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Managing climate change adaptation in forests: a case study from the U.S. Southwest

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Summary

1. Forest mortality related to climate change is an increasingly common global phenomenon. We provide a case study of the U.S. Southwest to investigate the interactions among forest restoration treatments that alter stand density, tree growth and drought resistance in trees of different size classes.

2. Using cores taken from five positions in large trees (coarse roots, breast height, base of live crown, midcrown branch and treetop) and breast height in small trees, we investigated how radial growth response to thinning and precipitation availability varied in 72 ponderosa pines *Pinus ponderosa* Dougl. in northern Arizona.

3. Ten years after thinning, growth of small trees did not respond significantly to thinning, whereas growth of large trees increased following moderate and heaving thinning, and this response was similar across within-tree core sample positions.

4. The intensity of thinning treatment did not significantly affect dry-year growth in small trees. In large trees, dry-year growth after thinning was maintained at pre-thinning levels in moderate and heavy thinning treatments but decreased in the light thinning and control treatments.

5. *Synthesis and applications*. Our findings indicate that more aggressive thinning treatments used for forest restoration stimulate growth throughout large residual trees from coarse roots to branches and also improve drought resistance, providing a greater resilience to future climate-related stress. These responses to treatment are more pronounced in large trees than small trees. Forest thinning is therefore recommended in systems that are likely to experience increased temperature and decreased precipitation as a result of climate change.

Key-words: Arizona, carbon allocation, dendrochronology, drought, ponderosa pine, restoration, stand density, thinning, tree ring

Introduction

Increased temperature and drought attributable to changing climate are increasing forest mortality (Allen *et al.* 2010). Tree mortality influences forest structure, ecological communities and ecosystem function and services (Anderegg, Kane & Anderegg 2012). At the global scale, forest mortality alters biosphere–atmosphere interactions by affecting carbon uptake and sequestration (Bonan 2008; Allen *et al.* 2010) as well as albedo (Lee *et al.* 2011). Examples of recent increases in tree mortality related to drought are well-documented and can be found on all wooded continents in a range of diverse forest types and climatic zones (Allen *et al.* 2010).

Using the U.S. Southwest as a case study, we investigated the interactions between climate change and forest management. In this region, models project continued warming and drying (Seager *et al.* 2007) and shifts in the bimodal precipitation regime of the region (Kim 2002; Cook *et al.* 2004). Based on dendrochronological analyses, the combination of high summer vapour pressure deficit (VPD) and low winter precipitation strongly reduces tree growth, and as this condition becomes more common, it will likely lead to widespread loss of south-western ponderosa pine *Pinus ponderosa* Dougl. forests (Williams *et al.* 2012). These ongoing

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impacts are occurring in a system that has already undergone substantial change as a result of human intervention in natural disturbance cycles. Since European settlement in the late 1800s, fire suppression and overgrazing in the Southwest have produced today's dense ponderosa pine forests characterized by stunted young trees (Covington *et al.* 1997), declining old trees (Kolb *et al.* 2007) and dangerously high fuel loading. Thinning of these forests is now a major management initiative to improve forest condition and reduce the risk of fire and insect outbreaks, with an overall goal of returning the forest to the natural range of variability that existed prior to fire exclusion (Covington *et al.* 1997). However, it is unclear how management actions may interact with climate drivers of tree growth and forest productivity, an important consideration given the uncertainty associated with projected changes in climate (Millar, Stephenson & Stephens 2007).

Thinning ponderosa pine forests can reduce competition and increase resource availability (Covington *et al.* 1997; Hurteau, Stoddard & Fulé 2011), sometimes producing a 'release effect' observed as an increase in annual radial growth at breast height (Feeney *et al.* 1998; Kolb *et al.* 1998; Latham & Tappeiner 2002; Skov, Kolb & Wallin 2005). While smaller trees consistently show a release effect, larger trees may be more variable in their response. A release effect was reported in old ponderosa pines in western Oregon, USA (Latham & Tappeiner 2002), but not at sites in northern Arizona in the first 3 years after thinning (Skov, Kolb & Wallin 2005).

Characteristics of large, old trees such as increased maintenance respiration (Ryan, Binkley & Fownes 1997) and decreased hydraulic conductance (Ryan & Yoder 1997; Koch *et al.* 2004), foliar CO_2 diffusion (Mullin *et al.* 2009) and leaf photosynthetic rate (Ryan & Yoder 1997; Koch *et al.* 2004) are associated with slowing of growth as trees age (Yoder *et al.* 1994); however, large and old trees often retain the ability to respond to environmental change (Phillips, Buckley & Tissue 2008; Sillett *et al.* 2010). Detection of a release effect may require measurements at appropriate temporal and spatial scales. Latham & Tappeiner (2002) found that large ponderosa pines often did not show a release effect until 15 years after thinning. That Skov, Kolb & Wallin (2005) did not observe a release effect in large ponderosa pines in Arizona 3 years after thinning may indicate a delay between the onset of physiological responses and a detectable change in radial growth (Feeney *et al.* 1998; Latham & Tappeiner 2002; Skov, Kolb & Wallin 2004).

Failure to detect a release effect in large, old trees also may result from changing within-tree allocation patterns masking the growth response inferred from measurements at breast height. Thinning often increases leaf area relative to sapwood area (Feeney *et al.* 1998; Kolb *et al.* 2007). If this is accompanied by greater radial growth in the tree crown than the bole, then a release effect may go undetected in the near term by measurements at breast height. Consistent with the importance of crown position, Kerhoulas & Kane (2012) previously showed that the sensitivity of ponderosa pine radial growth to climate is greater at the treetop than in coarse roots or positions lower on the bole.

