

Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems

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Abstract. Reducing tree densities through silvicultural thinning has been widely advocated as a strategy for enhancing resistance and resilience to drought, yet few empirical evaluations of this approach exist. We examined detailed dendrochronological data from a long-term (>50 years) replicated thinning experiment to determine if density reductions conferred greater resistance and/or resilience to droughts, assessed by the magnitude of stand-level growth reductions. Our results suggest that thinning generally enhanced drought resistance and resilience; however, this relationship showed a pronounced reversal over time in stands maintained at lower tree densities. Specifically, lower-density stands exhibited greater resistance and resilience at younger ages (49 years), yet exhibited lower resistance and resilience at older ages (76 years), relative to higher-density stands. We attribute this reversal to significantly greater tree sizes attained within the lower-density stands through stand development, which in turn increased tree-level water demand during the later droughts. Results from response–function analyses indicate that thinning altered growth–climate relationships, such that higher-density stands were more sensitive to growing-season precipitation relative to lower-density stands. These results confirm the potential of density management to moderate drought impacts on growth, and they highlight the importance of accounting for stand structure when predicting climate-change impacts to forests.

Key words: *climate change; growth–climate relationships; Minnesota, USA; Pinus resinosa.*

INTRODUCTION

Climate change represents the greatest challenge facing resource managers today due to the uncertainty in future conditions and urgency to develop strategies that increase adaptive capacity and/or minimize ecosystem vulnerability (Spies et al. 2010). In forests, recommended strategies include manipulating forest structure and composition to reduce impacts and increasing the representation of functional traits to enhance adaptation potential (Puetzmann 2011). Although these and other approaches are grounded in ecological theory, their effectiveness at minimizing climate change impacts is poorly understood due largely to the long time frames necessary for empirical evaluation. This uncertainty poses a daunting challenge

for policy makers and practitioners tasked with developing long-term strategies for addressing climate change.

A key question related to managing forests within the context of climate change is how to minimize the impacts of increasing drought frequency and intensity. Droughts strongly affect tree growth and mortality, and changes in drought frequency and intensity are expected to elevate mortality rates, shift species composition, and reduce carbon sinks over broad geographic regions (Klos et al. 2009, Allen et al. 2010). Although drought impacts on forest systems are most severe in water-limited regions (Allen and Breshears 1998), recent global trends of elevated tree mortality during droughts within temperate, boreal, and tropical ecosystems highlight the importance of future drought impacts in all forested regions (Klos et al. 2009, Michaelian et al. 2011, Granzow-de la Cerda et al. 2012).

One promising strategy for minimizing forest drought vulnerability is tree density reduction (via silvicultural

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thinning) to increase resource availability to the remaining trees within a given population (Linder 2000). Despite widespread endorsement of this strategy, few empirical studies have evaluated the long-term effectiveness of this approach at sustaining forest ecosystem functioning during drought events (but see McDowell et al. 2006). Such a long-term perspective is critical given the documented changes in drought vulnerability associated with increasing tree size and/or age for many species (Martínez-Vilalta et al. 2012), which suggests that changes in individual tree- and population-level structure may elicit dynamic drought responses during forest development.

Our objective was to assess how long-term forest density management reduced drought vulnerability. Specifically, we addressed the following questions: (1) Do reductions in tree densities confer greater population-level resistance and resilience to droughts? (2) How does this response vary with population density (i.e., thinning intensity) and age? (3) Can population density alter growth–climate relationships for a given tree species? We examined growth responses during known droughts occurring over the past 65 years in the Great Lakes region, USA. We relied on extensive dendrochronological data from red pine (*Pinus resinosa* Ait.) forests thinned repeatedly from 1957 to 2011 and maintained at a range of population densities.

MATERIALS AND METHODS

This study capitalized on a long-term experiment (the Birch Lake experiment) established by the USDA Forest Service in 1957 within a *P. resinosa* forest in northeastern Minnesota, USA (47°42' N, 91°56' W; see Bradford and Palik 2009 for more details on site conditions and the experiment). The forests were planted at the same initial density (2500 trees/ha) and were 45 years old when treatment began in 1957. The experiment consists of six levels of thinning intensity (7, 14, 21, 28, and 35 m²/ha basal area remaining) crossed with three thinning methods (thinning from above, from below, and proportional), and untreated controls. Treatment combinations and controls were randomly assigned to 4-ha units and replicated three times in a randomized block design. Thinnings were applied in 1957, 1962, and at 10-year intervals from 1962 to 2012. Relative densities ranged from 8–40%, 22–56%, 28–44%, 34–54%, 47–67%, and 58–91% for the 7, 14, 21, 28, 35 m²/ha, and unthinned treatments, respectively, over the period of active management (1957–2012; see Powers et al. 2010 for a detailed summary of stand structure over time at these areas). One 0.08 ha plot was randomly located within each unit, and species and diameter at breast height (dbh) were recorded for all trees greater than 8.9 cm dbh on ~5-yr intervals beginning in 1957.

