

Growth–climate relationships across topographic gradients in the northern Great Lakes

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ABSTRACT

Climatic conditions exert important control over the growth, productivity, and distribution of forests, and characterizing these relationships is essential for understanding how forest ecosystems will respond to climate change. We used dendrochronological methods to develop climate–growth relationships for two dominant species, *Populus tremuloides* (quaking aspen) and *Pinus resinosa* (red pine), in the upper Great Lakes region to understand how climate and water availability influence annual forest productivity. Trees were sampled along a topographic gradient at the Marcell Experimental Forest (Minnesota, USA) to assess growth response to variations in temperature and different water availability metrics (precipitation, potential evapotranspiration (PET), cumulative moisture index (CMI), and soil water storage). Climatic variables were able to explain 33–58% of the variation in annual growth (as measured by ring-width increment) for quaking aspen and 37–74% of the variation for red pine. Climate–growth relationships were influenced by topography for quaking aspen but not for red pine. Annual ring growth for quaking aspen decreased with June CMI on ridges, decreased with temperature in the November prior to the growing season on sideslopes, and decreased with June PET on toeslopes. Red pine growth increased with increasing July PET across all topographic positions. These results indicate the sensitivity of both quaking aspen and red pine to local climate and show several vulnerabilities of these species to shifts in water supply and temperature because of climate change. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS dendrochronology; quaking aspen; red pine; PET; soil moisture

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INTRODUCTION

Globally, the distribution and productivity of forests is strongly influenced by water availability (Churkina *et al.*, 1999; Whittaker, 1975), and available water in the form of soil moisture has strong localized effects on patterns of annual tree growth and forest dynamics (Graumlich, 1993; Hogg *et al.*, 2002; Hogg *et al.*, 2008; Pederson *et al.*, 2014). The role of soil moisture in governing patterns of tree growth is particularly important along the prairie-forest border in the upper Great Lakes region of North America, where annual precipitation is only slightly above potential evapotranspiration (Rodríguez-Iturbe *et al.*, 1999; Rodríguez-Iturbe, 2000). Given that climate in the Great Lakes region has already warmed (Sebestyen *et al.* 2011; Dymond *et al.* 2014) and is expected to continue to warm

with more extreme precipitation events (Kirtman *et al.*, 2013), a thorough understanding of how the annual growth of different tree species in this region responds to climatic variables is necessary. These climate–growth relationships can then be used to assess and project the sensitivity, resilience, and resistance of different tree species to changes in climate at localized scales.

Soil moisture is unevenly distributed along hillslopes (Grayson *et al.*, 1997), and soil moisture distribution is dependent upon soil depth and the percent slope, aspect, and curvature of the hillslope (Gómez-Plaza *et al.*, 2001; Qiu *et al.*, 2001; Tromp-van Meerveld and McDonnell, 2006; Penna *et al.*, 2009). From a forest community structure and function standpoint, topographic position influences the species that are present as well as their productivity (Meiners *et al.*, 1984; Fralish, 1994; Iverson *et al.*, 1997). In the Great Lakes region, elevation across a landscape varies by only tens of metres. Despite the low elevational profile, differences in species concur with topographic positions, with peatland species (e.g. *Picea mariana* and *Larix laricina*) dominating the lowlands and upland hardwoods

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and pines dominating the higher topographic positions. Even with its profound influence on water availability and species productivity, the influence of topography on annual tree growth has only been considered in a handful of dendrochronology studies (Kulakowski and Veblen, 2002; Anning *et al.*, 2013).

The effect of climate in regulating tree growth has largely been documented through dendrochronological studies, which have shown that precipitation and temperature alone can explain over 50% percent of the variation in annual tree growth (e.g. Fritts *et al.*, 1979; Cook *et al.*, 1987; Graumlich, 1993). Traditionally, soil moisture effects on tree growth have been examined using meteorological records of precipitation or approximations of soil moisture deficit, such as the Palmer Drought Severity Index (PDSI), which are derived from temperature and precipitation records (Stockton and Meko, 1975; Adams and Kolb, 2005; Keyan *et al.*, 2015). This work has demonstrated the importance of water availability and moisture stress in affecting patterns of annual wood formation (e.g. Meko *et al.*, 1993), but the coarse scale nature of these measures may obfuscate more fine-scale species and site-level responses to soil moisture patterns. For instance, the same amount of precipitation may fall on two adjacent stands, one that is fine-textured with a shallow-rooted species and one that is coarse-textured with a deep-rooted species. Despite having identical water inputs and climate-derived indices of water stress (i.e. PDSI), the plant available water in these two systems would be very different, given their differences in infiltration rates, hydraulic conductivity, antecedent moisture conditions, species physiology, and other factors. As such, using precipitation as a proxy for plant available water in dendrochronological analyses may greatly oversimplify complex ecohydrological processes.

The goal of this study was to understand how different soil moisture parameters interact with temperature to influence annual tree growth along a topographic gradient in two species that are dominant in the Great Lakes region. The specific objectives of this study were the following:

1. To identify the climate factors and water availability metrics that determine the growth of two dominant tree species (red pine, *Pinus resinosa*, and quaking aspen, *Populus tremuloides*) in northern Minnesota;
2. To identify if and how climate–growth relationships differ between tree species and landscape positions.

MATERIALS AND METHODS

Study site

The sites for this study were all located within the Marcell Experimental Forest (MEF; 47°52'N, –93°46'W) in north-central Minnesota (Figure 1). The MEF is located

approximately 150 km from the boundary of the forest–prairie tension zone. Vegetation across this tension zone shifts from deciduous and coniferous trees to prairie grasses, a transition predominantly driven by moisture availability and soil type (Curtis, 1971). Upland forested vegetation in the region consists primarily of mixed hardwoods and pines, with quaking aspen (*P. tremuloides* Michx.) and red pine (*P. resinosa* Sol.) dominating the landscape. Smaller quantities of bigtooth aspen (*Populus grandidentata* Michaux), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marshall), American basswood (*Tilia americana* L.), paper birch (*Betula papyrifera* Marshall), eastern white pine (*Pinus strobus* L.) and jack pine (*Pinus banksiana* Lamb.) are also common.

