

1 **Perpetuating Old Ponderosa Pine**

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21 **Abstract**

22 We review current knowledge about the use of management treatments to reduce human-
23 induced threats to old ponderosa pine (Pinus ponderosa) trees. We address the following
24 questions: Are fire-induced damage and mortality greater in old than younger trees? Can
25 management treatments ameliorate the detrimental effects of fire, competition-induced stress,
26 and drought on old trees? Can management increase resistance of old trees to bark beetles? We
27 offer the following recommendations for the use of thinning and burning treatments in old-
28 growth ponderosa pine forests. Treatments should be focused on high-value stands where fire
29 exclusion has increased fuels and competition and where detrimental effects of disturbance
30 during harvesting can be minimized. Fuels should be reduced in the vicinity of old trees prior to
31 prescribed burns to reduce fire intensity, as old trees are often more prone to dying after burning
32 than younger trees. Raking the forest floor beneath old trees prior to burning may reduce
33 damage from smoldering combustion under certain conditions, but also may increase fine-root
34 mortality. Thinning of neighboring trees often increases water and carbon uptake of old trees
35 within one year of treatment, and increases radial growth within several years to two decades
36 after treatment. However, stimulation of growth of old trees by thinning can be negated by
37 severe drought. Evidence from young trees suggests that management treatments that cause
38 large increases in carbon allocation to radial xylem growth also increase carbon allocation to
39 constitutive resin defenses against bark beetle attacks, but evidence for old trees is scarce.
40 Prescribed, low-intensity burning may attract bark beetles and increase mortality of old trees
41 from beetle attacks despite a stimulation of bole resin production.

42 **Keywords:** bark beetle; forest management; fire, Pinus ponderosa; prescribed burn; restoration;
43 thinning

44 **1. Introduction**

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

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

62 Definitions of old-growth ponderosa pine forests vary among authors and agencies, yet
63 all emphasize the existence of old trees (Kaufmann et al., 1992). For example, attributes of old-
64 growth ponderosa pine forests include containing trees with a diameter at breast height (DBH)
65 greater than 41 cm and at least 200 years old in the Front Range of the Rocky Mountains, DBH
66 greater than 41 cm and at least 160 years old in the Black Hills, South Dakota, and DBH greater

67 than 46 cm and at least 160 years old in Arizona and New Mexico (Mehl, 1992). The mean age
68 of ponderosa pines in old-growth stands in Arizona and New Mexico is about 279 years, with the
69 oldest known tree 742 years old (Swetnam and Brown, 1992). In southern Oregon, mean age of
70 ponderosa pine in two mixed conifer stands ranged from 230-315 years, with the oldest tree over
71 400 years (Agee 2003, Perrakis and Agee 2006). In Montana, mean age of ponderosa pine in
72 old-growth mixed conifer stands ranged from 179 to 374 years with the oldest tree over 450
73 years (Arno et al. 1995, 1997; E. Keeling and A. Sala, unpublished data). Trees older than about
74 400 years in remote unlogged areas are rare, perhaps because of extensive mortality from severe
75 drought in the late 1500s (Swetnam and Brown, 1992). In addition to age, crown characteristics
76 differ between old and younger, but mature trees. Height growth is slow in old trees producing a
77 flattened crown top compared to the more conical crown top of younger trees with more rapid
78 height growth (Keen, 1936; Bond, 2000). In this review, we use the term “old” to refer to
79 ponderosa pines that are at least 160 years old or have a DBH greater than 40 cm, and the terms
80 “young” or “younger” to refer to trees that are less than 160 years of age or have a DBH less than
81 40 cm.

82 Old ponderosa pine in areas historically subjected to frequent low-severity fire regimes is
83 currently threatened by several factors that are distinct from the logging that reduced their
84 abundance over the past 150 years. The first of these factors is wildfire. Recent increases in
85 wildfire activity and severity in the western U.S. that often kill old pines have been linked to
86 temperature increases since the mid 1980s (Westerling et al., 2006) and fuel accumulation
87 resulting from a century of fire exclusion (Habeck 1994; Arno et al. 1995, 1997; Covington et
88 al., 2001; Keane et al. 2002; Fulé et al., 2004; Moore et al., 2004). The increase in fuels due to
89 fire exclusion, however, appears to be less predictable in old-growth forests of the northern

90 Rocky Mountains relative to drier forests of the southwestern U.S. (Keeling et al. 2006).
91 Increasing evidence also suggests that historic logging disturbance may also promote
92 regeneration and increase fuel accumulation in the long-term beyond that caused by fire
93 exclusion (Minnich et al. 1995; Kauffman et al. 2000). In ponderosa pine forests where current
94 fire regimes are clearly outside the historic range of variability, wildfire severity and frequency
95 are expected to increase in the future in the western U.S. as temperatures rise and relative
96 humidity decreases (Brown et al., 2004). Restoration treatments, consisting of thinning or
97 prescribed burning to reduce fuels and modify fuel structure, have been recommended to reverse
98 the current trend of large, stand-replacing wildfires (e.g. Covington, 2000; Fiedler, 2000; Fulé et
99 al., 2001; Allen et al., 2002; Fitzgerald, 2005).

100 A second threat to old ponderosa pine is competition with mid- or under-story trees. This
101 threat may be natural, or non-anthropogenic, in some mixed-species higher-elevation forests
102 containing ponderosa pine whose fire regime does not deviate much from historic variability
103 (Brown et al., 1999; Schoennagel et al., 2004), but is of anthropogenic origin in regions where
104 fire exclusion has increased tree density beyond its natural range of variability. For instance,
105 increased tree density in the understory and in former openings and meadows over the last
106 century of fire exclusion has increased competition between old and younger trees in some areas
107 (Biondi, 1996; Feeney et al., 1998; Stone et al., 1999; McDowell et al., 2003). The use of
108 silvicultural treatments to reduce competition stress on old trees is a relatively new idea
109 (Harrington and Sackett, 1992; Kaufmann et al., 1992; Fiedler, 2000). Several experiments have
110 been started recently to address impacts of thinning and prescribed burning on old ponderosa
111 pine (Covington et al., 1997; Oliver, 2000; Ritchie, 2005), yet only a few conclusive results have

112 been published and synthesis of these results is currently lacking. Information on the growth rate
113 of old trees in low-competition environments is scarce for all tree species (Bond, 2000).

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

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

130 **2. Response of old ponderosa pine to fire**

131 Impacts of prescribed fire on growth of ponderosa pine have been addressed in several
132 studies of trees that were mature but younger than our definition of an old tree. Studies on old
133 trees are rare. In Oregon, height, basal area, and volume growth of young ponderosa pine were
134 reduced over an eight-year period after prescribed fire, and the effect was more pronounced in

135 burned areas with higher duff consumption (Landsberg et al., 1984). In northern Arizona,
136 prescribed fire reduced radial growth of young, mature ponderosa pine for several years after
137 burning even in the absence of obvious crown damage from fire, after which growth recovered to
138 pre-burn rates (Sutherland et al., 1991). Prescribed fire with and without prior thinning had little
139 effect on radial growth of young ponderosa pine in Montana (Sala et al., 2005). Prescribed fire
140 intervals of four or six years have been reported to stimulate radial growth of young trees
141 slightly, whereas intervals of one, two, eight and ten years decreased growth relative to no
142 burning (Peterson et al., 1994). Prescribed, low-intensity fire rarely kills young ponderosa pine
143 unless fire intensity is severe enough to girdle the tree by killing cambium or removing much of
144 the canopy by scorch or consumption (Ryan, 1982; Ryan, 1990; McHugh and Kolb, 2003; Sieg
145 et al., 2006).

