

Thinning increases climatic resilience of red pine

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Abstract: Forest management techniques such as intermediate stand-tending practices (e.g., thinning) can promote climatic resiliency in forest stands by moderating tree competition. Residual trees gain increased access to environmental resources (i.e., soil moisture, light), which in turn has the potential to buffer trees from stressful climatic conditions. The influences of climate (temperature and precipitation) and forest management (thinning method and intensity) on the productivity of red pine (Pinus resinosa Ait.) in Michigan were examined to assess whether repeated thinning treatments were able to increase climatic resiliency (i.e., maintaining productivity and reduced sensitivity to climatic stress). The cumulative productivity of each thinning treatment was determined, and it was found that thinning from below to a residual basal area of 14 m²·ha⁻¹ produced the largest average tree size but also the second lowest overall biomass per acre. On the other hand, the uncut control and the thinning from above to a residual basal area of $28 \text{ m}^2 \cdot \text{ha}^{-1}$ produced the smallest average tree size but also the greatest overall biomass per acre. Dendrochronological methods were used to quantify sensitivity of annual radial growth to monthly and seasonal climatic factors for each thinning treatment type. Climatic sensitivity was influenced by thinning method (i.e., thinning from below decreased sensitivity to climatic stress more than thinning from above) and by thinning intensity (i.e., more intense thinning led to a lower climatic sensitivity). Overall, thinning from below to a residual basal area of 21 m²·ha⁻¹ represented a potentially beneficial compromise to maximize tree size, biomass per acre, and reduced sensitivity to climatic stress, and, thus, the highest level of climatic resilience.

Résumé : Les techniques d'aménagement forestier, telles que les pratiques d'éducation des peuplements au stade intermédiaire (p.ex. l'éclaircie), peuvent faciliter la résilience climatique des peuplements forestiers en atténuant la compétition entre les arbres. Les arbres résiduels ont un meilleur accès aux ressources environnementales (c.-à-d. l'eau du sol et la lumière), ce qui peut les protéger des stress climatiques. L'influence du climat (température et précipitation) et de l'aménagement forestier (méthode et intensité d'éclaircie) sur la productivité du pin rouge (Pinus resinosa Ait.) au Michigan a été étudiée pour évaluer si des traitements répétés d'éclaircie étaient en mesure d'augmenter la résilience climatique (c.-à-d. maintenir la productivité et réduire la sensibilité aux stress climatiques). À partir de la productivité cumulée qui a été déterminée pour chaque traitement d'éclaircie, nous avons trouvé que l'éclaircie par le bas laissant une surface terrière résiduelle de 14 m²·ha⁻¹ était associée à la plus forte taille moyenne des arbres, mais aussi à la deuxième plus faible biomasse totale à l'hectare. D'un autre côté, le témoin non coupé et l'éclaircie par le haut laissant une surface terrière résiduelle de 28 m²·ha⁻¹ étaient associés à la plus faible taille moyenne des arbres, mais aussi à la plus forte biomasse totale à l'hectare. Des méthodes dendrochronologiques ont été utilisées pour quantifier la sensibilité de la croissance radiale annuelle aux facteurs climatiques mensuels et saisonniers pour chaque type d'éclaircie. La sensibilité climatique était influencée par la méthode d'éclaircie (c.-à-d. que l'éclaircie par le bas diminuait davantage la sensibilité aux stress climatiques que l'éclaircie par le haut) et par l'intensité de l'éclaircie (c.-à-d. qu'une éclaircie plus intense menait à une moins grande sensibilité climatique). Généralement, l'éclaircie par le bas laissant une surface terrière résiduelle de 21 m²·ha⁻¹ représentait un compromis potentiellement avantageux pour maximiser la taille des arbres et la biomasse à l'hectare, et pour réduire la sensibilité aux stress climatiques et ainsi atteindre le plus haut degré de résilience climatique. [Traduit par la Rédaction]

Introduction

The instrumental climatic record has indicated that global average surface temperatures have increased by 0.74 °C from 1906 to 2005 (IPCC 2007). Projections of future climate change based on general circulation models and different emission scenarios of greenhouse gases indicate a further warming of 1.1-6.4 °C by the end of the 21st century (2090-2099) relative to 1980-1999 (IPCC 2007). While little change is expected in annual average precipitation, higher temperatures are expected to increase rates of evapotranspiration in plants. Future climate change (i.e., global warming and increased summer dryness) is expected to generally reduce forest productivity and increase rates of tree mortality in water-limited forest regions (Spittlehouse and Stewart 2003; Chmura et al. 2011). Current forest management techniques must adapt to maintain the productivity of forest resources under

future conditions. Modification of thinning practices may represent a proactive forest management method to maintain productivity as opposed to relying on reactive forest management to salvage lost productivity.

The effects of climate (particularly the aspects of temperature and precipitation) have been shown to have a significant effect on tree productivity (Kilgore and Telewski 2004; Pichler and Oberhuber 2007; Chhin et al. 2008; De Luis et al. 2009; Dombroskie et al. 2010; Miyamoto et al. 2010). Similar region-wide climatic conditions can illicit similar productivity responses among different species and locations. For example, both Chhin et al. (2008) and Miyamoto et al. (2010) reported the influence of summer temperature on drought stress and reduced tree productivity. Site-specific studies provide details of localized conditions and tree growth responses that can differ from the general region-wide patterns. Pichler and

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Oberhuber (2007) reported how a heat wave caused different growth responses of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* Karst.) in a single stand based on the trees' canopy positions. Similarly, De Luis et al. (2009) described how larger Aleppo pine (*Pinus halepensis* Mill.) and Stone pine (*Pinus pinea* L.) are less susceptible to temperature and precipitation stress compared with their smaller counterparts.

