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Influence of climate and disturbance on the growth of *Tsuga canadensis* at its southern limit in eastern North America

Justin L. Hart · Saskia L. van de Gevel · John Sakulich · Henri D. Grissino-Mayer

Abstract It has long been hypothesized that trees growing at range limits likely also occur near the limit of their ecological amplitude and thus, should be more sensitive to climate variability than individuals growing nearer the range core. We developed a tree-ring chronology using *Tsuga canadensis* individuals from three disjunct stands at the species' southern limit to quantify the influence of climate and disturbance on radial growth patterns. The tree-ring record extended 158 years from 1850 to 2007. Significant negative relationships were found between the STANDARD chronology and monthly mean temperature, monthly maximum temperature, and monthly minimum temperature during the previous and current summer, while significant positive relationships were documented between the STANDARD chronology and monthly minimum temperature for September and October of the current year. Also, significant positive relationships were documented between the STANDARD chronology and monthly total precipitation for September of the previous year and May of the current year. Response function analysis showed that monthly climate variables ($r^2 = 0.22$) and prior growth ($r^2 = 0.40$) explained 62% of the variance in the *T. canadensis* tree-ring chronology. A time series plot for the *T. canadensis* chronology showed that actual tree growth agreed relatively well with the predicted growth based on significant climate variables. However, positive departures from the predicted growth were noted. Dendroecological analysis revealed these departures were likely related to disturbance events. Our results indicated that *T. canadensis* individuals at its southernmost extent are sensitive to regional climate, but not more so than trees nearer the range core. We hypothesize that microenvironmental conditions of *T. canadensis* stands at its southern limit are similar to conditions within the contiguous distribution of the species, which may explain this pattern.

Keywords *Tsuga canadensis* · Dendrochronology · Ecological amplitude · Climate · Biogeography

Introduction

Ecological amplitude is defined as the variety of environmental conditions within which a species may grow and reproduce (Fritts 1976). Species that only live and function on restricted sites have a narrow ecological amplitude, while species that occur over a range of different habitats have a wide ecological amplitude. In the field of dendrochronology, ecological amplitude is used as a guiding principle as trees most useful for the analysis of climatic influences on annual growth patterns often occur near the margins of their natural range (Fritts 1976). In theory, individuals near range margins are more sensitive to environmental conditions such as climate. Thus, mean sensitivity (i.e. year-to-year variation in growth) should be high and annual growth patterns of trees within peripheral populations should be consistent (Fritts and Swetnam

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1989). This principle in dendrochronology is based on the assumption that an environmental gradient exists throughout the range of a species. At some point within the range, generally hypothesized to be near the core, environmental conditions should be optimal (Brown 1984; Cox and Moore 2000; Sagarin and Gaines 2002). Conditions are assumed to become less favorable with increased distance from the optimal position until ultimately at the external range boundary (i.e. the outermost limit of occurrence) the species physiological and ecological requirements are not met (Brown 1984; Murphy et al. 2006). Although this theory has been widely discussed in the literature, surprisingly few studies have analyzed radial growth patterns of trees at southern range boundaries (Webb et al. 1993; Cook et al. 2001; Chhin et al. 2004). In this paper, we analyzed the radial growth of *Tsuga canadensis* (L.) Carr. for sensitivity to climate and disturbance events at its southern range limit in the southeastern USA.

Tsuga canadensis is a common component in Appalachian forests of eastern North America. The species exhibits many unique life-history characteristics. It is a gymnosperm that generally only co-occurs with angiosperm species. It is extremely tolerant of shade and often occurs in almost pure stands, especially on lower slopes and in stream valleys of Appalachian forests (Godman and Lancaster 1990; Kessell 1979; Ellison et al. 2005; Shankman and Hart 2007). *Tsuga canadensis* is also among the longest lived trees in the region with some individuals living for more than 500 years (Eastern OLDLIST 2009). The species is capable of long-term suppression under a closed canopy with sustained slow growth, but is capable of rapidly exploiting new resources after canopy disturbances (Kelty 1986; Foster and Zebryk 1993; Davis et al. 1996; Black and Abrams 2004). *Tsuga canadensis* is a noted foundation species that controls population and community dynamics and regulates ecosystem processes (Orwig et al. 2002; Ellison et al. 2005). Litter of *T. canadensis* decomposes slowly, which creates deep acidic humus with low rates of nitrogen mineralization and nitrification (Rogers 1978; Finzi et al. 1998; Lovett et al. 2004). *Tsuga canadensis* trees also have dense canopies and transpiration characteristics (e.g. year-round) that differ from co-occurring deciduous species (Catovsky et al. 2002; Ford and Vose 2006). These characteristics modify the quantity and quality of light, temperature, and moisture conditions of the understory environment, create conditions favorable for other species, and stabilize ecosystem processes (Hadley 2000; Rankin and Tramer 2002; Ellison et al. 2005).

The range of *T. canadensis* extends from southern Quebec and Ontario southward along the Appalachian Highlands to Georgia and Alabama (Fig. 1). Although the species is rather widespread, stand characteristics differ throughout its distribution (Ellison et al. 2005). Disjunct
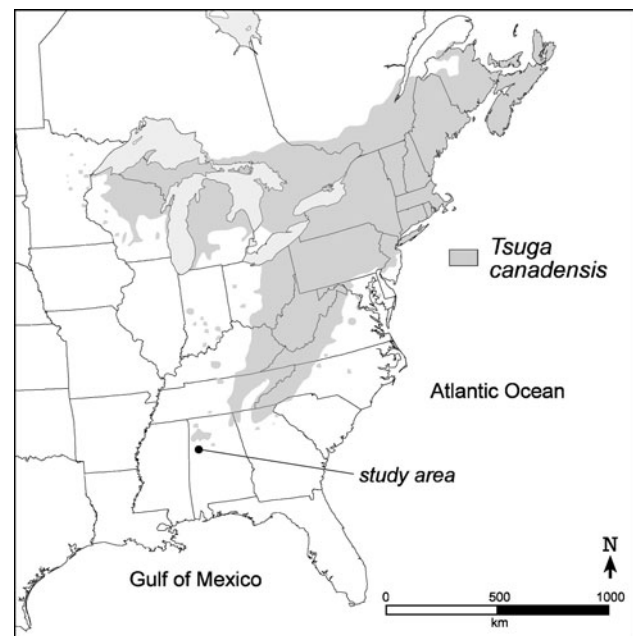

Fig. 1 Range of *Tsuga canadensis* and location of the study area in eastern North America

stands are common in the southern and western portions of its range and stand characteristics and abiotic conditions of some isolated stands have been studied (Segars et al. 1951; Harper 1952; Oosting and Hess 1956; Bormann and Platt 1958). The southern range limit of the species is represented by disjunct stands that are separated from the contiguous range by ca. 300 km.

