

Density-dependent vulnerability of forest ecosystems to drought

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Summary

1. Climate models predict increasing drought intensity and frequency for many regions, which may have negative consequences for tree recruitment, growth and mortality, as well as forest ecosystem services. Furthermore, practical strategies for minimizing vulnerability to drought are limited. Tree population density, a metric of tree abundance in a given area, is a primary driver of competitive intensity among trees, which influences tree growth and mortality. Manipulating tree population density may be a mechanism for moderating drought-induced stress and growth reductions, although the relationship between tree population density and tree drought vulnerability remains poorly quantified, especially across climatic gradients.

2. In this study, we examined three long-term forest ecosystem experiments in two widely distributed North American pine species, ponderosa pine *Pinus ponderosa* (Lawson & C. Lawson) and red pine *Pinus resinosa* (Aiton), to better elucidate the relationship between tree population density, growth and drought. These experiments span a broad latitude and aridity range and include tree population density treatments that have been purposefully maintained for several decades. We investigated how tree population density influenced resistance (growth during drought) and resilience (growth after drought compared to pre-drought growth) of stand-level growth during and after documented drought events.

3. Our results show that relative tree population density was negatively related to drought resistance and resilience, indicating that trees growing at lower densities were less vulnerable to drought. This result was apparent in all three forest ecosystems, and was consistent across species, stand age and drought intensity.

4. *Synthesis and applications.* Our results highlighted that managing pine forest ecosystems at low tree population density represents a promising adaptive strategy for reducing the adverse impacts of drought on forest growth in coming decades. Nonetheless, the broader applicability of our findings to other types of forest ecosystems merits additional investigation.

Key-words: climate change adaptation, drought impacts, ecosystem services, *Pinus ponderosa*, *Pinus resinosa*, semi-arid forests, temperate forests, thinning, tree population density

Introduction

Climate change is expected to increase drought frequency and intensity (Dai 2013; Cook, Ault & Smerdon 2015),

with potentially serious negative consequences for forest ecosystem structure and function (Allen *et al.* 2010; Anderegg, Kane & Anderegg 2013). Coping with these consequences represents one of the greatest contemporary challenges facing forest resource managers tasked with sustaining the delivery of ecosystem services under unprecedented moisture deficits (Millar, Stephenson & Stephens 2007; Lindner *et al.* 2014). In many forested regions, increases in drought frequency and intensity can

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impede tree recruitment (Rigling *et al.* 2013), reduce growth (McDowell *et al.* 2008; Vicente-Serrano *et al.* 2013; Castagneri *et al.* 2015) and increase mortality (Breshears *et al.* 2005; Bigler *et al.* 2006; van Mantgem *et al.* 2009), potentially triggering large-scale changes in forest distribution, structure and composition (Rigling *et al.* 2013; McIntyre *et al.* 2015) and threatening terrestrial net primary production (Ciais *et al.* 2005; Zhao & Running 2010). Forecasting how forest ecosystems might respond to future droughts, as well as developing adaptation strategies to changing climate, hinges on an adequate understanding of the ecological mechanisms governing drought vulnerability of tree populations (Williams *et al.* 2013).

The importance of plant population density in governing patterns of resource competition and availability and hence rates of recruitment, growth and mortality is well established (McDowell *et al.* 2006; Adams *et al.* 2009). In forest ecosystems tree population density is used as an indirect measure of competition intensity, and it influences growth and mortality in forests around the world (Hille Ris Lambers, Clark & Beckage 2002). However, it is less clear how tree population density influences the response of forests to environmental stressors such as drought. Tree population density can be calculated from the number and sizes of all trees present, and compared to an upper biological maximum tree population density to estimate *relative tree population density*, which facilitates comparisons across diverse species, sites and stand ages (Jack & Long 1996). Because tree population density is directly reduced by forest thinning practices, examining long-term thinning experiments can refine our understanding of the relationships between tree population density and drought vulnerability, and assess the potential for thinning to provide a convenient and powerful framework for adapting forest ecosystems to increased drought intensity. Nonetheless, only a few studies have quantified the role of tree population density on forest growth in response to episodic drought (e.g. Sohn *et al.* 2016), leaving key knowledge gaps regarding the ecological response of forest ecosystems to drier climatic conditions and hampering efforts to develop climate-adapted management strategies.

The vulnerability of tree growth to drought can be measured with indices of resistance and resilience (Lloret, Keeling & Sala 2011). Resistance reflects the ability of a forest to avoid growth reductions during drought; resilience reflects the ability of a forest to regain growth following drought (Scheffer *et al.* 2001; Lloret, Keeling & Sala 2011).

Here we assessed resistance and resilience of forest growth during and after multiple drought periods in two of the most widely distributed pine species in North America: ponderosa pine and red pine. We capitalized on unusually rich historical and dendrochronological (tree-ring) data sets to evaluate the relationships between tree population density and growth patterns during and after past drought events. Specifically, we examined three

replicated long-term forest ecosystem experiments that span a broad geographical and aridity gradient within the USA, including a temperate humid red pine forest in Minnesota, a temperate dry sub-humid ponderosa pine forest in South Dakota and a semi-arid ponderosa pine forest in Arizona (Smith *et al.* 2001). These data allowed us to test if the relationships between tree population density and growth resistance and resilience to drought hold across these climatic conditions, and at different forest ages.