Regional climate forecasts for the state of Michigan and the Great Lakes Region indicate that average temperatures will rise 3-11 °C in the summer and 3-7 °C in the winter (Kling et al. 2003). Changes in future climate are predicted to shift the range of red pine (Pinus resinosa Ait.) 600-800 km northeast as well as to decrease the total area in which red pine is found (Flannigan and Woodward 1994). Some prior studies have examined the degree of sensitivity of red pine radial growth to climate factors in the Great Lakes region and in Michigan. In the Great Lakes region, Graumlich (1993) used a principle component analysis to determine that climate was the principle environmental factor effecting growth of trees. In one of the main studies conducted in Michigan, red pine at the Grayling Beal Plantation was reported to respond to April temperatures but not to precipitation at any point in the year (Kilgore and Telewski 2004). It was postulated that this was because of local conditions that caused low amounts of evaporative water loss and root development that granted access to more consistent stores of water (Kilgore and Telewski 2004).

Thinning is an effective forest management technique to reduce competition and promote growth in the remaining individuals (Nyland 2007). The number of trees removed is a factor of thinning intensity and is expressed in terms of residual basal area. Generally speaking, increased thinning intensity results in increased measures of tree-level productivity (Smith 2003; Gilmore et al. 2005; Bradford and Palik 2009; Powers et al. 2010). Once a residual basal area that provides sufficient growing space has been achieved, increased thinning intensity will not increase treelevel productivity (Nyland 2007). Furthermore, high intensity thinnings can decrease tree-level productivity under certain circumstances. For example, tree crowns are more susceptible to wind damage in a stand with a low residual basal area (Everham and Brokaw 1996). Additionally, with more trees removed from a stand there is a greater chance of logging damage to the remaining trees (Heitzman and Grell 2002). The most common thinning intensity for red pine is thinning to a residual basal area of 21-25 m²·ha⁻¹ after the stand reaches 32 m²·ha⁻¹ (Johnson 1995; Gilmore and Palik 2005).

Thinning is further defined in terms of thinning method, which determines the trees to be removed (Nyland 2007). Several thinning methods are based on a tree's crown classification. For example, thinning from above removes some of the dominant and codominant trees to promote growth of the best trees of the same classes, while the understory trees are left to provide even stand density. Thinning from below removes the intermediate and overtopped trees to promote growth of the trees in the dominant and codominant crown classifications (Buckman et al. 2006). Thinning method does not have the same universal impact on productivity as thinning intensity. In terms of red pine, there are conflicting results in which some report thinning method has no effect on productivity (Smith 2003; Gilmore et al. 2005), whereas others indicate it does affect productivity (Bradford and Palik 2009; Powers et al. 2010). For instance, Bradford and Palik (2009) reported that thinning from above generated greater growth rates than thinning from below. Such variation is most likely due to differences in region, age of the stand, and unit of productivity in question. For instance, Bradford and Palik (2009) worked with older trees (80-130 years) while Gilmore et al. (2005) and Smith (2003) studied stands that were much younger (35-50 years). The higher growth rate of younger trees potentially dominates any impact of thinning method.

Ecosystem resilience is defined as the capacity of an ecosystem to absorb some disturbance (i.e., drought), which in turn may induce some minor degree of ecosystem change but still maintain its essential structure and functions (Folke et al. 2004). In the context of forested ecosystems, forest management practices can moderate the degree of competition for environmental resources (i.e., soil moisture and light), which in turn has the potential to buffer residual trees from stressful climatic conditions (Millar et al. 2007; Chmura et al. 2011). This resource buffering effect in turn may result in the general decoupling of growth from the prevailing regional climate, although extreme resource limitations (e.g., high competition levels) may also lead to decoupling. From a growth and yield perspective, climatic resiliency is defined as the maintenance of an adequate degree of stand- and tree-level productivity in spite of poor climatic conditions, and a decoupling or reduced sensitivity between stand- and tree-level growth with climate conditions (Piutti and Cescatti 1997; Chmura et al. 2011). For example, Cescatti and Piutti (1998) found that an intermediate thinning intensity of European beech (Fagus sylvatica L.) resulted in resiliency to drought and temperature stress, while maintaining a valuable yield. Laurent et al. (2003) reported more intense thinnings increased the drought resiliency of Norway spruce but also increased susceptibility to other limiting factors that may include atmospheric pollution. With additional research, including more species and regions, it may be possible to predict growth patterns under future climate conditions and help maintain productivity (Spittlehouse and Stewart 2003; Dombroskie et al. 2010; Chmura et al. 2011).

Tree-ring analysis (dendrochronology) provides insight into the physiological ecology of tree species including the seasonal timing of growth-climate relationships (Fritts 1976; Vaganov et al. 2006). Therefore, dendrochronology studies can assist with the parameterization of climatically sensitive forest growth models. While tree-ring analyses represent an insightful approach to revealing past climatic drivers of tree growth, it has been an underutilized tool to examine whether forest management practices can modify sensitivity of tree growth to climatic stress (Cescatti and Piutti 1998; Laurent et al. 2003).

With this need in mind, the three objectives of this study of red pine sampled in Manistee National Forest, Michigan, were to (1) quantify the effects of thinning method (thinning from above and thinning from below), as well as thinning intensity (residual basal areas of 14, 21, and 28 m²·ha⁻¹) on red pine productivity; (2) examine which thinning treatment will result in reduced sensitivity of red pine to climatic stress using dendrochronological methods; and (3) determine which thinning treatment will result in higher levels of climatic resiliency that incorporates both growth and the frequency of significant relationships between growth and climatic variables.

Methods

Study site

The study was conducted on a forest research plantation in the Manistee National Forest, Michigan (44°17′45″N, 85°47′00″W), located west of Cadillac, Michigan (Fig. 1A). The site is commonly referred to as the Sooner Club plantation and is maintained by the USDA Forest Service (Fig. 1A). The stand was planted with 2–0 red pine planting stock in 1931 on approximately 14 ha (35 acres). Annual mean temperature averaged 6.13 °C from 1931 to 2010 in Cadillac, Michigan. In the same time period, the total annual precipitation averaged 819.0 mm and the total annual climatic moisture index averaged 231.6 mm (National Climatic Data Center 2012). Temperature and precipitation are greatest from April to October, which marks the length of the growing season (Fig. 2A). However, the increase in temperature from May to August also increases evapotranspiration, negating the influx of water into the system and causing a net loss of water available for growth.