The dendrochronological principle of ecological amplitude, predicts that individuals in disjunct stands outside the contiguous range of the species should be highly sensitive to climatic conditions and changes in the surrounding environment that may be caused by disturbance events. This prediction is based on the more general ecological concept of the abundant center distribution, which presumes the distribution of abundance of a taxon to be associated with multiple limiting environmental variables (Sagarin and Gaines 2002; Gaston 2003). Areas near the center of a species' geographic range are assumed to be most suitable for that species' survival, because few environmental variables are limiting. Suitable growing conditions are hypothesized to occur less frequently with increased distance from the range core; thus, species abundance should decline with increased distance from the range center (Brown 1984; Brown et al. 1995; Sagarin and Gaines 2002). In addition to abundance, other measures of vitality such as growth rate, reproductive rate, and productivity would also be expected to decline as the range limit is approached (Hengeveld 1990). At its southern range limit, *T. canadensis* only occurs where a rare suite of microenvironmental conditions, which are rare for the

region, exist. Although not quantified, field observation indicates these microenvironments are somewhat similar to conditions near the core of the range. Thus, trees in these disjunct stands at the southern boundary may not actually be sensitive to climate or more sensitive to climate than stands within the contiguous distribution. This observation originally led us to question the theory of ecological amplitude for this species and initiate this study. Quantitative information on the climate–growth relationships and sensitivity of trees at range limits may be especially useful for the management of the species under a changing climate (Cook and Cole 1991; Chhin et al. 2004; Pederson et al. 2004).

In addition to climate conditions, forest disturbance events may be strong controls on radial growth rates of trees. Disturbance effects may be especially influential on tree growth near range boundaries, where conditions are hypothesized to be more limiting. Thus, reconstructions of forest disturbance history are useful for our understanding of forest stand development patterns. In particular, information on the frequency, magnitude, and spatial extent of disturbance events in disjunct *T. canadensis* stands near its southern limit is lacking.

The overall purpose of our study was to document the influence of climatic conditions and forest disturbance events on the growth of *T. canadensis* at its southernmost extent. Our specific objectives were to (1) develop a master tree-ring chronology for *T. canadensis* at its southern range limit; (2) analyze the relationships between climate variables and radial tree growth; (3) statistically separate the influence of climate from that of forest disturbance in the tree-ring chronology; and (4) compare the sensitivity of stands at the southern range limit to those throughout the range and nearer the core of the contiguous distribution. Results were viewed in the context of ecological amplitude and climatic conditions limiting the southern extent of the species.

Materials and methods

Study area

We sampled *T. canadensis* individuals from three disjunct stands in Fayette County, Alabama in late-November of 2007 (Fig. 2). These *T. canadensis* stands all occurred along incised reaches of the Sipsey River with ca. 10 km separating the southernmost and northernmost stands studied. All three stands were located immediately upstream of the Fall Line, which separates the Appalachian Highlands from the Coastal Plain. All stands occurred on steep north to east facing slopes where a combination of sandstone outcrops, seepage, springs, permanent watercourses, and thick moss
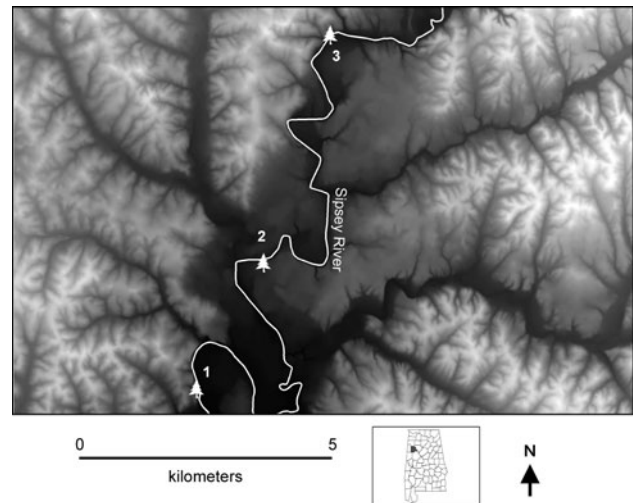

Fig. 2 Shaded relief map of the study sites in Fayette County, Alabama. *Tree symbols* represent locations of the three sampled stands at an elevation of ca. 120 m asl. *Higher elevations* on the map (indicated in *white*) are ca. 150 m asl. *Shaded area* on Alabama inset map is Fayette County

on the forest floor contributed to the habitat conditions required for growth and reproduction of *T. canadensis*.

These *T. canadensis* stands were quantified by Hart and Shankman (2005). In all sampled stands, *T. canadensis* dominated the canopy. Other canopy species included *Quercus alba* L., *Q. montana* Willd., *Fagus grandifolia* Ehrh., *Acer rubrum* L., and *Liriodendron tulipifera* L. Abundant understory species included *Kalmia latifolia* L., *Ilex opaca* Ait, *Juniperus virginiana* L., and *Magnolia macrophylla* Michx. These were small linear stands adjacent to the Sipsey River that ranged from ca. 90 to 130 m in length along the watercourse. All stands had discrete boundaries with a high density of *T. canadensis* trees within the stands and no isolated individuals outside of the stands. The stands consisted of 106–213 total individuals with the majority being seedling and understory trees (Hart and Shankman 2005). In all three stands, *T. canadensis* exhibited low numbers of individuals in the large diameter size classes and progressively higher numbers in the small diameter classes indicative of continuous regeneration.

Field and laboratory methods

We used increment borers to extract tree cores from all accessible *T. canadendis* individuals in the main forest canopy from the three study stands. We attempted to collect two cores per tree with each core sample separated by 180°. However, steep slopes made sampling difficult and in some cases only one sample could be safely collected. The majority of trees were cored parallel to slope contour to avoid the sampling of reaction wood in the radial growth patterns (Scurfield 1973; Fritts 1976; Grissino-Mayer

2003), however, three trees could only be safely sampled from the upslope portion of the bole. All cores were collected at ca. 30 cm above the root collar to maximize the number of annual growth rings (Grissino-Mayer 2003). Core samples were placed in labeled paper straws for storage and protection.