Materials and methods

EXPERIMENTAL SITES

This study is part of the Experimental Forest Monitoring for Climate Change project (<https://www.researchgate.net/project/Experimental-Forest-Monitoring-for-Climate-Change-EFMCC>), which capitalizes on long-term silvicultural research of the USDA Forest Service Experimental Forest network (Adams, Loughry & Plaugher 2004) to show how forest management may enhance climate change adaptation (D'Amato *et al.* 2011). In this study, we focused on three Experimental Forests dominated by red pine and ponderosa pine (Fig. 1a).

The red pine forest in northern Minnesota, USA, located on the Cutfoot Experimental Forest (CEF) (Table 1), naturally regenerated after a fire in the late 1860s. Prior to the establishment of the experiment, the forest was entered twice to salvage trees that were damaged by storms in the early 1940s. The ponderosa pine forest in southwestern South Dakota, USA, located on the Black Hills Experimental Forest (BHEF) (Table 1), naturally regenerated in the early 1900s. The ponderosa pine forest in northern Arizona, USA, located on the Fort Valley Experimental Forest (FVEF) (Table 1), naturally regenerated around 1919 following a wet period in the early 20th century (Savage, Brown & Feddema 1996; Brown & Wu 2005).

The different tree population densities analysed in this study refer to levels of stand basal area, as well as untreated controls (i.e. treatments), which were maintained over time *via* periodic thinning (Table 1). Treatments, each replicated three times in each study, were randomly assigned at each site within stands with similar structure, origin, development, disturbance history, soil characteristics, slope and altitude (Myers 1967; Bailey 2008; Bradford & Palik 2009). This design was aimed at eliminating local confounding factors that could have affected the growth response to drought.

SAMPLING DESIGN, AND TREE-RING SAMPLE PROCESSING AND ANALYSES

One 0.08-ha circular plot was located within each of the replications of the treatment unit within a site, and species and tree diameter at 1.3 m height (DBH) were recorded for all trees greater than 10 cm DBH before each thinning from the beginning of the density management experiment for each of the three Experimental Forests. In 2010 (CEF), 2012 (FVEF) and 2014 (BHEF), one increment core was taken orthogonal to the slope at breast height from all living trees greater than 10 cm DBH within each plot to estimate annual growth rates, resulting in 1484 cores across the three Experimental Forests.

