


Competition amplifies drought stress in forests across broad climatic and compositional gradients

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Abstract. Forests around the world are experiencing increasingly severe droughts and elevated competitive intensity due to increased tree density. However, the influence of interactions between drought and competition on forest growth remains poorly understood. Using a unique dataset of stand-scale dendrochronology sampled from 6405 trees, we quantified how annual growth of entire tree populations responds to drought and competition in eight, long-term (multi-decadal), experiments with replicated levels of density (e.g., competitive intensity) arrayed across a broad climatic and compositional gradient. Forest growth (cumulative individual tree growth within a stand) declined during drought, especially during more severe drought in drier climates. Forest growth declines were exacerbated by high density at all sites but one, particularly during periods of more severe drought. Surprisingly, the influence of forest density was persistent overall, but these density impacts were greater in the humid sites than in more arid sites. Significant density impacts occurred during periods of more extreme drought, and during warmer temperatures in the semi-arid sites but during periods of cooler temperatures in the humid sites. Because competition has a consistent influence over growth response to drought, maintaining forests at lower density may enhance resilience to drought in all climates.

Key words: aridity; competitive intensity; dendrochronology; drought severity; drought stress; forest density; forest growth; forest response; long-term experimental forests; USA.

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INTRODUCTION

Climatic extremes (such as extreme heat and droughts) are expected to increase as a result of climate change (Lu et al. 2007, Dai 2011). Severe droughts cause widespread tree mortality and

decreased growth in forests (Williams et al. 2013, Allen et al. 2015), even in areas with cool and mesic climates where drought impacts are not widely recognized (Pederson et al. 2014, Clark et al. 2016). Simultaneously, forest density and the associated competitive intensity among trees

have increased across many areas of the United States since the late 1800s as a result of fire exclusion in fire-adapted systems (Agee 1996), and recovery from intensive land use (Foster 1992, Hanberry et al. 2012). Understanding how ecosystems respond to temporal fluctuations in resource availability or competitive intensity is a long-standing challenge in ecology (Grime 1979, Tilman 1987), and forecasting forest response to simultaneous changes in both stress and competition is even more difficult (Liancourt et al. 2005), especially over broad climatic gradients (Pugnaire and Luque 2001, Linares et al. 2010).

Increasing drought severity and high competitive intensity may interact, producing unexpectedly severe outcomes for forest ecosystems (Linares et al. 2010). Drought influences the composition and structure of forest communities, yet it can be difficult to understand because of confounding factors such as species-specific sensitivity to drought (Martín-Benito et al. 2008, Mérian and Lebourgeois 2011), stand diversity (Forrester et al. 2016, Metz et al. 2016), competitive interactions, and site variability (Elliott and Swank 1994). Drought, defined here as a meteorological moisture deficit relative to a site's mean condition, can directly affect trees by reducing growth and eventually causing mortality (Cailleret et al. 2016). Across many species, trees with slower growth and that respond more negatively to drought have a higher probability of mortality than faster-growing trees, at both short-term (Wyckoff and Clark 2002, Hanna and Kulakowski 2012) and long-term temporal scales (Kane and Kolb 2014, Vanoni et al. 2016). However, there are exceptions in some species (Cailleret et al. 2016), particularly slower-growing species with greater hydraulic safety margins which tend to be more drought tolerant and have higher post-drought recovery rates (Choat et al. 2012, Anderegg et al. 2015). Drought can also indirectly affect forests by predisposing trees to damage by abiotic (i.e., nutrient limitations) and biotic (i.e., insects and disease) factors (Olano and Palmer 2003). Trees experiencing high competitive intensity at a stand level may be particularly vulnerable to drought as the greater transpiration potential of the crowded environment exacerbates soil moisture deficits (Primicia et al. 2015). Thus, future potential changes in water and energy exchanges due to the

combination of drought and increased high forest density may have unexpected consequences for forest composition, structure, and function under future climate conditions (Clark et al. 2016).

Forest density has a recognized influence over tree demographic processes, including recruitment, growth, and mortality, given its strong relationship with average tree-level resource availability (Westoby 1984, Bottero et al. 2017, Bradford and Bell 2017). Reducing forest density increases the productivity of the remaining trees by increasing average resource levels, while reducing the vulnerability of forests to disturbances such as wildfire and insect outbreaks (Latham and Tappeiner 2002, Fettig et al. 2014). Several studies have shown that reducing forest density through thinning may directly reduce drought vulnerability (Grant et al. 2013, Thomas and Waring 2015), while others have shown that thinning may indirectly increase drought vulnerability due to increased understory evaporative losses (Aussenac 2000) and competition for soil moisture (Zahner 1958, Nilsen et al. 2001). Additional studies found that forest vulnerability to drought and competition depends on the species of interest (Rollinson et al. 2016), and particularly the species' strategies to tolerate drought and shade (Niinemets and Valladares 2006). These variable results suggest there may be differences in climate, site history, or age structure of the focal tree populations, and underscore the importance of unknown interactions that influence forest vulnerability to drought (D'Amato et al. 2013). Most forest drought studies have focused on individual tree responses to drought (Klos et al. 2009, Clark et al. 2014); however, stand-level responses may be more useful for understanding large-scale phenomena (Clark et al. 2016) and for developing forest management prescriptions, which are implemented at the stand level. To date, few studies have investigated stand-level forest responses to drought (D'Amato et al. 2013, Forrester et al. 2016, Metz et al. 2016).

Untangling the interactive effects of drought and competition on forest growth remains a critical knowledge gap. Our objective was to examine how growth of entire tree populations (quantified retrospectively by dendrochronology) has been influenced by drought and competitive intensity (represented by long-term, maintained, replicated

forest stand density experiments) using eight research sites that span a broad climatic gradient. The eight sites also represent a range of temperate forest ecosystems in the continental United States, from drier pine-dominated forests in the western USA, to more humid hardwood and mixed hardwood–conifer forests in the Midwestern and northeastern USA (Fig. 1). At each site, dendrochronology records (tree ring-width chronologies) were obtained from all trees within study plots (maintained at various forest densities) to quantify population-level, annual-scale forest growth. We used these unusually rich datasets to explore how density modifies forest growth response to drought.