In 2009, increment cores were taken at breast height (1.3 m) from all trees greater than 5 cm dbh within each 0.08-ha plot, resulting in 12–92 increment cores per plot and 2119 total cores across the experiment. Increment

cores were prepared, cross-dated, and measured using standard procedures. Basal area increment (BAI) of each cored tree was estimated for each available year based on back-reconstructed dbh values derived from dbh at time of coring and radial increments over time. We summed plot-level BAI for each year and used this population-level metric as our unit of analysis for examining resistance and resilience of growth to past drought and growth–climate relationships. This population-level analysis of drought vulnerability and climate response complements the more typically used average tree-level relationships. We have also included average tree-level analyses based on standard dendrochronological treatment of these data (i.e., standardized chronologies) in the supplementary material for comparison.

We focused on three known droughts to examine the effectiveness of thinning at reducing drought vulnerability. These droughts were identified from historic documents and meteorological records, vs. reconstructed meteorological proxies, such as Palmer Drought Severity Index (PDSI), which may overestimate long-term temporal trends in drought frequency (Sheffield et al. 2012). Despite these limitations, PDSI provides a useful measure of overall drought severity and soil moisture deficit; we thus utilized monthly growing season PDSIs simply to characterize the three droughts. The first drought (1948; moderate severity with PDSIs from –2.0 to –3.5) was selected to evaluate drought response prior to the onset of thinning in 1957. The second drought (1961; moderate severity with PDSIs from –2.0 to –3.3) was chosen to evaluate drought response after a single initial thinning. The third drought (1988; moderate to high severity with PDSIs from –3.3 to –4.8) allowed us to determine how drought response may have varied with stand age and long-term thinning, given this event occurred when these forests were 76 years old and had received four thinning treatments.

To quantify drought response, we expanded upon the tree-level approach developed by Kohler et al. (2010) to quantify population-level drought responses. We thus defined population-level drought resistance (D_{rs}) as the ability to experience drought without a change in population-level growth increment, calculated as $D_{rs} = \text{BAI}_D / \text{BAI}_{pre}$, where BAI_D is average stand-level BAI during a drought event and BAI_{pre} is the average stand-level BAI during the five years prior to the event. Because drought events and impacts often span multiple years, BAI_D included multiple years where appropriate. Similarly, drought resilience (D_{rl}) was defined as the ability to return to pre-drought growth, calculated as $D_{rl} = \text{BAI}_{post} / \text{BAI}_{pre}$, where BAI_{post} is average stand-level BAI five years following a drought event. We used drought resistance and resilience as inverse measures of drought vulnerability.

The effects of thinning method and intensity on drought resistance and resilience were examined using mixed-model analysis of variance (ANOVA). Because initial ANOVA results indicated no thinning method