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

156 Prescribed burning at Crater Lake National Park in Oregon between 1976 and 1986
157 increased mortality of old ponderosa pine compared with control, unburned stands (Swezy and

158 Agee, 1991). In burned stands, mortality was moderately high for the smaller diameter classes,
159 declined as diameter increased, and then increased sharply for the largest diameter trees.
160 Mortality of trees with diameters greater than 100 cm in burned stands varied between 21 and
161 50%, and trees in the oldest class with moderate to low vigor class had mortality of 71-100%
162 (Swezy and Agee, 1991). A majority (68%) of dead trees after a fire in 2002 had evidence of
163 western pine beetle (Dendroctonus brevicomis) attacks (Perrakis and Agee, 2006). Crown vigor,
164 measured with Keen's crown vigor classes, was significantly related to mortality after burning –
165 mortality was highest for low vigor trees.

166 Similar to experiences in Oregon, prescribed fire also can increase the mortality of old
167 ponderosa pine in northern Arizona. Prescribed fire applied to a stand in northern Arizona after
168 100 years of fire exclusion resulted in 39% mortality of old trees compared with 16% in a
169 control, unburned stand, within 20 post-fire years (Sackett et al., 1996). This mortality was
170 associated with complete consumption of the forest floor from the bole to the dripline. Mortality
171 of the old trees started 1.5 years after the fire and continued for 20 years after fire. Prescribed
172 fire at Grand Canyon National Park, Arizona, increased mortality of old ponderosa pine (10 to
173 23% depending on stand) compared with control, unburned stands (1 to 3%) (Kaufmann and
174 Covington, 2001). Following thinning and prescribed burning on shallow, lava-derived soils in
175 northern Arizona, Fulé et al., (2002) reported 67% mortality of large (>50 cm diameter)
176 ponderosa pine compared with 19% mortality for small (<50 cm diameter) pine within two years
177 of burning.

178 Old ponderosa pines are often more susceptible to mortality after fire than younger,
179 mature trees. For example, a “U-shaped” relationship between post-fire mortality and diameter
180 at breast height (Fig. 1) was reported for ponderosa pine in both southern Oregon (Agee, 2003)

181 and northern Arizona (McHugh and Kolb, 2003). In Arizona, mortality three years after fire was
182 highest for trees with the smallest diameter (<20 cm) as would be expected because of their thin
183 bark. Mortality decreased as diameter increased between 20 and 50 cm as would be expected
184 due to increasing bark thickness. However, mortality increased as diameter increased between
185 50 cm and the largest trees at 80 cm. A very similar relationship was found in the Oregon data
186 which included larger diameter trees (Fig. 1). While Harrington (1993) reported decreasing
187 mortality with increasing diameter for ponderosa pine, the largest size class of trees he studied
188 was 30 cm, which is consistent with Fig. 1. This “U-shaped” distribution between post-fire
189 mortality and diameter has also been reported in another study of ponderosa pine (Finney, 1999),
190 and for Scots pine (*Pinus sylvestris*) in Sweden (Linder et al., 1998). Relationships between the
191 probability of post-fire mortality and total crown damage from fire for stands in northern Arizona
192 suggest that fire can increase mortality of large-diameter, old trees more than smaller, younger
193 trees even when crown damage from fire is standardized over tree size classes (Fig. 2).

194 INSERT Fig. 1, Fig. 2

195 What reasons may account for high levels of mortality in old ponderosa pine after fire?
196 First, old, large trees may have previous fire and lightning scars, and damage from insects and
197 fungi, that enable fire to extend deeper into the cambium and higher up the bole causing higher
198 levels of crown damage (Weaver, 1943; Linder et al., 1998). Second, ponderosa pine sheds bark
199 pieces annually, in contrast to the persistent bark of Douglas-fir (*Pseudotsuga menziesii*) or true
200 firs (*Abies* spp.), and over decades the shed bark mixed with leaf litter can build up to 20 cm in
201 thickness or more (Fig. 3). A single prescribed fire can consume much of this material, and these
202 old trees can therefore experience greater root or cambial temperatures than younger trees
203 (Sackett and Haase, 1998; Finney, 1999). Third, old trees may have low amounts of

204 carbohydrate available to replace or repair damaged tissues because of low net photosynthetic
205 rate (Yoder et al., 1994; Bond, 2000; Kolb and Stone, 2000), low leaf area relative carbon sink
206 demands (Ryan et al., 1997), and large carbon allocation to roots and mycorrhizae (Ryan et al.,
207 1997). Fourth, large trees have thicker phloem than small trees (Kolb et al., 1998; Kolb et al.
208 2006) and thus may be a better food source for phloem-feeding insects such as the western pine
209 beetle that can cause tree mortality after fire (Miller and Keen, 1960; McHugh et al., 2003;
210 Breece, 2006).

211 INSERT Fig. 3

212 Other factors may predispose old ponderosa pine to accelerated mortality after fire. Old
213 trees with substantial fire scars can burn through to the cambium and die more easily than
214 younger trees with fewer scars (Perrakis and Agee, 2006). Depending on the timing of drought
215 (before or after the fire), stress may be exacerbated by a low-intensity fire that would have less
216 effect during non-drought periods (Agee, 2003). Interception of precipitation prior to burning by
217 the thick forest floor beneath old-growth ponderosa pine (Fig. 3) may cause additional water
218 stress that exacerbates effects of fire. Older stands may be severely infested with dwarf mistletoe
219 (Arceuthobium spp.), which can cause localized torching and may be associated with higher
220 mortality after fire (Kaufmann and Covington, 2001; Parker et al., 2006).

221

222 **3. Management amelioration of detrimental fire effects**

223 The previous section showed that prescribed- and wild-fire often increase mortality of old
224 ponderosa pine. Here, we address management treatments that have been used to reduce such
225 mortality. The results have not been universally successful, and monitoring of mortality from

226 such treatments has usually been short-term, despite evidence that post-fire mortality of old trees
227 can continue over a 10 to 20 year period after burning (Sackett and Haase, 1998; Agee, 2003).

228 3.1 Raking

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

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

244 Other studies indicated that within burned areas, trees that were raked had similar
245 mortality to those not raked. Kaufmann and Covington (2001) reported low mortality after
246 prescribed burning at Grand Canyon, Arizona, but cautioned that their study extended only five
247 years after burning. Perrakis (2004) found no difference in mortality of old trees for either

248 spring or fall burning between trees with fuels raked around their base and control trees in
249 Oregon.

250 Yet other studies have found that mortality of old trees was high on certain soils even
251 with a raking treatment. Two years after a prescribed fire, 35% of all trees growing on shallow,
252 lava-derived soils at Mount Trumbull in northern Arizona died, and 67% of the trees above 50
253 cm diameter died (Fulé et al., 2002). They observed that on other soils burned in the same fire,
254 unusual levels of mortality did not occur. In Oregon on soils developed from avalanche deposits
255 of gravel and pumice, raking of the surface organic horizons allowed the lower horizons to dry,
256 so that a higher proportion of the forest floor was consumed in spring burns (Swezy and Agee,
257 1991). Fine-root biomass was lower in the rake-burn treatment than a burn-only treatment.
258 These studies were conducted on soils derived from volcanic deposits where many of the roots
259 are concentrated in surface mineral and organic horizons, and this may negate the effect of an
260 ameliorating treatment such as raking. The results of these studies suggest that the effects of
261 raking treatment may be site specific.