Tree growth generally responds negatively to drought (i.e., less growth when conditions are dry and more growth when conditions are wet) and negatively to forest density (i.e., less individual tree growth in stands with more trees). Alternately, stand-level forest growth generally responds

positively to forest density (i.e., more stand-level forest growth with more trees). However, it is unknown how the magnitude of forest growth response to drought is influenced by forest density relative to site aridity or drought severity. We thus defined three specific metrics to investigate the relationships and interactions of forest growth, drought, and density (Fig. 2). First, we quantified forest growth response to drought, calculated as the slope of the relationship between growth and drought, a metric that is independent of density. Second, we evaluated the relative explanatory power of drought (compared to density) on growth, calculated as the proportion of inter-annual growth variance attributable to drought versus density. Third, we assessed the magnitude of forest density impacts on the forest growth response to drought, calculated as the change in growth vs. drought slope resulting from a given variation in density. We examined these metrics both across the climatic gradient and through time

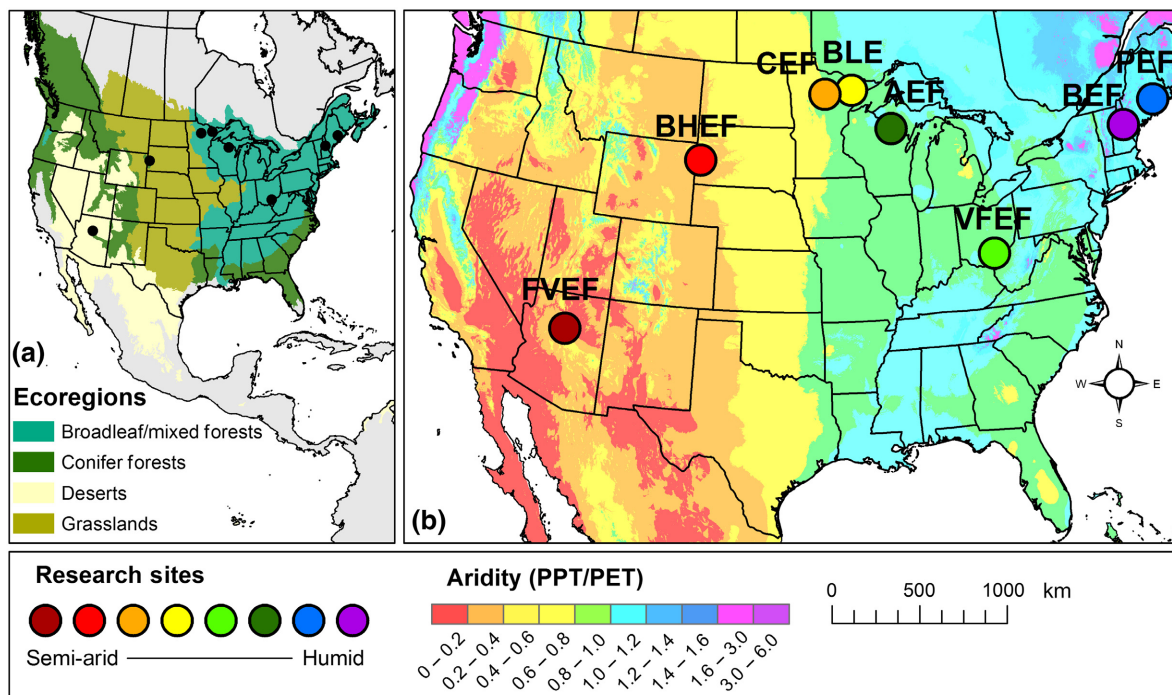


Fig. 1. (a) Eight research sites span the continental USA and are located in coniferous, broadleaf (hardwood), and mixed forest ecoregions (data product obtained from World Wildlife Fund). (b) Site map shows the distribution of the research sites across the North American aridity gradient. The research sites are all located in long-term forest density experiments and represent a climatic and forest composition gradient across the continental United States.