In the laboratory, all samples were allowed to air dry before they were glued to wooden core mounts. All cores were mounted with cells vertically aligned to provide a transverse view of the wood surface (Stokes and Smiley 1996). The cores were then surfaced with progressively finer sanding belts to reveal the cellular structure of the wood before dating (Orvis and Grissino-Mayer 2002).

Crossdating and chronology development

Growth rings on all core samples were visually inspected with the aid of a stereozoom microscope under 10× magnification for patterns of wide and narrow rings and other diagnostic characteristics that could be used to crossdate all series. Years with notable (e.g. unusually narrow or marker) rings and notable sequences of rings were recorded and compared to ensure these rings and patterns occurred across all core samples (i.e. the list method of crossdating; Yamaguchi 1991). Once crossdated, annual rings on each core were assigned calendar years starting with the first ring beneath the bark and continuing backward until the innermost ring or pith was reached, carefully noting troublesome areas of the cores identified during the crossdating process. All tree rings were then measured to the nearest 0.001 mm using a Velmex measuring stage interfaced with Measure J2X software. All measurement series were statistically analyzed as an additional check to ensure all growth rings were assigned the proper year of formation using the computer program COFECHA (Holmes 1983; Grissino-Mayer 2001a). The COFECHA program uses segmented time series correlation analyses to determine the strength of association between 50-year segments lagged 25 years from each individual series against a master chronology created from the remaining series. COFECHA removes all low-frequency trends using spline-fitting algorithms and autoregressive modeling to maximize the climate signal needed for accurate crossdating (Grissino-Mayer 2001a). Segments that fell below the predetermined significance threshold ($r = 0.32$, $P > 0.01$) were flagged by the program. All flagged segments were re-inspected for possible dating errors.

Crossdating quality was assessed by two statistical descriptors, the average mean sensitivity and the average interseries correlation. Mean sensitivity is a measure of the relative difference in the width of adjacent rings and is an indicator of climate sensitivity in the tree-ring record (Fritts

1976). The average interseries correlation is the average of all Pearson correlation coefficients calculated for each tree-ring series against the composite chronology once the series being tested is removed (Grissino-Mayer 2001a). The computer program ARSTAN was used to remove the age-related growth trend from each raw tree-ring series (Cook 1985). In ARSTAN, we standardized the raw measurement files by fitting a 30-year smoothing spline to the growth curve of each sample using the least squares technique. We chose the 30-year smoothing spline as a detrending option because this length removes the majority of non-climatic noise and approximates the default length of 32 years for detrending in COFECHA. This spline length was selected as the COFECHA default after experimenting with datasets from multiple regions, because it was shown to typically have the highest interseries correlations and therefore, strong correlations with climate data. Indeed, a 30-year smoothing spline was shown to be the best detrending option for another gymnosperm (*Pinus palustris* L.) in the southeastern USA (Grissino-Mayer 2001a). A 30-year spline may remove some low-frequency climate signal, but this is inevitable when trying to isolate a climate signal in closed canopy stands. Chronologies were developed by dividing the actual tree-ring measurements by the predicted values generated by the deterministic linear growth models fit to each individual series. Indices from all series were then averaged to create a single value for each year (Cook 1985). We used the three chronology types output by ARSTAN: (1) STANDARD (no further detrending other than by those methods listed above), (2) RESIDUAL (all low-frequency trends removed by autoregressive modeling), and (3) ARSTAN (low frequency trends built back in using autoregressive properties from the pooled dataset; Cook 1985).

Instrumental climate data

We analyzed the relationships between radial tree growth and climate using instrumental monthly mean temperature, monthly maximum temperature, monthly minimum temperature, monthly total precipitation, and monthly Palmer Drought Severity Index (PDSI) values. PDSI is used by the National Weather Service in the USA to monitor drought and wetness conditions. Dendroclimatological studies in eastern North America commonly use PDSI, because it is a good measure of available moisture conditions during the growing season (Cook et al. 1988, 1995; Cleaveland et al. 1992; Grissino-Mayer and Butler 1993; Dai and Trenberth 1998; Stahle et al. 1998). Data for monthly mean temperature, monthly total precipitation, and PDSI were obtained from the National Climate Data Center [National Climatic Data Center (NCDC) 2009]. We used divisional data rather than single station data because (1) our chronology was

developed from three separate sites, (2) average climate values typically have stronger relationships to tree growth, and (3) regional values are not biased by unique microclimatic conditions or recording histories (Blasing et al. 1981; Cook et al. 1995). Our study sites were located within the Upper Coastal Plain NOAA Climate Division (Division 3) of Alabama. Monthly maximum and minimum temperature data were obtained from the parameter-elevation regressions on independent slopes model dataset. The regression-based model uses interpolation of climate station data to create climate variable estimates (Daly et al. 1994, 2002).

Climate, biological, and response function analyses

Climatic variables that influence *T. canadensis* growth were assessed using both biological and statistical modeling. We calculated Pearson correlation coefficients using the STANDARD, RESIDUAL, and ARSTAN chronologies that were created with ARSTAN to determine which chronology had the strongest relationships with our climate datasets as measured by high variance explained by climate in our tree-ring chronologies. The three tree-ring chronologies were analyzed against the five climate variables over a 16-month period (previous July to current October; Fritts 1976).

The most recent 100 years of the STANDARD tree-ring chronology (1908–2007) were analyzed using correlation analysis and response function analysis (RFA) with the program PRECON (Fritts and Shashkin 1994). RFA was used in conjunction with correlation analysis to examine the climatic effects on ring widths by applying a multivariate, biological model of tree growth (Grissino-Mayer and Fritts 1995). The RFA examines the climatic effects on tree growth using principal components of the normalized climate dataset to remove the effects resulting from covariance among the independent climate variables (Grissino-Mayer et al. 1989). We included the growth indices from prior years to assess biological preconditioning in the tree-ring record (Grissino-Mayer and Fritts 1995). Biological preconditioning is the initiation of internal metabolic conditions that influence the growth or biochemical reactions in trees during their life spans (Fritts 1971, 1976). This is important as previous and current conditions influence the amount of carbon fixed and subsequently used for growth during the subsequent growing season (Kozlowski 1979; Kozlowski and Pallardy 1997; Gaudinski et al. 2009). RFA was conducted using the *T. canadensis* STANDARD chronology and 30 monthly variables: 15 variables for mean monthly temperature and 15 variables for monthly total precipitation. The 15 months began with the June of the previous year and ended with August of the current growing season.