In a water-limited forest, the positive effects of thinning on growth may be especially pronounced in dry years if thinning reduces competition for water. Released from competition for water, post-thinning dry-year growth is likely to exceed pre-thinning dry-year growth in residual trees. The variation in water relations within and among trees of different sizes (Ryan & Yoder 1997; Koch *et al.* 2004) suggests that the growth response to the reduction in water competition that accompanies thinning treatments may be expressed differently in small and large trees, at different positions within the crown and in dry vs. wet years. Examining these interactions is important for understanding whether and how management prescriptions can mitigate the effects of drought on forest productivity in warming and drying regions.

In the U.S. Southwest, ponderosa pines that established prior to the European settlement in the 1890s are currently a small fraction of total trees, but are valued for wildlife habitat, aesthetic considerations and the carbon protection afforded by their fire resistance (Hurteau & Brooks 2011; Hurteau, Stoddard & Fulé 2011). Previous work at our study site indicates that small trees responded to thinning with increased radial growth at breast height and this increase was more pronounced in heavier thinning treatments (Feeney *et al.* 1998; Skov, Kolb & Wallin 2005). Although large trees showed little growth increase in the first 3 years after thinning, regardless of thinning treatments (Skov, Kolb & Wallin 2005), physiological measurements indicated reduced water stress and greater photosynthesis in both small and large trees (Skov, Kolb & Wallin 2004). We reasoned that these positive physiological responses in large trees likely produced a growth response that was either undetected by measurements only at breast height or delayed in time compared with small trees because of lags in carbon allocation from the crown to the lower bole and root system. To test this, the present study extended the time period for assessing the growth response to thinning and examined the distribution of that response throughout large trees. Furthermore, because thinning lessens water stress (Skov, Kolb & Wallin 2004), it likely mitigates growth reductions in dry years. Specifically, we tested the following hypotheses: (i) ten years post-thinning, large trees will show a release effect comparable to that of small trees and (ii) thinning will mitigate growth reductions in dry years.

Materials and methods

STUDY SITE AND TREES

Our study sites were located in the Fort Valley Experimental Forest (USDA Forest Service, Rocky Mountain Research Station) 10 km north-west of Flagstaff, AZ, USA (N35°15′58″,W111°42′1″, elevation 2200 m). This ponderosa pine-dominated forest was experimentally thinned between December 1998 and September 1999. Treatments included three levels of thinning followed by prescribed burning and an unthinned and unburned control (Skov, Kolb & Wallin 2005). All pre-settlement trees were retained in thinned treatments. Post-settlement trees left after the thinning were selected to replace dead pre-settlement trees based on the occurrence of snags, downed trees, stumps and stump holes, and larger trees were favoured for retention over smaller trees. The light thinning treatment retained three trees ≥40 cm diameter at breast height (DBH) or six smaller trees for each indication of a dead pre-settlement tree. The moderate thinning treatment retained two trees ≥40 cm DBH or four smaller trees for each indication of a dead pre-settlement tree. The heavy thinning treatment retained an average of 1.5 trees ≥40 cm DBH or three smaller trees for each indication of a dead pre-settlement tree. All thinning treatments included understorey broadcast burns and burning of slash piles between 2000 and 2001; unthinned controls were not burned. The treatments yielded the following four post-treatment average basal areas: control 38.2 m^2 ha^{-1}, light thinning 22.4 m^2 ha^{-1}, moderate thinning 18.1 m^2 ha^{-1} and heavy thinning 15.8 m^2 ha^{-1}.

Two cohorts of trees comprise the population of ponderosa pines in our study sites: (1) older trees ('large trees' hereafter) established prior to the European settlement of the 1890s and, (2) younger trees ('small trees' hereafter) established in the 1900s after European settlement (Savage, Brown & Feddema 1996). Overgrazing and fire suppression throughout most of the twentieth century promoted survival of the second cohort and increased intraspecific competition (Covington *et al.* 1997). Eighteen large (≥60 cm DBH) and eighteen small (13–19 cm DBH) ponderosa pine trees were selected from each of the four treatments, for a total of 144 trees. Trees were selected by identifying individuals that were healthy, accessible, near vertical (large trees only) and safe to climb (large trees only). Nine large and nine small trees were then chosen from each treatment by a random number draw, yielding 72 study trees in total. Means and standard errors for height, DBH and age of the 36 large trees were 28.7 ± 0.7 m, 73.8 ± 1.4 cm and 219 ± 11 years, respectively. Corresponding values for the 36 small trees were 9.1 ± 0.4 m, 15.9 ± 0.3 cm and 59 ± 2 years.

CORE COLLECTION AND PROCESSING

Using a 5.15-mm increment borer, we collected tree cores from our 72 study trees (36 small and 36 large trees) in summer 2009. We collected cores from two radii at breast height from both small (SBH) and large trees (LBH). Additionally, in each large tree, we collected cores at base of live crown (BLC, average height of 10.1 ± 0.6 m), midcrown branch (BR, average height of 15.2 ± 0.6 m) and treetop (TT, average height of 22.1 ± 0.5 m) positions using arborist climbing techniques (Jepson 2000). We also took cores from one radius in two coarse roots (CR) of each large tree, for a total of ten cores per large study tree (small study trees only had two cores per tree). We limited within-tree sampling to large trees as we deemed the small trees unsafe to climb.