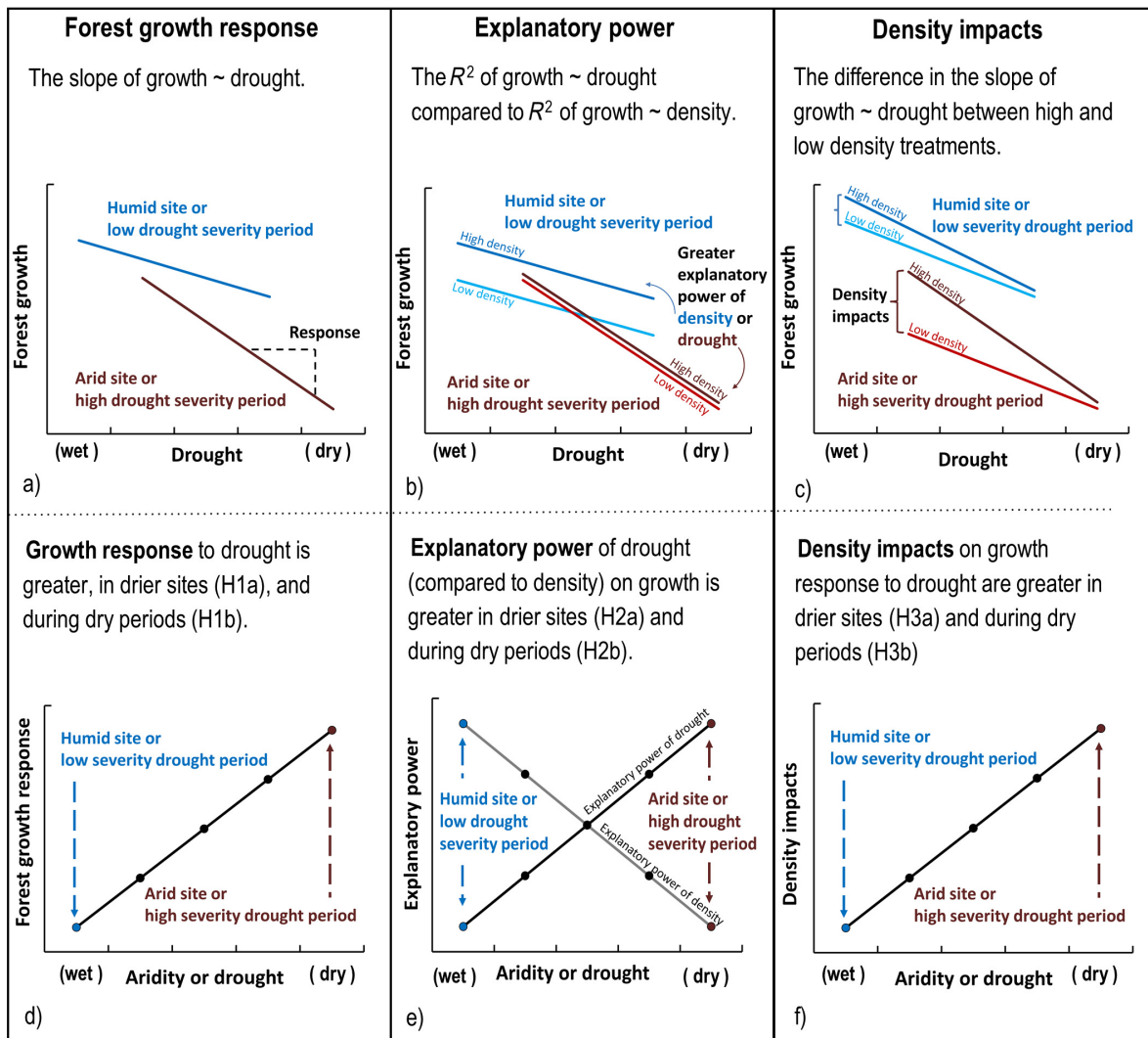


Fig. 2. (a–c) Top row describes the three metrics representing growth response to interactions of drought and competitive intensity. Red lines represent sites with more arid climates or periods with more severe drought, and blue lines represent more sites with more humid climates or periods with less severe drought. Dark colored lines indicate higher-density forests, whereas light colored lines indicate lower-density forests. (d–f) Bottom row shows proposed hypotheses of how each metric relates to either long-term site aridity or short-term drought severity. Aridity is defined as the long-term average of precipitation over potential evapotranspiration. Drought severity is defined as 20-yr median self-calibrated Palmer Drought Severity Index, which is relative to the site's long-term mean conditions.

as represented by our sites. Although there are numerous plausible alternative hypotheses, for simplicity we hypothesized that all three metrics (forest growth response, explanatory power of drought, and the magnitude of forest density impacts) would be highest in more arid sites and

during periods of more severe drought (Fig. 2). To our knowledge, this is the first study to evaluate how stand-level growth response to drought is influenced by forest density (competitive intensity) across broad spatial gradients of aridity, as well as temporal fluctuations in drought severity.

METHODS

We evaluated forest density impacts on forest growth response to drought using long-term, stand-level forest density measurements, dendrochronological records, and an annual drought severity index from eight long-term forest density experiments. Using 20-yr moving window analyses, we evaluated three metrics to address each of three hypotheses (Fig. 2). Each metric was evaluated relative to aridity and drought severity for all 20-yr windows during the study period for each site (from initial treatment to final sampling, ~40–60 yr).

Research sites

The eight research sites, all U.S. Department of Agriculture, Forest Service experimental forests or sites, span an aridity and compositional gradient of North American temperate forests and include (from west to east) Fort Valley Experimental Forest (FVEF), Black Hills Experimental Forest (BHEF), Cutfoot Experimental Forest (CEF), Birch Lake Experiment (BLE), Argonne Experimental Forest (AEF), Vinton Furnace State Experimental Forest (VFEF), Bartlett Experimental Forest (BEF), and Penobscot Experimental Forest (PEF). The sites dominated by ponderosa pine (*Pinus ponderosa*) are located in the Colorado Plateau in northern Arizona (FVEF), and the Black Hills in South Dakota (BHEF). The sites dominated by red pine (*Pinus resinosa*) are located in the drift and lake plains (CEF) and the northern Superior uplands (BLE) in northern Minnesota. The mixed hardwood-dominated site is in northern Wisconsin (AEF), the oak (*Quercus* spp.)-dominated site is in Ohio (VFEF), the mixed hardwood–conifer site is in New Hampshire (BEF), and the mixed conifer–hardwood site is in Maine (PEF; Fig. 1). All sites, except the northeastern sites (BEF and PEF), are located in long-term forest density experiments where forests have been maintained at a range of densities and repeatedly measured since the 1950–1960s. As an example of a typical western USA site, FVEF was thinned and maintained each decade to multiple density treatments based on retained basal area (m^2/ha), including a $45 \text{ m}^2/\text{ha}$ uncut control, and 34, 23, and $7 \text{ m}^2/\text{ha}$ experimental treatments. The northeastern sites, BEF and PEF, have long-term density measurements within

forest experiments including shelterwood, single-tree selection, and crop tree thinning. More detailed information on each research site including the species composition and treatment history is included in Table 1 and in Appendix S1: Table S1.

Aridity

As an index of climatological aridity for each site, we used a measure of moisture supply/moisture demand, namely the Global Aridity Index by the United Nations Food and Agriculture Organization and provided by the Consultative Group for International Agriculture, Consortium for Spatial Information (Trabucco and Zomer 2009). The Global Aridity Index was calculated as mean annual precipitation (PPT)/mean annual potential evapotranspiration (PET). Precipitation and PET were aggregated to mean annual values to represent the climatological aridity from 1950 to 2000. Throughout this paper, aridity is shown on reversed x-axes to show the increase in aridity associated with lower PPT/PET values.

Forest density and competitive intensity

In each research site, a range of forest densities have been maintained since the 1950–1960s in multiple replicate plots, although the specific densities and maintenance (treatment) schedules vary between sites. In each long-term density treatment plot, diameter at breast height (dbh) has been measured at regular intervals, usually every 5–10 yr in conjunction with thinning treatments. Forest density (m^2/ha) was derived from these historical dbh measurements for each treatment during each year of measurement.

Continuous density values were reconstructed across the study period by interpolating the historical forest density measurements for each treatment plot in each site. The inter-annual variability in density across the time interval between measurements was proportionally distributed based on the inter-annual variability in stand-level basal area increment (BAI) data derived from dendrochronological records. In sites where dbh was only measured before thinning, the reduction in forest density as a result of thinning was calculated by subtracting the basal area of the thinned trees from the total basal area of all trees measured. Although all sites have control stands, BLE and PEF are the only sites

Table 1. Experimental forest, climate, and treatment information for each of the eight research sites.