We used PRECON to develop a 100-year time series plot that incorporated the results from the regression that modeled tree growth as a function of climate. The regression used the months with significant climate effects to show those periods during the twentieth century when tree growth was above or below that modeled from the climate variables entered as being statistically significant in the model. Actual growth departures from modeled growth may be attributed to non-climatic influences, which may include common ecosystem disturbances, such as windthrow and insect outbreaks. However, we acknowledge that unexplained growth is not necessarily non-climatic. We used PRECON to create residual chronologies (in this case actual tree growth minus predicted tree growth and not to be confused with the RESIDUAL chronology created by ARSTAN) in the twentieth century to distinguish the separate influences of possible disturbance periods and climate in *T. canadensis* tree growth. Creating such residual chronologies also allowed us to infer possible disturbance trends over the past 100 years based on departures of the modeled tree growth from actual tree growth.

Disturbance history

We used dendroecological techniques to document the frequency and spatial magnitude of disturbance events in the three studied stands. This information is useful to document the influence of disturbance events on radial growth patterns. Release episodes were defined as changes in raw-radial growth relative to a predetermined criterion and were documented using a percentage growth change equation (Nowacki and Abrams 1997; Rubino and McCarthy 2004). We analyzed changes in raw-ring widths with respect to the running median of the previous and subsequent 10 years. Release events were identified as periods in which raw-ring width was ≥50% of the 10-year running median, sustained for a minimum of 3 years (Rubino and McCarthy 2004). We used FHX2 software to graphically display spatial and temporal disturbance patterns within and across the three stands (Grissino-Mayer 1995, 2001b; Hart and Grissino-Mayer 2008).

Comparison of mean sensitivity

We used two approaches to determine if *T. canadensis* individuals at the species' southern extent were more sensitive to climate than *T. canadensis* individuals located nearer the core of the range. First, we calculated the average mean sensitivity for all *T. canadensis* tree-ring chronologies in the International Tree-Ring Data Bank (ITRDB). Average mean sensitivity is the mean sensitivity of all tree-ring series in a chronology and is included in the COFECHA output file. Second, we used a two-tailed *t*-test

to determine if the average mean sensitivity of our tree-ring chronology was statistically different from the nearest *T. canadensis* chronology within the contiguous range of the species. The nearest *T. canadensis* chronology was developed from individuals at Savage Gulf State Natural Area (SGNA) in Tennessee, ca. 300 km nearer the range center than the sampled stands in Alabama. *Tsuga canadensis* trees at SGNA used to build the tree-ring chronology were collected from an old-growth remnant near the upper end of the gorge where the species dominated the canopy and was abundant in the shrub layer along with *Rhododendron maximum* L. (Quarterman et al. 1972; DeSelm and Sherman 1982). In fact, species richness and diversity (*H'*) in this portion of SGNA was low because of the dominance of *T. canadensis* in the overstory and understory (DeSelm and Sherman 1982). The mixed mesophytic forest in the upper portion of the gorge at SGNA has been observed to more closely resemble the forests of the Cumberland Mountains (nearer the core of the *T. canadensis* range) than adjacent mixed mesophytic communities (Quarterman et al. 1972).

Results

Tree-ring chronology

A total of 41 tree core samples (from 23 trees) were collected from three *T. canadensis* stands (number of trees sampled per stand: 6, 5, and 12). Some core samples contained large amounts of rot and many of the cores were broken. Of the 41 core samples collected, 37 (from 22 trees) could be accurately crossdated. The interseries correlation of the 37 tree-ring series was statistically significant ($r = 0.48$, $P < 0.01$). A total of 128 50-year segments were analyzed with the COFECHA program. Of the 128 segments tested, 18 (14%) were flagged by the program indicating they were not statistically significant with contemporary segments. All flagged segments were re-inspected to confirm original visual crossdating. We are confident all tree rings from the 37 cores were dated correctly. Average mean sensitivity was 0.24. Of note, no missing or locally absent rings were assigned to any series.

The tree-ring record extended 198 years from 1810 to 2007. The composite chronology extended 158 years from 1850 to 2007 (Fig. 3). We truncated the first 40 years of the tree-ring record to ensure that the start of the chronology would have a sample depth of three tree-ring series (representing two trees). Sample depth increased to seven series (representing four trees) in 1858. The STANDARD chronology revealed a sustained period of above average growth from 1900 to the mid-1920s. A notable peak of above average growth occurred in the 1880s and notable below average growth occurred in the mid-1950s.
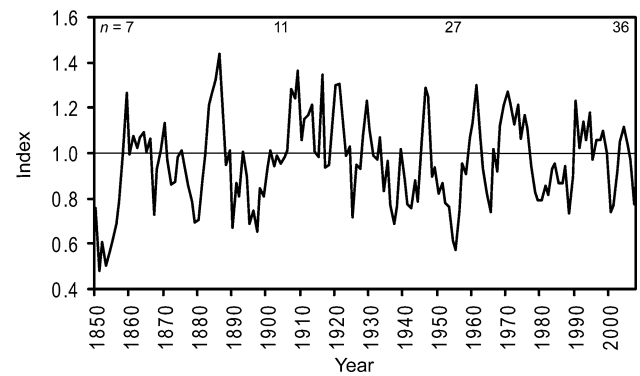

Fig. 3 Composite ring-width index generated from all *Tsuga canadensis* series sampled from three stands at its southern limit with mean growth standardized to 1.0 (*n* = number of series in that year)

Climate and disturbance influences

Radial growth of *T. canadensis* was significantly influenced by monthly climate variables. Correlation analysis of our climate variables against the STANDARD, RESIDUAL, and ARSTAN chronologies revealed similar results (i.e. similar months with significant relationships). However, the STANDARD chronology exhibited stronger relationships to the climate variables analyzed and more months with significant relationships. Significant negative relationships were found between the STANDARD chronology and monthly mean temperature, monthly maximum temperature, and monthly minimum temperature during the previous and current year summer (Fig. 4). Significant positive relationships were documented between the STANDARD chronology and monthly minimum temperature for September and October of the current year. Also, significant positive relationships were found between the STANDARD chronology and monthly total precipitation for September of the previous year and May of the current year (Fig. 5). Monthly PDSI showed a significant positive relationship to the STANDARD chronology for the entire 16-month period.