The climate at the MEF is continental and is strongly influenced by arctic air moving southward from Canada. Summers are warm and moist, while winters are cold and dry with abundant sunshine. Monthly mean temperature (1966–2013) is lowest in January (–15 °C) and highest in July (19 °C). Mean annual precipitation (1966–2013) is 78 cm, with the majority of precipitation falling during the summer months (Figure 2; Sebestyen *et al.*, 2011). Topographic relief on the forest is low, and elevation ranges from 1341 to 1446 m. Soils developed after glaciers retreated over 10 000 years ago and are generally well mixed and deep (>3 m) loamy sands and sandy clay loams (Johnson, 1994; Verry and Janssens, 2011).

Tree-ring sampling, cross-dating, and standardization

Increment cores were collected from 1/20th ha circular plots located along a topographic gradient (ridge, sideslope, and toeslope) within the three dominant cover types at the MEF (Figure 1, Table I). The design was replicated three times, for a total of 27 plots across the three cover types and topographic positions. Plot centres were co-located with soil moisture monitoring sites, which were established as part of a larger study on soil moisture dynamics (Dymond, 2014). As such, site characteristics such as stand age and management history were variable across plots. In each of the 27 plots, two increment cores were collected at breast height (1.37 m) from every dominant and co-dominant tree located within the plot. A total of 2380 cores from 18 different tree species were collected during field sampling.

All tree cores were mounted and prepared using standard dendrochronological procedures (Stokes and Smiley, 1968). Because of the large sample size, only the dominant tree species from each cover type (Table I) was measured and cross-dated. Cores were visually aged and cross-dated using a list method (Speer, 2010). Ring widths were then measured to the nearest 0.001 mm using a VELMEX measuring system (Velmex, Inc., Bloomfield, NJ, USA) outfitted with MeasureJ2X measuring software (VoorTech Consulting, Holderness, NH, USA). Accuracy of measurements and cross-dating techniques were statistically

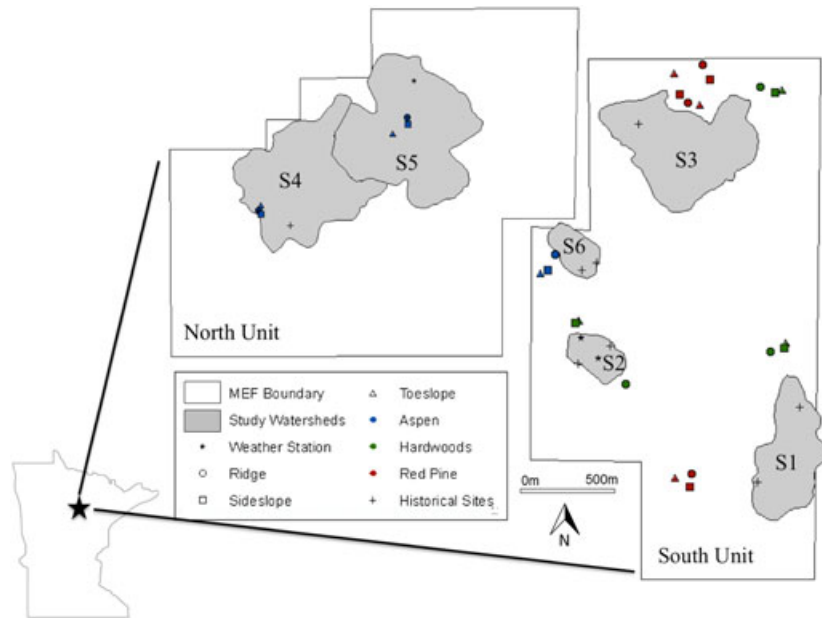


Figure 1. The MEF is located in north-central Minnesota and has six delineated research watersheds (S1–S6). From 2010–2011, nine sites in each of three cover types (aspen, hardwoods, and red pine) were cored for dendrochronological analysis and were measured for bi-weekly for volumetric soil moisture. Soil moisture data have been collected three times per year at the historical sites from 1966 to present.

verified using COFECHA software (Holmes, 1983). The sugar maple chronologies proved too unreliable to cross-date (likely because of a low sample size; Table I), and thus, the hardwoods' cover type was removed from further analyses and discussions.

Individual tree-ring series were detrended and converted to dimensionless ring-width indices using a two-third cubic smoothing spline with a 50% frequency response. The technique of detrending removes any growth patterns that may be a function of geometrically adding radial growth to an increasing tree diameter (Cook and Peters, 1981). Additionally, each series was prewhitened to remove temporal autocorrelation using autoregression. Residual chronologies from single trees were subsequently aggregated into one chronology per site and further aggregated into one species chronology per landscape position. All standardization techniques were applied using package *dpLR* in the R v. 3.1.1 statistical program (R Core Development Team, Vienna, Austria).

Climate and moisture variables

Meteorological records were collected at two weather stations on the MEF from 1961 to 2011 (Figure 1). Daily mean air temperature ($^{\circ}\text{C}$) and total daily precipitation (cm) were averaged across the two weather stations and then aggregated to determine mean monthly air temperature (T) and total monthly precipitation (P). P and T measurements at the north weather station were highly correlated with corresponding measurements from the south weather station ($p < 0.0001$). Monthly potential evapotranspiration (PET) was modelled

using the Thornthwaite equation (Thornthwaite and Mather, 1955). Monthly changes in moisture were also quantified using a cumulative moisture index (CMI), where CMI is equal to P less PET (Hogg, 1997).

Soil moisture storage

Soil moisture was measured *in situ* at each plot using a Troxler Series 4300 neutron probe (Troxler Electronic Laboratories, Inc., Research Triangle Park, NC, USA). Measurements were collected bi-weekly throughout the 2011–2013 growing seasons (approximately May to November) at 30-cm increments from 15 cm to approximately 200 cm depth. Soil moisture was measured gravimetrically from 0 to 15 cm in the soil profile, because moisture measured using the neutron probe technique can lead to spurious measurements because of a loss of neutrons from the soil surface (Brakensiek *et al.* 1979). Neutron probe measurements were calibrated on a site basis so that volumetric soil moisture readings could be compared across sites.