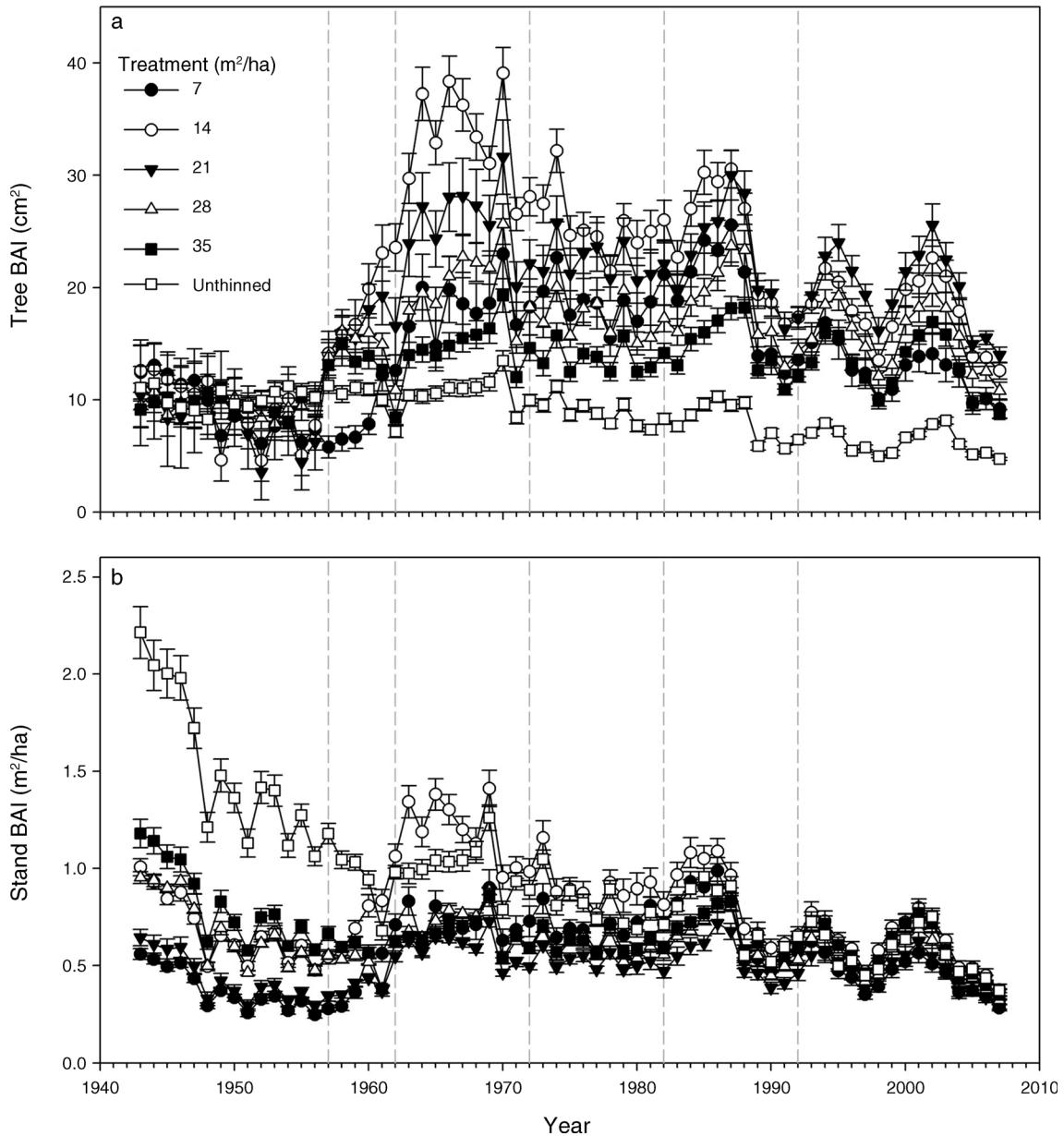


FIG. 1. (a) Tree-level and (b) stand-level basal area increment (BAI) for the five thinning intensities examined. Means are based on three replicates per treatment, and bars represent one standard error. Years in which thinning treatments were applied are indicated by the vertical dashed lines. Note that BAI is reconstructed based on trees surviving until sampling in 2009, leading to higher stand-level values for the unthinned controls relative to the other treatments during the pretreatment period (i.e., 1943–1956).

effects, we focused solely on thinning intensity, which was treated as a fixed effect with block as a random effect, following the SAS MIXED Procedure (SAS Institute 2008). Separate ANOVAs were conducted for each drought, and Tukey-Kramer multiple comparison tests were used to isolate specific differences among thinning intensities.

Relationships between climate and population-level BAI during active management (1957–2009) were evaluated for each thinning intensity with response-function analysis using Dendroclim2002 (Biondi and

Waikul 2004). We used annual monthly temperature (T) and precipitation (P) from June of the previous year through October of the current year (Kipfmüller et al. 2010). In addition, we used the ratio of monthly P to monthly potential evapotranspiration (PET) as an index of average monthly moisture stress (Martínez-Vilalta et al. 2012), with monthly PET calculated as per Hargreaves and Samani (1982). Response functions were calculated based on 1000 bootstrapped samples with significance tested at $\alpha = 0.05$ (Biondi and Waikul 2004).