Fig. 1. (A) The USDA research plantation sample site location (indicated by the white dot; situated near Wellston, Michigan) and the climate station (indicated by the black dot; Cadillac, Michigan) in Wexford County in the lower peninsula of Michigan. (B) Site map of the USDA research plantation. Shaded cells highlight treatment plots used in the study. Nonlabeled cells represent thinning treatments that were not considered in this study. Treatment plots covered 0.2 ha with a 0.04 ha measurement plot nested within each treatment plot.



This summer drought is demonstrated in Fig. 2B by a negative climatic moisture index (precipitation minus potential evapotranspiration) (Hogg 1997). The study site receives lake effect snow, which results in greater quantities of winter precipitation within approximately 80 km of the western shoreline of the Michigan's lower peninsula (Henne et al. 2007).

The plantation design includes 46 treatment plots in which a range of thinning treatments were applied (Fig. 1B). Each thinning treatment was replicated up to three times. The stand was initially thinned in 1960 to specifications of each thinning treatment of each plot, and had additional thinnings in 1965, 1986, and 2000 to maintain the integrity of each treatment as required. Soil at the site is a Montcalm–Graycalm complex, which is a well-drained loamy sand (Natural Resources Conservation Service 2012).

A total of 21 treatment plots were chosen to represent three replicates of the six different thinning treatments and one control treatment (Fig. 1B). The six thinning treatments consisted of a combination of two thinning methods and three thinning intensities. The two thinning methods represented in this study are thinning from above, in which the larger diameter trees are removed, and thinning from below, in which the smaller diameter trees are removed. The three thinning intensities considered in this study represent heavy, moderate, and light thinnings, with residual basal areas of 14, 21, and 28 m²·ha⁻¹, respectively. A control treatment that was never thinned was also included in the study and had a current average stand basal area of 47 m²·ha⁻¹. Each thinning treatment is denoted by a combination of thinning method and intensity parameters, e.g., Above 14 (AB14), Above 21 (AB21), Above 28 (AB28), Below 14 (BL14), Below 21 (BL21), and Below 28 (BL28), while the control plot is referred to as "Uncut".

Field sampling

In June of 2011, for each of the 21 selected treatment plots that covered 0.2 ha, measurements and samples were collected inside a single 0.04 ha measurement plot nested within each treatment plot. Field sampling was conducted in the measurement plots to avoid growth variation caused by edge effects. Each measurement plot was divided into four equal quadrants and the tree closest to the center of each quadrant was selected for sampling. The nearest neighbor of the center tree in each quadrant was also selected for sampling, totaling eight trees per measurement plot. In measurement plots with fewer than eight trees, all trees were sampled. For each of the selected trees, total height, height to live crown, diameter at breast height (DBH, 1.37 m), and bark thickness at breast height were measured. In addition, two cores were collected from each tree with an increment borer at breast height (1.37 m). Cores were taken from the north and south face of each tree. Additionally, DBH was measured for all trees in each measurement plot.

Sample processing, cross dating and tree-ring measurement

Tree cores were glued onto grooved wood strips to act as a stable base (Stokes and Smiley 1996). Samples were then sanded with progressively finer sandpaper (up to 600 grit) to achieve a polished surface in which the rings were clearly visible. Sanded cores were then scanned into a computer at an optical resolution of 1200 dpi.

Cores were cross dated with the list method to accurately assign a calendar date to each tree ring (Yamaguchi 1991). In addition to relative width of rings, characteristic ring structures such as missing rings, frost rings, and latewood width were also used to ensure maximum accuracy of the cross dating. Ring widths were measured using the programs CooRecorder and CDendro (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). A stage micrometer (Velmex, Bloomfield, New York) was used as a supplemental tool to measure sections of cores with very narrow rings that were unclear in the scanned image. Additional statistical quality control was provided through the use of the program COFECHA (Holmes 1983, 1994). COFECHA identifies samples that should be checked for cross-dating errors based on a poor correlation between individual ring-width series and an average treatment chronology.





Data analysis

Biomass calculations

Allometric equations were used to calculate tree biomass as a function of DBH. Total aboveground tree biomass (eq. (1)) was determined using the following equation (Jenkins et al. 2003):

(1) $T_{\rm bm} = \exp(-2.5356 + 2.4349 \ln \text{DBH})$

where $T_{\rm bm}$ is the total above ground biomass.

A tree component equation was used to calculate the ratio of stem biomass to total aboveground biomass (eq. (2)) (Jenkins et al. 2003)

(2) Ratio =
$$\exp[-0.3737 + (-1.8055/DBH)]$$

where Ratio is the ratio of stem biomass to $T_{\rm bm}$. The ratio was multiplied by the $T_{\rm bm}$ to calculate the stem biomass. Total and stem biomass were summarized as an average of the eight trees sampled in each measurement plot. Separate calculations summarized the total and stem biomass on a per hectare basis based on the DBH of all trees in a measurement plot as of June 2011.

Red pine productivity and growth form

Slenderness coefficient is a dimensionless value based on the ratio of the diameter and height of a tree and is calculated as the height divided by the DBH in the same units (m). Greater values indicate a taller and narrower tree, and trees with values over a threshold of 80 are prone to wind-induced breakage (Watt et al. 2008). Crown ratio represents the ratio of the crown length to the total height of a tree. All collected measures of tree-level productivity (DBH, total height, basal area, total biomass, and stem biomass) and growth form (crown ratio and slenderness coefficient) were subjugated to an one-factor analysis of variance (ANOVA) to identify significant thinning treatment effects using the program SYSTAT (Version 10.2). Furthermore, stand-level productivity (i.e., per hectare basis) was also compared between the treatments using a one-way ANOVA. Fisher's LSD was used to examine pairwise comparisons between thinning treatments (SYSTAT 2002). Any comparison with a P value that was less than 0.05 was considered significant. A two-factor (thinning method and thinning intensity) ANOVA was conducted to verify whether there was a method × intensity interaction (SYSTAT 2002).

