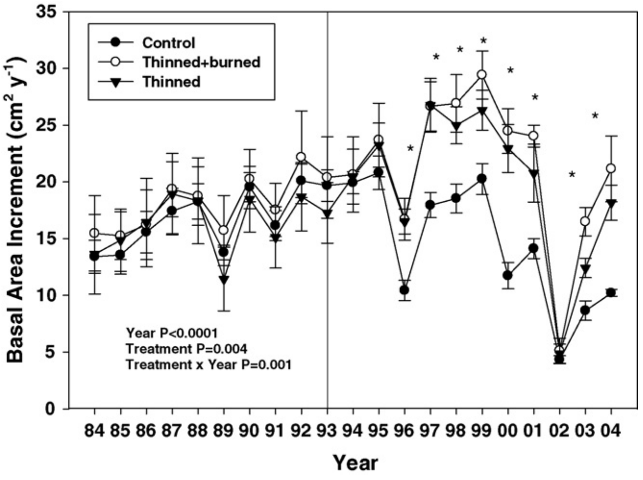

Fig. 5. Basal area increment of old ponderosa pine at the Gus Pearson Natural Area in northern Arizona was simulated by thinning treatments, and increment was similar for trees in thinned alone and thinned plus prescribed burned treatments. The vertical line shows the year of treatment. The *P*-values are from repeated measures MANOVA for the post-treatment years. Asterisk (*) indicates significant ($P < 0.05$) differences among treatments in ANOVA by year. Another MANOVA showed no difference in increment among trees in different treatments for the 10 pretreatment years (1984–1993). Error bars are one standard error of the mean.

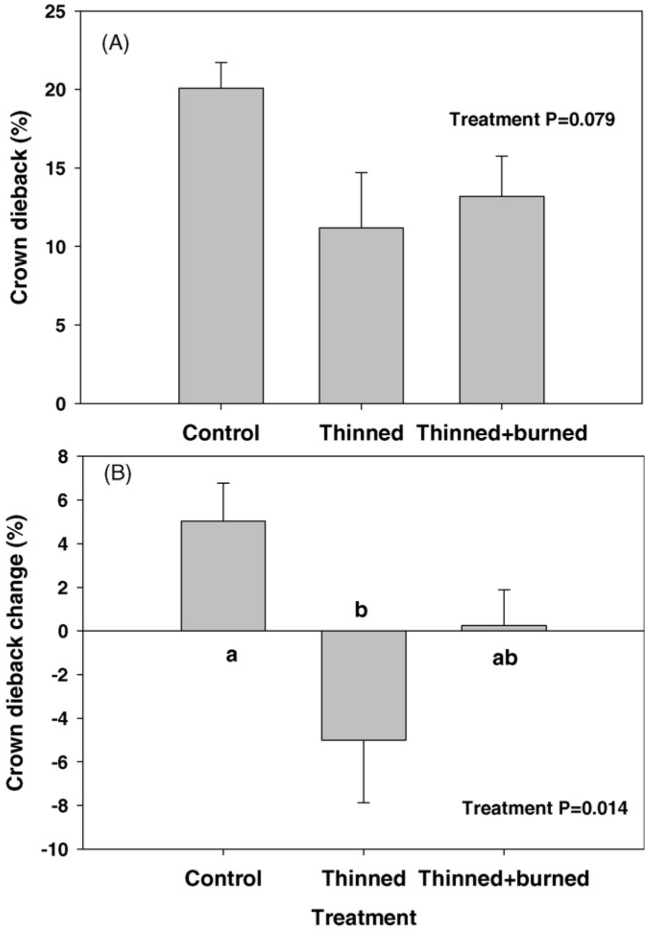

Fig. 6. Mean crown dieback (A) of old ponderosa pine at the Gus Pearson Natural Area in northern Arizona in year 2004, 10 years after treatment, was slightly greater in control compared with thinned alone and thinned plus prescribed burned treatments. Dieback increased for trees in the control between 1994 and 2004 (B), whereas dieback decreased (thinned) or did not change (thinned + burned) in the thinned treatments. The *P*-values are from ANOVA. Different letters indicate statistically significant differences among treatments (LSD, $P < 0.05$). The vertical bar shows one standard error of the mean.