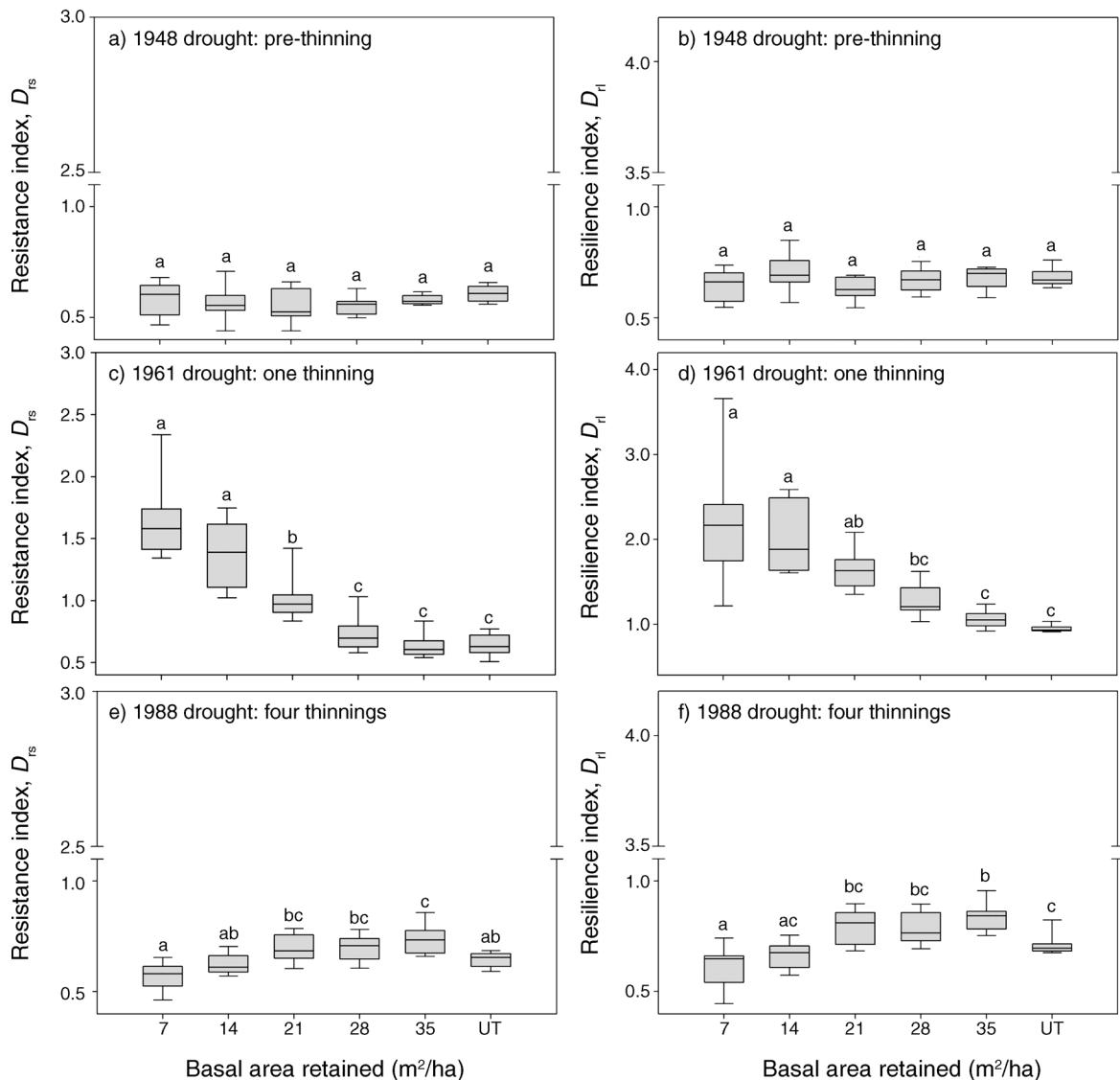


FIG. 2. Box plots of drought (a, c, e) resistance and (b, d, f) resilience across six *Pinus resinosa* population densities (7, 14, 21, 28, 35 m^2/ha , and unthinned [UT]) and three drought events (1948, 1961, 1988). Drought resistance (D_{rs}) values <1 indicate lower population-level growth rates during drought periods relative to pre-drought periods, whereas values >1 suggest higher growth. Drought resilience (D_{rl}) values <1 indicate lower population-level growth rates following drought events relative to pre-drought periods, whereas values >1 suggest higher growth. Box plots show 25% quartile, median, and 75% quartiles; error bars represent 90th and 10th percentiles. Population densities with different letters are significantly different at $\alpha < 0.05$.

RESULTS

Tree and population-level growth fluctuated markedly over the study period and reflected the periodic application of thinning treatments starting in 1957 (Fig. 1). The 1948 drought reduced growth in all populations; drought resistance or resilience did not differ among populations prior to thinning (Fig. 2a, b). In contrast, during the 1961 drought (after one thinning), the lower-density treatments (7 and 14 m^2/ha) displayed greater drought resistance and resilience relative to the higher-density (21, 28, 35 m^2/ha) and the unthinned treatments (Fig. 2c, d). Average tree size did

not differ among populations at the onset of this drought event (Fig. 3; Appendix A).