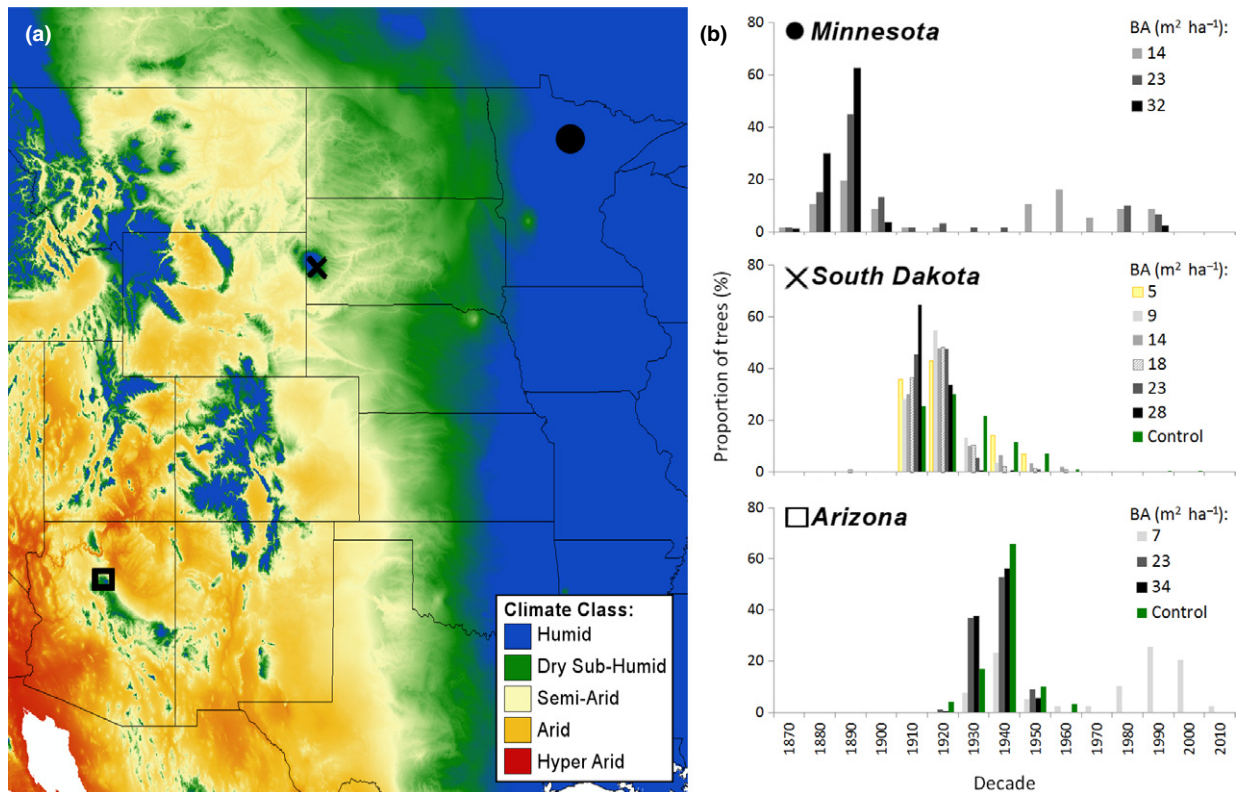


Fig. 1. (a) Location and (b) age structures for the three forest ecosystems (red pine in Minnesota, and ponderosa pine in South Dakota and Arizona) across different levels of residual basal area and untreated controls. Basal area levels in legends represent targeted residual basal areas following stand density reduction treatments. Means are based on three replications per treatment. The graphical representation of the climate classes (a) is based on mean aridity index values for the 1950–2000 period (Trabucco & Zomer 2009) and was generated with SAGA GIS. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1. Characteristics of the long-term thinning study sites used for examining the influence of forest density on drought vulnerability

<i>Site characteristics</i>			
Experimental forest (EF) name, Abbreviation	Cutfoot, CEF	Black Hills, BHEF	Fort Valley, FVEF
State, Country	MN, USA	SD, USA	AZ, USA
Latitude, Longitude	47°33' N, 94°05' W	44°10' N, 103°38' W	35°16' N, 111°43' W
EF area (ha)	1255	1400	2130
Year of study establishment	1949	1963	1962
Mean tree DBH (cm)*	22 [†]	16 [‡]	12 [§]
Age (years)*	80 [†]	65 [‡]	40 [§]
Reference levels of stand basal area for the different tree population densities analysed in this study ($\text{m}^2 \text{ha}^{-1}$)	14, 23, 32	5, 9, 14, 18, 23, 28, untreated controls	7, 23, 34, untreated controls
Periodic thinning (time of application)	1949–1964 (at 5-year intervals), 1964–2010 (at 10-year intervals)	1963, 1973, 1998	1962–2002 (at 10-year intervals)
Altitude range (m a.s.l.)	410–415	1646–1829	2250–2285
Topography	Flat	Irregular slopes	Flat
Mean annual sum of precipitation (mm)	570	610	574
Mean annual temperature (°C)	1.7	4.8	7.0

*Reference year: beginning of the density management experiment.

[†]Bradford & Palik (2009).

[‡]Myers (1967).

[§]Bailey (2008).

Increment cores were prepared, cross-dated, and measured using standard dendrochronological procedures (Speer 2010). The dating and ring-width measurements of each series were checked for errors with time-series correlation analyses using the

COFECHA software (Holmes 1983). Ring width chronologies covered the period 1880–2009 in Minnesota, 1910–2010 in South Dakota and 1920–2010 in Arizona. Ring width chronologies were converted to annual tree basal area increment (BAI) based on

back-reconstructed DBH values derived from DBH inside bark at time of coring and radial increments over time (Bunn 2008). Bark thickness was estimated with bark factor equations (Fowler & Damschroder 1988; Keyser & Dixon 2008), and subtracted from DBH to obtain the corresponding DBH inside bark. BAI was used instead of ring width, because BAI is less dependent on tree diameter and thus avoids the need for detrending (Biondi 1999), which could remove low-frequency variability, and produce larger errors towards the end of the tree-ring chronology (Kohler *et al.* 2010). Furthermore, the period of the growth series examined was well beyond the juvenile growth trend commonly observed for BAI series with competition induced growth patterns, having little impact on the period considered for drought year analysis. We summed tree-level BAI for each plot and year and used this population-level metric as our unit of analysis for examining resistance and resilience of growth to past droughts (D'Amato *et al.* 2013).

SELECTION OF DROUGHT YEARS

Past known droughts were identified from historical documents and meteorological records. The Standardized Precipitation Evapotranspiration Index (SPEI, unitless) (Vicente-Serrano, Beguería & López-Moreno 2010), during the growing season, was used to characterize these droughts. SPEI is a multiscalar index based on precipitation and temperature data, and it is suitable to detect, monitor, compare and analyse different drought types and impacts in the context of global warming. The SPEI reflects both water surplus (positive values) and water deficit (negative values) as standardized deviations from the average monthly climatic water balance (Vicente-Serrano, Beguería & López-Moreno 2010). In preliminary analyses (data not shown), we detected stronger correlations between growth and SPEI than we did using temperature or precipitation, the self-calibrating Palmer Drought Severity Index (sc-PDSI), or ratio between precipitation and potential evapotranspiration.

We used the 'spei' function (Beguería & Vicente-Serrano 2013) to obtain SPEI at different time-scales (from 1 to 24 months), using potential evapotranspiration data calculated according to the Hargreaves equation (Beguería & Vicente-Serrano 2013) for each site over the period 1901–2009. A 6-month SPEI (SPEI6) was chosen for all three study sites because we detected a stronger response with it than SPEI calculated at other time-scales (see Table S1, Supporting Information). SPEI6 was calculated for growing season months (June through August at CEF and June through September at BHEF and FVEF) using the target month (e.g. June) and the previous five month (e.g. Jan–May). To characterize the severity of past droughts for each site, a severe drought was defined as extraordinary departure from mean SPEI, lower than the mean by one standard deviation for the period 1901–2009 (see Fig. S1). Input meteorological data (monthly temperature and precipitation) for each study site were obtained from the PRISM Climate Group database (<http://www.prism.oregonstate.edu/>) based on climate observations, and modelled using climatologically aided interpolation for data sets prior to 1981.