These 432 cores were prepared using standard dendrochronological techniques (Stokes & Smiley 1968; Fritts 1976) and then were digitally scanned at 2400 dpi. All scanned cores were visually cross-dated, and annual ring widths were measured to the nearest 0.01 mm using WinDENDRO software (Regent Instruments, Inc., Quebec, Canada). We created separate ring width chronologies for small trees' breast height and each sample position in large trees. We used COFECHA (Holmes 1983) to verify the cross-dating for each chronology. Cores for which series intercorrelation was below 0.35 were deemed unfeasible to confidently cross-date and were removed from our analysis. We averaged the ring widths measured for all trees that had more than one core (i.e. radii) per tree position, resulting in the following sample size for each position: SBH $n = 32$, CR $n = 25$, LBH $n = 30$, BLC $n = 31$, BR $n = 26$ and TT $n = 29$. The cross-dated ring width series from each core was then standardized with first a negative-exponential function and then a cubic smoothing spline function with a 128-year wavelength using the program ARSTAN (Cook & Holmes 1986; Speer 2010) to remove size-related trends in growth (Fig. 1, Table 1). Northern Arizona ponderosa pines have a well-established, cross-dated chronology used in numerous earlier studies (Feeney *et al.* 1998; Skov, Kolb & Wallin 2005; Kolb *et al.* 2007; Kerhoulas & Kane 2012).

DATA ANALYSIS

To investigate the effects of treatment, within-tree position and tree size on annual growth, for each individual we calculated the ratio of average annual ring width index (RWI) after the 1998 thinning treatment (2003–2008) to average annual RWI before the 1998 thinning treatment (1992–1997). Hereafter we refer to this measure of growth response as 'post/pre'. For this post/pre RWI measurement, annual ring width included both earlywood and latewood growth. We excluded the years 1999–2002 from our post-thinning average to eliminate the possibility of thinning shock influencing our analyses (Harrington & Reukema 1983) and because the post-thinning prescribed burns of slash occurred over two of these years, 2000 and 2001 (Skov, Kolb & Wallin 2005). We limited our pre-thinning years to 1992–1997 so that our post-thinning and pre-thinning average annual RWI values were based on an equal number of years. This analysis of proportional change in radial growth allowed us to compare the growth response among five positions within large trees (CR, LBH, BLC, BR and TT) and BH between large and small trees, which have different absolute annual growth increments. For large trees, we also calculated a 'within-tree average' by averaging all five positions. If an effect (treatment, position or size) was not significant, data were pooled across that variable. All study trees were in the same geographical area and therefore experienced the same differences in weather between pre- and post-thinning years (Skov, Kolb & Wallin 2005).

We also investigated how trees in different treatments and size classes responded to dry years before and after the 1998 thinning treatment. For this analysis, we calculated average annual RWI values for each tree in dry years pre- and post-thinning to generate average dry-year post/pre values. Drawing from all years between 1950 and 2008, we used the Palmer Drought Severity Index (PDSI) to assign dry years (PDSI < −2). Local PDSI data from the Fort Valley weather station were assembled from the United States Historical Climatology Network (USHCN, http://cdiac.ornl.gov/epubs/ndp/ushcn/ushcn.html). For pre-thinning dry years, we used 1950, 1956, 1963, 1971 and 1989, which had PDSI values of −2.29, −3.58, −3.22, −3.02 and −2.98, respectively. For post-thinning dry years, we used 2000, 2002, 2003, 2006 and 2007, which had PDSI values of −2.65, −4.36, −3.47, −2.91 and −3.19, respectively.