Preconditioning was an important influence on the annual growth of *T. canadensis*. The RFA showed 62% of the *T. canadensis* variance was explained by climate ($r^2 = 0.22$) and prior growth ($r^2 = 0.40$). Specifically, the RFA showed a significant positive relationship between *T. canadensis* growth and the previous year's October and current year's February precipitation. We also found a strong negative relationship between *T. canadensis* growth and previous year August temperature (Fig. 6).

The influence of twentieth century disturbance patterns on *T. canadensis* growth was evident in the residual chronology developed using PRECON to examine the periodicity of departures from mean ring width independent of the climate variables (Fig. 7). The time series plot
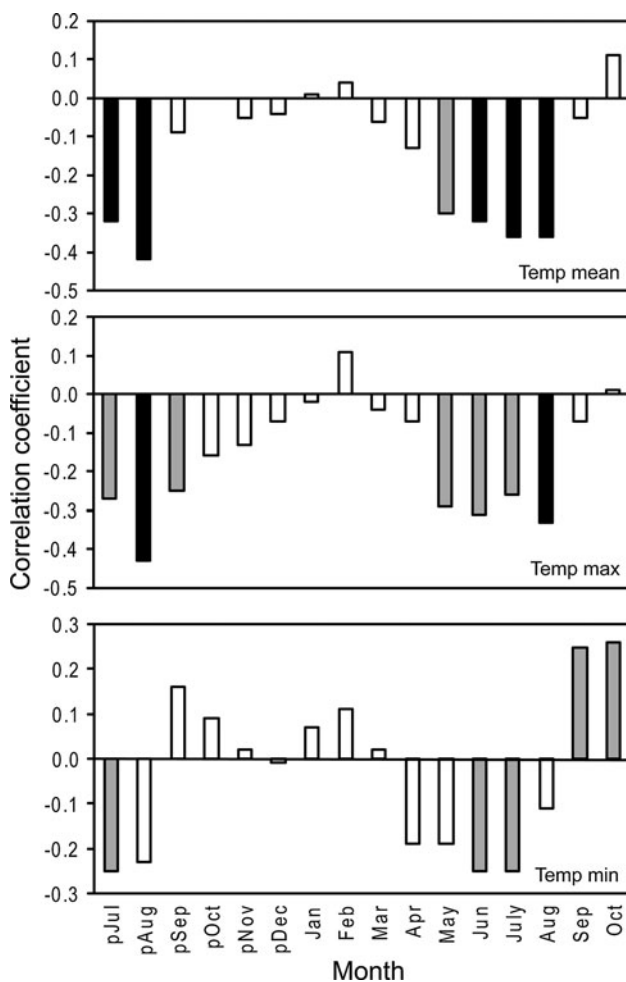
Fig. 4 Correlation analysis between the STANDARD tree-ring chronology and temperature variables. *Temp mean* monthly mean temperature, *Temp max* monthly maximum temperature, *Temp min* monthly minimum temperature. Month abbreviations preceded by 'p' indicate the previous year. *Solid bars* indicate significance values of $P < 0.01$ and *gray bars* indicate significance values of $P < 0.05$. Note that the *y*-scale varies
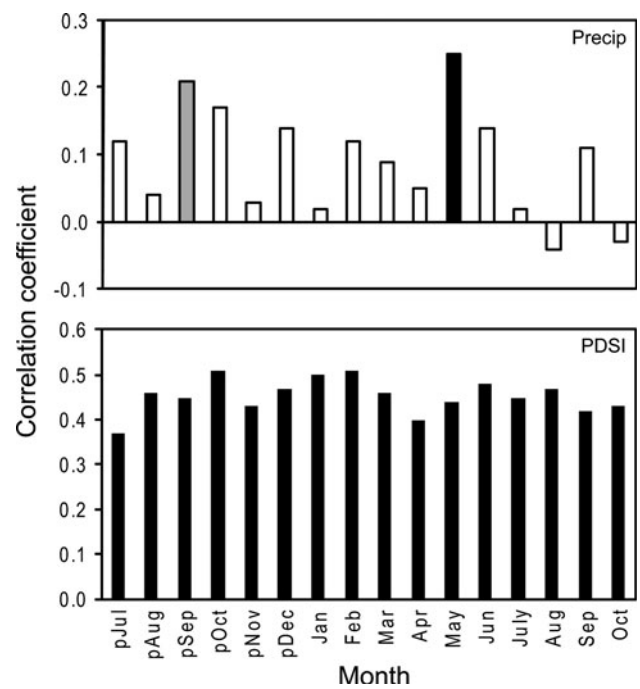

Fig. 5 Correlation analysis between the STANDARD tree-ring chronology and precipitation variables. *Precip* monthly total precipitation, *PDSI* Palmer drought severity index. Month abbreviations preceded by 'p' indicate the previous year. *Solid bars* indicate significance values of $P < 0.01$ and *gray bars* indicate significance values of $P < 0.05$. Note that the *y*-scale varies

for our *T. canadensis* chronology indicated that actual growth agreed relatively well with predicted growth, although positive departures (indicating likely non-climate growth increases) were found in 1920, 1929, 1946, 1961, 1970, and 1990.

Disturbance history was only analyzed for the 22 *T. canadensis* trees that could be crossdated with confidence. Of the 22 trees analyzed using the 10-year running median method, 14 (64%) exhibited release events. A total of 18 release events were detected from the 14 individuals (Fig. 8). Multiple release episodes were documented in three individuals, with one tree experiencing three separate release events during its life. Radial growth releases of greater than 100% over the 10-year running median sustained for a minimum of 3 years were documented in two individuals. Both of these releases were sustained for just

3 years and occurred in the same stand. Of note, these two releases with growth changes of over 100% were not contemporary with one another as one occurred in the late 1970s and the other in the late 1950s. Most episodes were short lived with the longest sustained release being 8 years. The mean release duration was 4.29 years ± 1.15 (SE). When release events were analyzed across the three stands the spatial magnitude of the events could be inferred. Three release episodes occurred simultaneously in more than one stand. Of these three episodes, one in the mid-1940s was evident in at least one tree from all three stands (Fig. 8). Also, the two releases with a growth change greater than the 100% threshold were contemporary with release events in other stands.