Sites	State	Latitude	Longitude	Aridity	Temp (°C)	PPT (mm)	Forest type	Treatments*	Density treatments sampled (m ² /ha)
AEF	Wisconsin	35.28	-111.72	0.95	4.3	791	Northern Hardwood	Stocking level, thinning method	14, 21, crop tree release, control (87)
BEF	New Hampshire	44.17	-103.63	1.39	5.6	1293	Northern Hardwood	Thinning method	Single-tree selection, light crop tree, control (35)
BLE	Minnesota	47.55	-94.09	0.92	3.3	720	Red Pine	Stocking level, thinning method	7, 14, 21, 28, 35, control (67)
BHEF	South Dakota	47.7	-91.93	0.68	5.1	584	Ponderosa Pine	Stocking levels	5, 9, 14, 18, 23, 28, control (81)
CEF	Minnesota	39.2	-82.4	0.82	4.1	679	Red Pine	Stocking level, thinning method	14, 23, 32, control (41)
PEF	Maine	45.74	-88.99	1.24	6.5	1035	Mixed conifer	Regeneration method	Five-year selection, three-stage shelterwood, control (56)
FVEF	Arizona	44.85	-68.62	0.51	7.1	553	Ponderosa Pine	Stocking levels	9, 23, 34, control (45)
VFEF	Ohio	44.06	-71.3	0.93	10.8	1056	Oak Hardwood	Stocking levels	9, 14, 18, 23

Notes: AEF, Argonne Experimental Forest; BEF, Bartlett Experimental Forest; BLE, Birch Lake Experiment; BHEF, Black Hills Experimental Forest; CEF, Cutfoot Experimental Forest; PEF, Penobscot Experimental Forest; FVEF, Fort Valley Experimental Forest; VFEF, Vinton Furnace State Experimental Forest. Aridity values (mean precipitation [PPT]/mean potential evapotranspiration) were integrated from 1950 to 2010; temperature and PPT data were retrieved from PRISM monthly 4-km data and integrated from 1960 to 2010. Density treatments sampled (m²/ha) include the target basal area values maintained for each density treatment, and the basal area for the control treatment measured at the time of dendrochronology sampling. For other thinning method treatment basal area information, refer to the Appendix S1: Table S1.

* Three replications of each treatment and a control were sampled at each site, except VFEF and BLE.

where the control plots were measured throughout the entire study period. Control plots for the other sites were measured when tree increment cores were collected.

Competitive intensity was inferred by relative stand density, calculated from forest measurements using a stand density index (SDI) for each treatment plot in each research site, as a comparison of current forest density to potential maximum density (SDI_{max}, Reineke 1933). Stand density index characterizes competition based on size–density relations independent of site quality and stand age, and represents density in units of relative density, thereby allowing for quantitative comparisons of density impacts across species and climatic conditions (Woodall et al. 2005). Stand density index for each plot was calculated using the summation method (Shaw 2006) and was used in the calculation of the density impacts metric described below.

Drought severity

As an index of annual-scale drought severity, we used the monthly self-calibrated Palmer Drought Severity Index (scPDSI) retrieved from Schrier et al. (2013) at a 0.5° resolution (CRUscPDSI 3.21) and aggregated over the annual water year

(October–September). This global dataset of dry and wet spells for 1901–2009 has a similar range of variability in diverse climates, making it useful for cross-site comparisons. The index is derived from a moisture supply/moisture demand model, which uses a Penman–Monteith parameterization for PET based on the actual vegetation cover. The scPDSI values are locally scaled to be roughly between -4 and +4 based on the historical record of climate variability at each location. Negative scPDSI values indicate dry periods, whereas positive scPDSI values indicate wet periods. Drought, or years with a moisture deficit, was defined by years with negative scPDSI values. Throughout this paper, drought is shown on reversed *x*-axes to represent an increase in drought associated with decrease in scPDSI values.

Drought frequency and severity were variable and relative to each site, but most sites experienced some relative drought during the study period (Appendix S1: Fig. S2). Because the scPDSI values are calibrated across the period of record (1901–2009), and calculated at a coarse spatial resolution (0.5°), the index is useful to evaluate periods of relative drought across sites and over time; however, it may not be accurate for a precise

location in space and time. During the study periods, the more arid sites, FVEF and BHEF, experienced moderate to severe drought frequently, the northern Lake State pine sites (CEF and BLE) experienced relatively mild droughts, the Midwestern mixed hardwood (AEF) and oak (VFEF) sites experienced moderate to severe drought frequently, and the more humid eastern mixed hardwood–conifer sites (PEF and BEF) experienced a variable climate with moderately dry to very wet conditions.

Forest growth

We quantified forest growth as stand-level BAI data (m^2/ha) from tree cores sampled during 2009–2012 from every living tree >5 cm dbh (>10 cm at BHEF, FVEF, CEF) at 1.3 m above ground, in subplots within the long-term density treatment plots (FVEF, $n = 598$; BHEF, $n = 420$; CEF, $n = 956$; BLE, $n = 1477$; AEF, $n = 1038$; VFEF, $n = 321$; PEF, $n = 1031$; BEF, $n = 564$). At FVEF, BHEF, BLE, VFEF, and AEF sites, tree cores were sampled within the long-term density treatment plots. At CEF, PEF, and BEF sites, tree cores were sampled from “mirror” plots established in areas adjacent to and maintained at the same densities as the long-term forest density treatment plots. The COFECHA software was used to check dating errors and improve the cross-dating of tree ring-width chronologies (Grissino-Mayer 2001). We then estimated the DIB (diameter [dbh] inside bark) using empirical equations to remove the bark thickness from the field-measured dbh (Bunn 2008). Tree ring-width chronologies were adjusted to account for off-center piths (due to elliptical trunk shape) following methods and justification presented in Frelich (2002). Using back reconstruction starting from inside the bark toward the pith, BAI values were obtained using the *dplR* package in R (Bunn 2008). Stand-level BAI values were calculated as the sum of all individual tree BAIs within a plot for each year since establishment.

The stand-level BAI values were developed from cores of living trees and thus do not account for tree mortality or the trees that were harvested from treatment plots to maintain the target density throughout the experimental period. The greater the intensity of removal during the experiment, the greater the underrepresentation of the BAI values derived from tree cores. To account for

this underrepresentation in our continuous analysis, a correction was applied to the BAI values based on the proportion of trees historically measured prior to each treatment to trees cored at the time of tree core sampling. The raw BAI values were multiplied by the ratio of the basal area of the cored trees over the basal area of all trees in each plot measured every 5–10 yr (when historical plots were measured and data were available) after the start of the experiment. This ratio (correction factor) was derived for each year the trees were measured, and applied to annual stand-level BAI values for all years prior to measurement until another measurement (and correction factor) was available. Stand-level forest growth (BAI) values were de-trended using a cubic spline over the study period for each plot to remove low-frequency (long-term) variability and preserve the high-frequency (inter-annual) variability in forest growth using the “*dplR*” package in R (Bunn 2008).