Within each site and among known past drought years, we selected three severe droughts for examination. For each site, the earliest drought selected was used to evaluate drought response prior to the establishment of the density management experiments, i.e. the most severe drought that occurred in the period immediately preceding the establishment of the experiment at each site (CEF: 1936, SPEI6 (growing season) ranged from

–1.95 to –1.04; BHEF: 1954, SPEI6 ranged from –1.22 to –0.73; FVEF: 1951, SPEI6 ranged from –1.35 to –0.65). The second drought event was chosen to evaluate drought response relatively early in the progression of each experiment, i.e. the first severe drought that occurred after the beginning of the experiment at each site (CEF: 1956, SPEI6 ranged from –1.01 to –0.82; BHEF: 1966, SPEI6 ranged from –1.25 to –0.49; FVEF: 1963, SPEI6 ranged from –1.61 to –1.17). Finally, the third drought was selected to evaluate drought response after several thinning treatments, later in the progression of each experiment, i.e. the most severe drought that occurred at each site in the last 10–15 years of the study (CEF: 2006, SPEI6 ranged from –1.04 to –0.62; BHEF: 2002, SPEI6 ranged from –1.32 to –0.80; FVEF: 2002, SPEI6 ranged from –2.51 to –2.36).

RELATIVE TREE POPULATION DENSITY

Our analyses were based on a relative tree population density index of each stand. Relative tree population density (RD) quantifies the current tree population density of a forest stand in comparison to a potential maximum density. Stand density index (SDI) (Reineke 1933) is an effective index of competition based on size-density relations, used for estimating RD (Woodall, Miles & Vissage 2005). Indices based on size-density relations are independent of site quality and stand age, and allow for comparisons of different levels of site occupancy independently of other factors (Long & Daniel 1990). We obtained RD by dividing current SDI by maximum SDI for each plot, and including all tree species and size combinations. The current SDI was determined for each plot by using the summation method (Long & Daniel 1990):

$$SDI = \sum tphi_i \left(\frac{DBH_i}{25} \right)^{1.6}$$

where DBH_i is the mid-point of the i th diameter class (cm) and $tphi_i$ is the number of trees per hectare in the i th diameter class.

We calculated maximum SDI according to a 99th percentile maximum SDI model (Woodall, Miles & Vissage 2005):

$$E(SDI_{99}) = 2057.3 - 2098.6 * (SG_m)$$

where $E(SDI_{99})$ is the statistical expectation of the 99th percentile maximum SDI, and SG_m is the mean specific gravity for the study species. Input data for each study site were obtained from historical inventory measurements taken in 1954 and 2007 at the CEF, in 1968 and 2003 at the BHEF, and in 1962 and 2002 at the FVEF.

MODELLING POPULATION-LEVEL VULNERABILITY TO DROUGHT

Growth responses to drought were quantified at the population-level (all measured trees in a plot), and expressed as growth resistance and resilience (measures of vulnerability) (Kohler *et al.* 2010; D'Amato *et al.* 2013). These two indices allow for examination of forest growth performance before and after periods of stress and therefore characterize population-level growth response to drought. Population-level resistance was defined as the ability to avoid growth reduction during drought, expressed as BAI_D / BAI_{pre} , where BAI_D is average population-level BAI during a drought and BAI_{pre} is the average population-level BAI during

the 5 years prior to the drought. Resilience was defined as the ability to regain pre-drought growth following drought, calculated as BAI_{post}/BAI_{pre} , where BAI_{post} is the average population-level BAI during the 5 years after a drought.

For each Experimental Forest, the average DBH and resistance and resilience indices were compared prior to establishing the experiments and again after drought events using analysis of variance (ANOVA), after verifying the homoscedasticity of variance and the normal distribution of residuals. Tukey–Kramer multiple comparison tests were used to isolate specific differences among treatments (R Core Team 2014). Linear regression models were used to quantify the effect of relative tree population density on population-level resistance and resilience to drought at different forest stand ages (shortly after initiation of the experiment, and later in the progression of each experiment). To estimate model parameters the 'lm' function of the 'stats' package (version 3.2.1) in the statistical computing software R (version 3.2.1) (R Core Team 2014) was used. During model construction, the regression assumptions were assessed using histograms of predictor variables and scatter plots of model residuals on predictor values.

Results

FOREST STRUCTURE AND COMPOSITION

Pines dominated the canopies of all three forest ecosystems (Table 2), with ponderosa pine accounting for 100% of stand basal area at the sites in Black Hills and FVEF, and red pine accounting for 95% of stand basal area at the CEF. At the latter study site, eastern white pine *Pinus strobus* (L.), paper birch *Betula papyrifera* (Marsh.), and northern red oak *Quercus rubra* (L.) also occupied canopy positions, but were more common in the subcanopy. Mean living tree basal area and density reflected the periodic application of thinning (Table 2). In general, stands

maintained at low relative basal area were characterized by a smaller number of trees. Average tree size did not differ among populations at the onset of each experiment (Table 2). In contrast, at the time of our sampling, stands maintained at lower basal area had greater average tree size than untreated controls and stands maintained at high relative basal area. Most forest stands in the three Experimental Forests showed primarily single-cohort age structures (Fig. 1b); however, stands maintained at low relative basal area had two-cohort age structures (Cutfoot and Fort Valley Experimental Forests).

