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Managing red pine stand structure to mitigate drought impacts

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ABSTRACT

Reducing forest stand density through silvicultural thinning has demonstrated potential to mitigate drought impacts on growth; however, less has been studied on *how* changes in stand structure created by different thinning methods influence forest growth responses to drought. This research examined the growth responses to drought of natural-origin red pine in a long-term study contrasting thinning methods. Dendrochronological methods were used to examine growth responses during several drought events among stands where different thinning methods have been applied since 1950. Growth responses to drought were expressed as resistance (maintaining growth during drought), and resilience (regaining pre-drought growth). Results indicate that periodic thinning from above, which resulted in smaller diameters, has the potential to moderate drought-induced growth reductions. Larger tree diameters negatively influenced tree-level resistance and resilience across all treatments; however, the proportion of dominant trees in a stand had contrasting effects on stand-level drought responses. Stands thinned from above exhibited more complex vertical structure and increased stand-level resistance and resilience to drought-induced growth declines because competition is more stratified among smaller diameter trees. Opposite trends were observed in stands thinned from below, where the larger diameters and monolayered structure create greater competition among trees of similar size and crown position. The results of this study highlight the utility in managing for greater structural diversity to mitigate the negative effects of drought in red pine forest ecosystems.

1. Introduction

Projections of future climate predict increasing drought intensity and frequency in several regions of the Northern Hemisphere (Dai, 2012; IPCC, 2014), with negative effects on forest ecosystem structure and function resulting from climate-induced physiological stress and mortality, and the increased potential for severe disturbances (Allen et al., 2010; Anderegg et al., 2012; IPCC, 2018; Seidl et al., 2017). Forests play an important role in balancing global climate and providing innumerable ecosystem services (Bonan, 2008; Hassan et al., 2005; IPCC, 2014). The capacity of forests to continue this role in a future of unprecedented moisture deficits will be greatly challenged (McDowell et al., 2016), and largely dependent on effective adaptive management strategies.

Silvicultural thinning is used to enhance the growth of trees in stands managed for wood production, regulating site occupancy levels and consequent natural growth patterns, stand structure, and development (Nyland, 2016). Two of the main types of thinning approaches include: thinning from above (also known as crown or high thinning) in which trees from dominant and co-dominant crown classes are removed to favor the best trees of those same crown classes; and thinning from below (typically called low thinning), which removes trees from the lower crown classes, concentrating growth potential on the larger diameter canopy dominants. Thinning from below generally results in more uniform size distribution and monolayer vertical structure, whereas stands thinned from above have greater complexity in both tree diameters and height (Kerr and Haufe, 2011).

Thinning, as typically applied, can simplify the composition and structure of a stand, potentially creating large areas of relatively homogeneous forest cover and increasing vulnerability to abiotic and biotic disturbances (Franklin et al., 2007; Young et al., 2017), both of which are predicted to increase with advancing climate change (IPCC, 2014; Seidl et al., 2017). However, thinning practices applied to achieve growth and diameter management objectives (Bradford and Palik, 2009) have also been found to lower climate sensitivity when compared to unthinned control stands (Gleason et al., 2017; Magruder

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et al., 2013), indicating their potential utility as an adaptive forest management tool.

Reducing the basal area of a forest by thinning may help to ameliorate drought-induced tree mortality (Bradford and Bell, 2017; Powers et al., 2010). Thinning increases light and soil moisture availability by reducing competition from neighboring trees, offering a potentially effective climate change adaptation strategy for sustaining tree growth during and after drought events (Bottero et al., 2017; D'Amato et al., 2013). Conversely, thinning may also exacerbate drought impacts as lower densities increase light and wind exposure. Over time, thinning can influence the structure and functional diversity of forests (Curzon et al., 2017), offering a longer-term climate-adaptive management strategy (D'Amato et al., 2011). Enhancing the structural and functional diversity of forests not only helps to stabilize ecosystem processes in response to disturbances and variations in climatic conditions, it also enhances provision of ecosystem goods and services (Hooper et al., 2005).

Red pine (*Pinus resinosa* Aiton) forests of the western Great Lakes region have broad ecological and economic importance, for instance by providing wildlife habitat and timber resources. Natural origin, unmanaged red pine forests in Minnesota are highly diverse in cohort age structure and compositional diversity, possibly the result of non-stand replacing fires (Fraver and Palik, 2012). By contrast, managed red pine stands are often characterized by comparatively less structural and compositional diversity (Young et al., 2017). In managed forests, the reduction of basal area has proven benefits in reducing mortality and growth vulnerability during drought events (Bottero et al., 2017; Bradford and Bell, 2017; Gleason et al., 2017; Magruder et al., 2013); however, less has been documented on the drought resilience conveyed by structural changes resulting from applications of different thinning methods. In this study, we examined red pine stands of uniform basal area periodically thinned with different methods (above, below), and untreated controls, to determine how changes in diameter and vertical forest structure (achieved by removing dominant and co-dominant trees vs. smaller diameter, lower canopy trees) affect resistance and resilience to drought-induced growth declines. Specifically, we sought to (1) quantify the effects of thinning method (thinning from above and thinning from below) on red pine tree- and stand-level resistance and resilience to drought-induced growth declines using a dendrochronological approach; (2) examine which thinning method minimizes drought-induced growth decline; and (3) evaluate the effect of individual-tree and stand characteristics on these growth responses to drought.

2. Material and methods

2.1. Study area

This study utilized treatments from a long-term red pine thinning methods experiment established by the USDA Forest Service in 1950. The cutting methods study (47°33′ N, 94°05′ W), part of the Cutfoot Experimental Forest, is located on the Chippewa National Forest, in northern Minnesota, USA (Fig. 1). Red pine stands on the Cutfoot regenerated naturally following fires in the late 1860s. Species composition is primarily red pine, which comprises 95% of the basal area in the study plots. The cutting methods study includes stands thinned from above (removal of dominant and co-dominant trees from the upper canopy) and below (removal of smaller diameter trees in lower canopy positions) in 4.0 ha units with three replicates of each treatment type. Stands were thinned at 5–25 year intervals to maintain a uniform residual growing stock basal area ($25\ m^2\ ha^{-1}$). Following the initial thinning in 1950, all treatment stands (above and below) were subsequently thinned again in 1955, 1960, 1970, 1985, and 2010 (Fig. 4).