For the 1988 drought, the higher-density treatments (21, 28, 35 m^2/ha) had significantly greater drought resistance than the lowest-density treatment (7 m^2/ha ; Fig. 2e, f). In addition, the 35 m^2/ha treatment had greater drought resistance than the 14 m^2/ha and unthinned treatments (Fig. 2e). Drought resistance did not differ among the lower-density (7 and 14 m^2/ha) and unthinned treatments during this event (Fig. 2e). Drought resilience followed a similar trend for this event, with the greatest resilience apparent within the

higher-density thinned treatments (Fig. 2f). Average tree size in the lower-density (7 and 14 m²/ha) treatments was greater than the 35 m²/ha and unthinned treatment at the onset of this event (Fig. 3; Appendix A). The lowest-density treatment (7 m²/ha) also had greater average tree sizes than the 28 m²/ha treatment during this period (Fig. 3; Appendix A).

Population-level growth responses to climate during the active management period varied among densities, as reflected by the patterns in significant response functions for each thinning treatment (Table 1). The only common growth–climate response across treatments was a negative relationship between BAI and previous September temperatures (Table 1). This was the only significant response function for the lowest-density treatments (7 and 14 m²/ha; Table 1). Temperatures in previous August were also negatively related to BAI within the 21 m²/ha treatments, whereas previous October temperatures were positively associated with BAI within the unthinned treatment (Table 1).

Precipitation and moisture stress (Precip/PET) were strongly related to BAI in the highest-density treatments (28 and 35 m²/ha and unthinned; Table 1). BAI within the highest-density thinned treatment (35 m²/ha) was positively related to precipitation and Precip/PET for current June and July (Table 1). Similarly, BAI within the 28 m²/ha treatment was positively related to previous June, current June, and current July precipitation and Precip/PET (Table 1). BAI within the unthinned treatment was positively related to current August precipitation and Precip/PET (Table 1). Patterns in significant response functions were very similar between these population-level analyses and those conducted with standardized chronologies (i.e., average tree level; Appendices B and C).

DISCUSSION

Thinning is a recognized forest management tool for reducing inter-tree competition to increase tree- and stand-level growth (Assmann 1970). Correspondingly, the lower drought vulnerability in young thinned populations observed in this and other studies likely reflect the lower intensity of competition for soil moisture in lower-density populations relative to dense, unthinned forests (McDowell et al. 2006). These observed differences in drought vulnerability between thinned and unthinned systems have also been partially attributed to the larger root systems on trees in thinned populations (McDowell et al. 2006, Kohler et al. 2010), which allows greater access to groundwater stores during drought (Dawson 1996).

The long-term nature of this study allowed us to identify that, while thinning intensity also enhanced drought resistance and resilience, this relationship reversed as stands matured. At younger stand ages (i.e., 1961 drought, stand age 49 years), the lower-density populations exhibited the greatest drought resistance and resilience. In contrast, at more advanced ages (i.e.,

1988 drought, stand age 76), the thinned populations maintained at higher densities (i.e., 21, 28, 35 m²/ha treatments) exhibited the greatest drought resistance and resilience. Previous examinations of average tree-level responses to drought have generally found that trees growing in managed lower densities and natural populations have greater drought resistance than those from higher-density populations (Laurent et al. 2003, McDowell et al. 2006, Klos et al. 2009). The reversal of this trend through stand development has not been previously reported; its occurrence here suggests that density effects on population-level drought vulnerability may be more complex than previously recognized, and it underscores the value of long-term studies to reveal such trends.

The age-dependent reversal in drought vulnerability observed among population densities likely reflects the influence of different thinning intensities on tree-level architecture and physiology, including higher leaf area to sapwood area ratios, which increase tree water demand (McDowell et al. 2006). For example, the 1961 drought occurred four years after the onset of thinning, a point in stand development in which average tree size did not differ among the populations (Fig. 3; Appendix A). By the 1988 drought, population densities had been maintained for over 30 years, resulting in significant differences in tree size among treatments, particularly in the lowest and highest-density populations (Fig. 3; Appendices A and D). The differential response among populations to this later event was likely related to the greater proportion of large trees, and their correspondingly higher water demand, making up the low-density treatments (Fig. 3; cf. McDowell et al. 2006). In particular, long-term acclimation of hydraulic architecture to the lower-density treatments, including the development of greater leaf area, likely increased the vulnerability of trees in these stands to the later drought event. Although our indices of drought vulnerability (\pm SE) were based on proportional changes in stand-level growth, the absolute magnitude of growth reduction was also greatest in the lowest-density and unthinned stands during this event (0.52 ± 0.04 , 0.47 ± 0.05 , 0.32 ± 0.04 , 0.40 ± 0.06 , 0.34 ± 0.10 , 0.68 ± 0.05 m·ha⁻¹·yr⁻¹ for the 7, 14, 21, 28, 35 m²/ha, and unthinned treatments, respectively), further underscoring the effects of population density on drought vulnerability.