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

266 3.2 Understory removal and pruning

267 Understory trees have the potential to torch and increase crown scorch to old trees during
268 prescribed burning. Swezy and Agee (1991) suggested that felling, girdling, or removing small
269 trees in the vicinity of old trees before prescribed burning might result in less heat damage to the
270 older trees. In Oregon, understory shrubs are mown before burning to compact fuels and reduce

271 fireline intensity (Fitzgerald, 2005). Similarly, pruning of low-hanging mistletoe branches can
272 reduce the probability of torching of old trees (Youngblood et al., 2004).

273 3.3 Slash compression

274 We know of only one study that has evaluated the effect of compressing slash prior to
275 prescribed burning on post-fire mortality of old ponderosa pine (Jerman et al., 2004). The study
276 was performed in northern Arizona and the slash was compressed with a bulldozer. Slash and
277 forest floor were removed for a distance of 0.5-1 m around the base of the trees, and the
278 remaining slash (about 60 Mg ha⁻¹) from a thinning operation was either compressed or left
279 uncompressed before a prescribed fire was applied. Crown scorch volume was 14% in the
280 uncompressed slash burn compared to less than 1% in the compressed slash burn. After two
281 years, mortality of old trees in the uncompressed slash area was 14% compared to 0% in the
282 compressed slash area. This study (Jerman et al., 2004) and others (e.g., Hummel and Agee,
283 2003) suggest that arrangement of fuels, as much as total mass, may affect fireline intensity and
284 mortality of old ponderosa pine after prescribed burning.

285 Understory trees have the potential to torch and increase crown scorch to old trees during
286 prescribed burning (Scott and Reinhardt, 2001). Swezy and Agee (1991) suggested that felling,
287 girdling, or removing small trees in the vicinity of old trees before prescribed burning might
288 result in less heat damage to the older trees, and this recommendation has been incorporated into
289 broad perspectives for restoring southwestern ponderosa pine forests (Allen et al., 2002). Fule et
290 al. (2002) developed operational guidelines for two levels of understory thinning around old
291 pines in the Southwest. The intensive treatment included removing nearly all young trees in the
292 vicinity of old trees, while the less intensive treatment cleared most young trees within a radius
293 of 12-18 m of each old trees, with a longer radius in the downslope/downwind direction.

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

295 It is well known that resource uptake and growth of young ponderosa pine can be
296 increased by management treatments such as thinning that reduce inter-tree competition
297 (Schubert, 1971; Cochran and Barrett, 1993; Kolb et al., 1998; Sala et al., 2005; McDowell et al.,
298 2006). Accelerating the growth of young trees by thinning and prescribed burning treatments
299 has been recommended to promote more rapid development of old-growth conditions in
300 ponderosa pine forests (e.g., Sesnie and Bailey, 2003; Skov et al., 2005).

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

310 4.1 Ecophysiology of old tree response to management treatments

311 A number of physiological changes occur as trees become older and larger that likely
312 influence their response to management treatments. As the path length of water transport from
313 the roots to the foliage increases with tree size, both frictional and gravitational constraints on
314 water movement increase (Ryan et al., 2006). These constraints result in reduced stomatal
315 conductance to avoid cavitation, which subsequently limits photosynthesis due to limited CO₂
316 diffusion from the atmosphere to foliage mesophyll. Decreased stomatal conductance and

317 photosynthesis with increased tree size has been consistently observed in ponderosa pine (Yoder
 318 et al., 1994; Hubbard et al., 1999; Kolb and Stone, 2000; Skov et al., 2004; Sala, 2006).
 319 Moreover, cell turgor can decrease with increased tree size because tissue water potential
 320 becomes more negative (Koch et al., 2004; Woodruff et al., 2004). These hydraulic constraints
 321 on photosynthesis and cell growth have been proposed as mechanisms of the commonly
 322 observed decrease in growth efficiency, defined as stemwood growth per unit leaf area, at the
 323 individual tree- and stand-levels, with increasing tree age and size (Ryan et al., 1997; Ryan et al.,
 324 2006; Martinez-Vilalta et al., 2007).

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

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

$$339 \quad g_s = \frac{k_t(\Psi_s - \Psi_l)}{VPD} \quad (1),$$

340 in which k_1 is whole plant hydraulic conductance, Ψ_s is soil water potential (MPa), Ψ_l is daytime
341 leaf water potential, and VPD is vapor pressure deficit (kPa). From the framework in equation
342 (1) we made generalized predictions of how different size trees may respond to changes Ψ_s
343 associated with thinning. We applied equation (1) in a similar fashion to McDowell et al.
344 (2005). We assumed that Ψ_l is constant (isohydric) regardless of site water availability
345 (Maherali and Delucia, 2001; McDowell et al., 2006) and that hydraulic conductance of old, tall
346 trees is half that of young, short trees. Young, short trees with high hydraulic conductance are
347 predicted to have a broader range of stomatal conductance and a steep response of stomatal
348 conductance to Ψ_s , whereas old, tall, trees are predicted to be less responsive (Fig. 4).

349 INSERT Fig. 4

350 The model results from equation (1) suggest that management actions in ponderosa pine
351 forests that increase availability of soil water, such as thinning (Feeney et al., 1998; Kolb et al.
352 1998; Sala et al., 2005; McDowell et al., 2006), stimulate stomatal conductance of young, short
353 trees more than old, tall trees. Stomatal response of old, tall trees to increased soil water content
354 is constrained by lower hydraulic conductance from soil to leaf as a consequence of a longer path
355 length compared with young, short trees. Because stomatal conductance is strongly related to
356 photosynthesis in ponderosa pine (Feeney et al., 1998; Skov et al., 2004), we should expect larger
357 and faster stimulation of photosynthesis and growth in young, short trees than old, tall trees.
358 This theoretical expectation is consistent with results of an experiment in northern Arizona
359 where thinning stimulated stomatal conductance and net photosynthetic rate (Skov et al., 2004)
360 and bole radial increment (Skov et al., 2005) of small, mature ponderosa pine more than for old
361 pine in the same stand.

362 4.2 Empirical studies of response of old ponderosa pine to management

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

369 4.2.1 Arizona

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

378 The goal of the thinned treatment was to recreate as closely as possible the tree size class
379 distribution and spatial pattern that occurred on the site before the start of Euro-American
380 settlement of the region in 1876. The thinning removed most post-settlement trees, defined as
381 trees that established after Euro-American settlement of the region in 1876. A small number of
382 post-settlement trees were left on site to replace dead presettlement trees that were identified by
383 old logs and stumps. In addition, no trees with diameter at breast height greater than 40 cm were
384 cut. The thinning occurred in November 1993 and reduced tree basal area by about 62% (34.5
385 $\text{m}^2 \text{ha}^{-1}$ to 13.0 $\text{m}^2 \text{ha}^{-1}$) and tree density by 95% (3100 trees ha^{-1} to 151 trees ha^{-1}).

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

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

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

423 Increased resource uptake by old trees in the thinned plots at the GPNA ultimately
424 resulted in greater stem radial growth. Figure 5 shows an update of an earlier analysis of the
425 growth response of old trees at the GPNA (Feeney et al., 1998). Basal area increment of old
426 trees did not differ significantly among the treatment plots before treatment (1984-1993), in the
427 year of treatment (1994), nor in the first post-treatment year (1995) (Fig. 5). Starting with the
428 second post-treatment year in 1996, trees in the thinned only and thinned+burned treatments
429 typically had significantly greater increment than trees in the control treatment (Fig. 5). The
430 only exception was the severe drought year of 2002 when increment was similar in all
431 treatments. Increment was similar in the thinned only and thinned+burned treatments in all

432 years, except 2003 when increment was higher in the thinned+burned treatment. A significant
433 treatment x year interaction in increment (Fig. 5) resulted primarily from the larger negative
434 effect of the 2002 drought on increment in the thinned only and thinned+burned treatments than
435 the control.