2.2. Data collection

Three plots in each of the three replicates of cutting methods stands thinned from above and below (n = 18) were sampled in June 2015. Cutting methods plots were selected at random from the 90th percentile of density and diameter variability using 1950–1953 inventory data. Data collected in 2015 from unmanaged stands on the Cutfoot (n = 6), and in 2010 from Sunken Lake Natural Area (n = 3) served as the controls. Control plots were selected in stands with the same natural origin establishment date (ca. 1865) and similar density, diameter, and compositional variability as the cutting methods stands prior to the 1950 thinning treatments using 1940–1956 Cutfoot Experimental Forest inventory data (Young et al., 2017). The inventory data also confirmed the absence of management activities in the selected control plots from 1956 onward. To minimize sampling impacts in the experimental forest, one increment core was extracted from all living trees ≥10 cm diameter at breast height (dbh, 1.37 m height). Tree species and dbh were also measured and recorded for all sampled trees. Tree sampling in the cutting methods study was conducted in 0.04 ha fixed area circular plots, nested within the established 0.08 ha plots to reduce edge effects. In the unmanaged control plots, where edge effects were less of a factor, trees ≥10 cm dbh were sampled from the full 0.08 ha inventory plot.

2.3. Drought selection

The self-calibrating Palmer Drought Severity Index (scPDSI) was used as indicator for drought, and calculated using the function pdsi of the R package pdsi (Palmer, 1965; Wells et al., 2004). Monthly temperature and total precipitation were obtained from the PRISM gridded climate dataset (Di Luzio et al., 2008), and the available water capacity used in the scPDSI calculation was extracted from the web soil survey (NRCS, 2015). June-July temperature and precipitation are most correlated to red pine tree growth in northern Minnesota (Kipfmueller et al., 2010), thus extreme drought years were defined as years when the average June-July scPDSI was less than one standard deviation of the 1940–2010 mean (Fig. 2). The time period of 1940–2010 was selected to cover the duration of the cutting methods study and 10 years prior. The identified droughts occurred in 1940, 1941, 1956, 1958, 1961, 1977, 1980, 1988, 1990, 1991, 2000, and 2007. Of these, only droughts that occurred after the beginning of the cutting method study (1950) were considered for further analyses. Sequential droughts occurring within a three-year window were analyzed as a single drought event when scPDSI remained negative during that time span. Following this method, mean resistance and resilience response values were analyzed for the 1958–1961 and 1988-1990-1991 drought events.

2.4. Tree-ring samples and data analysis

Increment core samples were glued into grooved wooden mounting sticks and repeatedly sanded with progressively finer grit paper on a 36″ benchtop belt sander according to standard dendrochronological procedures (Speer, 2010). Prepared core samples were crossdated visually, measured under stereomicroscope using Velmex sliding stage/linear encoder and MeasureJ2X software (precision to nearest 0.001 mm), and the crossdating was validated with COFECHA (Holmes, 1983), for a total of 372 individual series measurements for analysis. The entire series covered a time span of 1785–2014, with series intercorrelation ranging from 0.527 to 0.601. Mean sensitivity (MS) and expressed population signal (EPS) ranged from 0.21 to 0.23 and 0.86 to 0.92, respectively (Table 1).

Tree-level basal area increment chronologies were calculated for each treatment (Fig. 4) and used in further drought response analyses. The time period considered for drought analysis is beyond the juvenile phase (1940–2010), avoiding potential bias at the beginning of the series due to rapid acceleration of ring width and tree productivity

