The Effects of Climate on Radial Growth of Disjunct Northern White Cedar (*Thuja occidentalis L.*) in Virginia

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ABSTRACT

Understanding the geographic range and growth of species is essential for effective land management in a landscape affected by anthropogenic activity and climate change. Climate change is expected to alter the distribution and growth of many tree species in eastern North America, including northern white cedar (*Thuja occidentalis* L.). This research examined the effects of climate on radial growth of *T. occidentalis* in disjunct populations south of its continuous range margin in eastern North America. A *T. occidentalis* tree-ring chronology was developed and examined for growth-climate interactions. Mean sensitivity of the *T. occidentalis* chronology was within the range of values reported for the species in northern portions of its range. Significant positive correlations existed between the *T. occidentalis* chronology and moisture variables late in the growing season of the previous year and current year. The relationship between the *T. occidentalis* chronology and temperature was more variable with significant positive and negative correlations throughout the previous year and current year. The Ordinary Least Squares (OLS) regression model suggested moisture conditions late in the growing season of the previous year and current year had a significant positive influence on the growth of *T. occidentalis*. In contrast, maximum temperature in March of the current year negatively influenced the growth of *T. occidentalis*. While the mean sensitivity of *T. occidentalis* appears similar throughout its range, there is geographic variability in the climate-growth response of *T. occidentalis*. More research is necessary to expand the scope of our knowledge concerning *T. occidentalis* growth throughout its range.

Keywords: *Thuja occidentalis,* Climate, Range, Tree rings, Disjunct

INTRODUCTION

Species located at or beyond the margins of their continuous range are often assumed to be more sensitive to ecological factors such as climate. It is hypothesized that one or more ecological factors become less favorable and more stressful for species located at increasing distances from their range center (Guo et al. 2005; Hart et al. 2010). If disjunct species are indeed more sensitive, then stress should be evident in their growth characteristics. Even if marginal ecological factors remain favorable for a species, conditions may differ from those experienced by more centrally located populations (Lesica and Allendorf 1995; Hardie and Hutchins 2010). Marginal populations are of particular interest to scientists because they may represent hearths for species with unique biological tolerances, variable genotypes, atypical morphologies and life history characteristics (Hardie and Hutchins 2010). With ongoing environmental transformation driven by anthropogenic activity and climate change, it is essential for effective land management that we understand the geographic range and growth characteristics of species. Climate change will likely alter the growth and distribution of many tree species in eastern North America. While climate change will increase the amount of suitable habitat for some species, other species such as *Thuja occidentalis* L. will experience great reductions in habitat (Iverson et al. 2008).

Thuja occidentalis, also known as arborvitae or northern white cedar, is a slow-growing and shade tolerant coniferous tree species native to eastern North America. The continuous range of *T. occidentalis* extends across southeastern Canada to the Great Lakes and New England regions of the United States. Isolated, disjunct populations exist south of the continuous range and throughout the Appalachian Mountains as far south as Tennessee, USA (Caplenor and Speir 1975; Walker 1987). Southern disjunct populations are typically small (0.1 to 1.0 ha) and rare, often restricted to steep, north-facing slopes or cliffs situated in stream or river valleys (Fleming 1999; Fleming and Coulling 2001). It has been suggested that these isolated habitats represented a glacial refugium for *T. occidentalis* and associated species (Larson et al. 1999).

Despite the extensive distribution of *T. occidentalis*, research examining the effects of climate on its growth has been limited in geographic scope, with most studies originating from northern portions of its range (e.g. Kelly et al. 1994; Kelly and Larson 1997; Tardiff and Bergeron 1997; Kipfmueller et al. 2010). Because heterogeneous conditions exist throughout a species range, previous research may be overlooking geographic variation in the growth characteristics of *T. occidentalis*. Previous studies have examined the growth of *T. occidentalis* in disjunct populations near its northern and northwestern range margins in Canada, but no such research originating from southern portions of the range exists (Tardiff and Stevenson 2001; Paul et al. 2014). Research examining *T. occidentalis* in southern disjunct populations has been limited to studies of forest community ecology and population biology (Walker 1987; Young 1996; Fleming 1999; Fleming and Coulling 2001).

The overall purpose of this research is to document the effects of climate on radial growth of *T. occidentalis* in disjunct populations south of its continuous range margin. Two specific objectives are posed by this research: 1) to develop a tree-ring chronology for *T. occidentalis* in Virginia; and 2) to quantify the relationship between *T. occidentalis* radial growth and climate variables.