Dendrochronological analysis

Ring widths were detrended to generate a radial growth index through the statistical program ARSTAN (Cook 1985; Holmes 1994). A radial growth index is a dimensionless expression of ring width and was calculated by dividing the observed ring width by the ring widths predicted from a 40-year cubic smoothing spline. Radial growth index values that are greater than one represent above average growth and values less than one represent below average growth. Ring widths were detrended to standardize the raw ring-width measurements through the removal of size- and age-related effects on ring width. A 40-year cubic spline preserves 99% of the variation in each ring-width series at a wavelength of about 13 years. Consequently, common trends (1-13 years) in radial growth between trees owing to stand-wide effects like climate and stand management practices are still preserved (Biondi, 1999). The radial growth index of each tree and year was averaged to create a standard chronology for each thinning treatment, which could then be compared with historical climate data. ARSTAN calculated an expressed population signal (EPS) to exceed 0.85 for all thinning treatments from 1948 to 2010; therefore, all growthclimate analysis is based on that timeframe (Briffa and Jones, 1990). The EPS quantifies how well a chronology based on a finite number of trees represents a hypothetically perfect chronology (Wigley et al. 1984).

Historical climate data was obtained from by the National Climatic Data Center at the Cadillac Municipal Airport (Station ID 201176) (44°16'50"N, 85°25'02"W) and Cadillac station (Station ID 201176) (44°15'55"N, 85°23'47"W) in Cadillac, Michigan, which is 31 km east of the study site. Both the weather station location and the study site had the same flat topography. Data collected included monthly averages of minimum, mean, and maximum daily temperature, and total monthly precipitation. Minimum and maximum monthly temperature and precipitation measurements were further combined into a climatic moisture index (CMI) representing estimated net water availability to trees. CMI is calculated as total precipitation minus water lost due to evapotranspiration, which is a factor of increasing temperature (Hogg 1997). Missing climate data points were extrapolated based on data from nearby climate stations at the Tippy Dam Pond (Station ID 208772) (44°15'31"N, 85°56'21"W) in Wellston, Michigan, and the Manistee 3SE station (Station ID 205065) (44°12'40"N, 86°17'37"W) in Manistee, Michigan. Additionally, monthly climate data was seasonalized into 3-month periods (averages of temperature and sums of precipitation and CMI) to represent longer term climatic trends.

The standard chronology and each individual set of climate data were run though the program DendroClim (Biondi and Waikul 2004) to identify significant monthly correlations between each climatic variable and standardized radial growth index from April of the previous year to October of the current year. Analysis

		, 0	Tree	Tree basal	Aboveground tree	Stem	Crown	
Treatment	п	DBH (cm)	height (m)	area (m ²)	biomass (kg)	biomass (kg)	ratio	Slenderness
Uncut	24	24.0 (1.7)b	23.6 (1.3)a	0.0473 (0.0070)b	194.3 (35.2)b	124.5 (23.3)b	0.33 (0.10)ab	101.9 (10.3)a
Above 14	24	29.9 (4.6)ab	22.5 (0.5)a	0.0720 (0.0204)ab	324.0 (109.8)ab	210.4 (72.8)ab	0.40 (0.03)ab	76.6 (12.8)ab
Above 21	24	25.9 (1.9)b	21.3 (1.6)a	0.0537 (0.0068)b	226.8 (33.0)b	145.9 (21.7)b	0.48 (0.01)a	83.7 (7.6)ab
Above 28	24	23.9 (2.1)b	21.9 (2.1)a	0.0463 (0.0070)b	190.4 (35.4)b	121.9 (23.3)b	0.39 (0.05)ab	91.9 (4.4)a
Below 14	21	34.6 (1.2)a	23.9 (0.7)a	0.0943 (0.0067)a	446.5 (37.2)a	291.7 (24.8)a	0.44 (0.03)a	68.4 (4.4)b
Below 21	24	34.3 (3.0)ab	23.9 (1.4)a	0.0932 (0.0148)ab	439.8 (84.2)ab	287.3 (56.2)ab	0.49 (0.02)a	69.2 (1.5)b
Below 28	24	27.7 (1.2)b	24.3 (0.4)a	0.0607 (0.0055)b	260.4 (27.4)b	168.0 (18.1)b	0.30 (0.02)b	86.3 (1.0)a

Table 1. Average (standard deviation) tree-level productivity (diameter at breast height (DBH), tree height, basal area, total aboveground biomass, and total stem biomass) and growth form (crown ratio and slenderness) of red pine in Michigan managed under seven thinning treatments.

Note: Thinning methods: Above, thinning from above; Below, thinning from below. Thinning intensities: 14, 21, and 28 m²·ha⁻¹ of residual basal area for each thinning treatment. Uncut, the unthinned control treatment. *n* is the the number of trees sampled per treatment type. Treatments with different letters are significantly different (P < 0.05).

begins in April of the previous year as growing conditions of the previous year can affect the current year's growth by how much carbon they store and how many needle buds are formed (Garrett and Zahner 1973; Pallardy 2007). Significant correlations were determined through bootstrapped samples, which are drawn at random with replacement from each year in the data set (Biondi and Waikul 2004). For every data set, Pearson's correlation coefficients were calculated between standardized radial growth index and each of the monthly and seasonal climate variables. A total of 1000 bootstrapped samples were calculated to compute correlation coefficients. Statistical significance was determined from the correlation coefficients from the original data set that fall outside of the 95% range of the 1000 bootstrapped data sets (Biondi and Waikul 2004).

Principal component analysis (PCA) was conducted on a covariance matrix (SYSTAT version 10.2, procedure FACTOR) of the radial growth index chronologies for each of the uncut and thinning treatments over the common period shared by all chronologies (1948–2010).