Analysis and metrics

We quantified forest density impacts on growth response to drought for each site across the entire study period using 20-yr moving window analyses. Density impacts were evaluated for each 20-yr window (period) in each site using the following three metrics (Fig. 2):

Growth response.—Forest growth response to drought was calculated for each site for each period, as the slope of a least-squares linear regression of annual forest growth (BAI) vs. annual drought severity (inverse of *scPDSI*) using data for all plots combined in each site.

Explanatory power.—The relative explanatory power (R^2) of drought vs. density on the inter-annual variability in forest growth was calculated for each site for each period, using hierarchical partitioning of the optimal regression model. A stepwise, multivariate least-squares linear regression was applied to each period using annual BAI values for the dependent variable of forest growth, and annual values of forest density, drought severity (inverse of *scPDSI*), and the drought \times density ($\text{Dr} \times \text{De}$) interaction, as independent drivers for all treatment plots in each research site. The “step” function in the R package “*stats*” determined the optimal model for each period based on Akaike’s information criterion values. We used

hierarchical partitioning in order to determine the relative explanatory power of drought vs. density to forest growth in these optimal models using the “hierpart” function in the R package “hier.part” (Walsh and Mac Nally 2013). Hierarchical partitioning evaluates both the independent variable and the interactive contributions of each independent variable to the overall model.

Density impacts.—When the relationship between growth and drought was significantly impacted by density in the optimal models, we quantified the impact of density as the difference in slope of a least-squares linear regression of forest growth (BAI) vs. drought severity (inverse of scPDSI), for treatment plots of high density minus treatment plots of low density. Density impacts were standardized by the difference in relative density (SDI) between the high-density treatment plots minus the low-density treatment plots. All possible combinations of density treatments were calculated between high- and low-density treatment plots and were used to evaluate density impacts across all sites. To minimize bias in standardizing differences between sites, we used all possible combinations of high- and low-density treatments with at least 0.1 difference in SDI (10% difference in relative density) to evaluate density impacts within sites. For each site, climate conditions during periods when the $Dr \times De$ interaction was significant in the optimal models were compared with periods where the interaction was not significant to identify conditions when forest density significantly impacted forest growth response to drought.

Each metric was evaluated relative to aridity and median drought severity in each site for all 20-yr periods, using least-squares linear regressions. Differences in climate characteristics of periods with and without significant $Dr \times De$ interactions were analyzed using two-tailed t tests. All analyses were performed in R 3.1.3 (R Core Team 2015). Significance of statistical relationships was determined using an α value of 0.05.

RESULTS

Forest growth response to drought

Forest growth responded negatively to drought (i.e., less growth during drier periods and more growth during wetter periods) over the entire study period in all sites but one

(Fig. 3a), including the semi-arid western pine forests (FVEF and BHEF), the sub-humid Lake States pine site (CEF), the mixed hardwood site (AEF), the oak site (VFEF), and the humid mixed hardwood–conifer forests of the northeast (PEF and BEF). However, in the red pine-dominated site (BLE), forest growth demonstrated the opposite relationship and responded positively to drought (i.e., more growth during drier periods than during wetter periods). In this higher-latitude site, long cold winters may create conditions in which growth is more limited by energy availability than by soil moisture availability (Running et al. 2004).

Temporal patterns within sites revealed that growth responses to short-term drought were greater during 20-yr periods with relatively drier conditions only in some sites. Specifically, growth response to drought was more negative during periods of more severe drought in the two driest pine sites, FVEF ($R^2 = 0.69$, $P < 0.001$; Fig. 3b) and BHEF ($R^2 = 0.26$, $P < 0.01$; Fig. 3c) as well as the oak site VFEF ($R^2 = 0.96$, $P < 0.001$; Fig. 3f). By contrast, we observed the opposite relationship, where forest growth response to drought was less negative during periods with more severe drought, at AEF the mixed hardwood site of intermediate aridity ($R^2 = 0.38$, $P < 0.001$; Fig. 3g) and at BEF the humid hardwood–conifer forest of the northeast ($R^2 = 0.53$, $P < 0.001$; Fig. 3i).

Relative explanatory power of drought vs. density on growth

Quantifying the combined influence of both drought and density over growth within all 20-yr periods revealed substantial variability in the relative importance among sites and within sites through time (Fig. 4). Across all sites, the mean explanatory power of drought on growth increased with long-term aridity (PPT/PET; $R^2 = 0.51$, $P < 0.05$; Fig. 3j). Drought had greater mean explanatory power on growth, compared to density, in the more arid pine-dominated sites (FVEF and BHEF; $\mu = 0.18$, $\sigma = 0.02$), and was less influential in the sites of intermediate climates (CEF, BLE, VFEF, and AEF; $\mu = 0.07$, $\sigma = 0.07$), as well as in the humid mixed hardwood–conifer sites (PEF and BEF; $\mu = 0.05$, $\sigma = 0.02$). Temporal variability in the explanatory power of drought was also greatest in the most arid sites. By contrast,