MATERIALS AND METHODS

Study area

Sampling for this research was conducted in Rockingham County, Virginia, USA (Figure 1). Rockingham County lies predominantly within the Ridge and Valley physiographic province but is bounded by the Appalachian Mountains to the west and Blue Ridge Mountains to the east. Elevation varies within the county from approximately 274 m to 1335 m. Mean annual precipitation in the study area is 852 mm with 61% of it occurring between May and October. The mean annual temperature is 13.3°C with a mean seasonal range of 2.9°C to 23.7°C (SERCC 2016). Frost-free conditions (i.e. the growing season) typically extend from April to October.

The *T. occidentalis* forests examined in this research occurred at a mean elevation of 367 ± 16.3 m. Each forest was located on a steep (31-47%), north to northwest-facing slope with soils derived from calcareous bedrock. The structures and disturbance dynamics of these forests were quantified by Kincaid (2016). *T. occidentalis* was a canopy dominant in the study area, representing > 60% of the basal area at each sample location. Despite its dominant position in the overstory, there were low numbers of *T. occidentalis* stems in the smallest size classes. Other canopy species included *Liriodendron tulipifera* L., *Pinus strobus* L., and *Tilia americana* L. Stand dynamics were characterized by canopy gap-scale processes that generally affected a small number of trees each decade (Kincaid 2016).

Field and Laboratory Methods

Two *T. occidentalis* forest stands were sampled for this study (Kincaid 2016). Increment borers were used to extract cores from canopy trees along a 100-m transect at each site. Each tree was cored at breast height (1.4 m) and parallel to slope contours to avoid reaction wood, which can distort radial growth patterns. Canopy tree selection was accomplished using the point-quarter method every 10 m along transects where slope conditions allowed safe access (Cottam and Curtis 1956). Each transect was situated midslope and parallel to slope contours to avoid forest-environment transitions. A single transect was used at each site because the forests exhibited oblong dimensions and were located on steep slopes.

In preparation for laboratory analyses, all cores were air-dried, glued to wood mounts, and sanded with progressively finer grits of sand paper (Phipps 1985; Stokes and Smiley 1996). The growth rings on all cores were visually enumerated and crossdated using the list method (Yamaguchi 1991). Individual cores were measured to the nearest 0.001 mm using a Velmex measuring stage and Measure J2X software. The accuracy of crossdating was assessed using the computer program COFECHA (Holmes 1983; Grissino-Mayer 2001). COFECHA uses correlation analyses to examine the association between a single measurement series and a master chronology created from the other series. Measurement series that were poorly correlated with the master chronology were checked and corrected or eliminated from further analyses. A total of 42 tree cores were examined in this research (Kincaid 2016).

Radial growth-climate analyses

The computer program ARSTAN was used to standardize the raw tree-ring measurements (Cook 1985). Detrending of the raw tree-ring measurements was accomplished using a 30-year cubic smoothing spline. Standardization reduces the effects of tree age and stand

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dynamics, which allows for comparisons among trees with different growth rates. I used the RESIDUAL chronology produced by ARSTAN because autoregressive modelling has removed autocorrelation in the tree-ring data, which can bias the results of statistical tests such as correlation and regression. However, removing autocorrelation from the chronology can make it less sensitive to the signal of interest (Speer 2010).

I evaluated the relationships between monthly climate data and the *T. occidentalis* RESIDUAL chronology using Pearson correlation analysis. Climate data for Virginia Climate Division 5 were obtained from the National Climate Data Center. Virginia Climate Division 5 data were interpolated from stations using a 5 km grid resolution (NCDC 2015). The monthly climate variables examined in this research included total precipitation, Palmer Drought Severity Index (PDSI), mean temperature, maximum temperature, and minimum temperature for the previous year (year t-1) and current year (year t). The RESIDUAL chronology and monthly climate variables were examined using a 17-month window from June of the previous year to October of the current year.

To complement the Pearson correlation analysis, I used ordinary least-squares (OLS) regression to model the overall relationship between the *T. occidentalis* RESIDUAL chronology and climate variables (Chang and Aguilar 1980; Grissino-Mayer and Butler 1993; Parker et al. 2001). OLS regression was used instead of response function analysis because regression explicitly permits interaction among multiple climate variables, providing for an integrative explanatory model (Parker et al. 2001). In addition to examining previous year and current year monthly climate data, I included seasonal variables such as June through August total precipitation and March through May mean temperature. The inclusion of variables representing multiple consecutive months allows for direct examination of the effects of seasonal climate on tree growth and facilitates the estimation of a parsimonious model (Parker et al. 2001). A best subsets regression approach was used to screen all variables and models.