To obtain values of soil moisture back in time for each of the plots, monthly soil water storage from 0 to 229 cm in the soil profile was modelled using a modified Thornthwaite approach (Kolka and Wolf, 1998). Modelled results of monthly soil water storage were compared with the measured values of soil moisture collected *in situ* from 0 to 229 cm depth at the 27 plots during the 2011–2013 growing seasons. The modified Thornthwaite approach was found to be an adequate predictor of monthly soil water storage at the MEF (Dymond, 2014). Using this approach, soil water storage was calculated as

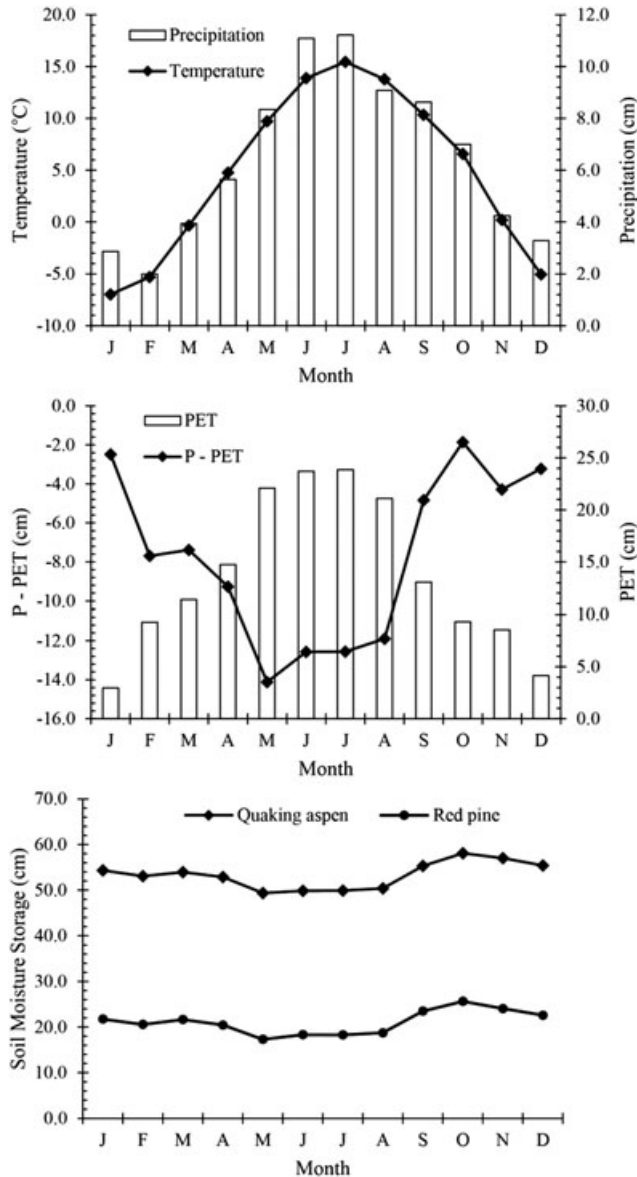


Figure 2. Mean monthly temperature, precipitation (top), PET, P-PET (middle), and soil moisture storage (0–229 cm depth) under two different cover types (bottom) from 1966 to 2011 at the MEF.

$$S_t = 10 \left[\log MSW - \left(\frac{0.525}{(MSW^{1.0371})} \right) \times ACPWL_{t-1} \right] \quad (1)$$

where S is soil water storage in month t , MSW is the maximum soil water (mm) that a particular soil can hold, and $ACPWL$ is the absolute value of accumulated potential water loss. The MSW for each site was obtained using the relationship between soil texture and percent volumetric water at field capacity. Soil texture values were found using the hydrometer method for particle size analysis (Gee and Bauder, 1986). Maximum soil water storage was estimated based on the average soil texture across the soil profile (Saxton and Rawls, 2006); percent volumetric water was

multiplied by soil depth to obtain the maximum soil water storage at field capacity in millimetres. $ACPWL$ is the amount of water lost from the soil when PET exceeds precipitation. Details of $ACPWL$ calculations as well as their application at the MEF can be found in Kolka and Wolf (1998) and Dymond (2014). Soil moisture storage was averaged across plots to obtain a mean value of S for each cover type/topographic combination; these values were used in subsequent dendroclimatological analyses.

Analyses

To investigate the relationship between climate and trees at the MEF, annual growth signals from the residual chronologies were related to local monthly and seasonal water variables (either P , CMI , or S) and monthly/seasonal temperature (T) using the SEASCORR package in R (Meko *et al.*, 2011; Zang and Biondi, 2015). Analyses included only years where the expressed population signal, or EPS , exceeded 0.85 (Briffa and Jones, 1990). SEASCORR was used such that the water variable (P , CMI , or S) was summarized with correlations, while temperature was summarized with partial correlations by adjusting for the dependence of the tree-ring index on the water variable. In SEASCORR, significance of the correlations and partial correlations is obtained using Monte Carlo simulation (Meko *et al.* 2011).

To determine which water parameter most effectively explains variability in annual tree rings, significant variables from the SEASCORR output were used to construct a series of linear regression models. Models predicted the residual ring width as a function of climate using the PROC MIXED procedure in SAS Version 9.0 (SAS Institute Inc., Cary, NC, USA). A series of candidate models were created based on the set of significant variables identified via SEASCORR. The fit of models of varying levels of complexity were created and compared with each other and a null model where ring width was solely a function of year using the corrected Akaike information criterion (AIC_c ; Akaike, 1974). Interaction terms were only included in these candidate models if they were deemed biologically plausible and significant. The squared correlation between predicted and observed values was used as a measure of model goodness of fit. We chose the best-approximating models in a given set based on a combination of AIC , R^2 , and Akaike weight. In cases in which there was strong support for multiple models ($\Delta AIC < 2$), we interpreted the most parsimonious model in these best-approximating sets.

The influence of topography on mean annual growth was first assessed by comparing the mean basal area increment (BAI) across the sampled topographies. BAI was calculated using the *bai.in* procedure in the *dplR* package in R. This procedure calculates BAI based on the diameter of the tree (which was measured in the field), assuming a circular cross-sectional area (Biondi, 1999). Topography–climate relationships were assessed using the mean sensitivity of

Table I. Site information and statistics for different cover types at the MEF.