Climate resilience index (CRI)

A climate resilience index (CRI) was determined for each thinning treatment by combining measures of productivity and sensitivity to climate using the following formula (Magruder et al. 2012):

$$(3) \qquad CRI = SLP + TLP - SMC - SSC$$

where SLP is the stand-level productivity, which is a relative index variable based on stand-level $T_{\rm bm}$; TLP is the tree-level productivity, which is a relative index variable based on tree-level $T_{\rm bm}$; SMC is the sensitivity to monthly climate, which is a relative index variable based on the total number of significant correlations to temperature, precipitation, and moisture index; and SSC is the sensitivity to seasonal climate, which is a relative index variable based on the total number of significant correlations to temperature, precipitation, and moisture index; and SSC is the sensitivity to seasonal climate, which is a relative index variable based on the total number of significant correlations to temperature, precipitation, and moisture index. SLP, TLP, SMC, and SSC were calculated by dividing their respective raw values for each treatment type by the thinning treatment with the smallest value. A relative index greater than 1 indicates a greater relative value for that variable, i.e., higher productivity or higher sensitivity to climatic stress. Larger values of CRI indicate greater climatic resiliency.

Results

Tree- and stand-level productivity

For both thinning methods, tree-level productivity (DBH, basal area, tree aboveground biomass, and stem biomass) increased as thinning intensity increased; however, the difference between the lowest and highest thinning intensities was significantly different only for thinning from below (Table 1). Given the same thinning intensity, thinning from below did not differ

Table 2. Average (standard deviation) stand-level productivity (basal
area per hectare, aboveground biomass per hectare, and stem biomass
per hectare) of red pine in Michigan managed under seven thinning
treatments.

Treatment	Stand basal area (m²·ha ⁻¹)	Total aboveground biomass (t·ha ⁻¹)	Total stem biomass (t·ha ⁻¹)
Uncut	47.08 (11.97)abcd	187.0 (40.5)abc	119.1 (25.0)abc
Above 14	17.41 (0.33)d	77.6 (6.2)c	50.3 (4.5)c
Above 21	24.71 (1.33)c	104.7 (3.5)b	67.4 (2.1)b
Above 28	34.66 (0.41)a	141.2 (4.8)a	90.3 (3.7)a
Below 14	17.56 (2.49)cd	83.4 (10.6)bc	54.5 (6.9)bc
Below 21	25.69 (1.62)bc	121.5 (5.2)a	79.4 (3.2)ab
Below 28	31.61 (1.37)ab	138.0 (4.0)a	89.5 (2.4)a

Note: Thinning methods include: Above, thinning from above; Below, thinning from below. Thinning intensities: 14, 21, and 28 m²·ha⁻¹ of residual basal area for each thinning treatment. Uncut, the unthinned control treatment. Treatments with different letters are significantly different (P < 0.05).

significantly from thinning from above for all the measures of productivity or growth form. For thinning from below, the slenderness coefficient was significantly greater under the lowintensity thinning regime compared with the other thinning intensities.

According to stand-level productivity measures on a per hectare basis, there was no significant difference in stand basal area and total stem biomass between the two thinning methods given the same thinning intensity (Table 2). For both thinning methods, the low-intensity thinnings generated a significantly higher standlevel basal area, total aboveground biomass, and total stem biomass per hectare compared with the high-intensity thinnings. The uncut plots had the greatest variability (i.e., standard deviation) of basal area and biomass per hectare (Table 2).

Two-factor ANOVA indicated that there was only significant interaction between thinning method and thinning intensity for tree crown ratio (P = 0.006) and stand-level total aboveground biomass (P = 0.049) (Table 3). Crown ratio was significantly lower for the lowest thinning intensity compared with the other thinning intensities but only for thinning from below. Total aboveground biomass was significantly greater for thinning from below than thinning from above but only at the moderate thinning intensity. For productivity variables that showed no significant interaction between thinning method and thinning intensity, thinning method resulted in significant differences in DBH, height, tree above-ground biomass, stem biomass, slenderness, and total stem biomass; and thinning intensity resulted in significant differences in DBH, tree basal area, tree aboveground biomass, stem biomass, slenderness, stand basal area, and total stem biomass.

Tree-ring chronologies

Basic patterns of relative ring width can be seen across all seven thinning treatments (Fig. 3). For the uncut control, lower than

Table 3.	Two-factor	(thinning metho	od and thinni	ng intensity)	analysis c	of variance	(ANOVA)	results for t	ree- and	stand-level	produc
tivity var	riables.										

	Tree-lev	el producti	vity	Stand-le	Stand-level productivity					
Source	DBH	Height	Tree basal area	Tree aboveground biomass	Stem biomass	Crown ratio	Slenderness	Stand basal area	Total aboveground biomass	Total stem biomass
Method										
df	1	1	1	1	1	1	1	1	1	1
SS	143.67	20.29	0.0029	82204	36151	0.00	404.20	1.86	187.8	114.9
F	21.26	12.43	21.12	19.84	19.79	1.35	9.22	0.88	4.91	6.81
Р	< 0.001	0.004	< 0.001	< 0.001	< 0.001	0.268	0.010	0.367	0.047	0.023
Intensit	y									
df	2	2	2	2	2	2	2	2	2	2
SS	129.23	1.25	0.0028	79739	35132	0.06	900.80	734.97	10513.7	4202.9
F	9.56	0.38	9.96	9.62	9.62	31.44	10.28	173.21	137.52	124.56
Р	0.003	0.689	0.003	0.003	0.003	< 0.001	0.003	< 0.001	< 0.001	< 0.001
Method	× Intensi	ty								
df	2	2	2	2	2	2	2	2	2	2
SS	18.23	1.22	0.0005	15700	6974	0.01	63.26	13.63	299.7	128.8
F	1.35	0.37	1.82	1.89	1.91	8.00	0.72	3.21	3.92	3.82
Р	0.296	0.695	0.203	0.193	0.191	0.006	0.506	0.076	0.049	0.052
Model										
df	5	5	5	5	5	5	5	5	5	5
SS	291.13	22.77	0.0062	177643	78257	0.07	1368.26	750.46	11001.2	4446.6
F	8.61	2.79	8.91	8.58	8.57	16.04	6.24	70.74	57.56	52.71
Р	0.001	0.067	< 0.001	0.001	0.001	< 0.001	0.004	< 0.001	<0.001	< 0.001
Error										
df	12	12	12	12	12	12	12	12	12	12
SS	81.11	19.60	0.0017	49717	21922	0.01	525.93	25.46	458.7	202.4
Total										
df	17	17	17	17	17	17	17	17	17	17
SS	372.23	42.37	0.0078	227360	100179	0.1	1894.2	775.92	11459.9	4649.0

Note: Thinning methods: Above, thinning from above; Below, thinning from below. Thinning intensities: 14, 21, and 28 m²·ha⁻¹ of residual basal area for each thinning treatment. DBH, diameter at breast height; df, degrees of freedom; SS, sum of squares; and *F*, *f* ratio.

average ring widths were observed in the early to mid-1960s, 1977, and the late 1980s, while ring widths were greater than average in the early 1970s and early 1980s (Fig. 3A). In the mid-1960s, decreasing thinning intensity resulted in greater reduction in radial growth, whereas in the 1990s, increasing thinning intensity resulted in reduced growth (Figs. 3B and 3C).