436 INSERT Fig. 5

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

452 INSERT Fig. 6

453 There is no evidence that careful, well-implemented thinning causes long-term stress to
454 old ponderosa pine in Arizona or elsewhere. Thinning shock, or a negative effect of thinning on

455 tree condition (Harrington and Reukema, 1983; Aussenac, 2000), has been documented in
456 northern Arizona only for small, suppressed ponderosa pines as a reduction in sapwood hydraulic
457 conductance per unit leaf area and canopy conductance after thinning during extreme drought
458 (Simonin et al., 2006). This type of thinning shock occurred only in the first year after thinning,
459 and thinning stimulated conductance in the second year after thinning.

460 4.2.2 Oregon

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

470 The second recent study in Oregon (McDowell et al., 2003) provides additional
471 understanding of physiological mechanisms of the response of old ponderosa pine to thinning.
472 This study compared BAI and water, carbon, and nitrogen relations of old trees between
473 untreated stands and stands treated with shelterwood cuts that reduced basal area 61 to 82%. A
474 retrospective reconstruction of leaf gas exchange in both types of stands modeled from carbon
475 isotope ratios in tree rings and level-level gas exchange (McDowell et al., 2003) suggested that
476 net photosynthetic rate (Fig. 7A) and stomatal conductance (Fig. 7B) increased in the first year
477 after thinning and were elevated above rates of trees in unthinned stands for at least 15 years

478 after thinning. Basal area increment (Fig. 7C) increased by two- to three-fold after thinning, and
479 the increase was sustained for up to 15 years after thinning. The increase in BAI after thinning
480 lagged behind the increase in net photosynthetic rate and stomatal conductance by two years
481 (Figs. 7 A-C). Thinning increased tree predawn water potential 15 years after treatment,
482 indicating an increase in soil water content in the rooting zone, but had no effect on leaf nitrogen
483 concentration (McDowell et al., 2003). These results show that heavy thinning can increase
484 radial growth, water uptake, and leaf gas exchange of old ponderosa pine for at least 15 years
485 after treatment if stand leaf area is not fully reestablished.

486 INSERT Fig. 7

487 4.2.3 Montana

488 Visual symptoms of decline of old ponderosa pine in the Blackfoot River Valley in
489 Montana in the early 1980s prompted the experimental application of thinning and prescribed
490 burning to improve the vigor and survival of old trees (Fiedler, 2000). The thinning treatment in
491 1984 removed most understory “ladder” fuels, including most Douglas-fir. Half of the thinned
492 plots were prescribed burned in the fall after thinning. Thinning of understory trees, with and
493 without prescribed burning, reduced mortality of old trees compared with the unthinned controls
494 (Fiedler, 2000). Mortality was 5.5-fold greater in control than in thinned or thinned and burned
495 plots. Thinning also increased diameter growth of the old trees by about 2.6 fold.

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

497 The ultimate measure of tree resistance to bark beetles is survival after bark beetle
498 attacks. Large numbers of lethal bark beetle attacks occur episodically in ponderosa pine forests;
499 however, such attacks rarely occur during experimental studies (e.g., Larsson et al., 1983).
500 Consequently, mechanisms of resistance are typically measured to provide insight on resistance

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

511 A mixture of direct and indirect evidence suggests that management actions that cause
512 large increases in stem radial growth rate of ponderosa pine also increase tree resistance to lethal
513 bark beetle attacks. Most of this evidence is for trees that are younger than 100 years. Early
514 research on the relationship between radial growth and bark beetle resistance emphasized the
515 importance of tree vigor, defined as wood production per leaf area, with leaf area predicted from
516 sapwood area (Larsson et al., 1983; Mitchell et al., 1983; Waring and Pitman, 1985). Attacks of
517 mountain pine beetle decreased when vigor of ponderosa (Larsson et al., 1983) and lodgepole
518 (Pinus contorta) pines (Mitchell et al., 1983) was greater than 100 g of wood produced per m² of
519 leaf area. McDowell et al. (2007) highlighted uncertainty in accurately predicting leaf area from
520 sapwood area, and thus vigor as defined above, because of changes in the ratio of leaf area to
521 sapwood area with tree competitive status (Simonin et al., 2006) and thinning (McDowell et al.,
522 2006). Instead, McDowell et al. (2007) emphasized the use of more direct measurements of

523 carbon allocation to stem radial growth, such as BAI, to predict tree carbon allocation to resin
524 defenses in the stem.

525 The indirect evidence concerning positive effects of management, especially thinning, on
526 ponderosa pine resistance to bark beetles is an association between stand structural conditions
527 and tree mortality or resin flow after wounding. Stand conditions associated with high mortality
528 of young ponderosa pine stands by mountain pine beetle (Dendroctonus ponderosae) in the
529 inland western U.S. include high stand basal area and tree density (Sartwell and Stevens, 1975;
530 Dahlsten and Rowney, 1983; Cochran and Barrett, 1993; Olsen et al., 1996; Fettig et al., 2007)
531 which are known to reduce diameter growth (e.g., Larsson et al., 1983; McDowell et al., 2006).
532 Probability of lethal attacks by mountain pine beetle (Negron and Popp, 2004) and roundheaded
533 pine beetle (Dendroctonus adjunctus) increases with stand density and decreases with radial
534 growth rate for ponderosa pine (Negron, 1997; Negron et al., 2000). Consistent with these
535 reports, flow of preformed resin from phloem wounds, a key defense of many conifers against
536 bark beetles (Smith, 1975; Raffa and Berryman, 1982, 1983), was positively related to BAI in a
537 region-wide synthesis of five studies of ponderosa pine in northern Arizona (McDowell et al.,
538 2007).

539 The direct evidence for a role of management in enhancing resistance of ponderosa pine
540 to bark beetles consists of changes in bark beetle attacks, tree survival, or resistance mechanisms
541 following experimental manipulation of tree density or stand basal area. Increased radial growth
542 of young ponderosa pine in heavily thinned stands has been linked to fewer attacks and
543 consequent tree mortality by mountain pine beetle in Oregon (Fig. 8) and South Dakota (Fettig et
544 al., 2007), and greater resin flow from phloem wounds in Arizona (Kolb et al., 1998). However,
545 heavy thinning (ca. 50% basal area) in Montana did not increase resin flow in June in spite of

546 increases in radial growth (Peters, 2003). Similarly, relatively light (reduction of basal area by
547 <30%) and infrequent thinning of young ponderosa pine stands can stimulate radial growth
548 slightly, but is not effective at stimulating resin flow (Zausen et al., 2005).

549 INSERT Fig. 8

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

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

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

587 Studies at the GPNA in northern Arizona also have investigated effects of management
588 treatments on leaf toughness, an important resistance mechanism against foliage-feeding insects
589 such as pine sawflies (McMillin and Wagner, 1993; Wagner and Zhang, 1993). Both thinning
590 and thinning+burning treatments consistently increased leaf toughness of old trees compared to

591 trees in the control (Feeney et al., 1998; Wallin et al., 2004). This result suggests reduced
592 performance of foliage-feeding insect on trees in thinned treatments, but this has not been
593 verified with insect performance experiments. Tougher foliage appears to be a long-term effect
594 of thinning at the GPNA as it was consistent in all measurements between one and seven years
595 after thinning.