Comparison of mean sensitivity

The average mean sensitivity of *T. canadensis* in the disjunct stands was not significantly different from other stands within the contiguous distribution of the species (Table 1). Average mean sensitivity of all 46 *T. canadensis* tree-ring chronologies in the ITRDB was 0.24 ± 0.005 (SE) with a maximum value of 0.34 and a minimum value of 0.19. The chronology with the highest average mean sensitivity was developed from individuals in Michigan while the chronology with the lowest average mean

Fig. 6 Results from the response function analysis (RFA) showing the effects of temperature and precipitation (1908–2007) on *Tsuga canadensis* growth. Statistically significant relationships are indicated by *Asterisk* ($P < 0.05$). On the *x*-axis Y1, Y2, and Y3 indicate effects of growth for one (Y1), two (Y2), and three (Y3) years prior
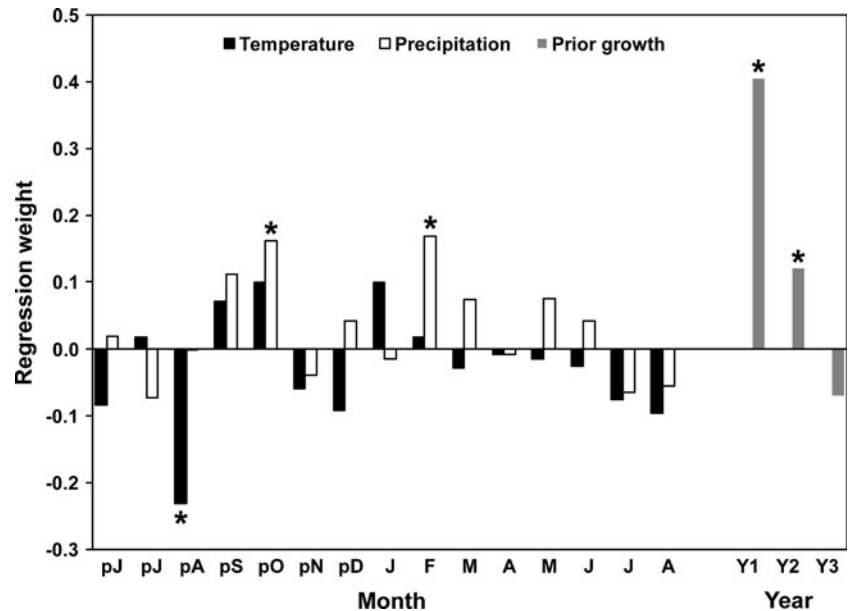

Fig. 7 Actual and estimated indices of tree growth and residuals developed for *Tsuga canadensis* individuals at its southern range limit. "Actual" indicates the actual *T. canadensis* growth (the STANDARD chronology), "estimated" indicates the estimated annual *T. canadensis* growth based on the significant climate variables, and "residual" is the difference between the actual and estimated chronologies. *Vertical gray bars* indicate periods of disturbances beyond the stand scale
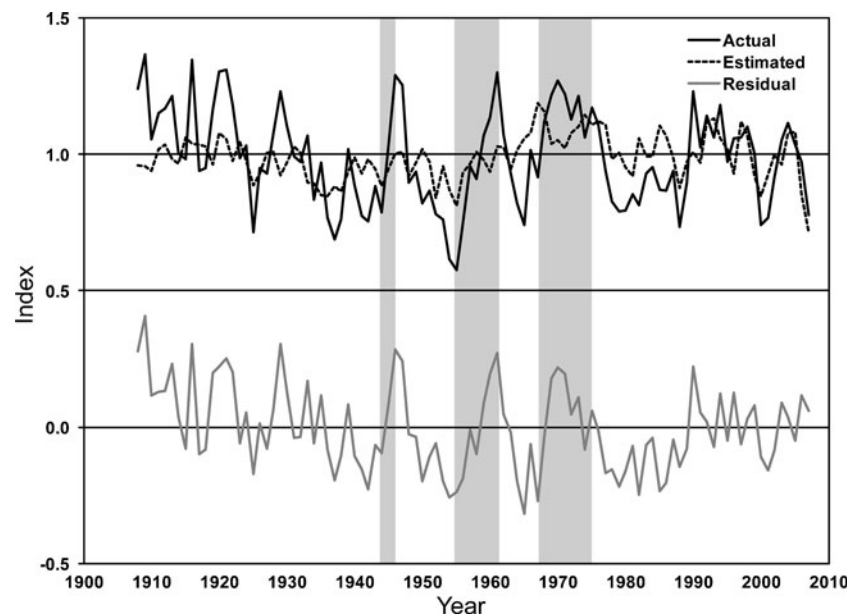

sensitivity occurred in North Carolina. Average mean sensitivity of the chronology developed in this study was 0.24, indistinguishable from the average mean sensitivity of all *T. canadensis* chronologies in the ITRDB. Mean sensitivity of the Alabama chronology was not statistically different ($P < 0.05$) from mean sensitivity of the Tennessee chronology from SGNA.

Discussion

Tree-ring series from the three disjunct *T. canadensis* stands showed strong agreement as the interseries

correlation of the tree-ring chronology was well above the minimum significance level required for confident cross-dating. Consistent annual ring width patterns over large spatial areas typically indicate regional climate has an important influence on tree growth (Fritts 1976; Fritts and Swetnam 1989). Indeed, statistically significant relationships were documented between regional climate variables and the *T. canadensis* chronology. The results of the correlation analyses and RFA were not in complete agreement. This is not necessarily surprising as the two methods are quite different. RFA performed in PRECON is a biological model that orthogonalizes all input climate variables and removes interdependence among them, unlike correlation