| Cover Type | Dominant Species | Landscape position | No. of cores | No. of trees | Start year | Mean tree age | Mean tree ring width, SD (mm) | R_{BAR}^a | MS^b |
|------------|------------------|--------------------|--------------|--------------|------------|---------------|-------------------------------|--------------------|---------------|
| Aspen | Quaking aspen | Ridge | 127 | 70 | 1972 | 29 | 2.22 (1.04) | 0.51 | 0.40 |
| | | Sideslope | 44 | 44 | 1976 | 31 | 2.00 (0.99) | 0.49 | 0.41 |
| | | Toeslope | 83 | 45 | 1969 | 36 | 1.91 (0.81) | 0.54 | 0.36 |
| Hardwoods | Sugar maple | Ridge | 11 | 6 | 1934 | 60 | 1.08 (0.61) | 0.03 | 0.34 |
| | | Sideslope | 40 | 21 | 1911 | 68 | 1.20 (0.67) | 0.16 | 0.32 |
| | | Toeslope | 27 | 14 | 1941 | 50 | 1.60 (0.79) | 0.01 | 0.34 |
| Red pine | Red pine | Ridge | 210 | 112 | 1968 | 38 | 2.61 (1.77) | 0.40 | 0.23 |
| | | Sideslope | 275 | 173 | 1968 | 39 | 2.30 (1.47) | 0.38 | 0.22 |
| | | Toeslope | 200 | 109 | 1968 | 38 | 2.48 (1.57) | 0.41 | 0.22 |

Each cover type and landscape position consisted of three plots. Sugar maple had a low sample size and thus was dropped from further analyses.

^aTotal mean series intercorrelation; the average correlation of individual series with the master chronology (Holmes 1983).

^bMean sensitivity as calculated by Equation (1) in Biondi and Qeadan (2008).

the residual chronologies as well as by comparing the significant models and SEASCORR output.

RESULTS

Cross-dating and growth patterns

Trees included in this sample were relatively young: the mean age of aspen and red pine was 32 and 38 years, respectively (Table I). The total mean series intercorrelation ranged from 0.38 to 0.54, with red pine having lower mean series intercorrelation (R_{bar}) values than quaking aspen (Table I). The mean annual BAI was significantly different ($p < 0.0001$) between the two species (Figure 3). Red pine had a higher mean annual growth rate ($709.0 \text{ mm}^2 \text{ year}^{-1}$) than quaking aspen ($372.5 \text{ mm}^2 \text{ year}^{-1}$). There were no significant differences in growth rates across topographic positions both within and across cover types (Figure 3).

For red pine, periods of higher than mean annual growth and lower than mean annual growth occurred across the chronological record (Figure 4). Low growth occurred in 1974–1980, 1987–1992, and 1996. The lowest growth for red pine, regardless of topographic position, was in 1988. Periods of high growth in red pine occurred in 1971–1974 and 1992–1995, with the highest growth in 1972 and 1973. For quaking aspen, low growth was evident in 1978–1979, 1990–1991, and 2001–2002. The low growth periods for quaking aspen all corresponded to periods of documented forest tent caterpillar outbreaks in the region (Albers *et al.*, 2014).

For both quaking aspen and red pine, there was little variation in the residual mean annual ring-width increment (RWI) for each topographic position (Figure 4). At the beginning of the quaking aspen chronology, mean residual RWI was not consistent among the topographic positions. There was no significant difference (Tukey's mean test, $\alpha < 0.05$) in the mean sensitivity of red pine trees at different topographic positions, while quaking aspen ridges and sideslopes were significantly ($\alpha < 0.001$) more sensitive than the toeslope positions (Table I).

Climate Analyses

SEASCORR results varied between the different topographic positions (Table II). For quaking aspen, precipitation in the September prior to the growing season was positively correlated with mean residual RWI for the toeslopes and sideslopes, with no correlation for quaking aspen located on ridges. PET was only correlated with quaking aspen growth in the toeslope positions; the residual RWI increased with higher April and June PET. Likewise, the toeslope position was the only location where quaking aspen growth responded to soil moisture storage. High soil moisture in the previous September resulted in higher quaking aspen growth. Quaking aspen had higher growth with higher CMI (precipitation less PET; meaning higher excess precipitation) in the previous September for toeslopes and sideslopes, while growth for quaking aspen located on the ridges was negatively correlated with June PET. In all cases, the secondary variable (temperature) was negatively correlated with quaking aspen growth. When grouped together, quaking aspen growth was positively correlated with precipitation in the previous September and showed varied response to the CMI (Table II).

Topographic response to climate was less evident in red pine. For the three topographic positions, July PET was positively correlated with RWI. With the exception of the sideslope position, March temperatures were also positively correlated with RWI. These two variables were also significant when the red pine were grouped across topographic positions. For both quaking aspen and red pine, there were no significant variables when the data were analysed across seasons (using a 3- and 6-month moving average; data not shown).

Climate-growth models

Using AIC, the best-approximating bioclimate models explained 33% to 58% of the annual variation in tree-ring growth for quaking aspen and 37% to 74% for red pine ($p < 0.05$; Table III; Appendix). For quaking aspen, the models varied between topographic positions, and there was no consistency in the significance of the water availability

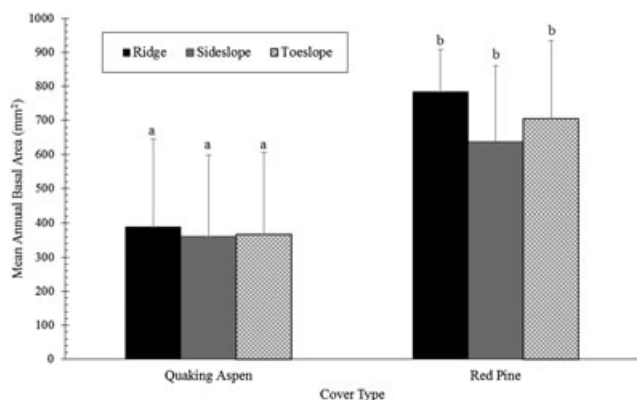


Figure 3. Mean annual basal area increment for dominant tree species across three different topographic positions at the MEF. Error bars indicate one standard deviation from the mean. Different letters indicate significantly different mean annual basal area ($\alpha < 0.0001$).