596

597 **6. Management amelioration of drought impacts on old ponderosa pine**

598 Increases in mortality of both ponderosa pine ([http://www.fs.fed.us/r3/resources/health/](http://www.fs.fed.us/r3/resources/health/beetle/index.shtml)
599 [beetle/index.shtml](http://www.fs.fed.us/r3/resources/health/beetle/index.shtml)) and pinyon pine (*Pinus edulis*) (Breshears et al., 2005; Shaw et al., 2005)
600 have been reported during drought over the last decade (1996-2006) in the Southwest US. We
601 utilized 3-PG, a physiologically-based tree growth model (Landsberg and Waring, 1997), to
602 contrast the implications of a reduction of nearly 50% in annual precipitation recorded near Los
603 Alamos, New Mexico between the period from 1996-1999 (mean, 490 mm yr⁻¹) and 2000-2003
604 (mean, 260 mm yr⁻¹) on tree growth. The model predicted a 1/3 reduction in tree growth and a
605 proportional reduction in maximum leaf area index (LAI) from 2.1 to 1.4. Similar reductions in
606 the normalized difference vegetation index have been reported in the region during severe
607 drought (Breshears et al., 2005). Self-thinning would necessarily increase, because, according to
608 the widely applied $-3/2$ power law, the maximum standing biomass at which mortality begins is
609 a function of maximum LAI (Landsberg and Waring, 1996). This simulation result suggest that
610 the increased frequency of severe droughts that are predicted to occur with future climate change
611 (Houghton et al, 2001; Coquard et al., 2004) will increase mortality of ponderosa pine in old-
612 growth stands. This mortality can be reduced by thinning that reduces the high LAI of many
613 current stands of 2.0 or greater by at least 33%. Removing younger trees by thinning will

614 increase water available to old trees during drought (e.g., Feeney et al., 1998; McDowell et al.,
615 2003; Wallin et al., 2004) and likely reduce their mortality.

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

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

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

650 Overall, results from the GPNA and related studies in northern Arizona (Feeney et al.,
651 1998; Skov et al., 2004; Skov et al., 2005; McDowell et al., 2006) suggest that thinning reduces
652 impacts of severe water stress on photosynthesis and growth immediately after treatment, but
653 may actually increase the relative impact of drought on growth (i.e., percent change between
654 non-drought and drought years) decades following treatment because of slow adjustments in tree
655 leaf area to sapwood area ratio. However, this is a relative response, i.e. trees in thinned stands
656 may show greater drought-related decreases than trees with low growth rates, but may still may
657 higher absolute growth. Trees in heavily thinned stands typically have greater absolute BAI than
658 trees in unthinned stands in both drought and non-drought years (Feeney et al., 1998; McDowell

659 et al., 2003; McDowell et al., 2006; Fig. 5). Therefore, resilience of growth to drought appears
660 to be greater for trees in thinned than unthinned stands.

661 **7. Management implications and recommendations for perpetuating old ponderosa pine**

662 Our review provides evidence that careful management of old-growth ponderosa pine
663 forests whose current stand structure deviates from historic conditions due to the effects of
664 grazing and fire exclusion often enhances resource uptake and growth of old trees in the short
665 term (up to 10 years). One might conclude that management involving thinning and burning of
666 all old-growth ponderosa pine forests is in order. However, such management should be
667 carefully considered. First, there is evidence that not all ponderosa pine forests are outside the
668 historic range of variability, either because fire regimes were not completely disrupted (e.g.,
669 Grand Canyon; Fulé et al., 2003), or because some mixed-conifer forests containing ponderosa
670 pine historically had relatively high density or infrequent fires (e.g., Colorado Front Range;
671 Brown et al., 1999; Schoenagel et al., 2004). In such cases, thinning for the purpose of restoring
672 historic structure would not be justified. Second, many old-growth forests in the western U.S.
673 are located in remote areas, where management often causes unavoidable disturbances such as
674 road construction, soil compaction, and exposure to mineral soil. Even in areas where old-
675 growth forests are clearly outside their range of natural variability the pros and cons of
676 management need to be carefully weighted. For instance, road construction and subsequent
677 increased access could increase invasive species (Korb, 2001), decrease native species diversity,
678 alter fire regimes, or change resource availability (Levine et al., 2003). Third, financial costs of
679 management treatments in old-growth forests can be high because of the careful attention
680 required to individual trees. Finally, while long-term monitoring data is lacking, increasing
681 evidence suggests that disturbance associated with harvesting may increase recruitment and

682 density in the long-term, which could be counter productive (Minnich et al., 1995; Kauffman et
683 al., 2000). For instance, in an ongoing study across Montana and central Idaho, tree density in
684 never-logged ponderosa pine stands not subjected to fire for the last 60 years was on average
685 over 40% lower than in paired stands (n=23 pairs) that had been subjected to historical logging
686 (C. Naficy and A. Sala, unpublished data). These results serve only to highlight the need to
687 consider long-term effects of disturbance, and the need for repeated maintenance actions, such as
688 prescribed fire, prior to management actions.

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

692 1. Results for removing the forest floor beneath old trees by raking prior to prescribed fire
693 to reduce fuels and smoldering combustion appear to be site specific. Raking appears to
694 ameliorate fire damage to old trees on fine-textured, basalt-derived soils in northern Arizona, but
695 results for other soils are variable. Raking one or two years before burning may ameliorate the
696 immediate loss of fine roots due to the raking treatment before further fine root loss is incurred
697 by burning.

698 2. Old ponderosa pine trees are often more prone to dying after prescribed burns and
699 wildfires than younger, mature trees. Their death often occurs more slowly after burns than for
700 younger trees. Fuels should be reduced in the vicinity of old trees prior to prescribed burns by
701 thinning the understory and removing the slash, or by compressing the slash to reduce fire
702 intensity.

703 3. Resource uptake and growth of old trees can be increased by careful thinning. Thinning
704 often reduces water stress of old trees starting one or two years after treatment. Radial growth

705 responses are slower, and often start several years to two decades after thinning. Growth
706 response to thinning is slower for old trees than young trees. Stimulation of growth of old trees
707 by thinning can be negated by severe drought. However, stimulation of growth by thinning
708 returns shortly after drought ceases. Overall, these results for old ponderosa pine are consistent
709 with a small, but growing number of experiments showing that resource uptake and growth of
710 old trees of various species are responsive to thinning (Bebber et al., 2004; Martinez-Vilalta et
711 al., 2007). An unresolved issue is whether stimulation of radial growth in old, large trees
712 increases their susceptibility to windthrow and breakage due to an increase in above-ground
713 mass or due to increased exposure.

714 4. Reduction of stand leaf area by management treatments should reduce mortality of old
715 trees during severe drought because of increased water availability to remaining trees.

716 5. Careful thinning does not often cause “thinning shock,” or a negative physiological or
717 growth response to thinning, in old ponderosa pine.

718 6. Management treatments that cause large increases in carbon allocation to radial xylem
719 growth also increase carbon allocation to constitutive resin defenses against bark beetle attacks,
720 based on studies with young ponderosa pine.

721 7. Prescribed, low-intensity burning that causes little crown scorch can stimulate bole resin
722 production in old trees. The mechanism of this stimulation is not known. Such burning also
723 tends to attract bark beetles and can increase tree mortality from beetle attacks.

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1167 prescribed burning on ponderosa pine physiology and bark beetle abundance in northern
1168 Arizona: A replicated landscape study. For. Ecol. Manage. 218, 291-305.
- 1169

1170 **List of Figures**

1171

1172 Figure 1. The U-shaped mortality trend in Southern Oregon (Agee 2003) and Northern Arizona
1173 (McHugh and Kolb 2003), showing highest post-fire mortality in the smallest and largest size
1174 classes of ponderosa pine. Missing columns indicate no data for that size class. A three-class
1175 running mean was used for the Arizona data to express it in the same classes as the Oregon data.