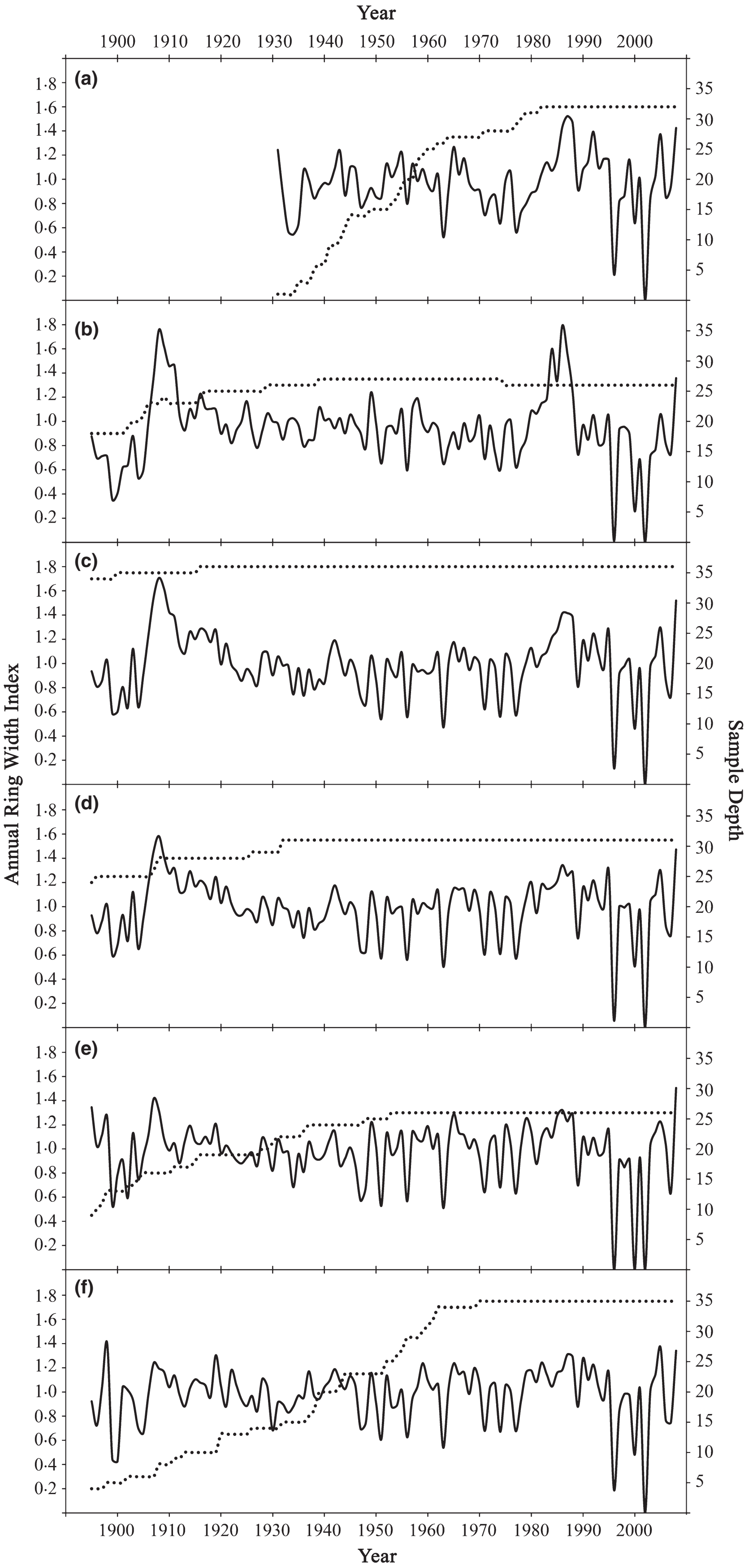

Fig. 1. The standardized 1895–2008 annual ring width chronology from ARSTAN for (a) small tree breast height, (b) large tree coarse root, (c) large tree breast height, (d) large tree base of live crown, (e) large tree midcrown branch, and (f) large tree treetop positions is plotted on the left vertical axis. Sample depth for each of these chronologies is plotted on the right vertical axis.

Table 1. Chronology statistics, including sample size (*n*), mean annual growth, mean sensitivity, series intercorrelation, first-order autocorrelation and expressed population signal (EPS, Holmes 1983), for cores taken from breast height of small trees (SBH) and from five positions in large trees (coarse roots, CR; breast height, LBH; base of live crown, BLC; midcrown branch, BR; and treetop, TT). Chronologies based on the time period 1895–2008

Position	*n*	Growth*	Sensitivity*	Series intercorrelation*	Autocorrelation†	EPS†
SBH	32	0.76	0.47	0.64	0.40	0.942
CR	25	0.98	0.42	0.52	0.54	0.867
LBH	30	1.18	0.39	0.68	0.34	0.950
BLC	31	1.22	0.34	0.70	0.34	0.962
BR	26	0.48	0.44	0.58	0.34	0.899
TT	29	1.08	0.39	0.72	0.24	0.943

*Denotes values taken from COFECHA (Holmes 1983).
†Denotes values taken from ARSTAN (Cook & Holmes 1986).

For all group comparisons, we used a two-way analysis of variance (ANOVA) when testing the significance of two effects and a one-way ANOVA when testing the significance of one effect. Levine and Bartlett tests were used to test the assumption of homogenous variance. When this assumption was violated, Welch tests were used to note the significant differences among groups. Group comparisons were followed with Tukey's honestly significant difference (HSD) orthogonal contrast post hoc tests. Significance was determined at the 95% confidence level ($\alpha = 0.05$). All ANOVAS were performed using JMP (SAS Institute, Cary, NC, USA).

Results

POST/PRE

Post/pre varied among treatments in large trees. Post/pre was significantly higher in the heavy and moderate thinning treatments compared with the light thinning and control treatments (Fig. 2, Table 2, $F = 6.45$, $P = 0.0004$), but did not vary significantly among positions ($F = 0.46$, $P = 0.77$), and response to treatment did not differ among positions (interaction $F = 0.66$, $P = 0.79$). The within-tree mean (all five positions averaged) of post/pre values for large trees in the control, light thinning, moderate thinning and heavy thinning treatments averaged 0.98 ± 0.10, 1.15 ± 0.12, 1.52 ± 0.12 and 1.52 ± 0.10, respectively.

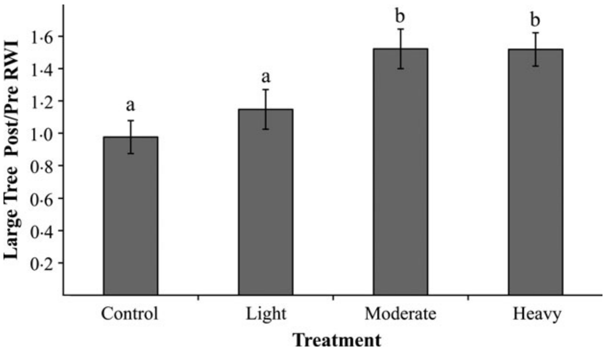

Fig. 2. Within-tree average (five positions pooled) post/pre annual ring width index (RWI) averages and standard errors in large study trees in the control, light, moderate, and heavy thinning treatments. Values above one represent increased post-treatment growth, with values below one representative of decreased growth. Treatments not sharing the same lowercase letter are significantly different ($F = 6.45$, $P = 0.0004$, $\alpha = 0.05$).