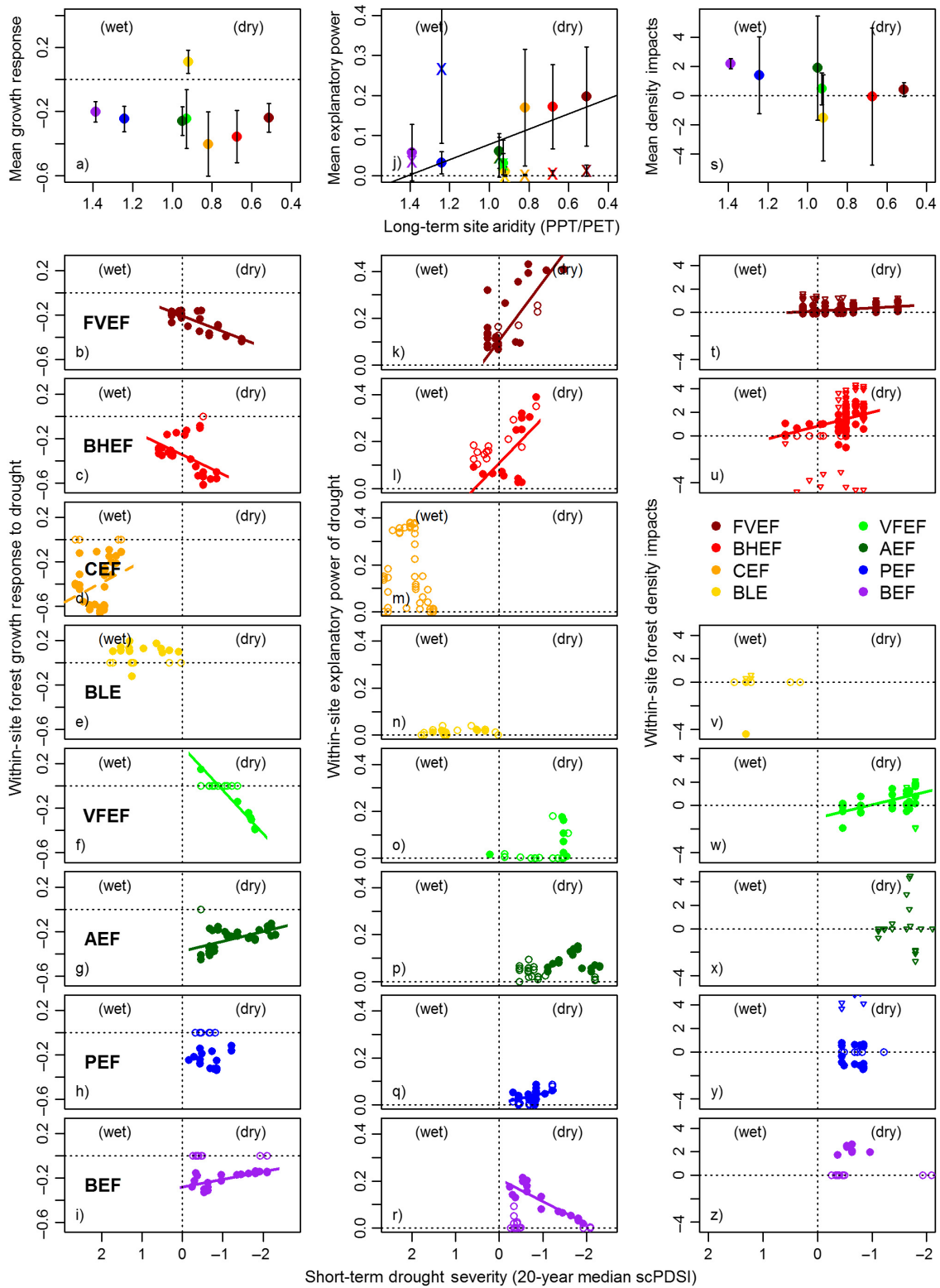


Fig. 3. (a) Geographic patterns in forest growth response to drought, indicating negative relationships of

(Fig. 3. Continued)

growth with drought across the climatic gradient for all but one site. Research sites include Fort Valley Experimental Forest (FVEF), Black Hills Experimental Forest (BHEF), Cutfoot Experimental Forest (CEF), Birch Lake Experiment State Forest (BLE), Vinton Furnace Experimental Forest (VFEF), Argonne Experimental Forest (AEF), Bartlett Experimental Forest (BEF), and Penobscot Experimental Forest (PEF). Error bars indicate ± 1 standard deviation (SD) among time periods within each site. (b–i) Within-site temporal variability in growth response to drought for all sites, indicating increased response during 20-yr periods with greater drought severity at FVEF, BHEF, and VFEF, and decreased response during 20-yr periods with greater drought severity at AEF and BEF. The periods with no significant growth response to drought are shown as zero values in open circles. (j) The mean explanatory power of drought on forest growth for all analysis periods in each site over aridity is shown in solid circles. The mean explanatory power of density on forest growth for all analysis periods in each site over aridity is shown in Xs. Density had greater explanatory power in the more humid sites than in the more arid sites. The black line shown indicates a linear regression of the explanatory power of drought on forest growth vs. aridity. Error bars indicate ± 1 SD of all analysis periods. (k–r) Temporal variability in the explanatory power of drought on forest growth over 20-yr drought (self-calibrated Palmer Drought Severity Index, scPDSI) for all sites, demonstrating that in more arid sites drought has a greater influence on forest growth during periods of more severe drought. The explanatory power of drought on forest growth during periods with no significant drought \times density interaction is shown in open circles. (s) The mean forest density impacts on the forest growth response to drought for all analysis periods over aridity. The CEF site showed no significant density impacts for any period and therefore was not included in the plots. The black line shown indicates a linear regression of density impacts vs. aridity. Error bars indicate ± 1 SD for all analysis periods. (t–z) Temporal variability in density impacts on the forest growth response to drought for each analysis period over drought severity (20-yr median scPDSI). In the more arid sites which experienced relatively severe drought during the experimental record (FVEF, BHEF, and VFEF), forest density impacts on the forest growth response to drought increased with increasing drought severity. The density impacts between treatments with less than 0.1 difference in stand density index are shown as open triangles and were not used in the least-squares linear regression analysis. The density impacts during periods with a significant drought \times density interaction across all treatments, but without significant response to drought within both treatments of comparison, are shown as zero values in open circles and were not used in the least-squares linear regression analysis.

density had relatively more influence over growth in the humid mixed hardwood–conifer sites (PEF and BEF; $\mu = 0.15$, $\sigma = 0.16$), than in the sites of intermediate climate (CEF, BLE, VFEF, and AEF; $\mu = 0.02$, $\sigma = 0.02$) and in the more arid sites (FVEF and BHEF; $\mu = 0.009$, $\sigma = 0.004$; Fig. 3j).

Within-site temporal patterns in the relative influence of drought vs. density suggest that drought had greater explanatory power on growth during drier periods in sites with more severe drought, specifically in FVEF ($R^2 = 0.55$, $P < 0.001$; Fig. 3k), BHEF ($R^2 = 0.36$, $P < 0.05$; Fig. 3l), and PEF ($R^2 = 0.32$, $P < 0.05$; Fig. 3q). In the most humid mixed hardwood–conifer forest, BEF, the influence of drought over growth was, counterintuitively, larger during periods with less severe drought ($R^2 = 0.7$, $P < 0.001$; Fig. 3r). Within-site temporal patterns in the explanatory power of density suggest that density had a greater explanatory power on growth during drier periods in two of the most humid sites namely

AEF ($R^2 = 0.72$, $P < 0.001$; Appendix S1: Fig. S5) and BEF ($R^2 = 0.19$, $P < 0.1$; Appendix S1: Fig. S5h). In the most arid forest, FVEF, the influence of density over growth was larger during periods of less severe drought ($R^2 = 0.35$, $P < 0.01$; Appendix S1: Fig. S5).