1176

1177 Figure 2. Distribution of predicted probability of ponderosa pine mortality for logistic regression
1178 models using total crown damage (percent of crown scorched + consumed) and diameter at
1179 breast height for two wildfires (A, Side wildfire; B Bridger Knoll Wildfire) that burned in late
1180 spring, 1996, in northern Arizona shows that large-diameter trees had a higher probability of
1181 mortality than small-diameter trees. Derived from McHugh and Kolb (2003).

1182

1183 Figure 3. Substantial buildup of organic material, including leaf litter and bark flakes, at the base
1184 of an old ponderosa pine can create substantial temperature increases around the base of the tree
1185 when burned by a prescribed fire. Photo by J.K. Agee.

1186

1187 Figure 4. Predictions of stomatal conductance verses soil water potential using the Whitehead
1188 (1984) modeling approach shows that conductance of old, tall trees is less sensitive to drying soil
1189 than young, short trees. Hydraulic conductance of tall trees was set to 50% of that of short trees.
1190 Model adapted from McDowell et al. (2005).

1191

1192 Figure 5. Basal area increment of old ponderosa pine at the Gus Pearson Natural Area in
1193 northern Arizona was simulated by thinning treatments, and increment was similar for trees in
1194 thinned alone and thinned plus prescribed burned treatments. The vertical line shows the year of
1195 treatment. The P values are from repeated measures MANOVA for the post-treatment years. *
1196 indicates significant ($P < 0.05$) differences among treatments in ANOVA by year. Another
1197 MANOVA showed no difference in increment among trees in different treatments for the 10
1198 pretreatment years (1984-1993). Error bars are one standard error of the mean.

1199
1200 Figure 6. Mean crown dieback (A) of old ponderosa pine at the Gus Pearson Natural Area in
1201 northern Arizona in year 2004, 10 years after treatment, was slightly greater in control compared
1202 with thinned alone and thinned plus prescribed burned treatments. Dieback increased for trees in
1203 the control between 1994 and 2004 (B), whereas dieback decreased (thinned) or did not change
1204 (thinned+burned) in the thinned treatments. The P values are from ANOVA. Different letters
1205 indicate statistically significant differences among treatments (LSD, $P < 0.05$). The vertical bar
1206 shows one standard error of the mean.

1207
1208 Figure 7. Net photosynthetic rate (A), stomatal conductance (B), and basal area increment (C)
1209 from a study of old ponderosa pine in central Oregon (McDowell et al. 2003) shows that thinning
1210 stimulated leaf gas exchange and radial growth one year after thinning, and increases growth
1211 four years after thinning. The shelterwood stand was thinned in 1987, and the neighboring
1212 control stand was never thinned. Net photosynthetic rate and stomatal conductance were
1213 modeled using tree-ring carbon isotope ratios and leaf level gas exchange measurements of the

1214 response of photosynthesis to internal CO₂ concentration as described in McDowell et al. (2003).

1215 Bars are one standard error of the mean.

1216

1217 Figure 8. The percentage of young ponderosa pine attacked by the mountain pine beetle

1218 decreased linearly with a decrease in stand basal area in a thinning experiment in central Oregon

1219 (derived from Larsson et al., 1983). The basal area levels were established by thinning 15 years

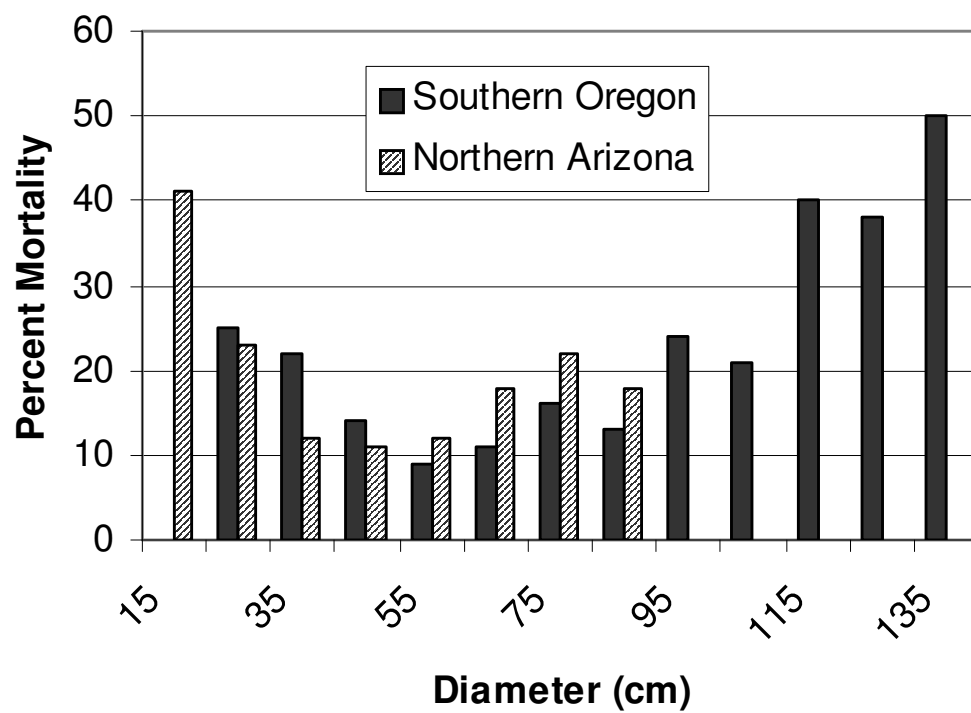
1220 prior to the measurement of bark beetle attacks and were maintained by periodic thinnings. The

1221 vertical bars show one standard error of the mean. Three stands were sampled for all thinned