GROWTH RATES AND VULNERABILITY TO DROUGHT

Prior to establishing the experiments, tree growth rates did not differ among the designated thinning treatments (Fig. 2a). The examined droughts reduced growth in all populations. After the experiments were established and various thinning treatments were imposed, tree and population growth rates fluctuated substantially over time throughout the study period in all three ecosystems, reflecting the periodic application of thinning (Fig. 2a,b). Divergence in growth rates among thinning treatments highlighted the influence of tree population density on tree-level growth. As expected, throughout the experiment, trees growing in less dense populations showed higher average growth rates in all three ecosystems.

Population growth resistance and resilience to drought did not differ among designated thinning treatments within each forest ecosystem prior to the implementation of the treatments (see Table S2). In contrast, after the beginning of the experiments, tree populations in lower density treatments generally showed higher resistance and resilience to

Table 2. Forest structural and compositional characteristics of the study sites. Site refers to Experimental Forest and tree population density treatment (expressed as m^2 per ha BA retained). Species composition is listed for tree species with relative basal area $>2\%$ (red pine = PIRE, eastern white pine = PIST, paper birch = BEPA, northern red oak = QURU, ponderosa pine = PIPO). Relative basal area by species, total basal area (BA, $m^2 ha^{-1}$), trees ($N ha^{-1}$) and mean diameter (DBH, cm) refer to stems >10 cm diameter at 1.3 m height shortly after initiation of each experiment (initial) and in 2010 (CEF), 2014 (BHEF) and 2012 (FVEF). Reported values are mean and standard error based on three replicates per thinning treatment. DBH values with different letters (within a column at each site) are statistically different at $\alpha < 0.05$

Site, BA	Relative basal area (%) for tree species _{II}					Live trees			
	PIRE	PIST	BEPA	QURU	PIPO	BA	Trees	DBH _{initial}	DBH
CEF, 14	90.4 ± 3.5	2.9 ± 2.0	2.0 ± 0.9	2.8 ± 0.2	–	14.9 ± 0.3	250 ± 26	26.4 ± 1.4 ^a	32.7 ± 3.7 ^a
CEF, 23	96.8 ± 2.1	1.1 ± 1.0	1.2 ± 1.1	0.5 ± 0.2	–	23.6 ± 0.2	271 ± 11	24.1 ± 1.3 ^a	34.1 ± 2.0 ^a
CEF, 32	99.5 ± 0.5	–	0.1 ± 0.1	0.2 ± 0.2	–	32.5 ± 0.5	346 ± 22	25.0 ± 2.9 ^a	37.7 ± 1.5 ^a
BHEF, 5	–	–	–	–	100	6.3 ± 0.03	38 ± 3	18.9 ± 0.3 ^a	44.8 ± 1.8 ^a
BHEF, 9	–	–	–	–	100	12.6 ± 0.2	114 ± 5	18.5 ± 0.5 ^a	36.7 ± 0.5 ^b
BHEF, 14	–	–	–	–	100	17.8 ± 0.1	189 ± 9	17.9 ± 0.5 ^a	33.9 ± 0.7 ^{bc}
BHEF, 18	–	–	–	–	100	22.6 ± 0.1	275 ± 21	18.4 ± 0.3 ^a	32.0 ± 1.0 ^{bcd}
BHEF, 23	–	–	–	–	100	27.0 ± 0.4	389 ± 73	17.7 ± 1.2 ^a	29.5 ± 2.2 ^{cd}
BHEF, 28	–	–	–	–	100	28.7 ± 2.4	473 ± 76	17.9 ± 0.9 ^a	27.4 ± 1.2 ^d
BHEF, Control	–	–	–	–	100	19.0 ± 1.6	614 ± 112	16.4 ± 0.4 ^a	18.7 ± 1.1 ^e
FVEF, 7	–	–	–	–	100	11.6 ± 1.2	108 ± 39	14.0 ± 0.6 ^a	37.6 ± 8.1 ^a
FVEF, 23	–	–	–	–	100	23.1 ± 0.3	250 ± 17	12.8 ± 0.6 ^a	34.0 ± 1.1 ^a
FVEF, 34	–	–	–	–	100	37.5 ± 1.1	634 ± 32	11.2 ± 0.2 ^a	26.9 ± 0.2 ^{ab}
FVEF, Control	–	–	–	–	100	54.1 ± 2.6	2051 ± 418	12.2 ± 1.8 ^a	18.0 ± 1.9 ^b