Post/pre varied between size classes in the heavy thinning treatment. Using a two-way ANOVA of breast height measurements to compare large and small trees, breast height post/pre varied significantly among treatments (Fig. 3a, Table 3, $F = 3.87$, $P = 0.01$) but not between tree size classes ($F = 1.85$, $P = 0.18$), and response to treatment did not differ among sizes (interaction $F = 1.03$, $P = 0.39$). However, a one-way ANOVA within each size class (Fig. 3b) showed that treatment was only a significant effect for large trees (large: $F = 4.19$, $P = 0.02$; small: $F = 2.29$, $P = 0.10$) and that only large trees in the moderate and heavy thinning treatments had increased growth response compared with control trees. Furthermore, in the heavy treatment, breast height growth response was greater in large trees compared with small trees ($F = 2.52$, $P = 0.05$). Average breast height post/pre values for all trees (two sizes pooled) in the control, light thinning, moderate thinning and heavy thinning treatments were 0.87 ± 0.13, 1.19 ± 0.15, 1.52 ± 0.15 and 1.30 ± 0.14, respectively.

DRY-YEAR POST/PRE

Both treatment and position significantly affected dry-year post/pre in large trees (Fig. 4, Tables 4 and 5). Dry-year post/pre in large trees was significantly higher in the heavy and moderate thinning treatments than in the control treatment (Fig. 4a, $F = 5.75$, $P = 0.001$). In large trees, average (five positions averaged) dry-year post/pre average values in control, light thinning, moderate thinning and heavy thinning were 0.61 ± 0.05, 0.75 ± 0.06, 0.82 ± 0.06 and 0.90 ± 0.05, respectively. Overall, coarse roots had lower dry-year post/pre than breast height, base of live crown and midcrown branch positions (Fig. 4b, $F = 2.66$, $P = 0.04$). Response of dry-year post/pre to treatment did not differ among positions (interaction $F = 0.63$, $P = 0.82$).

Table 2. Average post/pre ring width index (RWI) and standard error for within-tree average (WTA), coarse root (CR), breast height (LBH), base of live crown (BLC), midcrown branch (BR) and treetop (TT) positions of large trees in the control, light, moderate and heavy thinning treatments.

Treatment	WTA	CR	LBH	BLC	BR	TT
Control	0.98 ± 0.10^{a}	0.81 ± 0.10	0.91 ± 0.08	0.92 ± 0.07	1.17 ± 0.13	1.10 ± 0.07
Light	1.15 ± 0.12^{a}	1.14 ± 0.30	1.11 ± 0.31	0.95 ± 0.09	1.61 ± 0.23	1.04 ± 0.12
Moderate	1.52 ± 0.12^{b}	1.82 ± 0.84	1.68 ± 0.23	1.48 ± 0.28	1.34 ± 0.23	1.33 ± 0.15
Heavy	1.52 ± 0.10^{b}	1.81 ± 0.52	1.54 ± 0.26	1.44 ± 0.12	1.37 ± 0.29	1.57 ± 0.13

Within-tree average treatments not sharing the same lowercase letter are significantly different (F = 6.45, P = 0.0004, α = 0.05). Position did not significantly influence post/pre growth (F = 0.46, P = 0.77), and response to treatment did not vary across positions (interaction F = 0.66, P = 0.79)

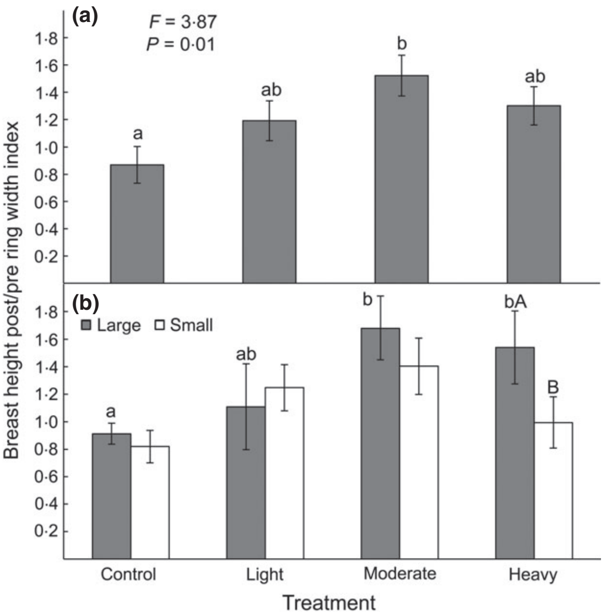

Fig. 3. Breast height post/pre ring width index averages and standard errors in the control, light, moderate, and heavy thinning treatments for (a) large and small trees pooled and (b) large and small trees separately. Values above one represent increased post-treatment growth, with values below one representative of decreased growth. Treatments not sharing the same lowercase letter and sizes not sharing the same capital letter are significantly different (α = 0.05). Two-way ANOVA shows size had no effect on breast height post/pre (F = 1.85, P = 0.18) and there was no interaction between treatment and size (F = 1.03, P = 0.39).