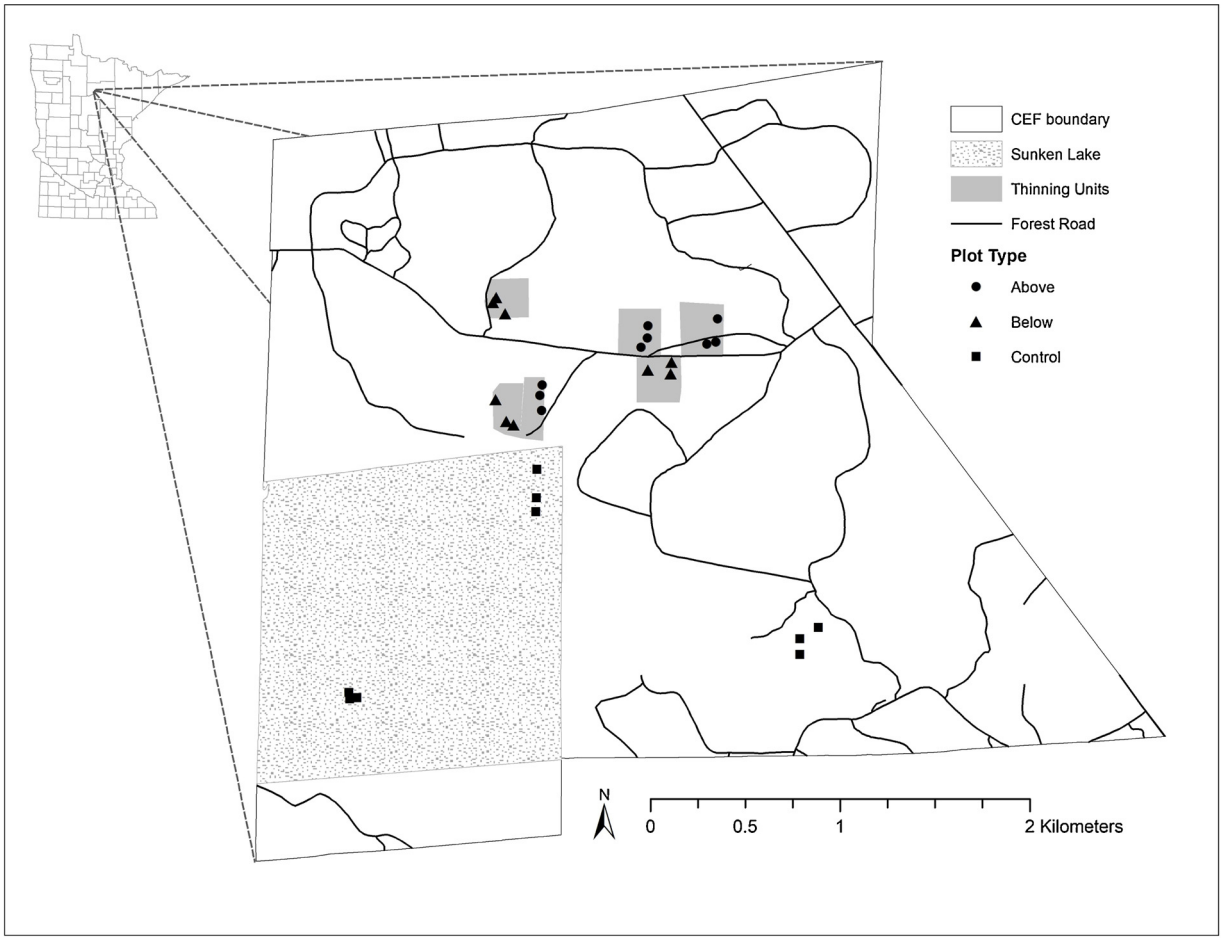

Fig. 1. Geographical distribution of sample plots within the cutting methods study and Sunken Lake Research Natural Area (RNA) in Cutfoot Experimental Forest (CEF) located, within Chippewa National Forest, Minnesota, USA.

observed during this initial phase of exponential growth. As an added provision, measured ring widths were converted to basal area increment (BAI) to remove geometric effects (Biondi, 1999). Diameter (dbh) inside bark at time of coring and radial increments were used to back-reconstruct BAI using the dplR package (Bunn, 2008). Bark thickness was obtained by multiplying the dbh (outside bark) by a species-specific bark ratio factor (Dixon and Keyser, 2008). The diameter inside bark was obtained by subtracting bark thickness from the measured dbh (outside bark).

Drought responses were evaluated at the tree- and stand-level using

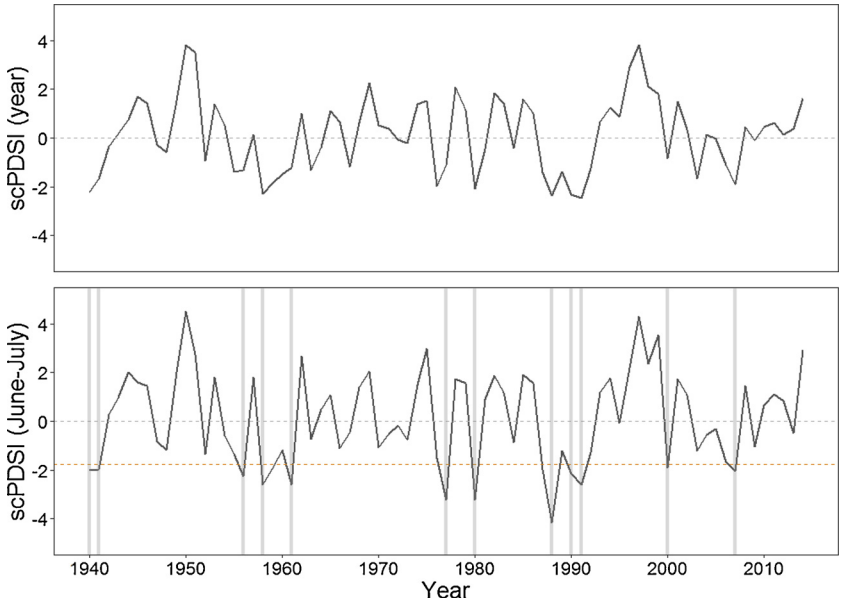

Fig. 2. Self-calibrating Palmer Drought Severity Index (scPDSI, year, top panel) and seasonal scPDSI (June-July, bottom panel) for the period 1940–2010. Grey horizontal dotted lines (top and bottom panels) differentiate between wet (values above 0) and dry (value below 0) years. The orange horizontal dotted line (bottom panel) shows the threshold (mean – 1SD) used to identify "extreme" years (vertical grey lines), under which scPDSI June-July was 1 SD below the mean.

Table 1
Forest composition and structural characteristics (reference year 2015 for Above, Below, and Cutfoot control plots; year 2010 for Sunken Lake control plots). Species composition is listed for tree species with relative basal area (BA) > 1% (balsam fir = ABBA, paper birch = BEPA, black spruce = PIMA, red pine = PIRE, eastern white pine = PIST). Trees (Trees ha^{-1}), mean diameter [dbh (cm)], and height [Ht. (m)], total number of cores (N. cores), mean sensitivity (MS), and expressed population signal (EPS) refer to live red pine ≥10 cm dbh. Height [Ht. (m)] was measured on a subset of trees (n = 44). Pearson correlation values (Correlation) indicate correlation between annual basal area increment (BAI mm^2) and self-calibrating Palmer Drought Severity Index (scPDSI).

		Above	SE	Below	SE	Control	SE
Relative BA (%) by species	ABBA	0	n/a	0	n/a	2.70	± 0.63
	BEPA	0.10	± 0.07	0	n/a	1.93	± 1.43
	PIMA	0	n/a	0	n/a	1.27	± 0.72
	PIRE	97.23	± 1.77	98.99	± 0.54	79.42	± 6.58
	PIST	2.01	± 1.46	1.01	± 0.54	12.36	± 5.36
Stand BA ($m^2 ha^{-1}$)		27	± 1.81	31	± 2.16	44	± 2.29
Trees ha^{-1}		314	± 21.29	200	± 17.18	536	± 42.05
Live red pine ≥ 10 cm dbh	dbh (cm)	33	± 0.86	47	± 0.48	36	± 0.77
	Ht. (m)	25	± 0.33	28	± 0.44	20	± 1.73
	N. cores	97	n/a	64	n/a	211	n/a
	MS	0.23	± 0.004	0.21	± 0.003	0.22	± 0.002
	EPS	0.86	± 0.014	0.92	± 0.010	0.87	± 0.046
	Correlation	0.037	± 0.007	0.036	± 0.003	0.029	± 0.006

a 3-year window to measure resistance and resilience (Lloret et al., 2011). The 3-year window was selected to account for the average duration of significant legacies in radial growth observed after severe drought (Anderegg et al., 2015). We defined resistance as the ability to avoid a growth reduction during a drought event (BAI_D/BAI_{pre}), where BAI_D is average tree- or stand-level BAI (obtained as sum of BAI of all trees within a plot) during a drought event, and BAI_{pre} is the average tree- or stand-level BAI during the three years before the event. Resilience was defined as the ability to regain pre-drought growth, calculated as BAI_{post}/BAI_{pre}, where BAI_{post} is the average tree- or stand-level BAI during the three years after a drought. Resistance and resilience are ratios of relative growth, and therefore less affected by overall growth patterns. Using a short (3-year) analysis window further minimizes the influence of overall growth trends on the resulting ratios of comparison.