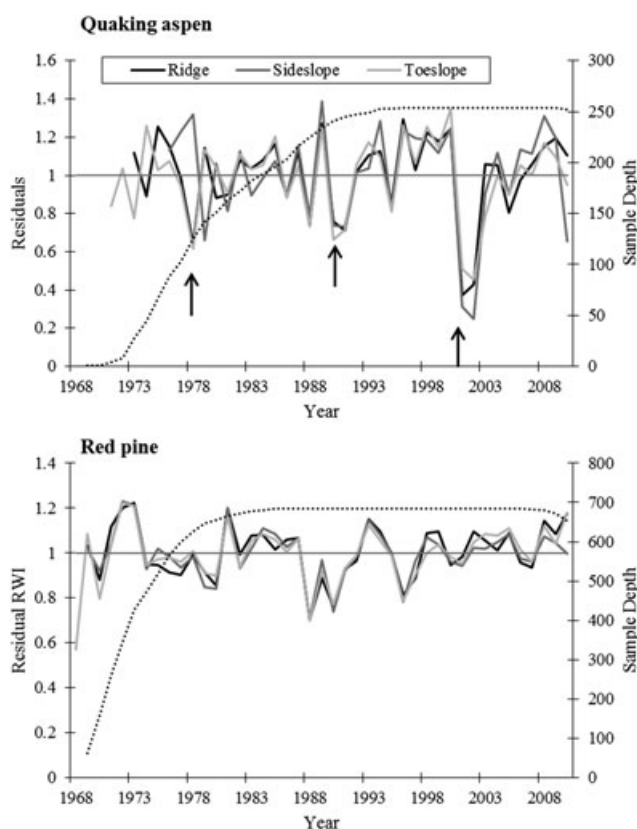


Figure 4. Standardized residual tree ring index (RWI) for two species at the MEF. Dotted lines indicate the sample depth or the number of individual cores per year. Arrows indicate periods of forest tent caterpillar outbreak.

metrics. For the ridges, RWI was best explained by June CMI or a combination of June CMI and mean temperature during the previous November ($R^2 = 0.33$ and 0.40 , respectively). The top models for the sideslope and toeslope positions were based on temperature from the previous November and June PET, respectively. Both of these models were at least two AIC units from the second-best model. When grouped across topographic position, annual RWI

was best explained by a combination of precipitation from the previous September and June temperatures.

For red pine, all of the topographic bioclimate models included July PET (Table III). All of the top models were at least two AIC units from the next model and had much higher weights (Appendix). When aggregated across the different topographic positions, June PET was also incorporated into the model. This final model of red pine growth was highly significant ($p < 0.0001$) and explained 75% of the variation in the annual ring-width index for red pine.

DISCUSSION

Tree growth in response to climate

We found strong climate-growth relationships for both quaking aspen and red pine in northern Minnesota. Across topographic positions, 51% of the variability in quaking aspen annual growth could be explained by precipitation and temperature. Tree growth was positively correlated with precipitation for the September prior to the growing season, while quaking aspen growth declined with warm temperatures early in the growing season (June). Previous studies have found declines in quaking aspen growth following droughts during the prior growing season, suggesting a lag effect of water availability on quaking aspen growth and mortality (Hogg *et al.*, 2008; Lapointe-Garant *et al.*, 2010). When broken into different topographic positions, the quaking aspen climate-growth models varied greatly. Annual quaking aspen growth on ridges and toeslopes responded negatively to early-season moisture stress (June CMI and June PET, respectively), while quaking aspen on sideslopes had a strong negative response ($R^2 = 0.58$, $p < 0.0001$) to temperatures in the November prior to the growing season. Quaking aspen located in the Québec region has also been shown to respond negatively to cold temperatures during the period of leaf senescence prior to the current growing season (Lapointe-Garant *et al.*, 2010). The negative response to temperature could be a result of cold temperatures impacting the cold hardening of buds. Growth-climate models of quaking aspen for ridges and toeslopes corroborate previous studies: aspen is known to be very drought sensitive (Hogg *et al.*, 2002, 2005; Kljun *et al.*, 2007).

While not part of the climate analysis, the three lowest ring-width years for quaking aspen (across all topographic positions) were associated with documented forest tent caterpillar (*Malacosoma disstria*) outbreaks in northern Minnesota (Albers *et al.* 2014). This may result in a dampening of the climate signals in our analyses. Forest tent caterpillar preferentially feeds on aspen, birch, basswood, and oak leaves, and many studies have also found that defoliating insects largely influence quaking aspen productivity and stand dynamics (Hogg *et al.* 2002; Hogg *et al.* 2008; Huang *et al.* 2008; Lapointe-Garant *et al.* 2010; Reinikainen *et al.* 2012). There is also evidence that defoliating insect outbreaks

Table II. Monthly climate variables that were significantly correlated ($\alpha=0.05$) with ring-width index for quaking aspen and red pine at three different topographic positions as well as grouped by species based on SEASCORR analysis.

| Species | Topographic position | Significant variables |
|---------------|----------------------|--|
| Quaking aspen | Ridge | <i>T</i> _{Apr} , <i>CMI</i> _{Jun} , <i>T</i> _{pNov} |
| | Sideslope | <i>P</i> _{pSep} , <i>T</i> _{pNov} , <i>CMI</i> _{pSep} |
| | Toeslope | <i>P</i> _{pSep} , <i>T</i> _{Jun} , <i>PET</i> _{Mar} , <i>PET</i> _{Jun} , <i>T</i> _{Jun} , <i>CMI</i> _{pSep} , <i>S</i> _{pSep} , <i>T</i> _{Aug} |
| | All | <i>P</i> _{pSep} , <i>T</i> _{Jan} , <i>T</i> _{Jun} , <i>CMI</i> _{pSep} , <i>CMI</i> _{pNov} , <i>CMI</i> _{Jan} , <i>CMI</i> _{Jun} |
| Red pine | Ridge | <i>P</i> _{Jul} , <i>PET</i> _{Jul} , <i>T</i> _{Mar} , <i>T</i> _{pSep} |
| | Sideslope | <i>PET</i> _{Jul} , <i>CMI</i> _{Mar} , <i>S</i> _{Mar} |
| | Toeslope | <i>PET</i> _{Jul} , <i>T</i> _{Mar} , <i>T</i> _{pAug} |
| | All | <i>P</i> _{Jul} , <i>T</i> _{Jun} , <i>PET</i> _{Jun} , <i>PET</i> _{Jul} , <i>CMI</i> _{May} , <i>T</i> _{Mar} , <i>S</i> _{May} |

Bold variables indicate positive correlations, while standard type indicates negative correlations. *T*, temperature (°C); *P*, precipitation (cm); *PET*, potential evapotranspiration (cm); *CMI*, cumulative moisture index (P–PET, cm); *S*, soil moisture storage (cm).