RESULTS

The *T. occidentalis* chronology examined in this research extended from 1895 to 2010 and contained a minimum sample depth of 3 trees. Sample depth consisted of 12 trees by 1929, and increased to 42 trees in 1963 (Figure 2). Intertree and intratree mean correlations were 0.489 and 0.558, respectively. Mean sensitivity of the chronology, which is a measure of the year-to-year variability in tree-rings, was 0.187 ± 0.19. Periods of above mean growth were sustained for 3 to 7 years while below mean growth events spanned 3 to 4 years.

Radial growth of *T. occidentalis* was significantly influenced by monthly precipitation variables. Significant positive relationships ($p < 0.01$) were observed between the *T. occidentalis* chronology and precipitation variables (Figure 3). Increases in *T. occidentalis* radial growth were associated with increases in total precipitation during the previous October and current August-September months. The correlation between *T. occidentalis* growth and monthly PDSI was higher and more significant than with precipitation or temperature. Monthly PDSI values were positively associated with *T. occidentalis* radial growth during the months of July through October of the current year. The PDSI integrates precipitation and temperature data, which may

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more closely reflect the conditions significant to tree growth. Positive PDSI values indicate moist conditions, while negative values reflect increasingly dry conditions.

Significant positive and negative relationships ($p < 0.01$) were observed between the *T. occidentalis* chronology and temperature variables (Figure 4). The radial growth of *T. occidentalis* was positively associated with previous August and current August temperatures. Temperatures in March, July, and September of the current year were negatively associated with *T. occidentalis* radial growth.

The OLS model produced an adjusted R^2 value of 0.311, which indicated a moderate amount of explanatory covariance between the climate variables and *T. occidentalis* chronology (Table 1). Two precipitation variables and one temperature variable were included in the final OLS model. Regression coefficients revealed that moisture conditions (i.e. precipitation and PDSI) near the end of the growing season of the previous year and current year positively affected *T. occidentalis* growth. Maximum temperature in March of the current year had a significant negative effect on the radial growth of *T. occidentalis*.

DISCUSSION

Climate was an important influence on the radial growth of *T. occidentalis* in southern disjunct populations. The mean sensitivity of *T. occidentalis* (0.187) in the study area was within the range of values documented for the species (range = 0.13 – 0.255) in northern portions of its range (Kelly et al. 1994; Tardiff and Bergeron 1997; Tardiff and Stevenson 2001; Kipfmueller et al. 2010). The mean sensitivity also was within the range of values expected for trees growing in eastern North America (DeWitt and Ames 1978). It is possible microsite conditions supporting southern disjunct populations of *T. occidentalis* are similar to conditions near the range center; therefore, the species is not necessarily more sensitive to ecological factors south of its continuous range margin (Brown 1984; Hart et al. 2010). Indeed, disjunct *T. occidentalis* populations in Virginia tend to occur along sheltered, north-facing slopes in stream or river valleys with limited solar exposure (Fleming 1999; Fleming and Coulling 2001).

The correlation coefficients and OLS model results revealed that moisture conditions during the late growing season of the previous year and current year were important influences on the radial growth of *T. occidentalis* in southern disjunct populations. Hart et al. (2010) documented a similar relationship between late growing season precipitation during the previous year and the growth of disjunct *Tsuga canadensis* (L.) Carr. south of its continuous range margin in eastern North America. Favorable moisture conditions late in the growing season may promote ongoing cambial activity and the storage of carbohydrates, which will be used to initiate new growth in the spring (Henderson and Grissino-Mayer 2009). The significance of late growing season moisture conditions to *T. occidentalis* growth in the study area contrasted with observations from northern portions of the range where early growing season conditions were more significant (Tardiff and Bergeron 1997; Tardiff and Stevenson 2001; Kipfmueller et al. 2010). The variation in growth responses of *T. occidentalis* to moisture conditions in particular portions of its range is likely related to a latitudinal gradient in growing season initiation and length.