Increased resource uptake by old trees in the thinned plots at the GPNA ultimately resulted in greater stem radial growth. Fig. 5 shows an update of an earlier analysis of the growth response of old trees at the GPNA (Feeney et al., 1998). Basal area increment of old trees did not differ significantly among the treatment plots before treatment (1984–1993), in the year of treatment (1994), nor in the first post-treatment year (1995) (Fig. 5). Starting with the second post-treatment year in 1996, trees in the thinned only and thinned + burned treatments typically had significantly greater increment than trees in the control treatment (Fig. 5). The only exception was the severe drought year of 2002 when increment was similar in all treatments. Increment was similar in the thinned only and thinned + burned treatments in all years, except 2003 when increment was higher in the thinned + burned treatment. A significant treatment × year interaction in increment (Fig. 5) resulted primarily from the larger negative effect of the 2002 drought on increment in the thinned only and thinned + burned treatments than the control.

Positive effects of the restoration treatments on resource uptake and growth of old trees at the GPNA are consistent with temporal changes in crown condition. Fig. 6 shows an update of an earlier analysis of crown condition at the GPNA (Kolb et al., 2001). Dieback in the upper crown was non-significantly less for trees in both thinned treatments than for trees in the control treatment in 2004, 10 years after thinning (Fig. 6). Comparison of the change in crown dieback over the 10 post-treatment years (1994–2004) shows an increase in dieback on trees in the control plot and a decrease (thinned) or no change (thinned + burned) in the treated plots (Fig. 6). Mortality of old trees at the GPNA over the 10 post-treatment years was 5.1% (3 of 59 trees) in the control, 8.1% (3 of 37 trees) in the thinned treatment, and 5.6% (3 of 53 trees) in the thinned + burned treatment. Broad inferences about treatment effects on mortality at the GPNA are limited by the small sample size, but our observations suggest greater incidence of tree mortality due to wind throw and stem breakage in the thinned treatments than the control. Between 1994 and 2002, three old trees in the thinned treatments broke or toppled during severe winter storms, whereas no mortality due to the storms occurred in the control (Kolb et al., 2001). In contrast, tree mortality in the control was preceded by a gradual decline of crown condition.

There is no evidence that careful, well-implemented thinning causes long-term stress to old ponderosa pine in Arizona or elsewhere. Thinning shock, or a negative effect of thinning on tree condition (Harrington and Reukema, 1983; Aussenac, 2000), has been documented in northern Arizona only for small, suppressed ponderosa pines as a reduction in sapwood hydraulic conductance per unit leaf area and canopy conductance after thinning during extreme drought (Simonin

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et al., 2006). This type of thinning shock occurred only in the 1st year after thinning, and thinning stimulated conductance in the 2nd year after thinning.

4.2.2. *Oregon*

Two studies in Oregon have been published recently on the response of old ponderosa pine to thinning treatments. In the first study (Latham and Tappeiner, 2002), old ponderosa pines, Douglas-fir, and sugar pines (*Pinus lambertiana*) in western Oregon increased diameter growth in response to thinning of understory trees or shelterwood thinnings compared with trees in untreated, control stands. The onset of increased growth after thinning for the old trees was often delayed and varied from 5 to 25 years after thinning. Thinning increased growth by 10% or more for 68% of trees, and by 50% or more for 30% of trees. Thinning decreased growth of only 1.5% of trees, which is consistent with studies of ponderosa pine in northern Arizona (Skov et al., 2005) that found little evidence of thinning shock in old ponderosa pine.