PCA of the uncut treatment and the six thinning treatments indicated that only the percentage of the total variance explained by the first principal component (PC1) (65.4%) was greater than that expected under the broken stick null model (37.0%); consequently, this indicates that PC1 is the only meaningful principal component to interpret (Legendre and Legendre 1998). The lowest chronology loading onto PC1 was thinning from below to a moderate thinning intensity (Below 21) followed by thinning from below to a moderate (Above 21) thinning intensity had the highest chronology loading onto PC1.

Climatic sensitivity

Sensitivity to monthly variables

All significant correlations between red pine radial growth and monthly temperature were negative in all treatments (Fig. 5A). Months of significant correlations were primarily in late spring (April) and early (May) and mid-summer (July) of the previous year and early (May) and later summer (September) of the current year. High intensity thinnings of both thinning methods (Above 14, Below 14) were correlated with temperature in July of the previous year.

Radial growth of red pine trees in unthinned forests showed no sensitivity to monthly total precipitation (Fig. 5B). The next treatment type that showed the lowest number of correlations with precipitation was the thinning from below at a moderate thinning intensity (Below 21). Radial growth was positively correlated with winter (December) and summer (June) precipitation of the current year for high intensity thinnings of both thinning methods (Above 14, Below 14; Fig. 5). Low-and moderate-intensity thinnings (Above 21, Above 28) were negatively correlated with precipitation in September of both the previous and current year.

Red pine trees in the thinning from below treatment at moderate thinning intensity (Below 21) showed no sensitivity to CMI (Fig. 5C). Growth responses to CMI closely resemble those of the precipitation correlations including the positive relationships in winter (December) and summer (June) of the current year for the high intensity thinnings of both thinning methods (Above 14, Below 14).

Sensitivity to seasonal variables

Similar growth–climate relationships are present for the seasonal temperature correlations compared with the growth responses to monthly climate variables (Fig. 6A). Red pine in moderate-and low-intensity thinnings of both thinning methods (Above 21, Above 28, Below 21, Below 28) and the unthinned control (Uncut) were all correlated with temperature in the April– May–June period of the previous year. Every thinning treatment except for the moderate-intensity thinnings thinned from below (Above 14, Above 21, Above 28, Below 14, Below 28, Uncut) were correlated with temperature in the May–June–July period of the previous year. Low-intensity thinnings of both thinning methods and the unthinned control (Above 28, Below 28, Uncut) were negatively correlated with temperature in the April–May–June and the May–June–July period of the current year.

Seasonal precipitation correlations reveal that high-intensity thinnings thinned from above (Above 14) were positively correlated with precipitation in two winter seasonal periods **Fig. 3.** Detrended ring-width chronologies of red pine grown in Wellston, Michigan. AB represents thinning from above; BL represents thinning from below; and 14, 21, and 28 represent the residual basal area (m²·ha⁻¹) of each thinning treatment.



(November–December–January and December–January–February; Fig. 6B). Moderate-intensity thinnings of both thinning methods (Above 21, Below 21) and low-intensity thinnings thinned from below (Below 28) were positively correlated to precipitation in the May–June–July period of the current year. The unthinned control (Uncut) and two other thinning treatments (i.e., Above 28 and Below 14) showed no significant correlation to monthly or seasonal precipitation.

Seasonal CMI correlations with growth were similar to growth responses to precipitation for the unthinned plots and all of the thinning from above treatments (Above 14, Above 21, Above 28; Fig. 6C). High-intensity thinnings done from below (Below 14) were correlated with CMI in the November–December–January period. Red pine trees in the thinning from below treatment at moderate thinning intensity (Below 21) showed no sensitivity to seasonal CMI.

Climatic sensitivity summary

An overall summary of growth sensitivity to monthly and seasonal climatic variables is provided in Table 4. Thinning from above at either a high (Above 14) or moderate (Above 21) thinning intensity had the highest number of significant correlation coefficients with monthly climate variables, whereas the unthinned and thinning from below to a moderate thinning intensity (Below 21) has the lowest number of significant correlation coefficients. Thinning from below to a low thinning intensity (Below 28) had the highest number of correlations with seasonal climate variables, whereas thinning from below to high (Below 14) **Fig. 4.** Principal component analysis (PCA) of the radial growth chronologies of the uncut and thinning treatments of red pine: (A) percentage of the observed total variance explained by each of the first four principal components (PC1–PC4) compared with the expected values from the broken stick null model and (B) loadings of each of the radial growth chronologies onto PC1. AB represents thinning from above; BL represents thinning from below; and 14, 21, and 28 represent the residual basal area (m²·ha⁻¹) of each thinning treatment.



or moderate (Below 21) had the fewest number of significant correlation coefficients.

Climatic resiliency

The CRI was greatest in the thinning from below to a moderate thinning intensity (Below 21) followed by thinning from below to a high thinning intensity (Below 14) (Table 5). Thinning from above to a high (Above 14) or moderate (Above 21) thinning intensity had the lowest CRI values.