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Geographic and seasonal differences were also apparent in the relationship between temperature and *T. occidentalis* radial growth. Maximum temperature in March of the current year appeared to have a significant negative influence on *T. occidentalis* growth. Higher temperatures with limited moisture during the early growing season may facilitate rates of evapotranspiration that favor respiration over carbon assimilation (Henderson and Grissino-Mayer 2009). In contrast, the growth responses of northern populations were positively influenced by early growing season temperatures (Kelly et al. 1994; Tardiff and Bergeron 1997; Tardiff and Stevenson 2001). Prior research from northern portions of the range has also reported negative relationships between previous August temperatures and *T. occidentalis* growth, but this was not evident in the current study (Kelly et al. 1994; Tardiff and Bergeron 1997; Tardiff and Stevenson 2001). The positive association between tree growth and late summer temperatures has been observed in *Chamaecyparis thyoides* L. (Atlantic white cedar; Hopton and Pederson 2005), as well as other conifers in the southern United States (Henderson and Grissino-Mayer 2009). Abundant precipitation and moderate temperatures late in the growing season may facilitate favorable rates of photosynthesis, respiration, and carbohydrate storage for *T. occidentalis* in southern disjunct populations. However, maximum temperatures in July and September of the current year were negatively related to growth, so there appears to be an upper limit, beyond which temperature begins to negatively affect *T. occidentalis* growth.

CONCLUSION

While the sensitivity of *T. occidentalis* growth to climate appears similar throughout its range, there is geographic and seasonal variation in the climate-growth relationships elucidated in this research. These differences in growth responses are likely the result of latitudinal variation in growing season conditions within the geographic range of *T. occidentalis*. Some researchers have suggested that *T. occidentalis* growth at its northern range margin is not significantly limited by climate, particularly temperature (Tardiff and Stevenson 2001; Paul et al. 2014). I hypothesize that maximum temperatures during the early growing season in conjunction with late growing season moisture availability influence the southern extent of *T. occidentalis* in disjunct populations. The current study has elucidated differences in the growth responses of *T. occidentalis* in southern disjunct populations compared to their northern counterparts. More research is clearly necessary to expand the geographic scope of our knowledge concerning *T. occidentalis* ecology and growth, particularly in more southern locations. This additional research should also explore the temporal stability of the climate-growth relationships documented in this research. Indeed, changes in climate have been associated with temporal shifts in the climate-growth relationships of other tree species, including *T. canadensis*, which frequently co-occurs with *T. occidentalis* in the study area (Marcinkowski et al. 2015; Saladyga and Maxwell 2015).

ACKNOWLEDGMENTS

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LITERATURE CITED

Brown, J. H. 1984. On the relationship between abundance and distribution of species. The American Naturalist 124:255-279.

Caplenor, D. and H. Speir. 1975. *Thuja occidentalis* L. on the Eastern Highland Rim in Tennessee. Journal of the Tennessee Academy of Science 50:74-75.

Chang, M. and G. J. R. Aguilar. 1980. Effect of climate and soil on the radial growth of loblolly pine (*Pinus taeda* L.) in a humid environment of Southeastern USA. Forest Ecology and Management 3:141-150.

Cook, E. R. 1985. A time series analysis approach to tree-ring standardization. Ph.D. thesis, University of Arizona, Tucson.

Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451-460.

DeWitt, E. and M. Ames. 1978. Tree-ring chronologies of eastern North America, Laboratory of tree-ring research, Chronology series IV, Volume 1. University of Arizona, Tucson.

Fleming, G. P. 1999. Plant communities of limestone, dolomite, and other calcareous substrates in the George Washington and Jefferson national forests, Virginia. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Natural Heritage Technical Report 99-4.

Fleming, G. P. and P. P. Coulling. 2001. Ecological communities of the George Washington and Jefferson national forests, Virginia. Preliminary classification and description of vegetation types. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Natural Heritage Technical report 01-1.

Grissino-Mayer, H. D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research 57:205-221.

Grissino-Mayer, H. D. and D. R. Butler. 1993. Effects of climate on growth of shortleaf pine (*Pinus echinata* Mill.) in northern Georgia: A dendroclimatic study. Southeastern Geographer 33:65-81.

Guo, G. Q., M. Taper, M. Schoenberger and J. Brandle. 2005. Spatial-temporal population dynamics across species range: from centre to margin. Oikos 108:47-57.

Hardie, D.C. and J. A. Hutchings. 2010. Evolutionary ecology at the extremes of species' ranges. Environmental Reviews 18:1-20.

Hart, J. L., S. L. van de Gevel, J. Sakulich and H. D. Grissino-Mayer. 2010. Influence of climate and disturbance on the growth of *Tsuga canadensis* at its southern limit in eastern North America. Trees 24:621-633.