The second recent study in Oregon (McDowell et al., 2003) provides additional understanding of physiological mechanisms of the response of old ponderosa pine to thinning. This study compared BAI and water, carbon, and nitrogen relations of old trees between untreated stands and stands treated with shelterwood cuts that reduced basal area 61–82%. A retrospective reconstruction of leaf gas exchange in both types of stands modeled from carbon isotope ratios in tree rings and level–level gas exchange (McDowell et al., 2003) suggested that net photosynthetic rate (Fig. 7A) and stomatal conductance (Fig. 7B) increased in the 1st year after thinning and were elevated above rates of trees in unthinned stands for at least 15 years after thinning. Basal area increment (Fig. 7C) increased by two- to three-fold after thinning, and the increase was sustained for up to 15 years after thinning. The increase in BAI after thinning lagged behind the increase in net photosynthetic rate and stomatal conductance by 2 years (Fig. 7A–C). Thinning increased tree predawn water potential 15 years after treatment, indicating an increase in soil water content in the rooting zone, but had no effect on leaf nitrogen concentration (McDowell et al., 2003). These results show that heavy thinning can increase radial growth, water uptake, and leaf gas exchange of old ponderosa pine for at least 15 years after treatment if stand leaf area is not fully reestablished.

4.2.3. *Montana*

Visual symptoms of decline of old ponderosa pine in the Blackfoot River Valley in Montana in the early 1980s prompted the experimental application of thinning and prescribed burning to improve the vigor and survival of old trees (Fiedler, 2000). The thinning treatment in 1984 removed most understory ‘‘ladder’’ fuels, including most Douglas-fir. Half of the thinned plots were prescribed burned in the fall after thinning. Thinning of understory trees, with and without prescribed burning, reduced mortality of old trees compared with the unthinned controls (Fiedler, 2000). Mortality was 5.5-fold greater in control than in thinned or thinned and burned plots. Thinning also increased diameter growth of the old trees by about 2.6-fold.