Table III. Bioclimate models of ring-width index for two dominant tree species across three different topographic positions at the MEF.

| Species | Topographic position | Water availability metric | Best-approximating model | <i>R</i> ² | <i>p</i> -value |
|----------|----------------------|---------------------------|--|-----------------------|-----------------|
| Aspen | Ridge | CMI | $y_{ij} = 1.7720 - 0.04704 * CMI_{Jun} + \epsilon_{ij}$ | 0.332 | 0.032 |
| | Sideslope | n/a | $y_{ij} = 17.1703 - 0.02828 * T_{pNov} + \epsilon_{ij}$ | 0.582 | <0.0001 |
| | Toeslope | PET | $y_{ij} = 2.0463 - 0.06407 * PET_{Jun} + \epsilon_{ij}$ | 0.470 | 0.002 |
| | All | Precipitation | $y_{ij} = 1.7665 + 0.01496 * P_{pSep} - 0.05470 * T_{Jun} + \epsilon_{ij}$ | 0.514 | 0.0008 |
| Red pine | Ridge | PET | $y_{ij} = 256.91 + 10.6104 * PET_{Jul} + \epsilon_{ij}$ | 0.413 | 0.0059 |
| | Sideslope | PET | $y_{ij} = 0.2464 + 0.03108 * PET_{Jul} + \epsilon_{ij}$ | 0.390 | 0.0097 |
| | Toeslope | PET | $y_{ij} = 0.2488 + 0.03115 * PET_{Jul} + \epsilon_{ij}$ | 0.370 | 0.0147 |
| | All | PET | $y_{ij} = 190.17 + 4.6457 * PET_{Jun} + 12.4241 * PET_{Jul} + \epsilon_{ij}$ | 0.735 | <0.0001 |

Best-approximating models were those with the lowest AIC values, and all top models were significant ($p < 0.05$). See the Appendix for a list of all of the evaluated models and their rankings. CMI, cumulative moisture index (cm); *PET*, potential evapotranspiration (cm); *T*, temperature (°C); *P*, precipitation (cm); y_{ij} , ring-width index for tree *i* in year *j*; ϵ , random error.

can be exacerbated by regional droughts (Worrall *et al.* 2013). The short (40-year) MEF quaking aspen chronology had no overlap between droughts and insect outbreaks, so this could not be explicitly tested in our dataset.

Climate explained a high and significant percentage of the variation in annual growth for red pine ($R^2=74\%$, $p < 0.0001$) when grouped across topographic positions. Across the topographic positions, red pine growth consistently responded positively to July PET. Prior studies have found that red pine growth responded most to warm early growing season temperatures and cool July temperatures (Graumlich, 1993; Kilgore and Telewski, 2004; Kipfmüller *et al.*, 2010; Magruder *et al.*, 2013). However, our results suggest that red pine growth is actually increasing with increased evaporative demand. Meanwhile, other studies have found some evidence that red pine growth is influenced by June and July precipitation (Kipfmüller *et al.*, 2010) or have found no association between red pine growth and water availability (Graumlich, 1993; Magruder *et al.*, 2013).

Recently, it has been shown that red pine management regimes may influence growth–climate relationships (D’Amato *et al.*, 2014; Magruder *et al.*, 2013). Of the nine red pine sites included in this study, five were from thinned stands and four were from unthinned stands (average basal area = 13.1 and 35.9 m² ha⁻¹, respectively). These sites were

placed into groups according to stocking status, and the growth–climate relationships were re-analysed. Despite a difference in mean annual basal area between the thinned and unthinned stands, the growth–climate relationships did not change according to management regime. However, this could be a result of the young stand age of the trees sampled, as tree size (and age) in managed red pine stands has been shown to affect growth–climate relationships (D’Amato *et al.*, 2014).

Water availability metrics

Many dendroclimatological studies use temperature and precipitation as the primary climate metrics (D’Arrigo and Jacoby, 1991; Graumlich, 1993; Salzer and Kipfmüller, 2005; Liang *et al.*, 2014; and others); measurements of these climate variables are geographically widespread, and long-term records (100+ years) are often available. However, the use of precipitation as a proxy for tree growth can be misleading, because monthly precipitation does not always directly correlate to plant available water (Loik *et al.*, 2004; Reynolds *et al.*, 2004; Schwinning *et al.*, 2004; Dymond *et al.*, 2014). Because of this, more dendroclimatological studies are incorporating the use of PDSI, Standardized Precipitation Index, Forest Drought Stress Index, soil moisture, and P–PET or P/PET as surrogates for moisture stress in their analyses (Kagawa *et al.*, 2003; Adams and Kolb, 2005; Li *et al.* 2007,

Williams *et al.*, 2013; Fang *et al.*, 2015). In our climate analyses, we found that the CMI (or P–PET) and PET could enhance typical climate–growth relationships. Because PET can easily be modelled from available temperature data, it is suggested that more dendroclimatological studies consider incorporating additional metrics of water availability into their analyses when possible to provide an independent representation of soil moisture availability.

Forest productivity and topography

Many studies have suggested that tree productivity is a function of topography (Whittaker, 1975; Oberhuber and Kofler, 2000; Fekedulegn *et al.*, 2003; Tsujino *et al.*, 2006), yet we found that mean annual BAI was not different across topographic positions for both quaking aspen and red pine at the MEF. For red pine, we found that one climate–growth model was adequate across topographic positions. However, we found that the annual growth (as measured by the RWI) of quaking aspen to climate differed according to topography. Quaking aspen RWI on ridge and toeslope sites responded positively to June water metrics, while RWI on sideslopes were negatively associated with temperatures late in the prior growing season. White oak growth–climate relationships also differ from ridges to toeslopes, with xeric ridge sites responding positively to January–July PDSI and mesic low-slope sites correlating to June PDSI alone (Anning *et al.*, 2013). These studies suggest that topography can strongly influence water availability and thus alter growth–climate relationships in hardwood species.

From a hydrologic standpoint, vegetation distribution and productivity will disperse along topographic gradients because of topographic influence on plant available water. In a mountainous system, soil moisture is typically lowest at the ridges and increases as you move down the hillslope and into the toeslopes and valleys. On sites with more gentle relief, soil wetness may be highest on the flat-topped ridges and toeslopes and lowest on the sideslopes (Anderson and Kneale, 1980). Quaking aspen located on sideslopes at the MEF may have access to less water than their counterparts that are located on ridges and toeslopes, making them more sensitive to climate factors not related to moisture, such as temperature.