Henderson, J. P. and H. D. Grissino-Mayer. 2009. Climate-tree growth relationships of longleaf pine (Pinus palustris Mill.) in the southeastern Coastal Plain, USA. Dendrochronologia 27:31-43.

Holmes, R.L. 1983. A computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43:69-78.

Hopton, H. M. and N. Pederson. 2003. Climate sensitivity of Atlantic White Cedar at its northern range limit. In: Burke M.K. and P. Sheridan (eds.) Atlantic White Cedar: ecology, restoration, and management. Proceedings of the Arlington Echo Symposium, Millersville, MD.

Iverson L. R., A. M. Prasad, S. N. Matthews, and M. Peters M. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. Forest Ecology and Management 254:390-406.

Kelly, P. E., E. R. Cook and D. W. Larson. 1994. A 1397-year tree-ring chronology of *Thuja occidentalis* from cliff faces of the Niagara Escarpment, southern Ontario, Canada. Canadian Journal of Forest Research 24:1049-1057.

Kelly, P. E. and D. W. Larson. 1997. Dendroecological analysis of the population dynamics of an old-growth forest on cliff-faces of the Niagara Escarpment, Canada. Journal of Ecology 85:467-478.

Kincaid, J. A. 2016. Structure and dendroecology of *Thuja occidentalis* in disjunct stands south of its contiguous range in the central Appalachian Mountains, USA. Forest Ecosystems 3:25.

Kipfmueller, K. F., G. P. Elliott, E. R. Larson and M. W. Salzer. 2010. An assessment of the dendroclimatic potential of three conifer species in northern Minnesota. Tree-Ring Research 66:113-126.

Larson D. W., U. Matthes-Sears, and P. E. Kelly. 1999. The cliff ecosystem of the Niagara Escarpment. In Anderson R. C., J. S. Fralish, and J. M. Baskin (eds.) Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, New York.

Lesica, P. and F. W. Allendorf. 1995. When are peripheral populations valuable for conservation? Conservation Biology 9:753-760.

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Marcinkowski, K., D. L. Peterson, and G. J. Ettl. 2015. Nonstationary temporal response of mountain hemlock growth to climatic variability in the North Cascade Range, Washington, USA. Canadian Journal of Forest Research 45:676-688.

NCDC. 2015. National Climatic Data Center. US Department of Commerce, National Oceanic and Atmospheric Administration, Asheville, North Carolina. http://www.ncdc.noaa.gov.

Paul V., Y. Bergeron and F. Tremblay. 2014. Does climate control the northern range limit of eastern white cedar (*Thuja occidentalis* L.)? Plant Ecology 215:181-194.

Parker A. J., K. C. Parker, T. D. Faust and M. M. Fuller. 2001. The effects of climatic variability on radial growth of two varieties of sand pine (*Pinus clausa*) in Florida, USA. Annals of Forest Science 58:333-350.

Phipps R. L. 1985. Collecting, preparing, crossdating, and measuring tree increment cores. US Geological Survey Water Resources Investigations Report 85-4148.

Saladyga, T. and R. S. Maxwell. 2015. Temporal variability in climate response of eastern hemlock in the central Appalachian Region. Southeastern Geographer 55:143-163.

SERCC. 2016. The Southeast Regional Climate Center. The University of North Carolina, Chapel Hill http://www.sercc.com/climate.

Speer J. H. 2010. Fundamentals of tree-ring research. University of Arizona Press, Tuscon.

Stokes M. A. and T. L. Smiley. 1996. An introduction to tree-ring dating. University of Arizona Press, Tucson.

Tardif J. and Y. Bergeron Y. 1997. Comparative dendroclimatological analysis of two black ash and two white white cedar populations from contrasting sites in the Lake Duparquet region, northwestern Quebec. Canadian Journal of Forest Research 27:108-116.

Tardif J. and D. Stevenson. 2001. Radial growth-climate association of *Thuja occidentalis* L. at the northwestern limit of its distribution, Manitoba, Canada. Dendrochronologia 19:179-187.

Walker G. L. 1987. Ecology and population biology of *Thuja occidentalis* in its southern disjunct range. PhD Dissertation, University of Tennessee, Knoxville.

Yamaguchi D. K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research 21:414-416.

Young J. 1996. The cliff ecology and genetic structure of northern white cedar (*Thuja occidentalis* L.) in its southern disjunct range. MS Thesis, University of Tennessee, Knoxville.