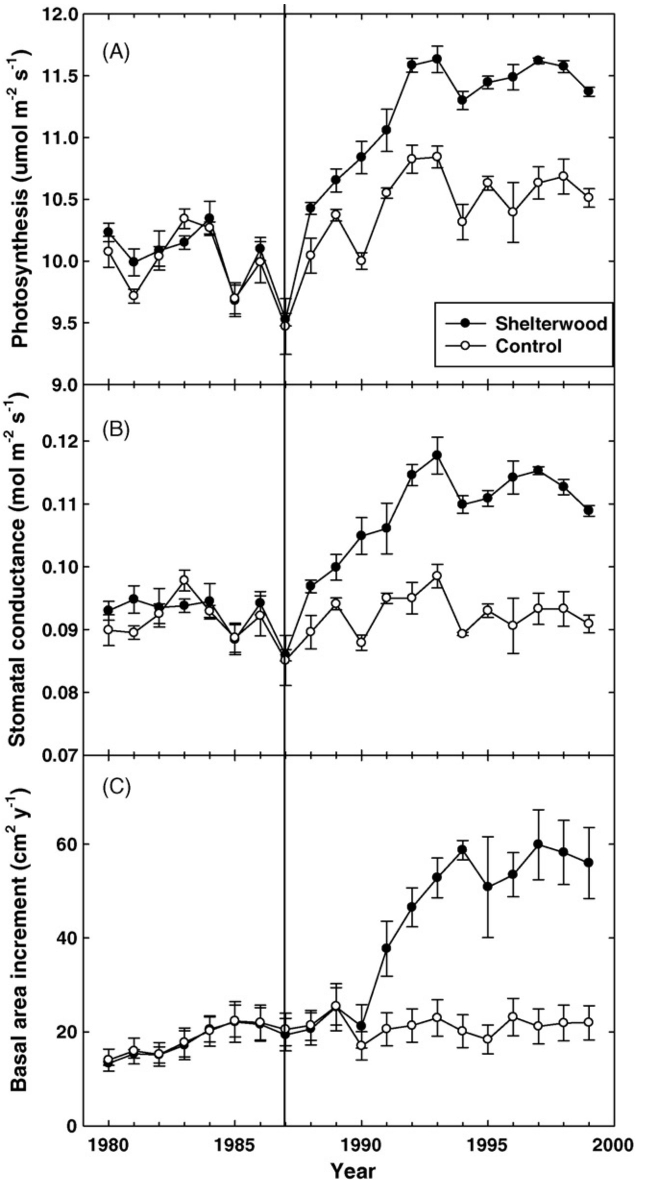

Fig. 7. Net photosynthetic rate (A), stomatal conductance (B), and basal area increment (C) from a study of old ponderosa pine in central Oregon (McDowell et al., 2003) shows that thinning stimulated leaf gas exchange and radial growth 1 year after thinning, and increases growth 4 years after thinning. The shelterwood stand was thinned in 1987, and the neighboring control stand was never thinned. Net photosynthetic rate and stomatal conductance were modeled using tree-ring carbon isotope ratios and leaf level gas exchange measurements of the response of photosynthesis to internal CO_2 concentration as described in McDowell et al. (2003). Bars are one standard error of the mean.

5. Management impacts on resistance of old ponderosa pine to insect attack

The ultimate measure of tree resistance to bark beetles is survival after bark beetle attacks. Large numbers of lethal bark beetle attacks occur episodically in ponderosa pine forests; however, such attacks rarely occur during experimental studies

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(e.g., Larsson et al., 1983). Consequently, mechanisms of resistance are typically measured to provide insight on resistance and to measure the likelihood of tree survival during attack. Resin, either released from storage in resin ducts located in phloem and xylem at the time of attack (preformed or constitutive resin), or synthesized in response to attack (induced resin), is generally hypothesized to be the most important mechanism of pine defense against initial attacks by bark beetles at low beetle densities (Raffa and Berryman, 1983; Lieutier, 2002). This hypothesis has been supported for young ponderosa pine by a negative relationship between resin flow and attack success of western pine beetle (Smith, 1975). After a successful initial attack, tree resistance to bark beetles depends in part on the attack density and the extent that current photosynthate can be quickly shifted to walling off blue-stain fungi introduced by the beetles (Christiansen et al., 1987; Franceschi et al., 2005).

A mixture of direct and indirect evidence suggests that management actions that cause large increases in stem radial growth rate of ponderosa pine also increase tree resistance to lethal bark beetle attacks. Most of this evidence is for trees that are younger than 100 years. Early research on the relationship between radial growth and bark beetle resistance emphasized the importance of tree vigor, defined as wood production per leaf area, with leaf area predicted from sapwood area (Larsson et al., 1983; Mitchell et al., 1983; Waring and Pitman, 1985). Attacks of mountain pine beetle decreased when vigor of ponderosa (Larsson et al., 1983) and lodgepole (*Pinus contorta*) pines (Mitchell et al., 1983) was greater than 100 g of wood produced per meter square of leaf area. McDowell et al. (2007) highlighted uncertainty in accurately predicting leaf area from sapwood area, and thus vigor as defined above, because of changes in the ratio of leaf area to sapwood area with tree competitive status (Simonin et al., 2006) and thinning (McDowell et al., 2006). Instead, McDowell et al. (2007) emphasized the use of more direct measurements of carbon allocation to stem radial growth, such as BAI, to predict tree carbon allocation to resin defenses in the stem.