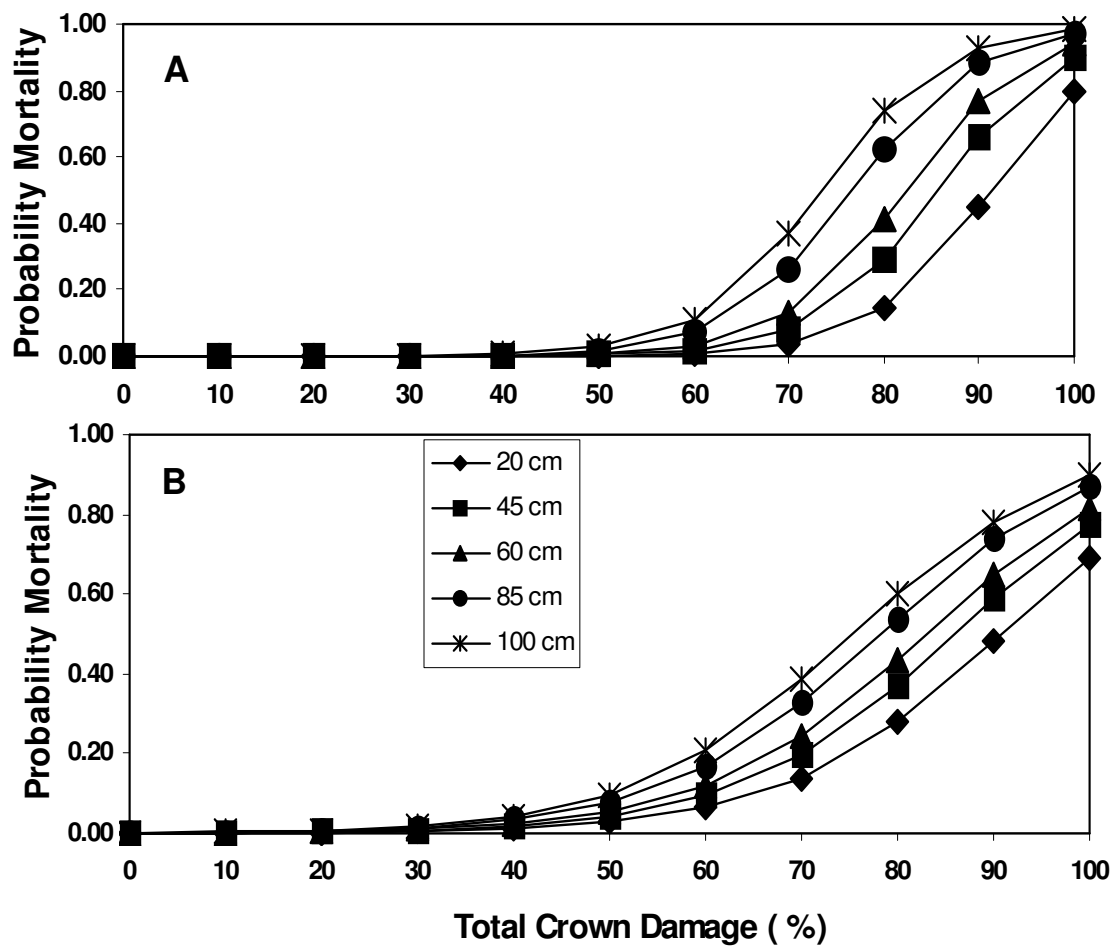
1222 stands (basal area less than 40 m² ha⁻¹), and nine stands were sampled for the unthinned control

1223 (basal area = 54 m² ha⁻¹).