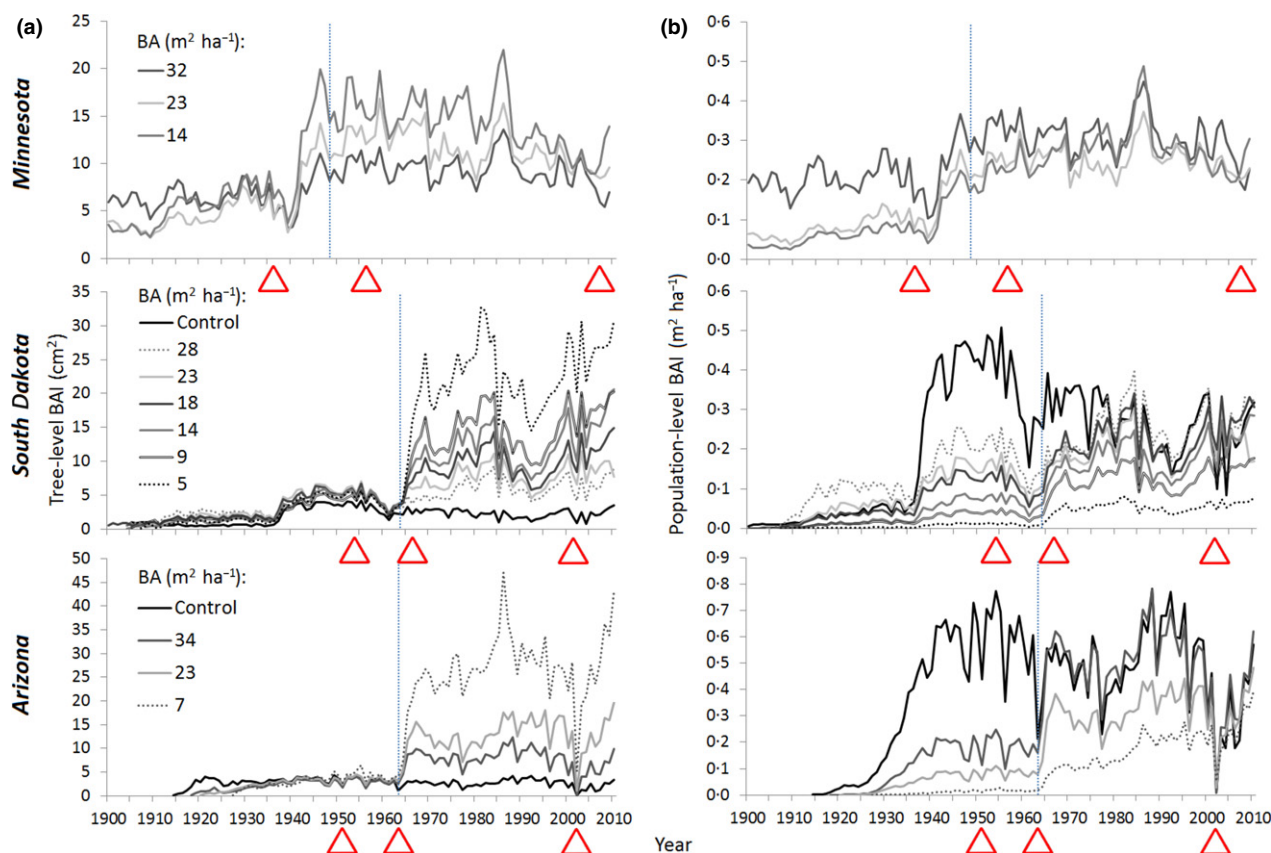


Fig. 2. (a) Tree- and (b) population-level basal area increment (BAI) for the three forest ecosystems (red pine in Minnesota, and ponderosa pine in South Dakota and Arizona) across different levels of residual basal area and untreated controls. Basal area levels in legends represent targeted residual basal areas following stand density reduction treatments. Means are based on three replications per treatment. Vertical dotted line shows the beginning of the tree population density reduction experiment for each forest. Triangles denote the analysed droughts at each site. Note that BAI is reconstructed based on trees surviving until sampling, leading to higher population-level values for untreated controls prior to the beginning of the experiment. [Colour figure can be viewed at wileyonlinelibrary.com]

drought, compared to populations in higher density treatments, regardless of the stand age at which the droughts occurred (Fig. 3). Notably, all three ecosystems had the same general trend in population-level growth resistance and resilience to drought. Tree population density explained much of the variability in resistance and resilience to drought at each site, especially during those droughts that occurred earlier in each experiment (Table 3).

Discussion

The impact of climate change on forest ecosystems globally may be strongly driven by increases in the intensity and frequency of drought events (Allen *et al.* 2010; Anderegg, Kane & Anderegg 2013; Vicente-Serrano *et al.* 2013). Water deficits can increase vulnerability of forests to stressors, and regional vegetation die-offs may trigger shifts in the distribution of forest ecosystems (Breshears *et al.* 2005; Choat *et al.* 2012; Rigling *et al.* 2013), potentially causing widespread changes in carbon stores and ecosystem services (Anderegg, Kane & Anderegg 2013). Our results clearly demonstrate that reducing tree population densities enhanced the resistance and resilience of

forest growth to drought, thereby potentially ameliorating these threats. We are aware of only one other study, from central Europe (Sohn *et al.* 2016), that examined a data set as temporally rich as ours and found similar results, i.e. reduced growth vulnerability in tree populations maintained at lower density. The added value of our study over that of Sohn *et al.* (2016), is that we demonstrated this relationship in two distinct *Pinus* species and across geographically and climatically diverse regions.