The indirect evidence concerning positive effects of management, especially thinning, on ponderosa pine resistance to bark beetles is an association between stand structural conditions and tree mortality or resin flow after wounding. Stand conditions associated with high mortality of young ponderosa pine stands by mountain pine beetle (*Dendroctonus ponderosae*) in the inland western U.S. include high stand basal area and tree density (Sartwell and Stevens, 1975; Dahlsten and Rowney, 1983; Cochran and Barrett, 1993; Olsen et al., 1996; Fettig et al., 2007) which are known to reduce diameter growth (e.g., Larsson et al., 1983; McDowell et al., 2006). Probability of lethal attacks by mountain pine beetle (Negron and Popp, 2004) and roundheaded pine beetle (*Dendroctonus adjunctus*) increases with stand density and decreases with radial growth rate for ponderosa pine (Negron, 1997; Negron et al., 2000). Consistent with these reports, flow of preformed resin from phloem wounds, a key defense of many conifers against bark beetles (Smith, 1975; Raffa and Berryman, 1982, 1983), was positively related to BAI in a region-wide synthesis of five studies of ponderosa pine in northern Arizona (McDowell et al., 2007).

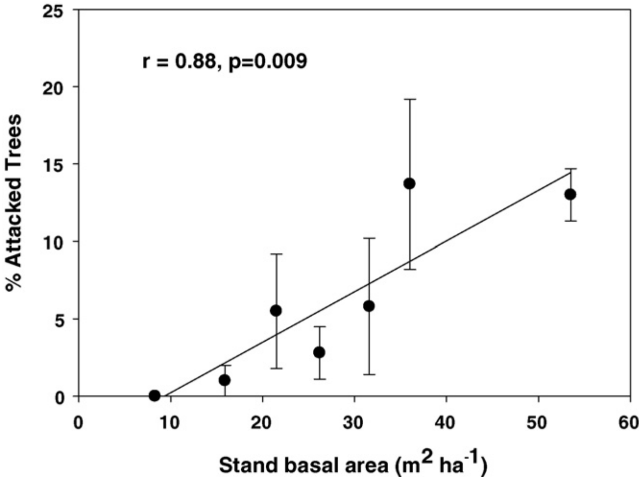

Fig. 8. The percentage of young ponderosa pine attacked by the mountain pine beetle decreased linearly with a decrease in stand basal area in a thinning experiment in central Oregon (derived from Larsson et al., 1983). The basal area levels were established by thinning 15 years prior to the measurement of bark beetle attacks and were maintained by periodic thinnings. The vertical bars show one standard error of the mean. Three stands were sampled for all thinned stands (basal area less than 40 m^2 ha^{-1}), and nine stands were sampled for the unthinned control (basal area = 54 m^2 ha^{-1}).

The direct evidence for a role of management in enhancing resistance of ponderosa pine to bark beetles consists of changes in bark beetle attacks, tree survival, or resistance mechanisms following experimental manipulation of tree density or stand basal area. Increased radial growth of young ponderosa pine in heavily thinned stands has been linked to fewer attacks and consequent tree mortality by mountain pine beetle in Oregon (Fig. 8) and South Dakota (Fettig et al., 2007), and greater resin flow from phloem wounds in Arizona (Kolb et al., 1998). However, heavy thinning (ca. 50% basal area) in Montana did not increase resin flow in June in spite of increases in radial growth (Peters, 2003). Similarly, relatively light (reduction of basal area by <30%) and infrequent thinning of young ponderosa pine stands can stimulate radial growth slightly, but is not effective at stimulating resin flow (Zausen et al., 2005).

With some exceptions, these results for young ponderosa pine are consistent with the hypothesis that trees in low density stands have greater resources, especially carbohydrates, to allocate to both radial growth and tissues bearing large numbers of resin ducts, such as phloem and xylem (Waring and Schlesinger, 1985; Christiansen et al., 1987). Other studies on young ponderosa pine suggest no strong trade-off between above-ground growth and differentiation processes, such as terpene concentration and resin production (Johnson et al., 1997; Gaylord et al., 2007). The lack of evidence for a strong trade-off between carbon allocation to growth versus resin for young ponderosa pine is not consistent with several reports for loblolly pine (*Pinus taeda*) that water stress shifts carbon allocation from growth to resin defenses and results in a positive relationship between stress and resin flow (Lorio, 1986; Blanche et al., 1992; Dunn and Lorio, 1993). The difference in results between loblolly pine and ponderosa pine may be explained by the different location of stress for each species on the bell-shaped relationship between carbon allocation to resin defense and water stress that has been described as the ‘‘growth-differentiation hypothesis’’ (Lorio, 1986, 1993; Lorio et al., 1990; Herms and Mattson, 1992). Studies of loblolly pine have compared resin flow between low and moderate water stress on this bell-shaped curve – thus stress and resin were positively related, whereas studies of ponderosa pine have compared resin flow between moderate and high water stress – thus stress and resin were negatively related.