Table 1. OLS regression model relating the RESIDUAL tree-ring chronology to temperature and precipitation variables. All variables are significant at $p < 0.01$.

| Model summary	Variable	Standardized regression coefficient	Tolerance
$F = 21.84$, $p < 0.01$ $R^2 = 0.328$ Adjusted $R^2 = 0.311$	September-November Mean PDSI	0.444	0.988
	March Maximum Temperature	-0.316	0.988
	Previous October Precipitation	0.255	0.999
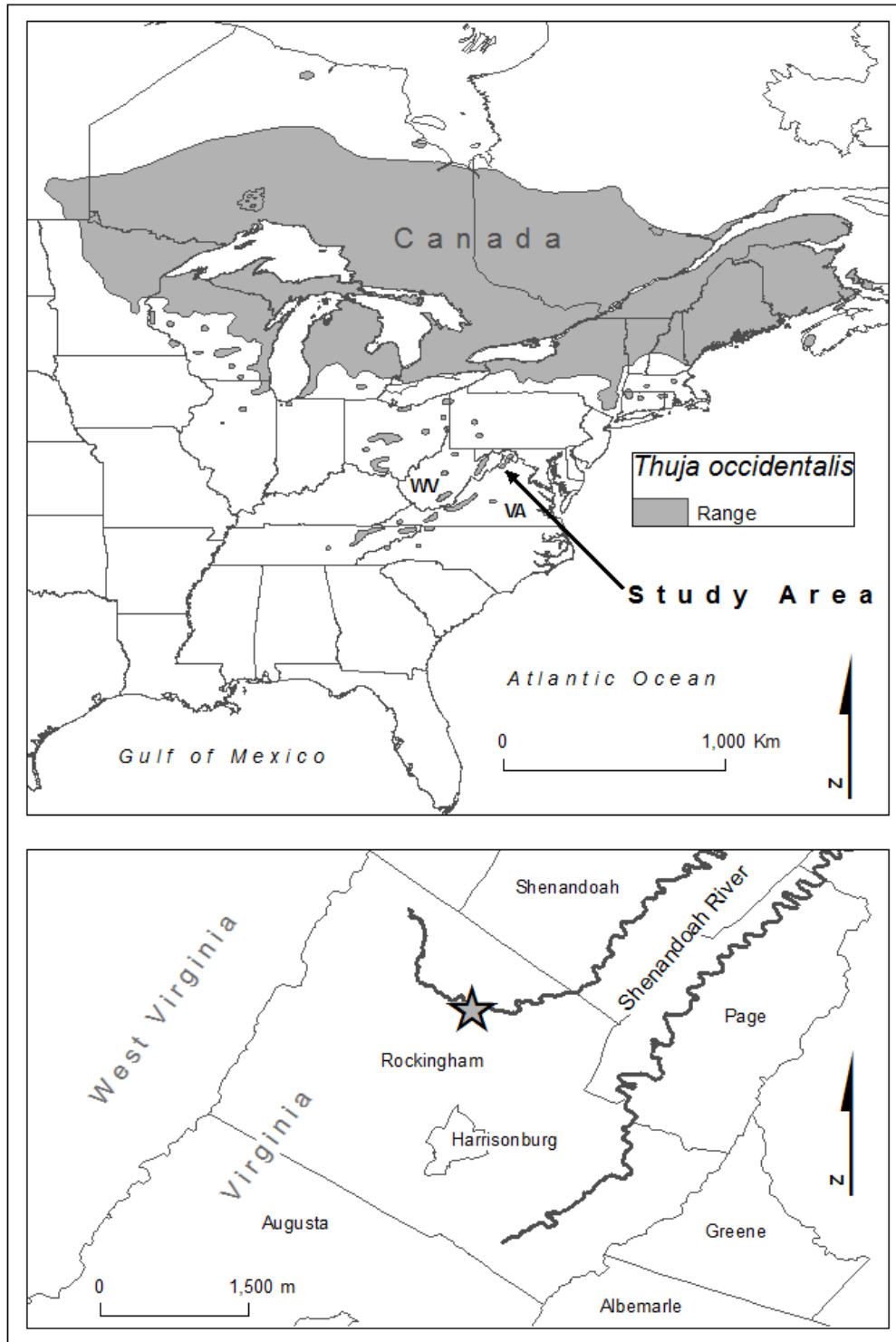
Figure 1. Map showing the range of *Thuja occidentalis* and study area.
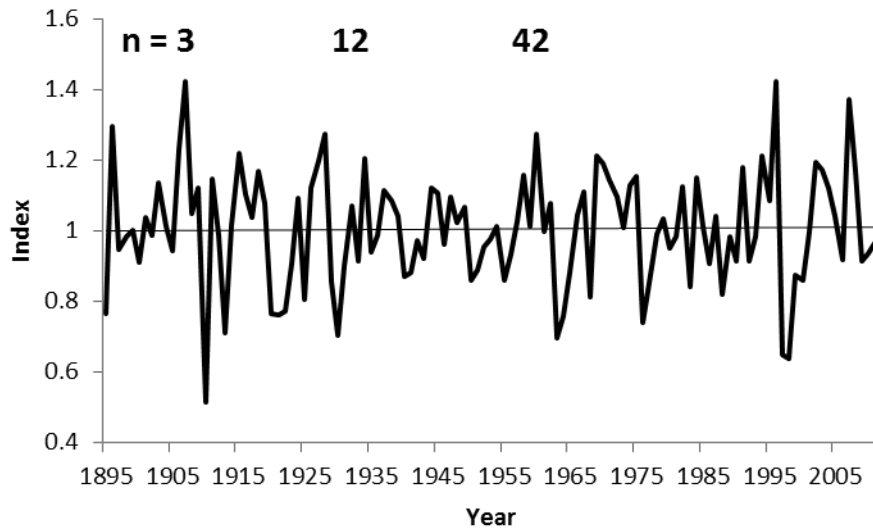
Figure 2. Composite ring-width index for *Thuja occidentalis* in the study area. Mean growth is standardized to 1.0 (n = number of trees represented in the index).