Height-diameter relationship models are often used to estimate the heights of trees from their diameters, being the two are highly correlated (Fulton, 1999; Lumbres et al., 2011; Sharma, 2016). We used relative dbh (calculated as ratio of dbh of $tree_i$ at $time_y$ to mean stand dbh at $time_y$) as a proxy for canopy position and tree height because the latter was not available for each sampled tree. Trees above mean stand dbh were considered "dominant" and those below were considered "non-dominant" trees to examine the influence of canopy position on tree growth response to drought events.

Linear mixed effect models were used to quantify the effect of canopy position (expressed as relative dbh), tree diameter, stand basal area, and scPDSI on tree- and stand-level resistance and resilience to drought in the different treatments. To estimate model parameters the lmer function in the lme4 R package (Bates, 2005) was used. Residual and normal quantile plots were visually assessed to ensure a normal distribution and homogeneity of residuals. In order to detect whether resistance and resilience to drought within the two treatments (above and below), and the control, followed different (i.e., counteracting) trends, we considered interactions between treatment and each of the fixed factors. Fixed factors were scaled and centered to improve parameter estimates and allow for direct comparison of the regression coefficients. A random effect was included in the models to account for variability in the growth response to drought among trees within the same plot and treatment (tree-level models) or among plots within the same treatment (stand-level models). Random effect was also defined for the intercept with drought years since adding this random structure to the models improved the model's quality (lower second-order Akaike's information criterion, AIC*c*). Years since previous drought were included in the models to account for the effect of close drought events. Potential multicollinearity among explanatory variables in the full model was examined with the variance inflation factor (VIF), and variables with high VIF value were removed from the full model. Successfully, a set of models with all combinations of fixed effect terms with their interactions included in the full model was ranked by the AIC*c*. The model with the lowest AIC*c* was chosen as the 'best' model. This model selection was performed with the function dredge from the MuMIn R package (Bartoń, 2018). The variance explained by the fixed effects and by the entire model was expressed computing marginal R-squared and conditional R-squared, respectively, using the function r.squaredGLMM from the R package MuMIn. All analyses were performed with the statistical computing software R (version 3.5.0) (R Core Team, 2018).

3. Results

3.1. Forest composition and structure

Our results show that red pine dominated the overstory across all cutting methods study sites (Table 1), comprising a majority of overstory basal area (thinned from above 97%, thinned from below 99%), with other species (removed during periodic thinning entries) occupying a minor presence in the understory. Basal area in the unmanaged control plots was also dominated by red pine (79%), with greater inclusions of other species such as white pine (12%), balsam fir (*Abies balsamea,* 3%), paper birch (*Betula papyrifa,* 2%), and black spruce (*Picea mariana, 1%*). The remaining basal area (< 3%) in control plots was comprised of red maple (*Acer rubrum*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), big tooth aspen (*Populus grandidentata*), and red oak (*Quercus rubra*).

Stand density and structure reflected the periodic application of thinning (Table 1, Figure 3).

Total basal area was similar in stands thinned from above (27 $m^2 ha^{-1}$) and below (31 $m^2 ha^{-1}$), but lower than basal area in the unmanaged control stands (44 $m^2 ha^{-1}$). Through the periodic removal of smaller diameter trees, target basal area in stands thinned from below was maintained at lower densities (mean 200 trees ha^{-1}), while the removal of larger diameter trees in stands thinned from above resulted in higher mean tree density (314 trees ha^{-1}). Total tree density in the unmanaged control stands was noticeably higher (mean 536 trees ha^{-1}).

Stands thinned from below contained larger diameter red pine (mean dbh 47 cm) compared to control plots (mean dbh 36 cm) and stands thinned from above (mean dbh 33 cm). Selective removal of large diameter canopy dominants in stands thinned from above resulted in shorter mean tree heights (25 m), and the removal of smaller diameter non-dominant trees in stands thinned from below resulted in

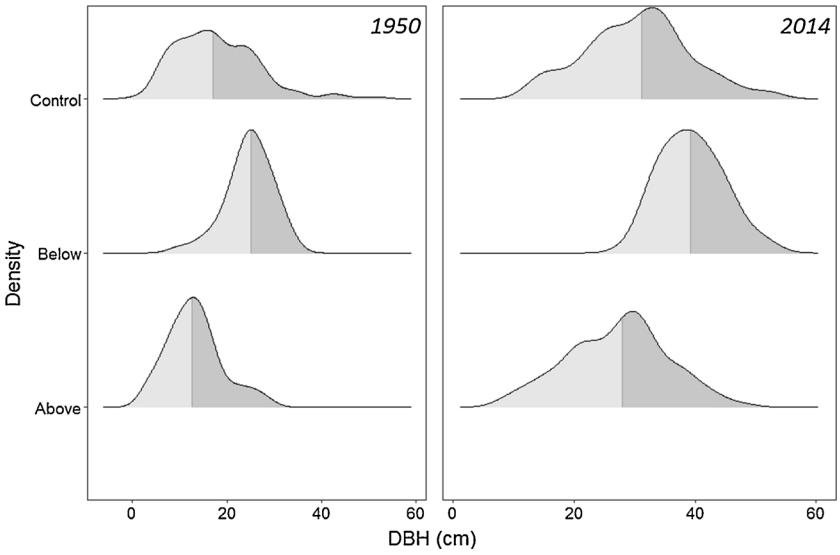

Fig. 3. Diameter distribution of trees in above and below treatments, and control at the onset of the cutting methods study (1950, left panel) and in 2014 (right panel). The different shading in the graphs indicate the intervals 0–50%, 50–100% (i.e., tree dbh below or above the mean, respectively). The vertical grey line in each graph corresponds to the mean dbh and indicates the threshold between dominant and non-dominant trees.

taller mean heights (28 m).