Discussion

Red pine productivity

Increased thinning intensity in the thinning from below treatments significantly led to increased tree-level productivity (i.e., DBH, basal area, and biomass). Less competition allows additional resource allocation for growth and results in greater tree-level productivity (increased DBH, basal area, biomass, increased crown size, and decreased slenderness) (Nyland 2007). The effect of greater thinning intensities resulting in greater tree-level productivity is a common theme in many managed red pine forests in the Great Lakes region (Bradford and Palik 2009; D'Amato et al. 2010; Powers et al. 2010). Increasing thinning intensity has also seen success in reinvigorating growth in older red pine stands (>90 years) (Bradford and Palik 2009; D'Amato et al. 2010). However, extremely high thinning intensities (7 m²·ha⁻¹) can be detrimental to tree-level productivity as the residual trees are susceptible to damage from the thinning process as well as windthrow (Bradford and Palik 2009; Powers et al. 2010).

No one thinning treatment is able to maximize all values of tree- and stand-level productivity, implying trade-offs among measures of productivity (Zeide 2001; D'Amato et al. 2011; Bradford and D'Amato 2012). In this study, stand-level productivity was expressed only with respect to the final residual basal area and biomass at the time of plot sampling in 2011. Thinning captures the potential mortality of trees (Nyland 2007). If the basal area and biomass of trees removed in past thinnings are included along with that of the residual trees (i.e., gross yield), the difference in stand-level productivity between the thinning methods and intensities could be smaller. It was found in this study that Below 14 and Below 21 had the largest average tree size in terms of height, diameter, basal area, and biomass. Not only did increasing the thinning intensity beyond Below 21 to Below 14 not result in an appreciable increase in tree-level productivity, but it decreased stand-level basal area and biomass. Therefore, the Below 21 treatment represents a potentially desirable thinning treatment that compromises high tree-level productivity while maintaining average stand-level productivity. Similar findings by D'Amato et al. (2010) indicate an above average basal area and volume per hectare in a plot that was thinned to 23.0 m²·ha⁻¹ compared with alternative thinning intensities that range from 13.8 to 32.1 m²·ha⁻¹. Additionally, Bradford and Palik (2009) reported that thinning to residual basal areas of 14 and 21 m²·ha⁻¹ generated the two largest quadratic mean diameters compared with higher and lower intensity thinnings.

Growth-climate relationships

The significant positive correlations between radial growth and monthly precipitation in June and July of the year of tree-ring formation represent drought stress reducing growth (Mäkinen et al. 2002; Martín-Benito et al. 2008; Pallardy 2007). The same pattern and reasoning applies for the correlation between radial growth and CMI. Seasonal correlations between radial growth and both precipitation and CMI indicate that summer drought stress is a persistent climatic variable. Red pine has been reported to be affected by summer drought (St. George et al. 2008; Kipfmueller et al. 2010). In contrast, Kilgore and Telewski (2004) found no significant correlation with precipitation at any point in the year. It is assumed that in Kilgore and Telewski's (2004) study that sufficient water storage capacity in the soil at their study site buffered the trees from drought and allowed them to grow independently from precipitation events (Kipfmueller et al. 2010).

In April of the previous year, the significant positive correlations between radial growth and both precipitation and CMI signify the reliance on water availability in early spring at the start of the growing season. This correlation could indicate a reliance on water availability to build up carbohydrate reserves that can to be used to drive growth in the following year (Garrett and Zahner 1973; Pallardy 2007).

Negative monthly temperature correlations with radial growth in both the previous and current year are likely a factor of increasing temperature causing an increase in the tree's respiration rate, which warrants further studies. Excessive respiration can consume carbon stores that had the potential to be used to increase productivity (Mäkinen et al. 2002; Pallardy 2007; Adams et al. 2009). The influence of temperature on growth is persistent across a number of consecutive months as these same patterns were observed in the seasonal temperature correlation. The negative association of growth and summer temperature is also likely due to the effect of increasing temperature on increasing rates of evapotranspiration, which was also reflected in the response of growth to summer CMI. Other studies have also shown that red pine growth is negatively correlated with summer temperature (St. George et al. 2008; Kipfmueller et al. 2010). This commonality indicates that summer temperature uniformly affects red pine across a wide area. Temperature at other times of the year has been reported to have a less uniform effect on tree growth within

Fig. 5. Significant correlation coefficients between radial growth of red pine with monthly climate variables: (A) mean temperature, (B) total precipitation, and (*C*) climatic moisture index. Analysis began in April of the previous year until October of the current year and over the period of 1948–2010. Significant positive (denoted by grey boxes) and negative (denoted by black boxes) correlation coefficients are outside the 95% range of coefficients derived from 1000 bootstrapped iterations. AB represents thinning from above; BL represents thinning from below; and 14, 21, and 28 represent the residual basal area (m²·ha⁻¹) of each thinning treatment.



the Great Lakes region. Graumlich (1993) and Kilgore and Telewski (2004) reported a positive correlation between red pine growth and temperature in April of the current year, which was attributed to increased growth elicited by warming temperatures that promoted an early start to the growing season. Continental climatic conditions prevail in Minnesota (Graumlich 1993) and central Michigan (Kilgore and Telewski 2004), resulting in lower winter temperatures that may delay the start of the growing season (Scott and Huff 1996). Conversely, the results of the current study indicate no correlation between radial growth and temperature in April of the current year. It is theorized that this lack of correlation is the result of the proximity of the Great Lakes moderating winter temperature to the point that temperature in April is no longer a limiting growth factor (Scott and Huff 1996).

Radial growth of red pine was positively correlated with monthly precipitation and CMI in December for the high thinning intensity plots. A potential ecophysiological-based explanation for this is that more snow is able to reach the ground of the high thinning intensity plots, insulating the soil by a few extra degrees (Brown and DeGaetano 2011). Greater soil temperature leads to earlier growth initiation in the spring and reduces the incidences of xylem cavitations in frozen tissue (Jyske et al. 2012). Furthermore, greater snow pack in the winter could drive increased soil moisture in the spring. Growth responses to seasonal precipitation and CMI suggest winter snow insulation as a persistent climatic variable.