Beyond changes in tree size, several studies have indicated that older trees may experience greater growth reductions during drought relative to younger individuals due to lower hydraulic conductance (Klos et al. 2009, Lloret et al. 2011, Martínez-Vilalta et al. 2012). We found little evidence for an age effect per se on drought resistance and resilience, as there was no difference in drought response in unthinned stands between the earliest and latest droughts (1948 and 1988; Fig. 2). Nevertheless, the tree ages we examined (36–76 years) were young relative to studies that

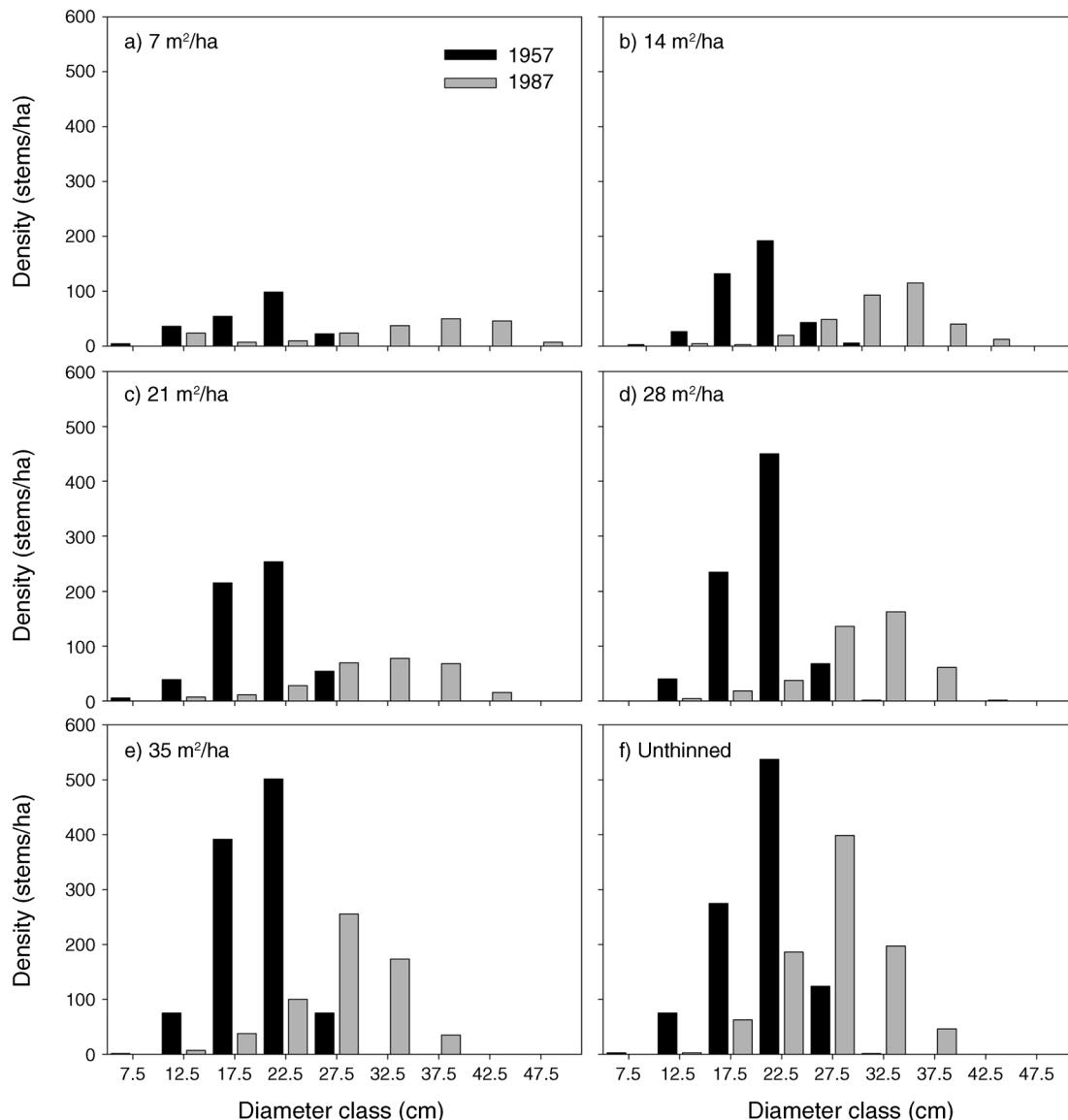


FIG. 3. Live-tree diameter distributions for the (a–e) thinned and (f) unthinned *Pinus resinosa* populations prior to the 1961 and 1988 droughts. Distributions are based on data collection periods occurring in years most closely preceding these events (i.e., 1957 and 1987).