Investigations at the GPNA in northern Arizona and Crater Lake National Park in Oregon have highlighted the influence of low-intensity prescribed burning on resin defenses of old ponderosa pine. At the GPNA, resin flow in response to wounding of the phloem for measurements taken in June two, three, and 7 years after treatment was higher for trees in the thinned + burned treatment than the thinned alone and control treatments (Feeney et al., 1998; Wallin et al., 2004). Higher resin flow for trees in the thinned + burned treatment may have resulted from stimulation of resin production in response to wounding of cambium or phloem by the understory burns, as has been reported for other pines (e.g., Santoro et al., 2001; Lombardero et al., 2006).

A recent study at Crater Lake National Park in Oregon (Perrakis and Agee, 2006) reported similar results on effects of prescribed burning on resin flow from old ponderosa pine. Both fall and spring prescribed burns increased resin flow in the first and second summers after treatment compared with unburned controls. The same burning treatments also increased tree mortality attributed to western pine beetle attacks, as has been found in other recent studies of prescribed fire in ponderosa pine forests in Arizona and New Mexico (Wallin et al., 2004; Breece, 2006). These results indicate that some species of bark beetles are attracted to burned stands and are successful at colonizing trees even when burning increases resin defenses, and suggest that tree resistance to bark beetles in burned stands cannot be predicted solely by quantitative changes in resin defenses.

Studies at the GPNA in northern Arizona also have investigated effects of management treatments on leaf toughness, an important resistance mechanism against foliage-feeding insects, such as pine sawflies (McMillin and Wagner, 1993; Wagner and Zhang, 1993). Both thinning and thinning + burning treatments consistently increased leaf toughness of old trees compared to trees in the control (Feeney et al., 1998; Wallin et al., 2004). This result suggests reduced performance of foliage-feeding insect on trees in thinned treatments, but this has not been verified with insect performance experiments. Tougher foliage appears to be a long-term effect of thinning at the GPNA as it was consistent in all measurements between one and 7 years after thinning.

6. Management amelioration of drought impacts on old ponderosa pine

Increases in mortality of both ponderosa pine (http://www.fs.fed.us/r3/resources/health/beetle/index.shtml) and pinyon pine (*Pinus edulis*) (Breshears et al., 2005; Shaw et al., 2005) have been reported during drought over the last decade (1996–2006) in the Southwest U.S. We utilized 3-PG, a physiologically based tree growth model (Landsberg and Waring, 1997), to contrast the implications of a reduction of nearly 50% in annual precipitation recorded near Los Alamos, New Mexico between the period from 1996 to 1999 (mean, 490 mm year^{-1}) and 2000 to 2003 (mean, 260 mm year^{-1}) on tree growth. The model predicted a one-third reduction in tree growth and a proportional reduction in maximum leaf area index (LAI) from 2.1 to 1.4. Similar reductions in the normalized difference vegetation index have been reported in the region during severe drought (Breshears et al., 2005). Self-thinning would necessarily increase, because, according to the widely applied −3/2 power law, the maximum standing biomass at which mortality begins is a function of maximum LAI (Landsberg and Waring, 1997). This simulation result suggest that the increased frequency of severe droughts that are predicted to occur with future climate change (Houghton et al., 2001; Coquard et al., 2004) will increase mortality of ponderosa pine in old-growth stands. This mortality can be reduced by thinning that reduces the high LAI of many current stands of 2.0 or greater by at least 33%. Removing younger trees by thinning will increase water available to old trees during drought (e.g., Feeney et al., 1998; McDowell et al., 2003; Wallin et al., 2004) and likely reduce their mortality.