Figure



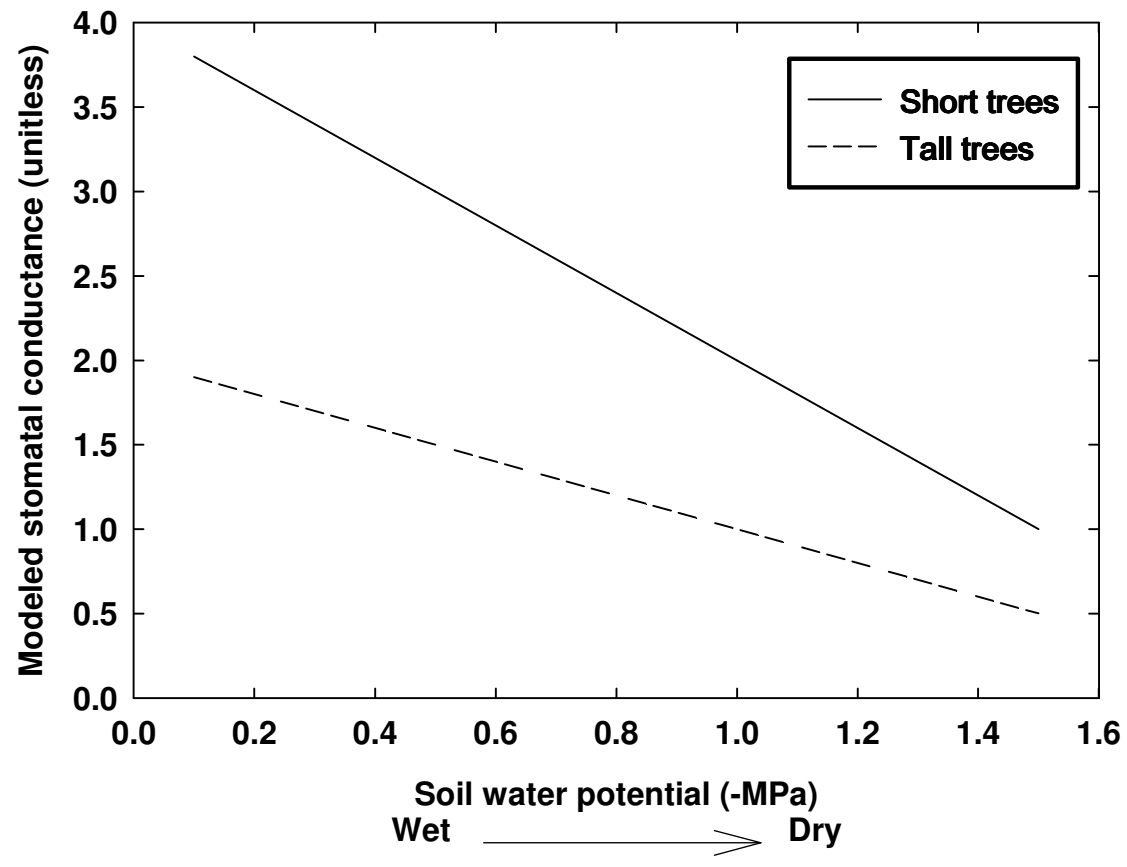
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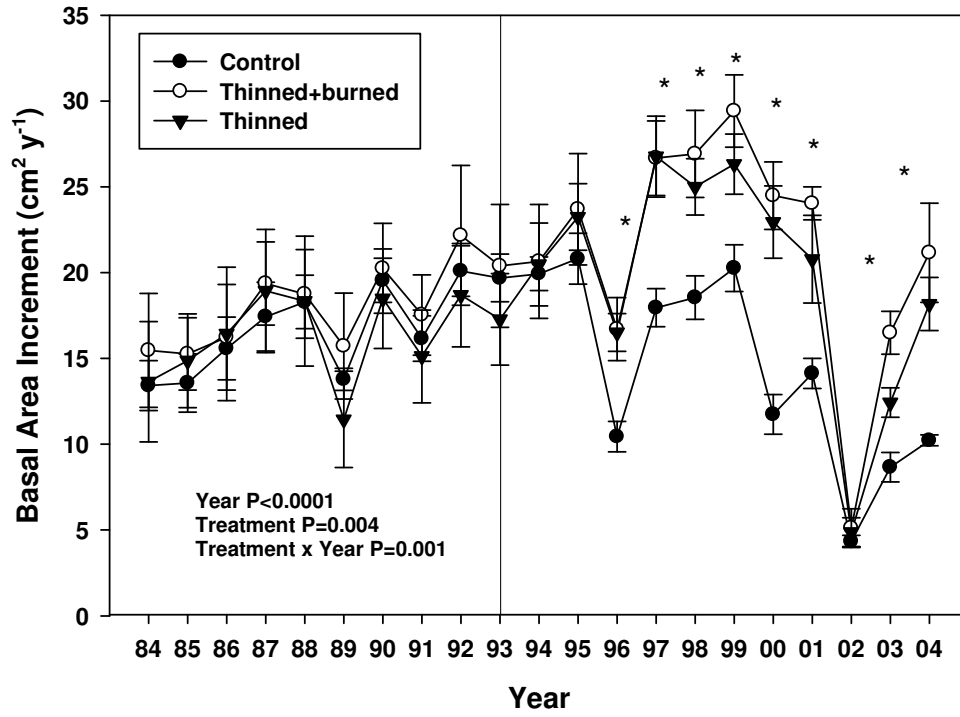
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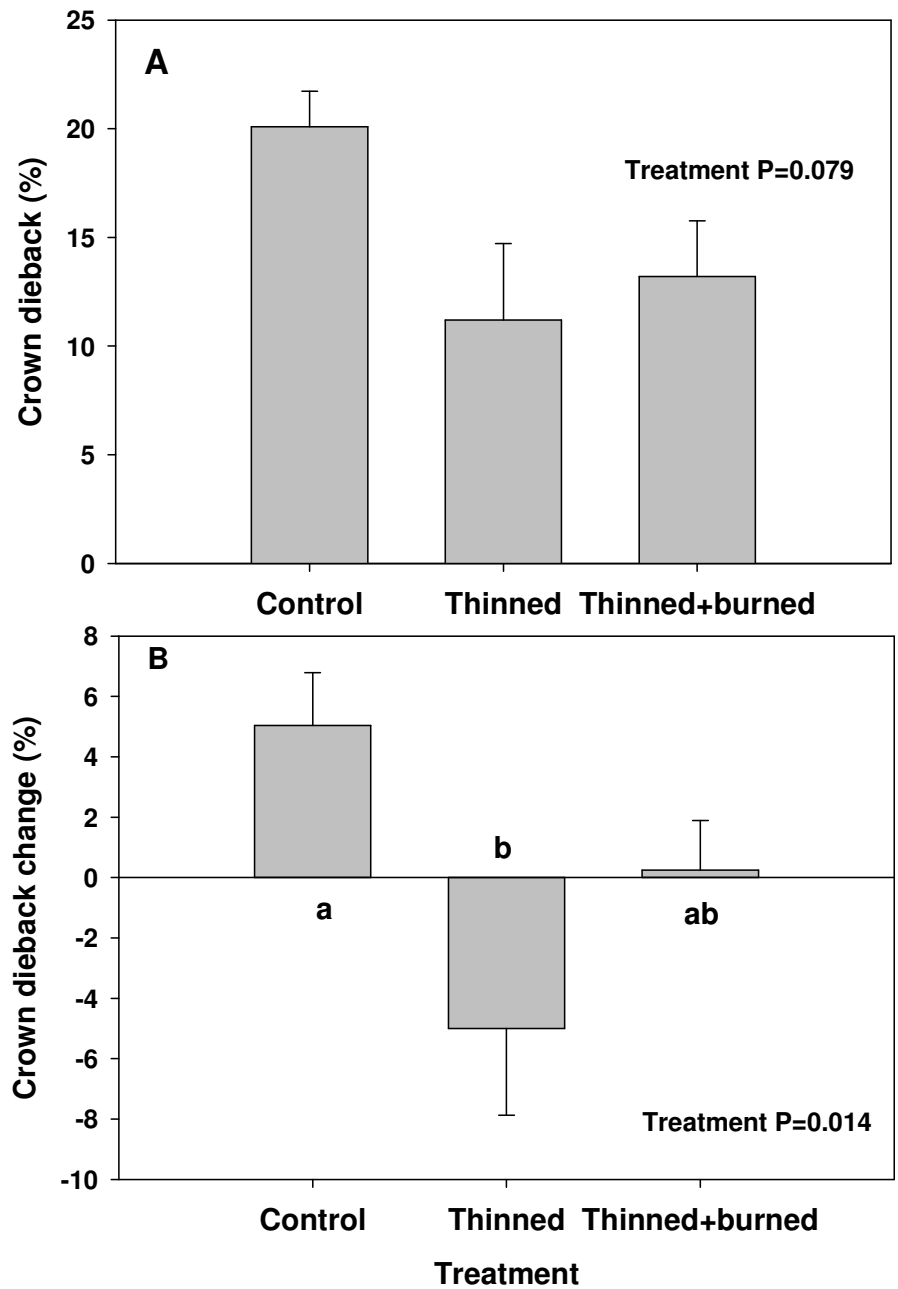
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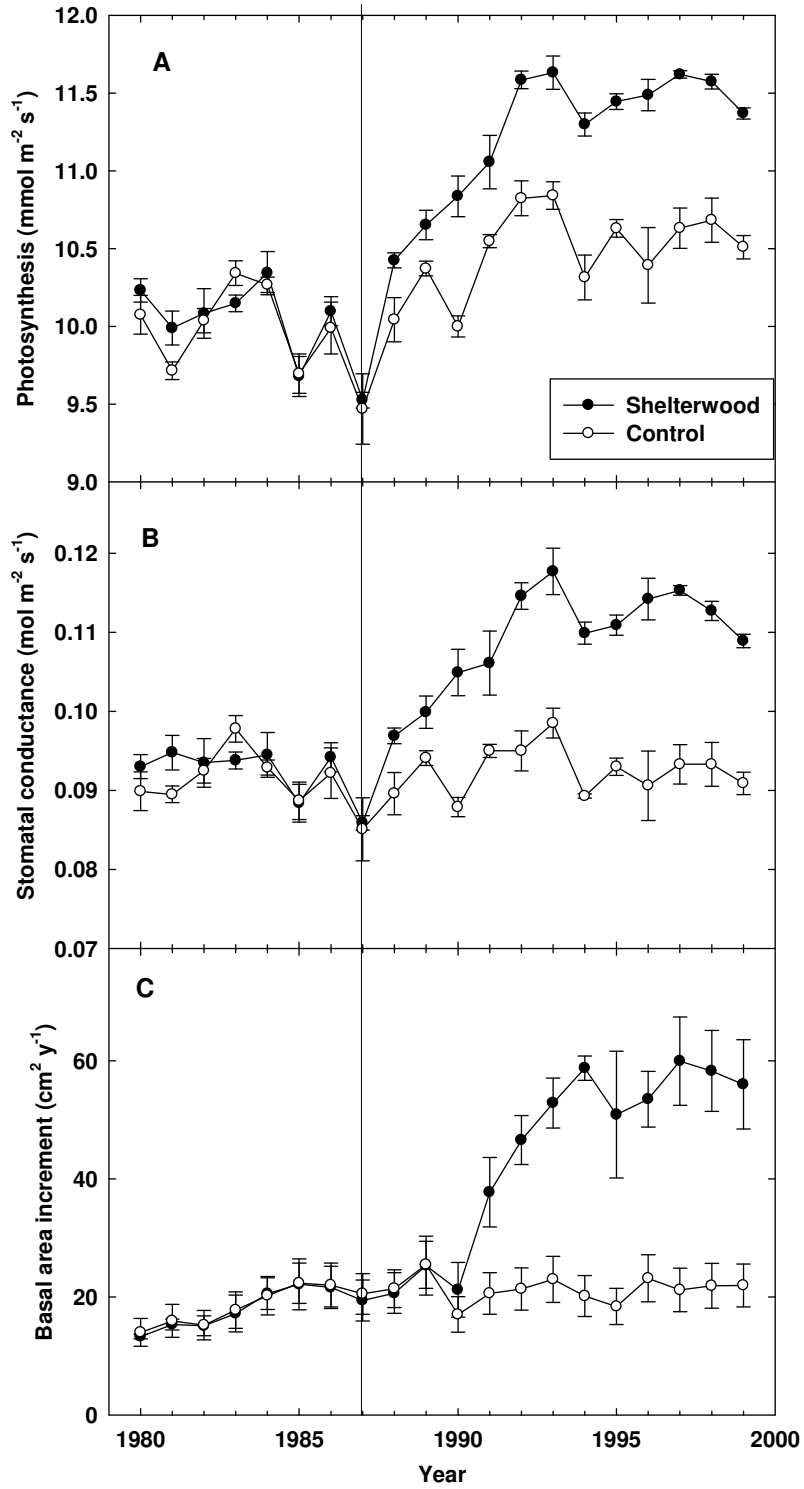
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