TABLE 1. Relationships between population-level basal area increment and monthly temperature, precipitation (Precip), and moisture stress (Precip/potential evapotranspiration [PET]) for thinned (7, 14, 21, 28, 35 m²/ha) and unthinned *Pinus resinosa* populations based on response function analysis.

Density (m ² /ha)	Temperature			Precipitation				Precip/PET			
	PAUG	PSEP	POCT	PJUN	JUN	JUL	AUG	PJUN	JUN	JUL	AUG
7	0.06	-0.23	-0.02	0.07	0.15	0.01	0.13	0.06	0.13	-0.01	0.10
14	-0.13	-0.24	0.02	0.03	0.02	-0.09	0.18	0.04	0.02	-0.09	0.15
21	-0.22	-0.26	0.03	0.09	0.05	-0.06	0.25	0.11	0.06	-0.05	0.18
28	-0.20	-0.23	-0.10	0.21	0.36	0.41	0.19	0.23	0.35	0.39	0.14
35	-0.07	-0.24	0.04	0.15	0.30	0.37	0.21	0.18	0.32	0.29	0.18
Unthinned	-0.16	-0.32	0.15	0.03	0.09	-0.08	0.26	0.05	0.10	-0.07	0.22

Notes: Months preceded by “P” represent monthly climate averages for the previous growing season. Significant response functions ($\alpha < 0.05$) are shown in boldface.

detected age effects, potentially limiting our ability to observe similar age-related trends.

Comparisons of drought response during the active management period suggest that younger thinned populations were less impacted by drought than older thinned stands (Fig. 2); however, these temporal differences are likely attributable to differences in population-level growth rate prior to each event. Recent work with other *Pinus* species has demonstrated that faster growing individuals experience a greater proportional impact than slower growing trees during drought (McDowell et al. 2006, Martínez-Vilalta et al. 2012). Pre-drought, stand-level growth rates were generally higher for thinned populations in the 1988 event relative to the 1961 drought (Fig. 1), which likely contributed to greater impacts during the later event.

Our examination of climate–growth relationships among population densities showed that thinning treatments also influenced the climate factors most important to growth. The only relationship consistent across populations was a negative association between previous September temperatures and growth. This relationship has been documented in other determinate conifer species (Tardif et al. 2003) and could represent lower levels of carbohydrate reserves to support radial growth in years preceded by high late-season temperatures due to thermal or moisture stress (Tjoelker et al. 2001).

Higher-density populations were generally more sensitive to climate based on their higher number of significant response functions (Table 1). Precipitation in the current and prior growing season was positively associated with stand-level growth in the higher-density populations (i.e., 28, 35m²/ha, and unthinned), a finding consistent with tree-level growth–climate analyses for this same species (Kipfmüller et al. 2010). This greater climate sensitivity with increasing stand density may reflect a tighter coupling with climate conditions, particularly precipitation, as population-level competition for resources increases (Laurent et al. 2003). Laurent et al. (2003) documented a similar trend as those detected by our response function analyses toward greater climate sensitivity, particularly in relation to soil water availability, with increasing density in young *Picea abies* stands in the Belgian Ardenne. These findings have important implications for efforts aimed at forecasting climate change impacts on tree species growth, as well as for developing appropriate management strategies. In particular, most forecasts of species' responses to future climate assume uniform responses within a species, independent of population structure (Iverson et al. 2011). Importantly, our findings suggest non-uniform responses, even within a species, the result of changes in tree and population-level structures over time.

Conclusions and management implications

This study provides a critical evaluation of the long-term effectiveness of tree density management at

reducing drought impacts and illustrates that the relative effectiveness of such strategies may vary depending on long-term thinning history. In particular, heavy thinning treatments applied to younger populations, although beneficial at reducing drought vulnerability at this stage, may predispose these populations to greater long-term drought vulnerability due to higher tree-level physiological burden developed by individuals maintained at these densities, primarily due to greater hydraulic constraints typically associated with larger trees (McDowell et al. 2006). Our findings also demonstrate that thinning can alter population-level climate–growth relationships, particularly as they relate to the relative importance of growing season moisture. These findings underscore the utility of tree density reductions (via silvicultural thinning) for reducing drought vulnerability. Thinning should be viewed as a near-term solution to reducing drought vulnerability relative to longer term approaches aimed at increasing the functional diversity of forest tree communities, including greater representation of drought tolerant species.