Results from the GPNA in northern Arizona provide insight on how thinning treatments and drought interact to affect the performance of old trees. The second growing season after thinning, 1995, was unusually wet with winter–spring precipitation 42% higher than average. A severe drought occurred in 1996 with winter–spring precipitation 60% lower than average. The effect of thinning on net photosynthetic rate and BAI varied between years (Feeney et al., 1998). Thinning had little effect on net photosynthetic rate and BAI (Fig. 5) in the wet year (1995). In contrast, thinning increased photosynthesis compared with the control during the driest weeks of the drought year (1996) (Feeney et al., 1998), and also increased annual BAI (Fig. 5). Similar interactions between drought and the early response (i.e., within 3 years of treatment) of photosynthesis to thinning treatments for old ponderosa pine have been reported in related studies in northern Arizona (Skov et al., 2004). These results suggest that increases in water availability to old trees for at least the first few years after thinning ameliorates the negative effect of severe drought on tree photosynthesis and radial growth.

Effects of thinning on sensitivity of radial growth to drought of old trees likely varies with drought severity and changes in tree architecture induced by thinning. Fig. 5 from the GPNA illustrates this influence. The 1996 drought, which occurred in the third growing season after thinning, had a greater negative effect on BAI of trees in the control than both thinned treatments, and BAI was greater during the drought in the thinned treatments than the control. In contrast, the more severe 2002 drought had a greater negative effect on BAI of trees in both thinned treatments than the control (Fig. 5). The greater sensitivity of growth to the 2002 drought for trees in the thinned treatments resulted in similar BAI among treatments.

Changes in tree architecture after thinning may explain the variable effects of thinning on sensitivity of radial growth to drought. A recent study on young, mature ponderosa pine in northern Arizona showed that periodic thinning increased the ratio of leaf area to sapwood area (McDowell et al., 2006). This architectural shift of trees in thinned stands results in increased canopy demand for water relative to supply via the sapwood, which predisposes trees to severe leaf-level hydraulic (and hence photosynthetic) limitation during drought relative to trees in unthinned stands. The increase in the ratio of leaf area to sapwood area with thinning was documented by McDowell et al. (2006) about four decades after the onset of decadal thinnings applied to 40-year-old, pole-size trees. The occurrence of this type of response to thinning for old trees is unclear as studies of long-term architectural responses of old trees to thinning have not been conducted. However, the same response to thinning for old trees at the GPNA over one decade after thinning would explain the increasing sensitivity of BAI to drought for trees in thinned plots (Fig. 5).

Overall, results from the GPNA and related studies in northern Arizona (Feeney et al., 1998; Skov et al., 2004, 2005; McDowell et al., 2006) suggest that thinning reduces impacts of severe water stress on photosynthesis and growth immediately after treatment, but may actually increase the relative impact of drought on growth (i.e., percent change between non-drought and drought years) decades following treatment because of slow adjustments in tree leaf area to sapwood area ratio. However, this is a relative response, i.e., trees in thinned stands may show greater drought-related decreases than trees with low growth rates, but may still may higher absolute growth. Trees in heavily thinned stands typically have greater absolute BAI than trees in unthinned stands in both drought and non-drought years (Feeney et al., 1998; McDowell et al., 2003, 2006; Fig. 5). Therefore, resilience of growth to drought appears to be greater for trees in thinned than unthinned stands.