Density-dependent competition influences stand dynamics and development across all forest types and biomes (Callaway & Walker 1997; Silvertown & Charlesworth 2009). Competition for soil moisture may exacerbate drought stress caused by water deficits and altered water availability patterns, and therefore influence the overall vulnerability of forest ecosystems to drought (Zhang, Huang & He 2015). Prolonged severe droughts may, in fact, profoundly impact tree physiological responses, leading to irreversible alterations in the xylem hydraulic system, loss of hydraulic conductivity and depletion of stored carbohydrates (McDowell *et al.* 2011; Rigling *et al.* 2013; Rowland *et al.* 2015). Consequently, quantifying the contribution of tree population density (an expression of

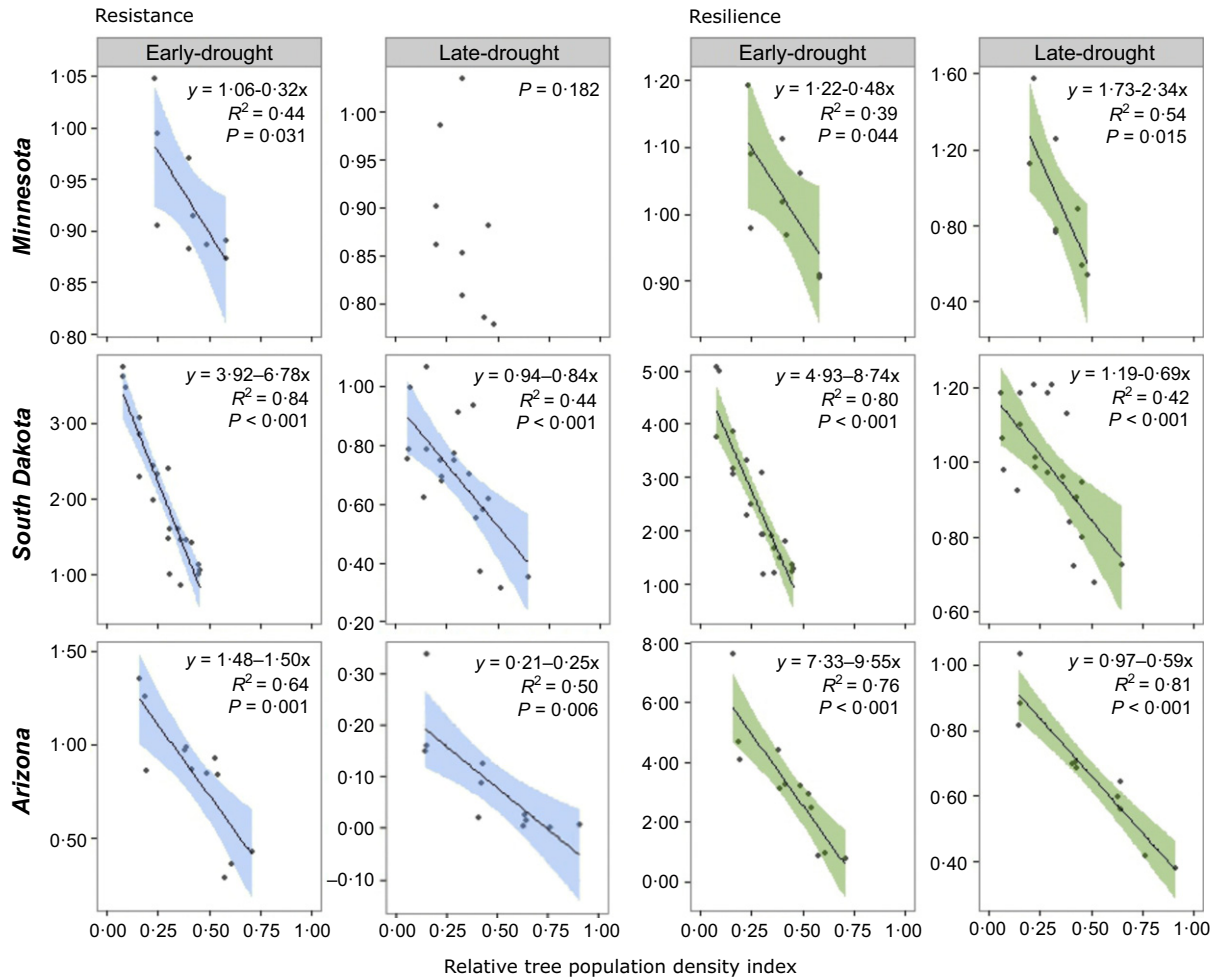


Fig. 3. Trends in drought resistance and resilience in relation to tree population density (expressed as relative tree population density index) for the three forest ecosystems examined in this study (red pine in Minnesota, and ponderosa pine in South Dakota and Arizona). Filled dots are observations (i.e. replications of the treatments). Solid lines show statistically significant relationships ($P < 0.05$). Corresponding equations, R^2 , P values and 95% confidence intervals (shaded areas) are given for each significant relationship. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 3. Parameters of linear regression models for predicting forest vulnerability to early- (shortly after initiation of each experiment) and late-droughts (later in the progression of each experiment) as a function of relative tree population density (RD) for each site