3.2. Drought vulnerability

Growth declines (measured in basal area increment) were observed across all sites (thinning treatments and control) during the analyzed drought events (Fig. 4). Stands thinned from below had the highest increments (greatest growth) until the late 1990s, then increments of all stands tended to be very similar. In addition, since the early 1960s, stands thinned from above and control stands had very similar increments.

Periodic thinning treatments affected tree-level growth responses to drought, with trees in stands thinned from below showing lower resistance and resilience to drought than trees in stands thinned from above (Fig. 5). Lower values of tree-level resistance and resilience were observed in relation to lower scPDSI values across the analyzed drought years (Fig. 2, Fig. 5). At the tree-level larger diameter trees were generally less resistant and resilient to drought (Table 2). June-July drought severity also influenced the tree-level growth responses to drought; as scPDSI (June-July) values decreased, resistance and resilience values also decreased (Table 2).

At the stand-level a higher proportion of dominant trees generally conferred lower stand-level resistance and resilience to drought-induced growth decline (Table 3). However, opposite patterns emerged in stands thinned from above, where a higher proportion of larger diameter trees conferred greater stand-level resistance and resilience to drought. Lower drought severity (June-July scPDSI) positively influenced stand-level growth resistance and resilience to drought (Table 3). Conversely, basal area had significant negative influence on resistance and resilience in both treatments (above and below).

4. Discussion

4.1. Structural diversity

As expected, higher values of stand basal area had a negative effect on stand-level growth responses (resistance and resilience) to drought events (Table 3). This result is consistent with other research examining the effects of thinning on drought vulnerability (Bottero et al., 2017; D'Amato et al., 2013; Gleason et al., 2017). Reducing stand density reduces the vulnerability of stand growth to drought by increasing the availability of limited soil moisture resources (Bradford and Bell, 2017),

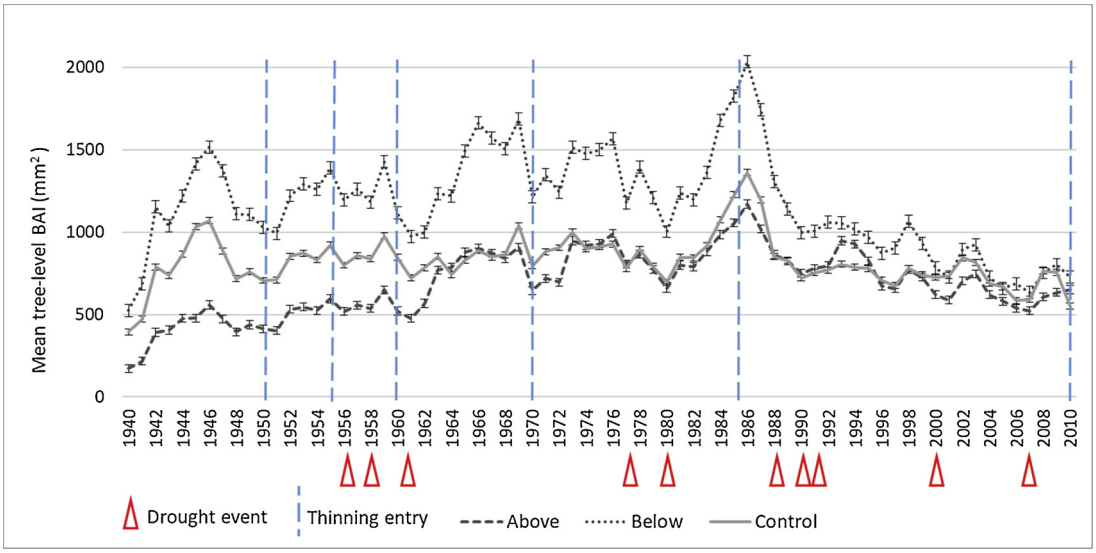

Fig. 4. Tree-level basal area increment (mm^2) and standard error for above treatments (dashed), below treatments (dotted) and control stands (solid). Vertical dashed lines indicate thinning entries (above and below treatments only). All stands were thinned within the same season. Triangles denote analyzed drought events.