Density impacts on growth response to drought

Density impacts were prevalent across most sites regardless of aridity (Figs. 3s, 4). Only one site of intermediate aridity, CEF, showed no significant density impacts during the study. The magnitude of density impacts on the growth response to drought (i.e., change in growth vs. drought slope across density levels) decreased with long-term site aridity across all sites but this trend was not significant due to large variability within sites (Fig. 3s). Inter-annual variability in density impacts on the growth response to drought was large in most sites. Density impacts on the growth response to drought increased

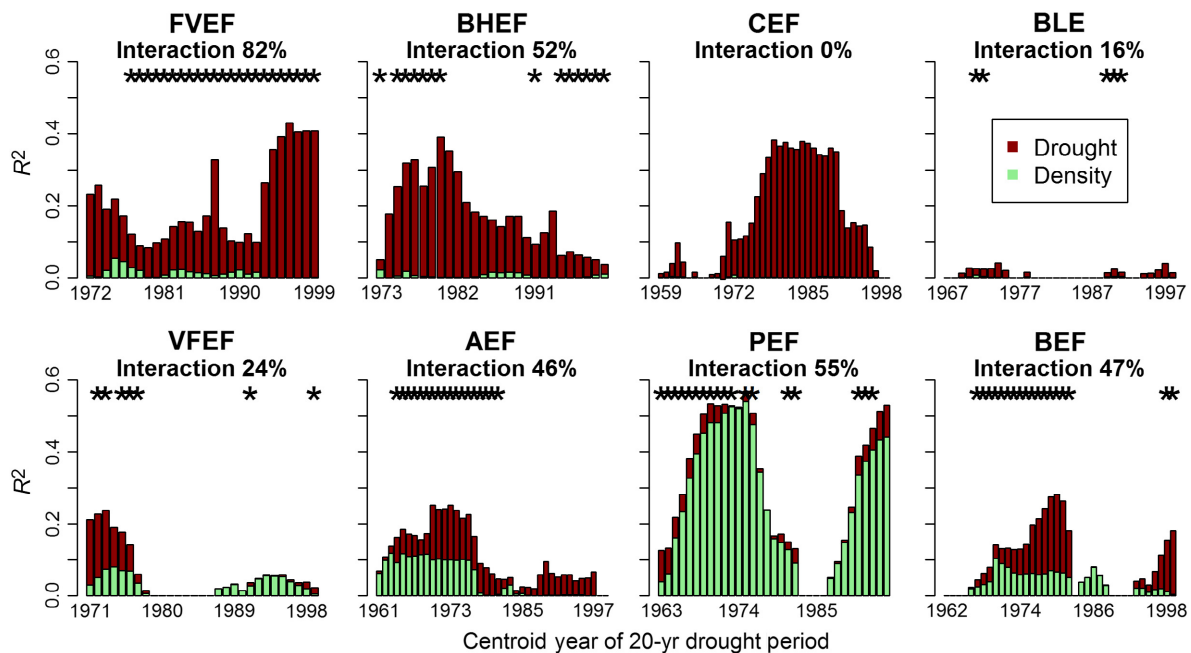


Fig. 4. Relative explanatory power of drought and density on forest growth for 20-yr analysis periods from initial treatment to tree core sampling at each site. Total bar height indicates the overall R^2 value of the stepwise multivariate model, and the colors indicate the partitioning of the overall model into the relative explanatory power of annual drought severity (self-calibrated Palmer Drought Severity Index) and forest density. Black asterisks indicate analysis periods with a significant drought \times density interaction. Drought has greater explanatory power in the more arid pine-dominated sites (upper row), whereas density has an increasing influence in the more humid hardwood and mixed forest sites (lower row). For explanation for abbreviations, please refer to Fig. 3 caption.

during drier periods across all sites ($R^2 = 0.24$, $P < 0.001$; Appendix S1: Fig. S6), but was variable within sites (Fig. 3t–z). Within sites, density impacts increased during periods with more severe drought in the three more arid sites that have experienced more severe relative drought during the study, namely FVEF ($R^2 = 0.26$, $P < 0.001$; Fig. 3t), BHEF ($R^2 = 0.19$, $P < 0.01$; Fig. 3u), and VFEF ($R^2 = 0.38$, $P < 0.001$; Fig. 3w). Furthermore, the characteristics of 20-yr periods when density impacts were significant in the optimal growth models differed across the sites. At all sites except VFEF, density impacts were significant during intervals with more extreme drought (minimum scPDSI; Fig. 5). Density impacts on growth response were significant during warmer periods in the western pine-dominated forests, but cooler periods in the humid eastern mixed forest sites, compared to periods when density impacts were not significant.

DISCUSSION

The health and functioning of forests are projected to be adversely impacted by increases in drought frequency and severity under climate change (Clark et al. 2016), with effects already manifesting in many regions of the globe. Promoting healthy and productive forest ecosystems requires understanding where and when competition among trees may mitigate or exacerbate the adverse effects of climate extremes. The direct and indirect impacts of drought and competition on forest growth are difficult to tease apart due to their complex interactions (Linares et al. 2010, Clark et al. 2016). We determined how growth of entire tree populations was influenced by drought and competitive intensity using compositionally different sites spanning broad spatial gradients of long-term aridity and short-term temporal variability in drought severity.