At breast height, dry-year post/pre was significantly different between size classes, but there was no effect of treatment. A two-way ANOVA revealed that dry-year breast height post/pre was significantly higher in large compared with small trees (Fig. 5a, F = 12.39, P = 0.001). However, treatment (F = 0.93, P = 0.43) and the interaction between size class and treatment (F = 1.62, P = 0.20) were not significantly different. When pooled across treatments, dry-year average post/pre values for large and small trees were 1.06 ± 0.07 and 0.72 ± 0.07, respectively (Fig. 5a, Table 6). Dry-year post/pre growth remained close to one for large trees but was always below one in small trees, indicating that small trees declined in dry-year growth after thinning relative to before thinning for reasons independent of treatment. A one-way ANOVA revealed that it is the moderate and heavy thinning treatments driving the difference in dry-year post/pre between large and small trees (Fig. 5b, Table 6). This analysis shows that in moderate (F = 9.00, P = 0.01) and heavy (F = 7.85, P = 0.01) thinning treatments, dry-year growth in large trees remained constant between pre- and post-thinning years but decreased in small trees.

Table 3. Average post/pre ring width index (RWI) and standard error at breast height (BH) in large (LBH) and small (SBH) trees in the control, light, moderate and heavy thinning treatments. Post/pre RWI varied significantly among treatments (F = 3.87, P = 0.01) but not between size classes (F = 1.85, P = 0.18), and response to treatment did not vary with size (interaction F = 1.03, P = 0.39).

Treatment	Pooled BH	LBH	SBH
Control	0.87 ± 0.13^{a}	0.91 ± 0.08^{a}	0.82 ± 0.12
Light	1.19 ± 0.15^{ab}	1.11 ± 0.31^{ab}	1.25 ± 0.17
Moderate	1.52 ± 0.15^{b}	1.68 ± 0.23^{b}	1.40 ± 0.21
Heavy	1.30 ± 0.14^{ab}	1.54 ± 0.26^{bA}	0.99 ± 0.19^{B}

When breast height post/pre measurements from large and small trees are pooled, treatments not sharing the same lowercase letter are significantly different (α = 0.05). One-way ANOVA in each size class shows that treatment has a significant effect on post/pre LBH RWI (F = 4.19, P = 0.02, Welch test used) but not on SBH RWI (F = 2.29, P = 0.10). Furthermore, LBH post/pre RWI was greater than SBH post/pre RWI in heavy treatments (F = 2.52, P = 0.05), as indicated by different capital letters

Discussion

World-wide increased drought related to climate change is resulting in widespread forest mortality with a cascade of secondary effects from the ecosystem to global scales (Allen *et al.* 2010; Anderegg, Kane & Anderegg 2012). In the U.S. Southwest, decreases in winter precipitation and snowpack (Hereford 2007) reduce snowmelt and deep recharge of soil water, ultimately resulting in a drier growing season. These types of climate change negatively affect tree growth and increase drought stress on forests (Williams *et al.* 2010, 2012). Furthermore, this drought stress renders forests more vulnerable to increasingly frequent intense wildfires (Westerling *et al.* 2006), bark beetle attacks (Williams *et al.* 2012) and mortality (Allen *et al.*

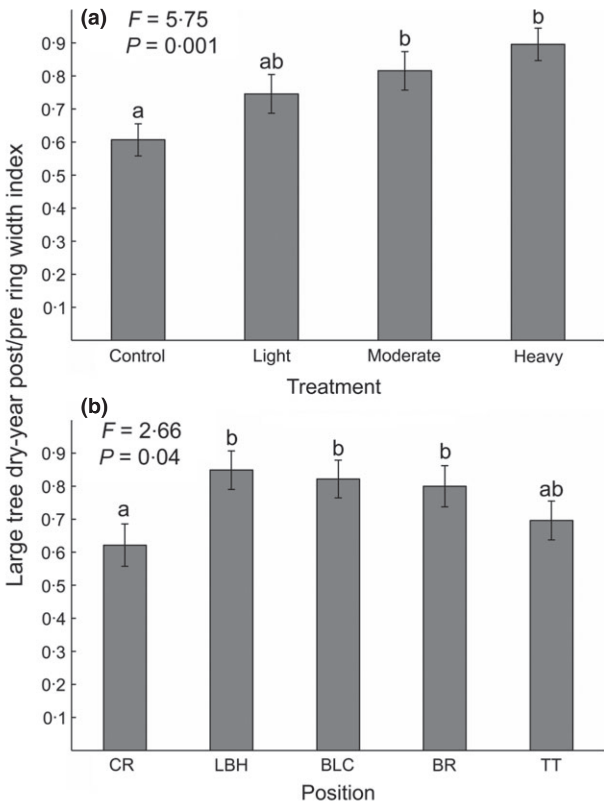

Fig. 4. Large tree dry-year post/pre growth averages and standard errors as influenced by (a) treatment and (b) position: coarse root (CR), breast height (LBH), base of live crown (BLC), midcrown branch (BR), and treetop (TT). In panel (a) positions are pooled, and in panel (b) treatments are pooled. Values above one represent increased post-treatment growth, with values below one representative of decreased growth. Treatments (a) or positions (b) not sharing the same lowercase letter are significantly different ($\alpha = 0.05$). There was no interaction between treatment and position ($F = 0.63$, $P = 0.82$).

2010). As in the U.S. Southwest, thinning is being considered as a means to reduce competition for water and lessen drought stress in other semi-arid regions of the world (Gyenge *et al.* 2011; Rodríguez-Calcerrada *et al.* 2011; Molina & del Campo 2012). Our analyses of post/pre growth provide new insights into the buffering effects of thinning against changing climate.