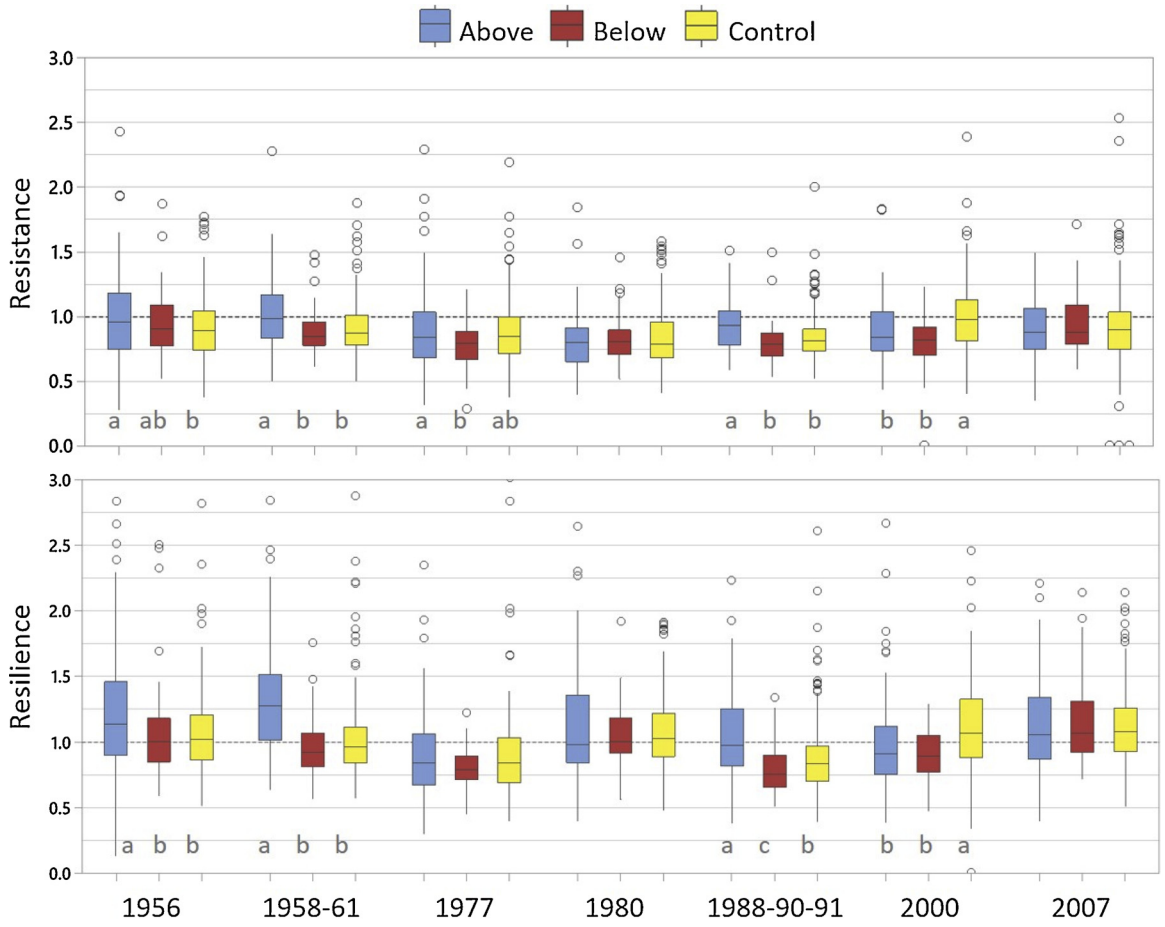

Fig. 5. Boxplots of tree-level growth resistance and resilience responses across Above and Below treatments and Control stands for each of the analyzed drought events. Lowercase letters (a,b,c) indicate significant differences at $\alpha < 0.05$ (ANOVA tests). Groups that do not have lowercase letters displayed no statistical difference in drought response.

presenting a short- to medium-term climate adaptive management strategy to moderate drought-induced growth declines (Bottero et al., 2017).

In this study, we found that tree diameter and vertical structure also appeared to influence the growth response of trees to drought. The stands in this study were thinned at periodic intervals to maintain uniform residual growing stock densities, making basal area less of a controlling factor on tree growth during drought events, relative to the structural characteristics created over time by the *type* of thinning treatment applied. Stands that were thinned from above displayed more varied diameter distributions, similar to that of control stands, while diameters in stands thinned from below were more uniform (Fig. 3), characteristic of managed forests (Curzon et al., 2017).

Tree-level responses to drought revealed that diameter had a negative effect on growth across stands thinned from above and below, and control stands (Table 2). Larger trees were less resistant to drought-induced growth declines and less resilient in recovering pre-drought growth levels, presumably as a result of having higher water demands (McDowell et al., 2006) and being more prone to hydraulic failure (Phillips et al., 2003; Ryan and Yoder, 1997). Hydraulic resistance increases as trees grow and the pathways that water must travel from roots to canopy expand. Water conduction processes are further stressed in times of soil moisture deficit (drought), which can lead to the temporary breakdown (cavitation) of water and nutrient transport, limiting growth (Ryan and Yoder, 1997), and mortality when water potential drops below the levels necessary to support hydraulic and stomatal conductance, photosynthesis, and carbohydrate production (McDowell et al., 2016). Smaller trees are less susceptible to these physiological limitations, thereby maintaining and/or recovering growth during and/or following drought events.

Resilience responses were largely driven by drought intensity (Table 2), with more structurally complex stands (thinned from above, control) showing greater resilience to drought (Fig. 5). Increased frequency and intensity of drought will negatively impact forest productivity, potentially compromising ecological function and timber production capacity (Anderegg et al., 2012). Managing forests to facilitate greater vertical structure and complexity in diameter distribution (i.e. unmanaged stand characteristics) may mitigate the negative impacts of drought through reducing direct canopy competition (D'Amato et al., 2011; Xu et al., 2018). Furthermore, greater variation in vertical structure mitigate the impacts of light penetration and wind exposure that may exacerbate drought conditions. As suggested by the growth responses observed in the control plots, increased compositional diversity may also mitigate the negative impacts of drought, presumably through differential competition for resources among different tree species.

4.2. Social position

Using relative dbh as a proxy for height (Sharma, 2016) to further examine vertical structure (i.e. canopy or social position) revealed interesting growth responses with regard to the quantity of dominant trees in a stand (Table 3). A higher proportion of dominant trees (those above mean stand dbh) reduced stand-level resistance to drought-induced growth decline in stands thinned from below and control stands. Conversely, in stands thinned from above the ratio of dominant trees

Table 2
Estimates, standard error (SE), and significance for tree-level drought resistance and resilience models. Abbreviations: rt = resistance, rs = resilience, treatm = treatment (3 levels: Above, Below, reference Control), dbh_cm = dbh (cm), scpdsi_jj = scPDSI (June-July), AIC*c* = second-order Akaike's information criterion, R^2marg = R-squared marginal (fixed effects), and R^2cond = R-squared conditional (fixed + random effects). Random effects for drought year, and plots within sites. Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1.

Model 'tree-level drought resistance'			
Best model: rt ~ dbh_cm x treatm + scpdsi_jj x treatm			
	estimate	**SE**	**Pr (> t)**
intercept	0.896	0.026	0.000***
dbh_cm	−0.054	0.006	0.000***
Above	−0.006	0.025	0.824
Below	−0.014	0.029	0.650
scpdsi_jj	0.064	0.020	0.012*
dbh_cm x Above	−0.055	0.012	0.000***
dbh_cm x Below	0.004	0.018	0.819
scpdsi_jj x Above	−0.025	0.010	0.017*
scpdsi_jj x Below	−0.024	0.012	0.042*
AIC*c*	705.2		
R^2marg / R^2cond	0.096 / 0.154		
Model 'tree-level drought resilience'			
Best model: rs ~ dbh_cm x treatm + scpdsi_jj			
intercept	1.009	0.034	0.000***
dbh_cm	−0.094	0.009	0.000***
Above	0.009	0.033	0.791
Below	−0.025	0.040	0.537
scpdsi_jj	0.100	0.027	0.006**
dbh_cm x Above	−0.119	0.018	0.000***
dbh_cm x Below	0.019	0.026	0.479
AIC*c*	3553.3		
R^2marg / R^2cond	0.145 / 0.192		

had a positive effect on stand-level resistance.