Broader implications

Our results suggest that quaking aspen and red pine trees at the MEF are responding significantly to climate. For quaking aspen, site and stand-level factors (e.g. insect outbreaks and local topography) may be of importance as well. The trees in this study were relatively young to develop climate–growth relationships – approximately 40 years as compared with 50 to 100 years for common dendroclimatological studies (Fritts 1976; Briffa *et al.* 1990; Meko *et al.*, 1993; Cook *et al.*, 1999). Additionally, many dendroclimatological studies target trees that are

located in harsh climatic zones and thus exhibit strong signals in regional temperature and precipitation. There is a need, however, to understand how trees living outside of such severe conditions respond to climate, especially given concerns of warming global temperatures and species range shifts (McKenney *et al.*, 2007; Chen *et al.*, 2011).

The response of tree growth to climate is becoming increasingly important as the climate in the northern Great Lakes region is expected to become warmer with more extreme wet and dry periods (Kirtman *et al.* 2013). In the past 45 years alone, mean annual temperature at the MEF has increased by 2.5 °C, and mean available soil water in May (0–229 cm depth) has declined by 3 cm, despite no change in annual or seasonal precipitation (Dymond *et al.* 2014). Recent studies have found that dominant trees in savanna and semi-arid ecosystems may experience mortality following an increase in drought conditions (Williams *et al.* 2010; Williams *et al.* 2013; Fensham *et al.* 2015). Our results suggest that annual tree basal area growth may decline following exaggerated drought conditions (increased temperatures; thereby increasing PET combined with decreased precipitation). This could lead to a shift in the suitable habitat for red pine and quaking aspen with corresponding effects on the species composition of forests in the Great Lakes region.

CONCLUSIONS

Tree growth in the northern Great Lakes region is generally believed to be limited by cold temperatures as opposed to soil moisture availability. However, the region contains broad physiognomic shifts from forest to prairie with the eastern boundary of the tallgrass prairie abutting the western edge of this region. If water availability were to decrease because of longer droughts as is expected under climate change projections, some tree species in the northern Great Lakes may be susceptible to declining vigour and local extirpation. At the MEF, dendrochronological analysis showed quaking aspen and red pine responded differently to climate metrics and that water availability metrics such as PET and CMI were more important in determining annual growth than precipitation. The significant water availability metrics varied by species and topographic position (for quaking aspen), indicating the importance of species and stand dynamics in determining how trees respond to climate.

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APPENDIX. MODEL DESCRIPTORS FOR THE GROWTH–CLIMATE MODELS FOR DIFFERENT SPECIES AND TOPOGRAPHIC POSITIONS AT THE MEF.

| Species | Topographic position | Water availability metric | Model variables | AIC | <i>k</i> | Weight |
|---------------|----------------------|---------------------------|---|-------|----------|--------|
| Quaking aspen | Ridge | CMI | CMI_{Jun} | -5.9 | 3 | 0.312 |
| Quaking aspen | Ridge | CMI | $CMI_{Jun} + T_{pNov}$ | -5.9 | 4 | 0.307 |
| Quaking aspen | Ridge | CMI | $T_{pNov} + T_{Jun}$ | -5.2 | 3 | 0.221 |
| Quaking aspen | Ridge | None | Null | -3.7 | 2 | 0.104 |
| Quaking aspen | Ridge | PET | T_{Apr} | -2.5 | 3 | 0.055 |
| Quaking aspen | Sideslope | Precipitation | T_{pNov} | 61.7 | 3 | 0.678 |
| Quaking aspen | Sideslope | Precipitation | $P_{pSep} + T_{pNov}$ | 63.2 | 4 | 0.322 |
| Quaking aspen | Sideslope | Precipitation | P_{pSep} | 137.0 | 3 | 0.000 |
| Quaking aspen | Sideslope | CMI | CMI_{pSep} | 137.0 | 3 | 0.000 |
| Quaking aspen | Sideslope | None | Null | 178.9 | 2 | 0.000 |
| Quaking aspen | Toeslope | PET | PET_{Jun} | -17.0 | 3 | 0.504 |
| Quaking aspen | Toeslope | PET | $PET_{Jun} + T_{Jun}$ | -15.2 | 4 | 0.203 |
| Quaking aspen | Toeslope | PET | $PET_{Mar} + PET_{Jun}$ | -14.8 | 4 | 0.169 |
| Quaking aspen | Toeslope | PET | $PET_{Mar} + PET_{Jun} + T_{Jun}$ | -13.0 | 5 | 0.070 |
| Quaking aspen | Toeslope | Storage | S_{pSep} | -10.0 | 3 | 0.015 |
| Quaking aspen | Toeslope | None | Null | -9.1 | 2 | 0.010 |
| Quaking aspen | Toeslope | Storage | $S_{pSep} + T_{Aug}$ | -7.6 | 4 | 0.004 |
| Quaking aspen | Toeslope | Precipitation | P_{pSep} | -7.5 | 3 | 0.004 |
| Quaking aspen | Toeslope | CMI | CMI_{pSep} | -7.5 | 3 | 0.004 |
| Quaking aspen | Toeslope | PET | T_{Jun} | -7.3 | 3 | 0.004 |
| Quaking aspen | Toeslope | Storage | T_{Aug} | -7.2 | 3 | 0.004 |
| Quaking aspen | Toeslope | PET | PET_{Mar} | -7.0 | 3 | 0.003 |
| Quaking aspen | Toeslope | Precipitation | $P_{pSep} + T_{Jun}$ | -6.0 | 4 | 0.002 |
| Quaking aspen | Toeslope | CMI | $CMI_{pSep} + T_{Jun}$ | -6.0 | 4 | 0.002 |
| Quaking aspen | Toeslope | PET | $PET_{Mar} + T_{Jun}$ | -5.2 | 4 | 0.001 |
| Quaking aspen | All | Precipitation | $P_{pSep} + T_{Jun}$ | -15.6 | 4 | 0.223 |
| Quaking aspen | All | Precipitation | $P_{pSep} + T_{Jan} + T_{Jun}$ | -15.4 | 5 | 0.198 |
| Quaking aspen | All | Precipitation | T_{Jun} | -13.5 | 3 | 0.078 |
| Quaking aspen | All | CMI | $CMI_{pSep} + CMI_{Jan}$ | -13.4 | 4 | 0.076 |
| Quaking aspen | All | Precipitation | $T_{Jan} + T_{Jun}$ | -13.3 | 4 | 0.070 |
| Quaking aspen | All | CMI | $CMI_{pSep} + CMI_{Jan} + CMI_{Jun}$ | -12.6 | 5 | 0.051 |
| Quaking aspen | All | CMI | $CMI_{pSep} + CMI_{Jun}$ | -12.4 | 4 | 0.044 |
| Quaking aspen | All | CMI | $CMI_{pSep} + CMI_{pNov} + CMI_{Jun}$ | -12.0 | 5 | 0.038 |
| Quaking aspen | All | CMI | $CMI_{pSep} + CMI_{pNov} + CMI_{Jan}$ | -11.7 | 5 | 0.032 |
| Quaking aspen | All | Precipitation | $P_{pSep} + T_{Jan}$ | -11.5 | 4 | 0.028 |
| Quaking aspen | All | CMI | CMI_{Jan} | -11.3 | 3 | 0.027 |
| Quaking aspen | All | CMI | $CMI_{pSep} + CMI_{pNov} + CMI_{Jan} + CMI_{Jun}$ | -10.8 | 6 | 0.020 |
| Quaking aspen | All | CMI | $CMI_{pSep} + CMI_{pNov}$ | -10.8 | 4 | 0.020 |
| Quaking aspen | All | CMI | CMI_{pSep} | -10.2 | 3 | 0.015 |
| Quaking aspen | All | CMI | P_{pSep} | -10.0 | 3 | 0.014 |
| Quaking aspen | All | Precipitation | T_{Jan} | -9.9 | 3 | 0.013 |
| Quaking aspen | All | CMI | $CMI_{pNov} + CMI_{Jan}$ | -9.7 | 4 | 0.012 |
| Quaking aspen | All | CMI | CMI_{Jun} | -9.7 | 3 | 0.012 |
| Quaking aspen | All | CMI | $CMI_{pNov} + CMI_{Jun}$ | -9.4 | 4 | 0.010 |
| Quaking aspen | All | CMI | CMI_{pNov} | -9.0 | 3 | 0.008 |
| Quaking aspen | All | None | Null | -8.5 | 2 | 0.006 |
| Quaking aspen | All | CMI | $CMI_{pNov} + CMI_{Jan} + CMI_{Jun}$ | -8.3 | 5 | 0.006 |
| Red pine | Ridge | PET | PET_{Jul} | -45.2 | 3 | 0.650 |
| Red pine | Ridge | PET | $PET_{Jul} + T_{Mar}$ | -42.7 | 4 | 0.188 |
| Red pine | Ridge | Precipitation | P_{Jul} | -41.2 | 3 | 0.090 |
| Red pine | Ridge | None | Null | -39.5 | 2 | 0.038 |
| Red pine | Ridge | Storage | T_{Mar} | -37.7 | 3 | 0.015 |
| Red pine | Ridge | Storage | T_{pSep} | -37.5 | 3 | 0.014 |
| Red pine | Ridge | Storage | $T_{pSep} + T_{Mar}$ | -35.7 | 4 | 0.006 |
| Red pine | Sideslope | PET | PET_{Jul} | -53.7 | 3 | 0.825 |
| Red pine | Sideslope | None | Null | -49.0 | 2 | 0.077 |
| Red pine | Sideslope | CMI | CMI_{Mar} | -48.7 | 3 | 0.066 |
| Red pine | Sideslope | Storage | S_{Mar} | -47.2 | 3 | 0.032 |