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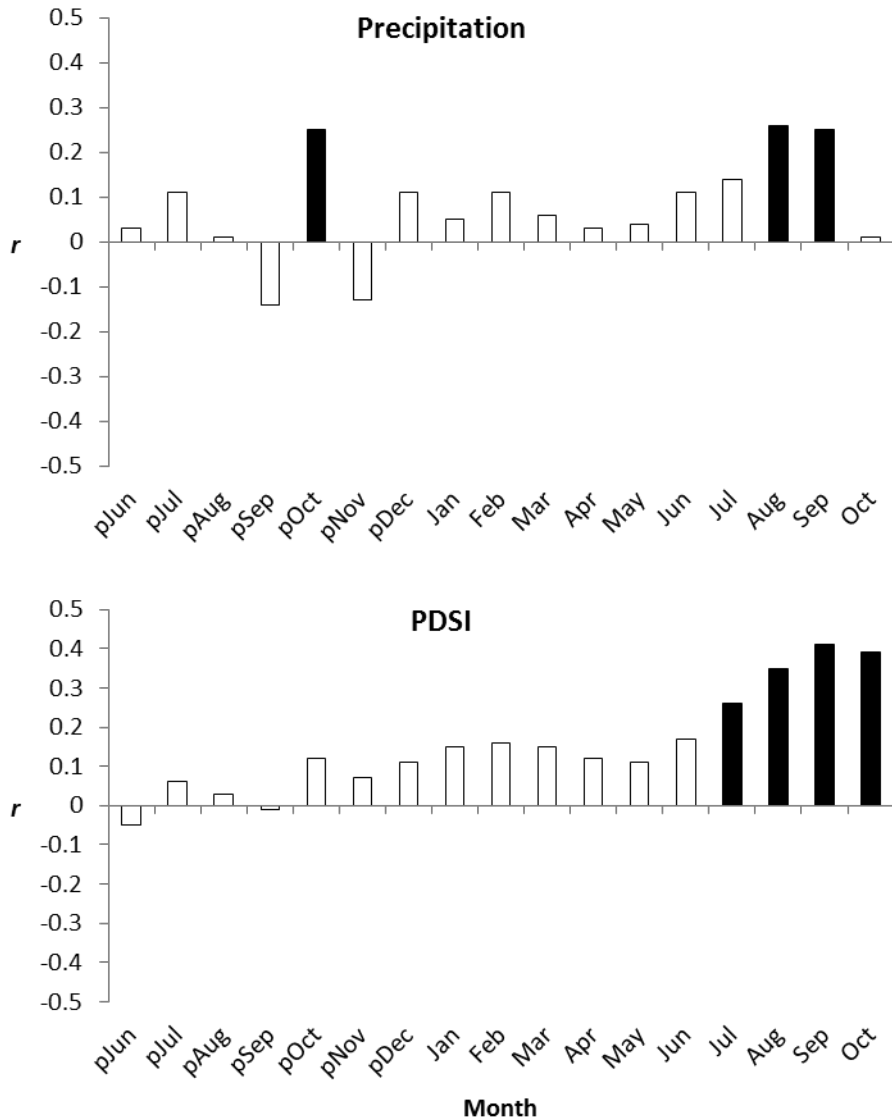
Figure 3. Pearson correlation coefficients showing the relationship between the *T. occidentalis* RESIDUAL chronology and precipitation variables. Black bars indicate a significance level of *p* < 0.01 and grey bars indicate a significance level of *p* < 0.05.