Prior research at our site found that large south-western ponderosa pine trees do not exhibit a growth response within the first few years following thinning (Skov, Kolb & Wallin 2005). Our results show that large tree growth did eventually respond positively to thinning, and the response was greatest in moderate and heavy thinning treatments (Fig. 2, Table 2). Increased growth in heavy and moderate thinning treatments despite a series of post-thinning dry years (2000, 2002, 2003, 2006, 2007) indicates that thinning reduced drought stress in these large trees.

Our results do not support the hypothesis that the lack of a release effect immediately after thinning in large south-western ponderosa pine (Skov, Kolb & Wallin 2005) is due to a redistribution of growth within the tree. Rather, the uniformity of response among positions suggests a time delay between the onset of physiological and growth responses (Feeney *et al.* 1998; Latham & Tappeiner 2002; Skov, Kolb & Wallin 2004) rather than growth increases to branch and root carbon sinks (Urban, Lieffers & MacDonald 1994; Kolb *et al.* 2007; Sillett *et al.* 2010) as the likely cause of slow growth response to thinning in large trees. The constancy of growth patterns observed among large tree positions demonstrates that breast height is an acceptable coring location to detect whole-tree growth patterns in south-western ponderosa pine forests.

Our analyses of post/pre dry-year growth in large trees advance understanding of the relationships among climate, treatment intensity and growth distribution within trees. Large trees in the moderate and heavy thinning treatments had significantly higher post/pre dry-year growth relative to large trees in the control treatment (Fig. 4a, Table 4). This response is especially important from a drought stress resistance perspective, as only the moderate and heavy thinning treatments maintained post-thinning dry-year growth at pre-thinning levels despite a succession of dry years, while in the other treatments, post-thinning dry-year growth decreased (Fig. 5b, Table 6). There is one potential caveat to this finding: it is possible that because average PDSI was more negative post-thinning (−3.3) than pre-thinning (−3.0), a nonlinear response of ring width to drought at the dry-extreme amplified post-thinning drought effects, thereby lessening the drought resistance observed in heavily thinned plots. Nevertheless, our results suggest that reducing forest density increases drought resistance of large trees, an effect

Table 4. Average dry-year post/pre ring width index (RWI) and standard errors for within-tree average (WTA), coarse root (CR), breast height (LBH), base of live crown (BLC), midcrown branch (BR) and treetop (TT) positions in large trees in control, light, moderate and heavy thinning treatments.

Treatment	WTA	CR	LBH	BLC	BR	TT
Control	0.61 ± 0.05^{a}	0.52 ± 0.10	0.65 ± 0.06	0.60 ± 0.05	0.65 ± 0.08	0.61 ± 0.06
Light	0.75 ± 0.06^{ab}	0.65 ± 0.10	0.79 ± 0.26	0.74 ± 0.07	0.96 ± 0.25	0.61 ± 0.08
Moderate	0.82 ± 0.06^{b}	0.51 ± 0.16	0.99 ± 0.15	0.97 ± 0.11	0.78 ± 0.15	0.77 ± 0.10
Heavy	0.90 ± 0.05^{b}	0.79 ± 0.17	0.99 ± 0.14	1.01 ± 0.07	0.84 ± 0.11	0.81 ± 0.08

Within-tree average treatments not sharing the same lowercase letter are significantly different ($\alpha = 0.05$). Within-tree average dry-year post/pre growth was significantly higher in moderate and heavy thinning treatments compared with the control ($F = 5.75$, $P = 0.001$), and response to treatment did not vary among positions (interaction $F = 0.63$, $P = 0.82$)

Table 5. Average dry-year post/pre ring width index (RWI) and standard errors for coarse root (CR), breast height (LBH), base of live crown (BLC), midcrown branch (BR) and treetop (TT) positions in large trees in control, light, moderate and heavy thinning treatments. When dry-year post/pre growth measurements are pooled across treatments, CR had significantly lower growth compared with LBH, BLC and BR positions ($F = 2.66$, $P = 0.04$). Response to treatment did not vary among positions (interaction $F = 0.63$, $P = 0.82$). Positions not sharing the same lowercase letter are significantly different ($\alpha = 0.05$)

Position	Pooled treatments	Control	Light	Moderate	Heavy
CR	0.62 ± 0.06^{a}	0.52 ± 0.10	0.65 ± 0.10	0.51 ± 0.16	0.79 ± 0.17
LBH	0.85 ± 0.06^{b}	0.65 ± 0.06	0.79 ± 0.26	0.99 ± 0.15	0.99 ± 0.14
BLC	0.82 ± 0.06^{b}	0.60 ± 0.05	0.74 ± 0.07	0.97 ± 0.11	1.01 ± 0.07
BR	0.80 ± 0.06^{b}	0.65 ± 0.08	0.96 ± 0.25	0.78 ± 0.15	0.84 ± 0.11
TT	0.70 ± 0.06^{ab}	0.61 ± 0.06	0.61 ± 0.08	0.77 ± 0.10	0.81 ± 0.08