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LITERATURE CITED

- Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences USA* 95:14839–14842.
- Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259:660–684.
- Assmann, E. 1970. *The principles of forest yield study*. Pengamon Press, Oxford, UK.
- Biondi, F., and K. Waikul. 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers and Geosciences* 30:303–311.
- Bradford, J. B., and B. J. Palik. 2009. A comparison of thinning methods in red pine: consequences for stand-level growth and tree diameter. *Canadian Journal of Forest Research* 39:489–496.
- Dawson, T. E. 1996. Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology* 16:263–272.
- Granzow-de la Cerda, I., F. Lloret, J. E. Ruiz, and J. H. Vandermeer. 2012. Tree mortality following ENSO-associated fires and drought in lowland rain forests of Eastern Nicaragua. *Forest Ecology and Management* 265:248–257.
- Hargreaves, G. H., and Z. A. Samani. 1982. Estimating potential evapotranspiration. *Journal of the Irrigation and Drainage Division ASCE* 108:225–230.
- Iverson, L. R., A. M. Prasad, S. N. Matthews, and M. P. Peters. 2011. Lessons learned while integrating habitat, dispersal,

- disturbance, and life-history traits into species habitat models under climate change. *Ecosystems* 14:1005–1020.
- Kipfmüller, K. F., G. P. Elliott, E. R. Larson, and M. W. Salzer. 2010. An assessment of the dendroclimatic potential of three conifer species in northern Minnesota. *Tree-Ring Research* 66:113–126.
- Klos, R. J., G. G. Wang, W. L. Bauerle, and J. R. Rieck. 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. *Ecological Applications* 19:699–708.
- Kohler, M., J. Sohn, G. Nagele, and J. Bauhus. 2010. Can drought tolerance of Norway spruce (*Picea abies* (L.) Karst.) be increased through thinning? *European Journal of Forest Research* 129:1109–1118.
- Laurent, M., N. Antoine, and G. Joel. 2003. Effects of different thinning intensities on drought response in Norway spruce (*Picea abies* (L.) Karst.). *Forest Ecology and Management* 183:47–60.
- Linder, M. 2000. Developing adaptive forest management strategies to cope with climate change. *Tree Physiology* 20:299–307.
- Lloret, F., E. G. Keeling, and A. Sala. 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120:1909–1920.
- Martínez-Vilalta, J., B. López, L. Loepfe, and F. Lloret. 2012. Stand- and tree-level determinants of the drought response of Scots pine radial growth. *Oecologia* 168:877–888.
- McDowell, N. G., H. D. Adams, J. D. Bailey, M. Hess, and T. E. Kolb. 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecological Applications* 16:1164–1182.
- Michaelian, M., E. H. Hogg, R. J. Hall, and E. Arsenaault. 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology* 17:2084–2094.
- Powers, M. D., B. J. Palik, J. B. Bradford, S. Fraver, and C. R. Webster. 2010. Thinning method and intensity influence long-term mortality trends in a red pine forest. *Forest Ecology and Management* 260:1138–1148.
- Puettmann, K. J. 2011. Silvicultural challenges and options in the context of global change: simple fixes and opportunities for new management approaches. *Journal of Forestry* 109:321–331.
- SAS Institute. 2008. SAS/STAT 9.2 User's Guide. The MIXED Procedure. SAS Institute, Cary, North Carolina, USA.
- Sheffield, J., E. F. Wood, and M. L. Roderick. 2012. Little change in global drought over the past 60 years. *Nature* 491:435–438.
- Spies, T., T. Giesen, F. Swanson, J. Franklin, D. Lach, and K. Johnson. 2010. Climate change adaptation strategies for federal forests of the Pacific Northwest, USA: ecological, policy, and socio-economic perspectives. *Landscape Ecology* 25:1185–1199.
- Tardif, J., J. J. Camarero, M. Ribas, and E. Gutierrez. 2003. Spatiotemporal variability in tree growth in the Central Pyrenees: Climatic and site influences. *Ecological Monographs* 73:241–257.
- Tjoelker, M. G., J. Oleksyn, and P. B. Reich. 2001. Modelling respiration of vegetation: evidence for a general temperature-dependent Q10. *Global Change Biology* 7:223–230.

SUPPLEMENTAL MATERIAL

Appendix A

Diameters of thinned *Pinus resinosa* populations (*Ecological Archives* A023-088-A1).

Appendix B

Population-level response function analysis (*Ecological Archives* A023-088-A2).

Appendix C

Tree-level response function analysis (*Ecological Archives* A023-088-A3).

Appendix D

Pinus resinosa canopy photos (*Ecological Archives* A023-088-A4).