Thinning generally reduces competition for resources by reducing tree population density (Bottero et al., 2017; Gleason et al., 2017); however, the *type* of thinning method applied may have more nuanced long-term effects on stand structure and drought response. Canopy competition remains relatively constant in stands thinned from below, whereas thinning from above changes canopy structure and thereby competition for resources. Selecting large diameter, dominant trees for removal reduces canopy competition, leaving the remaining smaller diameter trees in more favorable social positions to capitalize on light resources. Trees that have been very suppressed over time might not fully recover growth potential (McDowell et al., 2008). However, trees that were non-dominant, but occupied a better relative crown position (co-dominant or intermediate), may benefit from the removal of upper canopy competition. Therefore, in stands thinned from above, a higher proportion of dominant trees conferred an increased stand-level resistance to drought-induced growth declines.

5. Conclusion

Stands thinned from above exhibited increased resistance and resilience to drought-induced growth declines as a result of being populated by a larger proportion of smaller diameter trees (but not suppressed) in more favorable canopy positions to compete for light and water resources. While other studies have documented the benefits of managing stand density to mitigate drought vulnerability, this study highlights the importance of also considering the influence of periodic thinning entries on structural diversity. The effectiveness of managing for structural complexity should be tested in other stands of different age and compositional structure.

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Table 3
Estimates, standard error (SE), and significance for stand-level drought resistance and resilience models. Abbreviations: rt = resistance, rs = resilience, treatm = treatment (3 levels: Above, Below, reference Control), ratio_dom = proportion of dominant trees, scpdsi_jj = scPDSI (June-July), pl_ba_m2 = stand basal area (m^2), AIC*c* = second-order Akaike's information criterion, R^2marg = R-squared marginal (fixed effects), and R^2cond = R-squared conditional (fixed + random effects). Random effects for drought year, and sites. Signif. codes: '***' 0.001, '**' 0.01, '*' 0.05, '.' 0.1.

Model 'stand-level drought resistance'			
Best model: rt ~ ratio_dom x treatm + scpdsi_jj x treatm + pl_ba_m2 x treatm			
	estimate	**SE**	**Pr (> t)**
intercept	0.869	0.029	0.000***
ratio_dom	−0.029	0.003	0.000***
Above	−0.099	0.029	0.009**
Below	−0.084	0.029	0.020*
scpdsi_jj	0.066	0.021	0.015*
pl_ba_m2	−0.007	0.003	0.027*
ratio_dom x Above	0.049	0.004	0.000***
ratio_dom x Below	0.020	0.004	0.000***
scpdsi_jj x Above	−0.035	0.003	0.000***
scpdsi_jj x Below	−0.025	0.004	0.000***
pl_ba_m2 x Above	−0.109	0.010	0.000***
pl_ba_m2 x Below	−0.064	0.013	0.000***
AIC*c*	−8008.0		
R^2marg / R^2cond	0.254 / 0.598		
Model 'stand-level drought resilience'			
Best model: rs ~ ratio_dom x treatm + scpdsi_jj x treatm + pl_ba_m2 x treatm			
intercept	0.939	0.035	0.000***
ratio_dom	−0.054	0.004	0.000***
Above	−0.210	0.029	0.000***
Below	−0.131	0.028	0.001***
scpdsi_jj	0.101	0.031	0.011*
pl_ba_m2	−0.018	0.005	0.000***
ratio_dom x Above	0.088	0.005	0.000***
ratio_dom x Below	0.062	0.006	0.000***
scpdsi_jj x Above	−0.011	0.004	0.015*
scpdsi_jj x Below	−0.010	0.005	0.052
pl_ba_m2 x Above	−0.259	0.014	0.000***
pl_ba_m2 x Below	−0.103	0.018	0.000***
AIC*c*	−5411.8		
R^2marg / R^2cond	0.371 / 0.646		

References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., et al., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001.

Anderegg, W.R.L., Kane, J.M., Anderegg, L.D.L., 2012. Consequences of widespread tree mortality triggered by drought and temperature stress. Nat. Clim. Chang. 3, 30.

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Shevliakova, E., Williams, A.P., Wolf, A., Ziaco, E., Pacala, S., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science (80-.) 349, 528–532. https://doi.org/10.1126/science.aab1833.

Bartoń, K., 2018. Package "MuMIn" Title Multi-model Inference [WWW Document]. Available at. CRAN-R. www.cran.r-project.org/web/packages.

Bates, D.M., 2005. Fitting linear mixed models in R. Using the lme4 package. R News 5, 27–30. https://doi.org/10.1159/000323281.

Biondi, F., 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. Ecol. Appl. 9, 216–227. https://doi.org/10.1890/1051-0761(1999)009[0216:CTRCAR]2.0.CO;2.

Bonan, G., 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science (80-.) 320, 1444–1449. https://doi.org/10.1126/science.1155121.

Bottero, A., D'Amato, A.W., Palik, B.J., Bradford, J.B., Fraver, S., Battaglia, M.A., Asherin, L.A., 2017. Density-dependent vulnerability of forest ecosystems to drought. J. Appl. Ecol. 54, 1605–1614. https://doi.org/10.1111/1365-2664.12847.

Bradford, J.B., Bell, D.M., 2017. A window of opportunity for climate-change adaptation:

easing tree mortality by reducing forest basal area. Front. Ecol. Environ. 15, 11–17. https://doi.org/10.1002/fee.1445.
Bradford, J.B., Palik, B.J., 2009. A comparison of thinning methods in red pine: consequences for stand-level growth and tree diameter. Can. J. For. Res. 39, 489–496. https://doi.org/10.1139/X08-201.
Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124.
Curzon, M.T., D'Amato, A.W., Fraver, S., Palik, B.J., Bottero, A., Foster, J.R., Gleason, K.E., 2017. Harvesting influences functional identity and diversity over time in forests of the northeastern U.S.A. For. Ecol. Manage. 400, 93–99. https://doi.org/10.1016/j.foreco.2017.05.056.
D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. Ecol. Appl. 23, 1735–1742.
D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2011. Forest management for mitigation and adaptation to climate change: insights from long-term silviculture experiments. For. Ecol. Manage. 262, 803–816. https://doi.org/10.1016/j.foreco.2011.05.014.
Dai, A., 2012. Increasing drought under global warming in observations and models. Nat. Clim. Chang. 3, 52.
Di Luzio, M., Johnson, G.L., Daly, C., Eischeid, J.K., Arnold, J.G., 2008. Constructing retrospective gridded daily precipitation and temperature datasets for the conterminous United States. J. Appl. Meteorol. Climatol. https://doi.org/10.1175/2007JAMC1356.1.
Dixon, G.E., Keyser, C.E., 2008. Lake States (LS) Variant Overview - Forest Vegetation Simulator (revised January 2014). Fort Collins, CO USA. .
Franklin, J.F., Mitchell, R.J., Palik, B.J., 2007. Natural Disturbance and Stand Development Principles for Ecological Forestry. https://doi.org/10.2737/NRS-GTR-19.
Fraver, S., Palik, B.J., 2012. Stand and cohort structures of old-growth Pinus resinosa-dominated forests of northern Minnesota. USA. J. Veg. Sci. 23, 249–259. https://doi.org/10.1111/j.1654-1103.2011.01348.x.
Fulton, M.F., 1999. Patterns in height-diameter relationships for selected tree species and sites in eastern Texas. Can. J. For. Res. 29, 1445–1448.
Gleason, K.E., Bradford, J.B., Bottero, A., D'Amato, A.W., Fraver, S., Palik, B.J., Battaglia, M.A., Iverson, L., Kenefic, L., Kern, C.C., 2017. Competition amplifies drought stress in forests across broad climatic and compositional gradients. Ecosphere 8. https://doi.org/10.1002/ecs2.1849.
Hassan, R., Scholes, R., Ash, N., 2005. Ecosystems and human well-being: current state and trends. The Millennium Ecosystem Assessment Series 1 Ecosystems and human well-being, Washington, DC. https://doi.org/10.1007/BF02987493.
Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. https://doi.org/10.1016/j.ecoleng.2008.01.004.
Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. https://doi.org/10.1890/04-0922.
IPCC, 2018. Summary for Policymakers, Global Warming of 1.5°C. An IPCC Special Report on the Impacts of Global Warming of 1.5°C Above Pre-industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change. Geneva, Switzerland. .
IPCC, 2014. Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland.
Kerr, G., Haufe, J., 2011. Thinning practice: a silvicultural guide. Forestry Commission. https://doi.org/10.1111/j.1749-6632.2012.06474.x.
Kipfmueller, K.F., Elliott, G.P., Larson, E.R., Salzer, M.W., 2010. An assessment of the dendroclimatic potential of three conifer species in northern Minnesota. Tree-Ring Res. 66, 113–126. https://doi.org/10.3959/2009-12.1.
Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x.
Lumbres, R.I.C., Lee, Y.J., Seo, Y.O., Kim, S.H., Choi, J.K., Lee, W.K., 2011. Development and validation of nonlinear height-DBH models for major coniferous tree species in Korea. Forest Sci. Technol. 7, 117–125. https://doi.org/10.1080/21580103.2011.594610.
Magruder, M., Chhin, S., Palik, B., Bradford, J.B., 2013. Thinning increases climatic resilience of red pine. Can. J. For. Res. 43, 878–889. https://doi.org/10.1139/cjfr-2013-0088.
McDowell, N.G., Adams, H.D., Bailey, J.D., Hess, M., Kolb, T.E., 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. Ecol. Appl. 16, 1164–1182. https://doi.org/10.1890/1051-0761(2006)016[1164:HMOPPG]2.0.CO;2.
McDowell, N.G., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? New Phytol. 178, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x.
McDowell, N.G., Williams, A.P., Xu, C., Pockman, W.T., Dickman, L.T., Sevanto, S., Pangle, R., Limousin, J., Plaut, J., Mackay, D.S., Ogee, J., Domec, J.C., Allen, C.D., Fisher, R.A., Jiang, X., Muss, J.D., Breshears, D.D., Rauscher, S.A., Koven, C., 2016. Multi-scale predictions of massive conifer mortality due to chronic temperature rise. Nat. Clim. Chang. 6, 295–300. https://doi.org/10.1038/nclimate2873.
NRCS, 2015. Web Soil Survey [WWW Document]. Nat. Resour. Conserv. Serv. United States Dep. Agric. URL http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx.
Nyland, R.D., 2016. Silviculture: Concepts and Applications, third ed. Waveland Press.
Palmer, W.C., 1965. Meteorological Drought. Research Paper No. 45. US Dep. Commerhttps://doi.org/10.1074/jbc.M109.095992.
Phillips, N.G., Ryan, M.G., Bond, B.J., McDowell, N.G., Hinckley, T.M., Čermák, J., 2003. Reliance on stored water increases with tree size in three species in the Pacific Northwest. Tree Physiol. 23, 237–245.
Powers, M.D., Palik, B.J., Bradford, J.B., Fraver, S., Webster, C.R., 2010. Thinning method and intensity influence long-term mortality trends in a red pine forest. For. Ecol. Manage. https://doi.org/10.1016/j.foreco.2010.07.002.
R Core Team, 2018. R: a Language and Environment for Statistical Computing.
Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth. Bioscience 47, 235–242. https://doi.org/10.2307/1313077.
Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nat. Clim. Chang. https://doi.org/10.1038/nclimate3303.
Sharma, M., 2016. Comparing height-diameter relationships of boreal tree species grown in plantations and natural stands. For. Sci. 62, 70–77.
Speer, J.H., 2010. Fundamentals of Tree-ring Research. University of Arizona Presshttps://doi.org/10.1002/gea.20357.
Wells, N., Goddard, S., Hayes, M.J., 2004. A self-calibrating palmer drought severity index. J. Clim. https://doi.org/10.1175/1520-0442(2004)017<2335:ASPDSI>2.0.CO;2.
Xu, P., Zhou, T., Yi, C., Fang, W., Hendrey, G., Zhao, X., 2018. Forest drought resistance distinguished by canopy height. Environ. Res. Lett. 13, 075003. https://doi.org/10.1088/1748-9326/aacadd.
Young, B.D., D'Amato, A.W., Kern, C.C., Kastendick, D.N., Palik, B.J., 2017. Seven decades of change in forest structure and composition in Pinus resinosa forests in northern Minnesota, USA: comparing managed and unmanaged conditions. For. Ecol. Manage. 395, 92–103. https://doi.org/10.1016/j.foreco.2017.04.003.