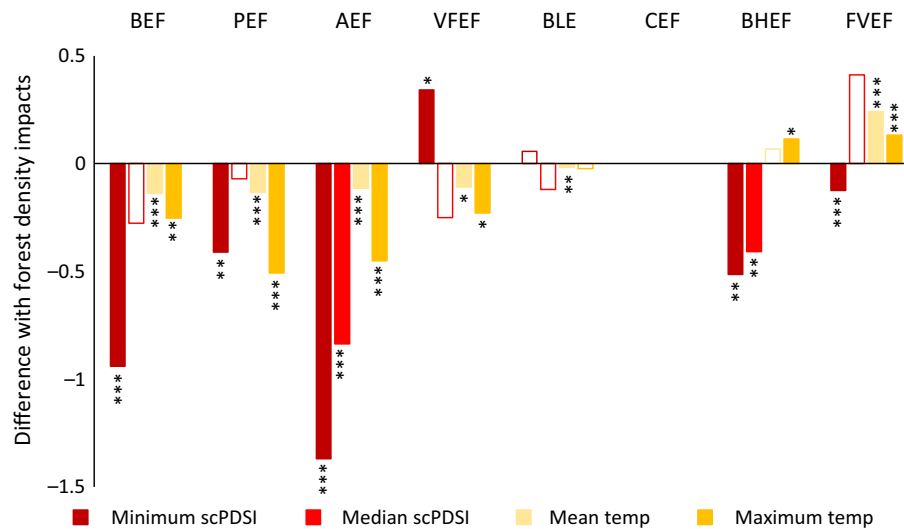


Fig. 5. The difference in median self-calibrated Palmer Drought Severity Index (scPDSI), minimum scPDSI, mean temperature, and maximum temperature during periods with significant density impacts minus during periods with no significant density impacts for all sites. Asterisks indicate the significance of the difference ($*P < 0.1$, $**P < 0.01$, $***P < 0.001$). Periods with significant drought \times density interactions were characterized by more severe drought, warmer temperatures in the arid sites and cooler temperatures in the humid sites. Empty bars indicate values of insignificant differences between periods with and without forest density impacts. Sites are organized in plot by increasing long-term aridity. For explanation for abbreviations, please refer to Fig. 3 caption.

Geographic patterns of growth response to drought and competition

The negative response of forest growth to drought was reasonably consistent across essentially all sites, and was unrelated to aridity across this broad climatic and compositional gradient (Fig. 3a), indicating no support for hypothesis 1a (Fig. 2d). Surprisingly, these responses were generally of similar magnitude in humid and arid climates, suggesting that most temperate forests are vulnerable to drought. However, in support of hypothesis 2a (Figs. 2e, 3j, 4), drought was the dominant control on forest growth in the more arid sites, whereas density, drought, and their interactions were controlling factors in the more humid sites. Growth at humid sites may be responsive because the component tree species are often drought sensitive and are adapted to take advantage of moist conditions (Clark et al. 2014), whereas tree species in more arid sites may have more conservative strategies aimed at avoiding negative impacts of stress, such as investing in non-structural carbohydrates to store carbon for future dry years (Richardson et al. 2013).

Furthermore, density impacts on growth response to drought (e.g., difference in slopes between high- and low-density stands) were greater in humid sites than in sites of intermediate and arid climates, rejecting hypothesis 3a (Figs. 2f, 3s), and supporting the idea that competition may be more (or at least consistently) intense in productive areas than in resource-limited forests (Grime 1979). These results suggest that competitive intensity is a relatively modest driver of growth (when interacting with drought) in drier locations, where water resources are typically scarce and trees may already be adapted to water limitations. These results indicate that drought exerts a dominant control on growth in arid sites, whereas growth controls in humid sites likely represent a complex interaction of both drought and competitive intensity. These results differ from previous work which found a stronger effect of density on mortality at more arid sites (Young et al. 2017), and reinforces that the mechanisms driving growth declines following drought may not be the same for forest mortality following drought. Particularly in the mixed species hardwood–conifer forests, the spatial and temporal

variability in water-use efficiency between competing individuals may alter the stand-level responses to soil water limitations (Kelty 1992). This could be related to the low drought tolerance of shade-tolerant species (Niinemets and Valldares 2006), particularly in the humid sites with mixed composition, where increases in density also reflect an increasing amount of shade-tolerant species over time. In contrast, the drier pine-dominated and fairly monotypic forests do not experience substantial compositional variability over time. Drought was more extreme during periods with significant density impacts across most sites; these periods were warmer in the more arid sites and cooler in the more humid sites, than periods without significant density impacts (Fig. 5). These results suggest that there may be varying mechanisms by which forests experience water limitations under varying climatological conditions across the aridity and compositional gradient.

Within-site temporal patterns of growth response to drought and competition

Forest growth response, explanatory power of drought, and density impacts were greater as drought severity increased at some of the sites, indicating partial support for hypotheses 1b, 2b, and 3b. Forest growth response to drought can be variable depending on drought duration, timing, integration period, and post-drought recovery of the species (Anderegg et al. 2015), which may introduce uncertainty in these results. In support of hypothesis 3b (Figs. 2f, 3t–z; Appendix S1: Fig S6), density impacts on growth response to drought were greater during periods of more severe drought across all sites, but were variable within sites. Some of the among-site variation in significance of temporal patterns was related to the severity of the drought periods experienced during the long-term studies. Specifically, the magnitude of temporal variability in growth and drought and/or competitive intensity was lowest for each metric in the two sites that experienced the mildest relative droughts during the several decades of the study (CEF and BLE). Also, two of the sites where drought severity consistently impacted forest growth (FVEF and VFEF) are also the two warmest sites, underscoring that temperature conditions during droughts can be very important. Such “hot droughts” may become a more regular occurrence as climate changes in the

future (Williams et al. 2013, Cook et al. 2014, Allen et al. 2015). Some sites displayed temporal patterns exactly opposite to our expectations. For example, at BEF, both the relative explanatory power of drought and the magnitude of density impacts were greater when conditions were wetter, which may be related to the overall humid climate of BEF where cloudy conditions and/or low temperatures associated with unusually wet years may be limiting to growth. The complexity of these temporal dynamics emphasizes the value of long-term manipulative experiments for understanding complex ecological processes, especially across wide environmental gradients.

CONCLUSIONS

Particularly in North America, drought is expected to increase in frequency and severity as the jet stream moves poleward, reducing PPT and summer soil moisture (Lu et al. 2007). If land-use change and fire suppression continue to increase forest density and climate change elevates drought frequency and severity, forests are likely to become more vulnerable to soil water limitations. Drought can be a triggering factor in tree death through prolonged reductions in forest growth, even in relatively mesic climates where competition for resources is considered one of the main factors driving mortality (Bigler et al. 2007, Aakala and Kuuluvainen 2011). Climate extremes, together with competition among trees, may interact to exacerbate forest growth declines and, in some cases, further increase forest mortality (Panayotov et al. 2016).

Our results demonstrate that competition amplifies population-level forest growth response to drought across a broad spatial gradient of aridity and forest composition, and these density impacts are particularly important during periods of more severe drought. Management to reduce forest density through thinning may enhance growth resilience to drought in all climatic conditions, particularly during periods of increasingly extreme drought. Further research is required to identify how the physical mechanisms influencing forest growth vary depending on climate (i.e., in cold climates) vs. competitive intensity (i.e., with mixed species diversity). Possible future research, including detailed ecophysiological investigations, soil moisture modeling, and remote sensing,

may continue to disentangle the direct and indirect effects of climate, structure, and composition on stand-level forest growth under drought conditions.

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