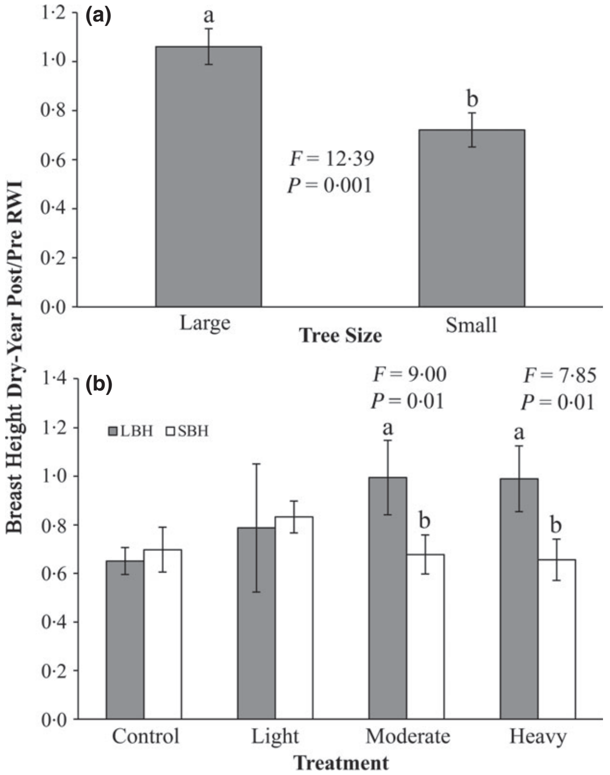

Fig. 5. Breast height dry-year post/pre ring width index (RWI) averages and standard errors for large (LBH) and small trees (SBH) with (a) treatments pooled and (b) treatments not pooled. Values above one represent increased post-treatment growth, with values below one representative of decreased growth. Treatment did not affect dry-year breast height post/pre ($F = 0.93$, $P = 0.43$) and there was no interaction between treatment and size in dry-year breast height post/pre ($F = 1.62$, $P = 0.20$). Different lowercase letters between sizes represent a significant difference ($\alpha = 0.05$).

that will become increasingly important given the increasing frequency of dry years projected for many semi-arid forests (Seager *et al.* 2007). From a carbon sequestration perspective, this effect is especially important because of the disproportionate amount of carbon stored in large trees (Sillett *et al.* 2010).

Forest thinning prescriptions often include the retention of smaller trees for the replacement of large trees lost to a variety of causes, including logging. Thus, understanding the influence of tree size on growth response to thinning is necessary for characterizing post-thinning forest growth. Our analyses showed significant variation in the release effect among thinning treatment intensities and tree sizes. We found that thinning had positive effects on growth of small and large trees five to ten years after treatment. Although growth response was similar in large and small trees in the control, light thinning and moderate thinning treatments, the heavy thinning treatment stimulated growth in large trees more than in small trees (Fig. 3, Table 3). Our research suggests that despite a delayed growth response to thinning, the positive effects of thinning on growth may be longer lived in large trees compared with small trees. Even with the long succession of dry years following thinning, large trees in the heavy thinning treatment increased their annual growth rate by roughly 50% (post/pre ≈ 1.54), while small trees in this treatment merely maintained pre-thinning annual growth rates (post/pre ≈ 0.99). This finding suggests that heavy thinning treatments imparted a greater buffer against drought to large tress than to small trees. Our findings that post/pre growth in large trees was equal to or greater than that in small trees demonstrate that large trees are responsive to thinning and that they are likely to be more resistant to drought than small trees.

At breast height, post/pre dry-year growth was greater in large trees compared with small trees independent of thinning treatments (Fig. 5a, Table 6). The significant influence of tree size, not treatment, on dry-year post/pre at breast height indicates a difference in growth over time between large and small trees. When pooled across treatments, dry-year breast height growth of large trees did not change between pre- and post-thinning periods (post/pre ratio is close to one), but in small trees, this ratio is less than one, suggesting that small tree growth declined for reasons that are unclear. We speculate that variable response by tree size was caused by something other than treatment that differed between the selected pre- and post-thinning years, such as other aspects of climate or weather, the degree of change in local basal area density with thinning or access to limiting resources. Further investigation on what resources limit post-thinning growth in small trees is needed.

Table 6. Average dry-year post/pre ring width index (RWI) and standard errors for breast height measurements in large (LBH) and small (SBH) trees in control, light, moderate and heavy thinning treatments applied in 1998. A two-way ANOVA shows that treatment did not significantly affect dry-year post/pre growth ($F = 0.93$, $P = 0.43$), and growth response to treatment did not vary between sizes in dry years (interaction $F = 1.62$, $P = 0.20$). When all treatments are pooled, large trees had significantly higher dry-year post/pre growth ($F = 12.39$, $P = 0.001$, $\alpha = 0.05$). One-way ANOVAS show that moderate ($F = 9.00$, $P = 0.01$) and heavy ($F = 7.85$, $P = 0.01$) thinning treatments increased dry-year post/pre growth in large trees compared to small trees

Size	Pooled Treatments	Control	Light	Moderate	Heavy
LBH	1.06 ± 0.07	0.65 ± 0.06	0.79 ± 0.26	0.99 ± 0.15	0.99 ± 0.14
SBH	0.72 ± 0.07	0.70 ± 0.09	0.83 ± 0.07	0.68 ± 0.08	0.66 ± 0.09

As the global climate warms and dries and precipitation inputs become more variable, tailoring management prescriptions to optimize forest drought resistance is crucial. We show that forest thinning can increase tree drought resistance and thereby may reduce vulnerability to other mortality agents. Our findings demonstrate increased growth in favourable years and improved drought resistance in dry years following thinning treatments. This combination has the potential to prolong forest persistence in regions that are likely to experience unprecedented climate-driven forest mortality (Allen *et al.* 2010). Broadly, our recommendation to thin forests for increased tree growth and drought resistance is particularly applicable to tree species in systems likely to experience increased temperature and decreased precipitation as a result of climate change.

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