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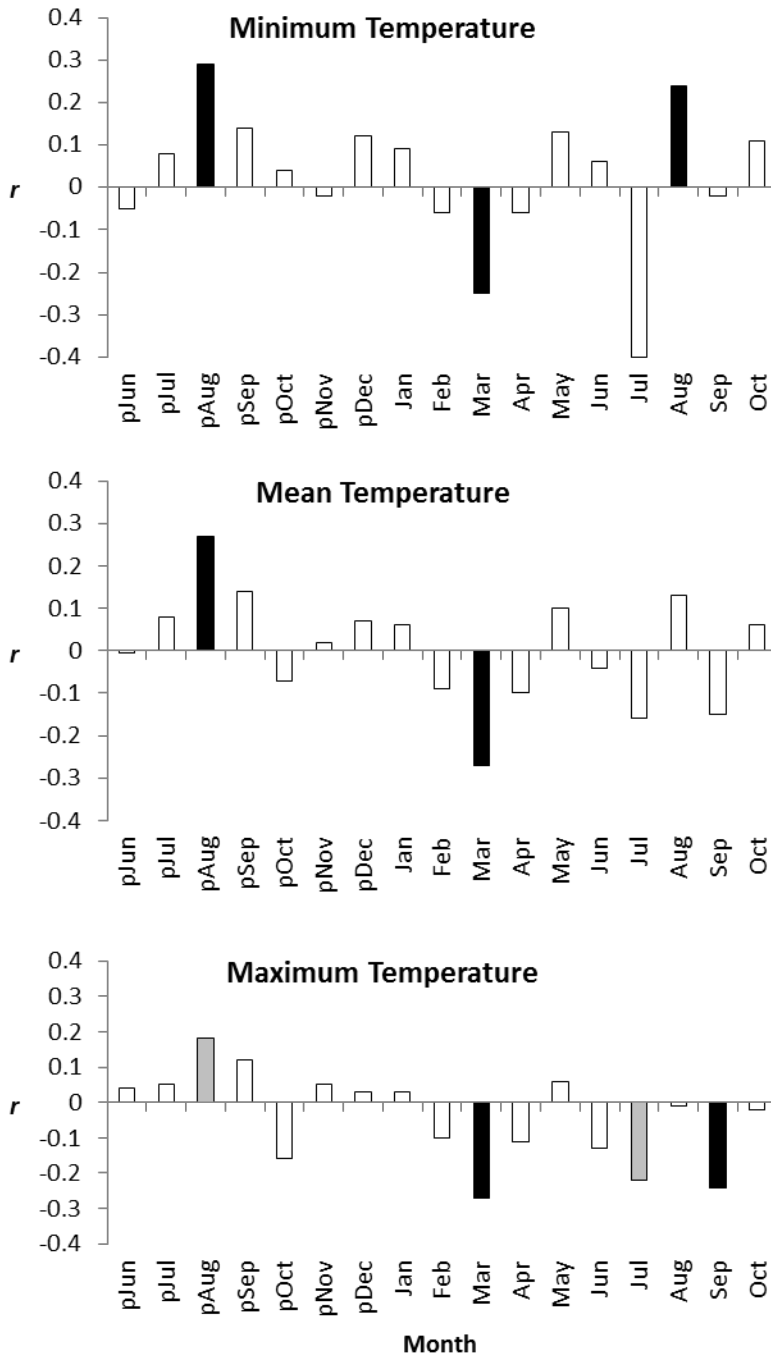
Figure 4. Pearson correlation coefficients showing the relationship between the *T. occidentalis* RESIDUAL chronology and temperature variables. Black bars indicate a significance level of $p < 0.01$ and grey bars indicate a significance level of $p < 0.05$.

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