(Continues)

APPENDIX. (Continued)

| Species | Topographic position | Water availability metric | Model variables | AIC | <i>k</i> | Weight |
|----------|----------------------|---------------------------|---------------------------|-------|----------|--------|
| Red pine | Toeslope | PET | <i>jul_pet</i> | -48.1 | 3 | 0.769 |
| Red pine | Toeslope | PET | <i>jul_pet mar_temp</i> | -45.6 | 4 | 0.222 |
| Red pine | Toeslope | None | Null | -37.8 | 2 | 0.005 |
| Red pine | Toeslope | Storage | <i>mar_temp</i> | -36.0 | 3 | 0.002 |
| Red pine | Toeslope | Storage | <i>paug_temp</i> | -35.5 | 3 | 0.001 |
| Red pine | Toeslope | Storage | <i>paug_temp mar_temp</i> | -33.8 | 4 | 0.001 |
| Red pine | Toeslope | Precipitation | P_{pSep} | -7.5 | 3 | 0.004 |
| Red pine | Toeslope | CMI | CMI_{pSep} | -7.5 | 3 | 0.004 |
| Red pine | Toeslope | PET | T_{Jun} | -7.3 | 3 | 0.004 |
| Red pine | Toeslope | Storage | T_{Aug} | -7.2 | 3 | 0.004 |
| Red pine | Toeslope | PET | PET_{Mar} | -7.0 | 3 | 0.003 |
| Red pine | Toeslope | Precipitation | $P_{pSep} + T_{Jun}$ | -6.0 | 4 | 0.002 |
| Red pine | Toeslope | CMI | $CMI_{pSep} + T_{Jun}$ | -6.0 | 4 | 0.002 |
| Red pine | Toeslope | PET | $PET_{Mar} + T_{Jun}$ | -5.2 | 4 | 0.001 |
| Red pine | All | PET | $PET_{Jun} + PET_{Jul}$ | 402.7 | 4 | 0.784 |
| Red pine | All | PET | PET_{Jul} | 405.3 | 3 | 0.211 |
| Red pine | All | Storage | T_{Mar} | 413.6 | 3 | 0.003 |
| Red pine | All | Storage | $S_{May} + T_{Mar}$ | 416.1 | 4 | 0.001 |
| Red pine | All | CMI | $CMI_{May} + T_{Mar}$ | 416.1 | 4 | 0.001 |
| Red pine | All | None | Null | 431.3 | 2 | 0.000 |
| Red pine | All | Precipitation | P_{Jul} | 432.0 | 3 | 0.000 |
| Red pine | All | Precipitation | T_{Jun} | 432.4 | 3 | 0.000 |
| Red pine | All | PET | PET_{Jun} | 433.3 | 3 | 0.000 |
| Red pine | All | Storage | S_{May} | 433.5 | 3 | 0.000 |
| Red pine | All | CMI | CMI_{May} | 433.5 | 3 | 0.000 |
| Red pine | All | Precipitation | $P_{Jul} + T_{Jun}$ | 433.7 | 4 | 0.000 |

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