Fig. 8 Release events using the 10-year running median method for 22 *Tsuga canadensis* individuals sampled from three stands in Fayette County, Alabama. Each horizontal line represents the record from one individual tree, *long vertical bars* indicate release initiation, and *short vertical bars* indicate release duration. A composite of release events for all stands is shown across the bottom. *Gray bars* indicate release episodes that occurred in more than one stand
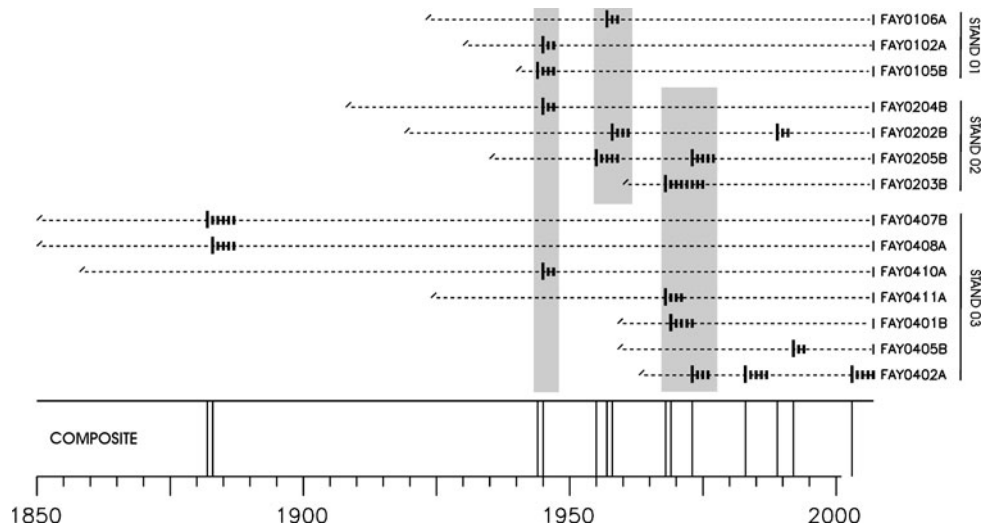
analysis. As such, it builds a model with multiple climate variables that affect tree growth. While RFA is more robust, because the climate variables are no longer dependent on each other, the methods are complementary.

The RFA revealed that precipitation in October of the previous year and February of the current year exerts a strong influence on radial growth. Precipitation in the region is limited in autumn and October is typically the driest month (NCDC 2009). A strong relationship exists between plant water status and photosynthesis rates for *T. canadensis* (Hodges and Scott 1968; Adams and Loucks 1971). Although October is late in the growing season, we have observed that many if not most deciduous tree species may retain green foliage well into November in this region and we speculate October precipitation influences autumn phenology. Relationships with February precipitation of the current year are likely related to water availability prior to the main growing season. As an evergreen species, *T. canadensis* can fix carbon outside of the main growing season. In fact, *T. canadensis* trees have been shown to fix ca. one-third of their annual carbon outside of the main growing season and to begin annual growth up to 2 months before that of co-occurring deciduous species (Catovsky et al. 2002). Thus, February precipitation may be important for growth in the early spring. Also, some of this precipitation may be stored in the porous sandstone bedrock, which may be made available during the dry summer months (Lacefield 2000). Positive relationships between *T. canadensis* growth and precipitation of the current summer and prior fall have been documented in other studies focused on the northern portion of its range (Cook and Jacoby 1977; Abrams et al. 2000; D'Arrigo et al. 2001). The results of the PDSI correlation analyses are most likely related to the high degree of autocorrelation that exists in the index. The contribution of each successive month is given an increasing weight up to the month for

which the index is calculated so the contribution of each month may not be an accurate representation (Blasing et al. 1988). Other studies of gymnosperms in the southeastern US have also found strong relationships between PDSI and tree growth (Grissino-Mayer and Butler 1993; Foster and Brooks 2001; Henderson and Grissino-Mayer 2009). Nevertheless, we contend that the relationship between PDSI and radial growth of *T. canadensis* illustrated that the species is sensitive to moisture conditions at its southernmost limit and supports prior work that suggested *T. canadensis* in the southern portion of its range is an ecotype more responsive to moisture stress (Kessell 1979).

Significant negative relationships between our *T. canadensis* chronology and August temperature of the previous year were also found. August is typically the warmest month in the region (NCDC 2009). The optimum temperature range for photosynthesis of *T. canadensis* is narrow and when temperatures exceed the optimum range the rate of net photosynthesis declines with increased temperature (Adams and Loucks 1971). Thus, air temperature is important for net carbon dioxide fixation by the species. Because August is generally the warmest month of the year, we speculate that August temperatures often exceed the optimum range for photosynthesis and are an important control on tree productivity. Cook and Cole (1991) hypothesized that the temperature response of *T. canadensis* is site-independent as the species has been shown to have a negative response to prior summer temperatures at multiple sites throughout its range. Our results at the species' southern range boundary are consistent and support this hypothesis.

Prior growth explained more variance in the tree-ring record than temperature and precipitation variables. Conditions prior to the current growing season influence the amount of carbon fixed and used for growth (Kozlowski 1979; Kozlowski and Pallardy 1997; Gaudinski et al. 2009).

Table 1 Location, average mean sensitivity, and contributor(s) of the *Tsuga canadensis* tree-ring chronologies used from the International Tree-Ring Data Bank (http://www.ncdc.noaa.gov/paleo/treering.html)

State/province, country	Latitude	Longitude	Avg mean sens	Contributor(s)
North Carolina, USA	35.28	−83.93	0.187	Barefoot
Pennsylvania, USA	41.33	−77.72	0.188	Cook
Virginia, USA	38.33	−79.33	0.196	Cook
Pennsylvania, USA	41.75	−78.97	0.197	Cook
Virginia, USA	38.30	−79.35	0.202	Puckett and Phipps
Pennsylvania, USA	40.67	−77.70	0.202	Cook
Pennsylvania, USA	40.88	−77.32	0.210	Cook
New York, USA	41.77	−74.18	0.212	Cook
Virginia, USA	37.50	−79.52	0.216	Cook
Virginia, USA	36.67	−81.67	0.217	Cook
New York, USA	41.77	−74.18	0.220	Cook
Virginia, USA	38.97	−77.20	0.222	Puckett and Phipps
Pennsylvania, USA	41.87	−75.88	0.223	Cook
Tennessee, USA	35.67	−83.50	0.227	Young
Pennsylvania, USA	40.23	−77.65	0.227	Cook
New Hampshire, USA	44.22	−71.40	0.231	Cook
Nova Scotia, CAN	44.82	−64.00	0.232	Cook
Connecticut, USA	41.97	−73.22	0.232	Cook
North Carolina, USA	35.08	−83.18	0.234	Cook
Vermont, USA	44.03	−72.83	0.234	Cook
Pennsylvania, USA	41.37	−76.30	0.234	Cook
Pennsylvania, USA	39.83	−79.70	0.235	Cook
New York, USA	41.77	−74.17	0.237	Cook
Virginia, USA	38.63	−77.30	0.239	Puckett and Chittenden
North Carolina, USA	35.35	−83.92	0.242	Cook
Tennessee, USA	35.75	−83.23	0.243	Young, Keeland, and Nunes
Pennsylvania, USA	41.22	−74.92	0.245	Cook
Maine, USA	45.50	−68.28	0.247	Cook
New York, USA	44.13	−73.78	0.248	Cook
Maine, USA	45.32	−68.25	0.248	Cook
Tennessee, USA[a]	35.45	−85.57	0.250	Cook and Pederson
New York, USA	43.55	−73.80	0.256	Cook
Pennsylvania, USA	39.83	−78.52	0.257	Cook
Michigan, USA	46.32	−86.62	0.260	Cook
Connecticut, USA	41.95	−73.22	0.262	Cook
Massachusetts, USA	42.62	−72.97	0.265	Cook
Virginia, USA	38.47	−78.47	0.270	Dougherty
Michigan, USA	46.47	−84.87	0.272	Cook
Quebec, CAN	46.63	−71.88	0.280	Cook
Maine, USA	46.23	−69.00	0.280	Cook
Michigan, USA	46.72	−89.97	0.285	Cook
Ontario, CAN	45.17	−78.75	0.286	Cook
Michigan, USA	46.70	−88.75	0.287	Cook
New York, USA	44.13	−73.75	0.295	Cook
Wisconsin, USA	45.10	−88.88	0.302	Cook
Michigan, USA	46.20	−89.30	0.338	Cook