Models [†]	SE	d.f.	R^2	r
Early-drought				
$Rst_{CEF} = 1.06*** - 0.32RD^*$	0.045	7	0.44*	0.71*
$Rst_{BHEF} = 3.92*** - 6.78RD^{***}$	0.369	19	0.84***	0.92***
$Rst_{FVEF} = 1.48*** - 1.50RD^{**}$	0.197	10	0.64**	0.82**
$Rsl_{CEF} = 1.22*** - 0.48RD^*$	0.075	7	0.39*	0.68*
$Rsl_{BHEF} = 4.93*** - 8.74RD^{***}$	0.544	19	0.80***	0.90***
$Rsl_{FVEF} = 7.33*** - 9.55RD^{***}$	0.941	10	0.76***	0.89***
Late-drought				
$Rst_{CEF} = 1.00*** - 0.38RD$	0.081	7	0.13	0.49
$Rst_{BHEF} = 0.94*** - 0.84RD^{***}$	0.149	15	0.44***	0.68***
$Rst_{FVEF} = 0.21*** - 0.25RD^{**}$	0.071	10	0.50**	0.74**
$Rsl_{CEF} = 1.73*** - 2.34RD^*$	0.227	7	0.54*	0.77*
$Rsl_{BHEF} = 1.19*** - 0.69RD^{***}$	0.127	15	0.42***	0.67***
$Rsl_{FVEF} = 0.97*** - 0.59RD^{***}$	0.083	10	0.81***	0.91***

[†]Resistance (Rst) and resilience (Rsl) to drought as a function of relative tree population density (RD), where SE is the residual standard error, d.f. is degrees of freedom, R^2 is the adjusted R squared of the model and r is the Pearson correlation coefficient between the observed and predicted data. Subscripts 'CEF', 'BHEF' and 'FVEF' refer to Experimental Forest for which model corresponds to. Parameters' significance code: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

competition) to drought vulnerability is crucial for adequately predicting climate change impacts on forest dynamics and for developing adaptive management strategies to sustain forest ecosystems in the future. We found a consistent negative relationship between forest growth resistance and resilience to drought and tree population density, suggesting a unifying relationship that can inform adaptation planning and management interventions (Fig. 3). Growth rates of trees occurring in denser populations were more negatively impacted by drought, showing lower growth resistance and resilience to drought. This density-dependent vulnerability to drought was consistent across three climatically divergent forest ecosystems and was apparent in the two species examined and across stand ages (Fig. 3). The variability in mean site resistance and resilience to drought observed across these forest ecosystems (Fig. 3) might be partly explained by the differences in drought intensity. Under drought conditions, lower water availability in denser stands may be exacerbated by high levels of inter-tree competition that limits tree growth (McDowell *et al.* 2006, 2008), while the growth of individual trees might increase as competition intensity decreases in less dense stands. Nevertheless, the positive growth response to thinning might still be hindered by extraordinary droughts and warming, which would not allow for improvement in intrinsic water use efficiency.

APPLICATIONS AND MANAGEMENT IMPLICATIONS

Our results suggest that reducing vulnerable tree population densities (*via* periodic silvicultural thinning of the population) represents a viable adaptation strategy (Millar, Stephenson & Stephens 2007) that may be included in management approaches to enhance drought resistance and resilience, and minimize the potentially adverse ecological and socio-economic impacts of increased mortality and susceptibility to pests and diseases. In our study, the vulnerability to drought of different forest types covering a broad aridity gradient was lowered by the reduction in tree population densities, independent of stand age. Our population-level findings are in line with those of previous examinations of tree-level responses to drought, where growth and resistance of trees to drought was higher for trees growing in less dense stands (McDowell *et al.* 2006; Kerhoulas *et al.* 2013; Fernández-de-Uña, Cañellas & Gea-Izquierdo 2015).

The wide range of climatic conditions represented by the long-term experiments examined here suggests that our results about the benefits of silvicultural thinning are likely applicable to many coniferous temperate and subtropical forest ecosystems. Forests growing in arid and semi-arid locations and at their dry limits are particularly vulnerable to climate change (Lévesque *et al.* 2014), and can therefore benefit from the effects of silvicultural thinning. The relationship between tree population density and drought vulnerability in other forest ecosystems merits further investigation. Forests growing in mesic

locations, where species and trees are less drought tolerant, might show different responses to stand density reduction treatments. For instance, the application of silvicultural thinning in humid tropical forests may result in drier and more fire susceptible understories, making these forests vulnerable to large-scale fires, which would overwhelm the impact of droughts (Holdsworth & Uhl 1997; Barlow & Peres 2004). While there is evidence that drought-induced forest decline can occur in wet forests (Choat *et al.* 2012), empirical studies are needed that evaluate the potential trade-offs between density reduction, as a climate change adaptation strategy, and fire risk.

Authors' contributions

A.W.D., B.J.P., J.B.B. and S.F. conceived the ideas and designed methodology; A.W.D., B.J.P., J.B.B., S.F., M.A.B. and L.A.A. collected the data; A.B., A.W.D., B.J.P., J.B.B. and S.F. analysed the data; A.B. and B.J.P. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Tree ring data used in this study are available at Dryad Digital Depository <http://dx.doi.org/10.5061/dryad.cb2d2> (Bottero *et al.* 2016).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. SPEI chronologies for the three Experimental Forests.

Table S1. Correlations between SPEIs calculated over different time intervals and index curves for the three Experimental Forests.

Table S2. ANOVA tests for pre-experiment population growth resistance and resilience.