7. Management implications and recommendations for perpetuating old ponderosa pine

Our review provides evidence that careful management of old-growth ponderosa pine forests whose current stand structure deviates from historic conditions due to the effects of grazing and fire exclusion often enhances resource uptake and growth of old trees in the short term (up to 10 years). One might conclude that management involving thinning and burning of all old-growth ponderosa pine forests is in order. However, such management should be carefully considered. First, there is evidence that not all ponderosa pine forests are outside the historic range of variability, either because fire regimes were not completely disrupted (e.g., Grand Canyon; Fulé et al., 2003), or because some mixed-conifer forests containing ponderosa pine historically had relatively high density or infrequent fires (e.g., Colorado Front Range; Brown et al., 1999; Schoennagel et al., 2004). In such cases, thinning for the purpose of restoring historic structure would not be justified. Second, many old-growth forests in the western U.S. are located in remote areas, where management often causes unavoidable disturbances, such as road construction, soil compaction, and exposure to mineral soil. Even in areas where old-growth forests are clearly outside their range of natural variability the pros and cons of management need to be carefully weighted. For instance, road construction and subsequent increased access could increase invasive species (Korb, 2001), decrease native species diversity, alter fire regimes, or change resource availability (Levine et al., 2003). Third, financial costs of management treatments in old-growth forests can be high because of the careful attention required to individual trees. Finally, while long-term monitoring data is lacking, increasing evidence suggests that disturbance associated with harvesting may increase recruitment and density in the long-term, which could be counter productive (Minnich et al., 1995; Kaufmann et al., 2000). For instance, in an ongoing study across Montana and central Idaho, tree density in never-logged ponderosa pine stands not subjected to fire for the last 60 years was on average over 40% lower than in paired stands ($n = 23$ pairs) that had been subjected to historical logging (Naficy and Sala, unpublished data). These results serve only to highlight the need to consider long-term effects of disturbance, and the need for repeated maintenance actions, such as prescribed fire, prior to management actions.

We provide the following recommendations for the use of thinning and burning in dry, old-growth ponderosa pine forests where fire exclusion has increased fuels over time and where potential negative effects of management are minimized:

1. Results for removing the forest floor beneath old trees by raking prior to prescribed fire to reduce fuels and smoldering combustion appear to be site specific. Raking appears to ameliorate fire damage to old trees on fine-textured, basalt-derived soils in northern Arizona, but results for other soils are variable. Raking one or 2 years before burning may ameliorate the immediate loss of fine roots due to the raking treatment before further fine-root loss is incurred by burning.
2. Old ponderosa pine trees are often more prone to dying after prescribed burns and wildfires than younger, mature trees. Their death often occurs more slowly after burns than for younger trees. Fuels should be reduced in the vicinity of old trees prior to prescribed burns by thinning the understory and removing the slash, or by compressing the slash to reduce fire intensity.
3. Resource uptake and growth of old trees can be increased by careful thinning. Thinning often reduces water stress of old trees starting one or 2 years after treatment. Radial growth responses are slower, and often start several years to two decades after thinning. Growth response to thinning is slower for old trees than young trees. Stimulation of growth of old trees by thinning can be negated by severe drought. However, stimulation of growth by thinning returns shortly after drought ceases. Overall, these results for old ponderosa pine are consistent with a small, but growing number of experiments showing that resource uptake and growth of old trees of various species are responsive to thinning (Bebber et al., 2004; Martinez-Vilalta et al., 2007). An unresolved issue is whether stimulation of radial growth in

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old, large trees increases their susceptibility to windthrow and breakage due to an increase in above-ground mass or due to increased exposure.

4. Reduction of stand leaf area by management treatments should reduce mortality of old trees during severe drought because of increased water availability to remaining trees.
5. Careful thinning does not often cause ‘‘thinning shock,’’ or a negative physiological or growth response to thinning, in old ponderosa pine.
6. Management treatments that cause large increases in carbon allocation to radial xylem growth also increase carbon allocation to constitutive resin defenses against bark beetle attacks, based on studies with young ponderosa pine.
7. Prescribed, low-intensity burning that causes little crown scorch can stimulate bole resin production in old trees. The mechanism of this stimulation is not known. Such burning also tends to attract bark beetles and can increase tree mortality from beetle attacks.

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