[a] Tree-ring data from Savage Gulf Natural Area, Tennessee

The influence of prior growth was evident for up to 2 years. Thus, the effects of a drought (such as the drought of 2007) may be evident in the tree-ring record for up to 2 years after the event. Preconditioning has been noted in other climate–growth studies focused on *T. canadensis* (Avery et al. 1940; Cook and Jacoby 1977; D'Arrigo et al. 2001).

Disturbance was also an important control on annual growth of *T. canadensis* in these stands. Patterns of disturbance were interpreted from the synchrony of disturbance events affecting the three sampled stands. Three separate disturbance episodes influenced individuals in more than one stand and one episode in the 1940s was apparent across all stands. These release episodes in the tree-ring record were possibly caused by strong winds. Windthrow is a common occurrence in many *T. canadensis* stands (Davis et al. 1996) and is the most dominant disturbance mechanism in the study stands (Hart and Shankman 2005). Strong winds in the region often result from extreme low pressure systems or frontal movement. The ability of *T. canadensis* to survive long periods in the understory of a closed canopy forest with slow growth and to rapidly respond with increased growth after localized canopy disturbances has been well documented (Abrams et al. 2000; Black and Abrams 2004, 2005). However, our results show that disturbances beyond the stand scale (i.e. non-localized events) also exert an influence on annual radial growth of the species. Growth responses related to coarse-scale disturbance events may be a characteristic of disjunct stands in the region and may not be indicative of conditions through the entire range.

The average mean sensitivity of our chronology was within the range expected for tree-ring series of the eastern US (DeWitt and Ames 1978). Additionally, mean sensitivity was not significantly different between these disjunct stands and a stand within the contiguous distribution of the species. The theory of ecological amplitude suggests that mean sensitivity would be high because the sampled individuals were located at the range limit of the species and would thus be sensitive to even subtle environmental changes. However, the stands studied were all located along permanent watercourses and on sites where seepage from the sandstone bedrock was common. Thus, we propose that microenvironmental conditions did not favor the documentation of slight changes in the year-to-year availability of water and may have reduced annual variability in ring width. However, in this region the species only occurs on sites with these microenvironmental conditions. Sensitivity of individuals at the species' southern range limit was not statistically different from individuals ca. 300 km nearer the range core and within the contiguous distribution. Interestingly, we noted no missing rings in *T. canadensis* series at the species' southern limit, while missing or locally absent rings were noted in the Tennessee chronology. We would expect to document such rings in

individuals at range boundaries that theoretically represent trees at physiological limits. This fact may provide additional evidence against the theory of ecological amplitude.

The species is known to occur in almost pure stands on sites where a suite of favorable environmental conditions exist, which include microclimatic conditions (Kavanagh and Kellman 1986; Godman and Lancaster 1990; Ellison et al. 2005; Hart and Shankman 2005; Lovett et al. 2006). While all species only occur on sites where conditions are within a required range and they can compete for necessary resources, *T. canadensis* occurs in almost pure stands when specific conditions are met, even at its external range limit. *Tsuga canadensis* may become relatively more sensitive to climate at any location in its range where one or more climatic variables are not optimal. Perhaps ecological amplitude for *T. canadensis* should be viewed on a local or regional scale rather than over the entire range of the species. In reality, environmental gradients occur throughout the distribution of a species and result in internal boundaries as most species are not ubiquitous within their external limits (Gaston 2003). We suggest that the microclimates of *T. canadensis*-dominated stands at the range extent may closely resemble conditions near the range center and are not necessarily more sensitive to climate than individuals nearer the range core. As further evidence, *T. canadensis* has been shown to be responsive to climate throughout its distribution (Cook and Jacoby 1977; Cook and Cole 1991; Abrams et al. 2000; D'Arrigo et al. 2001). While the climatic response of the species varies spatially (Kessell 1979; Cook and Cole 1991), the sensitivity of the species to climate conditions appears to be similar. Our primary goal was to test the theory of ecological amplitude using climate–growth relationships and sensitivity of *T. canadensis* trees in disjunct stands at its southernmost extent. Ecological amplitude theory does not hold true for this species based on our results.

Our findings also provide information on the possible factor or factors that may limit the southern distribution of the species. Based on the climate–growth relationships documented, we suggest that late-summer temperature and previous autumn and current spring and summer precipitation may influence the southern extent of *T. canadensis*. Shankman and Hart (2007) proposed that its southern limit was controlled by microclimatic and soil moisture conditions related to topography. The southern boundary of the species coincides with the terminus of the Appalachian Highlands where streams are incised and local relief of stream valleys is relatively high. Suitable sites for regeneration of the species do not occur on the relatively flat Gulf Coastal Plain where streams migrate laterally across broad floodplains. Our results do not contradict their hypothesis as *T. canadensis* stands near the southern boundary only occur on north to east facing slopes with

exposed sandstone that border permanent watercourses. These stands, however, are sensitive to climate. The occurrence of *T. canadensis* on these sites is likely related to topographic influences on microclimate conditions.

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