Density management and climatic sensitivity and resiliency

Little to no correlation between radial growth and both precipitation and moisture index of the uncut control and low thinning intensity plots is likely due to high levels of competition and not an inherent low sensitivity of red pine to precipitation and CMI. Because of the high density and competition in these plots, competition for light is likely the most limiting factor to productivity instead of water availability (Pallardy 2007; Castagneri et al. 2012). Nevertheless, competition for water and soil nutrients is also **Fig. 6.** Significant correlation coefficients between radial growth of red pine with seasonal (3-month periods) climate variables: (A) mean temperature, (B) total precipitation, and (C) climatic moisture index. All possible 3-month periods were considered that spanned April of the previous year until October of the current year and over the period of 1948–2010. Significant positive (denoted by grey boxes) and negative (denoted by black boxes) correlation coefficients are outside the 95% range of coefficients derived from 1000 bootstrapped iterations. AB represents thinning from above; BL represents thinning from below; and 14, 21, and 28 represent the residual basal area (m²-ha⁻¹) of each thinning treatment.



Table 4. Counts of significant bootstrapped correlation coefficients for monthly and seasonal periods between climatic variables (temperature, precipitation, and climatic moisture index (CMI)) and different thinning treatments.

Treatment	Monthly temp.	Monthly precip.	Monthly CMI	Monthly total	Seasonal temp.	Seasonal precip.	Seasonal CMI	Seasonal total
Uncut	2	0	1	3	4	0	0	4
Above 14	2	3	3	8	1	2	2	5
Above 21	3	2	3	8	3	1	1	5
Above 28	3	2	0	5	5	0	0	5
Below 14	1	2	3	6	1	0	1	2
Below 21	2	1	0	3	1	1	0	2
Below 28	2	2	2	6	4	1	2	7

Note: Fewer counts indicate climatic resiliency or high competition in high-density stands. Thinning methods: Above, thinning from above; Below, thinning from below. Thinning intensities: 14, 21, and 28 m²·ha⁻¹ of residual basal area for each thinning treatment. Uncut, the unthinned control treatment. Treatments with different letters are significantly different (P < 0.05).

Table 5. Climate resilience index (CRI) derived from a combination of relative indexes of productivity (stand-level productivity (SLP) and tree-level productivity (TLP)) and sensitivity to climatic stress (sensitivity to monthly climate (SMC) and sensitivity to seasonal climate (SSC)) of red pine in Michigan managed under seven thinning treatments.

Treatment	SLP	TLP	SMC	SSC	CRI
Uncut	2.37	1.02	1.00	2.00	0.39
Above 14	1.00	1.73	2.67	2.50	-2.44
Above 21	1.34	1.20	2.67	2.50	-2.63
Above 28	1.80	1.00	1.67	2.50	-1.37
Below 14	1.08	2.39	2.00	1.00	0.48
Below 21	1.58	2.36	1.00	1.00	1.94
Below 28	1.78	1.38	2.00	3.50	-2.34

Note: Thinning methods: Above, thinning from above; Below, thinning from below. Thinning intensities: 14, 21, and 28 m²·ha⁻¹ of residual basal area for each thinning treatment. Uncut, the unthinned control treatment. *n* is the the number of trees sampled per treatment type. SLP, TLP, SMC, and SSC are relative index variables calculated by dividing raw values for each treatment type by thinning treatment with the smallest value. A relative index greater than 1 indicates greater relative value for that variable. CRI = SLP + TLP – SMC – SSC.

another plausible mechanism for diminished sensitivity to climate in high-density stands. Significant relationships with precipitation are seen in higher intensity thinned plots in which competition was reduced enough for light to no longer be the most limiting growth factor (Above 14, Above 21, Below 14, and Below 21). Of these treatments, Below 21 exhibited the lowest sensitivity to monthly precipitation and moisture index.

Climate-growth relationships for a variety of species and regions have been well-researched (Kilgore and Telewski 2004; Pichler and Oberhuber 2007; Chhin et al. 2008; De Luis et al. 2009; Miyamoto et al. 2010; Mérian and Lebourgeois 2011). Such studies are mostly based on natural stands and can indirectly address climatic resiliency. Models have been used to predict climatic resiliency with the general consensus that it is possible for forest management to mediate changes in growth caused by climate change (Jacobsen and Thorsen 2003; Yousefpour et al. 2012). To directly approach quantifying climatic resiliency generated by forest management in terms of productivity, a retrospective analysis of forest research sites and silvicultural experiments through dendrochronological methods is generally used. However, such studies are rare, but a few examples are as follows. Laurent et al. (2003) utilized dendrochronological methods to examine the relationship between thinning intensity and drought resilience of Norway spruce. It was found that increased thinning intensity resulted in greater resilience to drought stress. Cescatti and Piutti (1998) also employed a dendrochronological approach to examine various thinning treatments of European beech (Fagus sylvatica L.) and found that an intermediate thinning intensity resulted in resiliency to drought and temperature stress while maintaining a valuable yield. The results of these studies are corroborated by the current study, which found that thinning from below to a moderate thinning intensity resulted in an increased resilience to temperature, precipitation variation, and moisture index variation while maintaining high tree-level productivity and moderate stand-level productivity. Furthermore, PCA indicated that thinning from below to a moderate thinning intensity showed the lowest response to the first principal component axis, which can be interpreted as reduced sensitivity to climatic stress.

Conclusion

A dendrochronological approach was applied to a long-term silvicultural experiment, which provided a rare opportunity to screen different methods and intensities of thinning with regard to their impact on climatic resilience of red pine. Overall, thinning from below at a moderate thinning intensity to a residual basal area of 21 m²·ha⁻¹ represents a potentially beneficial com-

promise to optimize the combination of higher productivity (both stand- and tree-level) and reduced climate sensitivity (both monthly and seasonal climate factors). This study underscored the importance of utilizing thinning as an important intermediate stand-tending approach to increase climatic resilience of the residual trees. This study provides added support to the general recommendation that adaptation to climate change in forest management should incorporate thinning to increase the vigor of residual trees to increase their resiliency to climatic stress and climate-induced changes in disturbance regimes such as fire, insects, and fungal pathogens (Spittlehouse and Stewart 2003; West et al. 2009). To sustain climatic resiliency, forest management techniques (such as density management) must be maintained, otherwise climatic resiliency may diminish over time (Vayreda et al. 2012).

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