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Structure and dendroecology of *Thuja occidentalis* in disjunct stands south of its contiguous range in the central Appalachian Mountains, USA

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Abstract

Background: Information on forest structure, growth, and disturbance history is essential for effective forest management in a dynamic landscape. Because most of our research concerning the ecology and growth of *Thuja occidentalis* comes from sites in northern portions of its range, highly contextual biotic and abiotic factors that affect the species in more southern locales may not be fully accounted for. This research characterized the structural attributes and growth dynamics of *Thuja occidentalis* in disjunct forest stands south of its contiguous range margin.

Methods: The *Thuja occidentalis* forests examined in this research were located in the central Appalachian Mountains, USA, approximately 440 km south of the contiguous range margin of the species. Forest structural attributes were characterized in two *Thuja occidentalis* forest stands, which are rare in the region. Tree-ring chronologies were used to examine the influences of disturbance and climate on the growth of *Thuja occidentalis*.

Results: The forests contained a total of 13 tree species with *Thuja occidentalis* contributing substantially to the basal area of the sites. *Thuja occidentalis* stems were absent in the smallest size class, while hardwood species were abundant in the smallest classes. *Thuja occidentalis* stems also were absent from the < 70 years age class. By contrast, *Thuja occidentalis* snags were abundant within stands. Growth-release events were distributed across the disturbance chronology and generally affected a small number of trees. The *Thuja occidentalis* tree-ring chronology possessed an interseries correlation of 0.62 and mean sensitivity of 0.25. The correlation between mean temperature and *Thuja occidentalis* growth was weak and variable. Growth and moisture variables were more strongly correlated, and this relationship was predominantly positive.

Conclusions: Structural attributes indicate the forests are in the understory reinitiation stage of forest development. Silvicultural manipulations may be necessary to promote *Thuja occidentalis* establishment. The sensitivity of *Thuja occidentalis* to climate appears similar throughout its range, but geographical variation in the growth response to climate factors is apparent. More research is necessary to expand the geographical and ecological scope of our knowledge concerning *Thuja occidentalis*, particularly at more southern and disjunct sites.

Keywords: Northern white cedar, Disturbance, Climate, Range, Disjunct, Radial growth, Regeneration

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Background

Information on stand structure, growth, and disturbance history is essential to our understanding of patterns and processes in forest ecosystems. By examining the structural attributes and radial growth patterns of trees, we can quantitatively characterize conditions that have influenced forest stand development (Lorimer 1980; Frelich and Lorimer 1991; Hart and Grissino-Mayer 2008; Hart et al. 2012). The range of variation elucidated by quantitative data facilitates more effective forest management in a landscape affected by both anthropogenic activities and climate change (Kincaid and Parker 2008; Hart et al. 2010; Hart et al. 2012). Climate change is expected to greatly reduce suitable habitat for many tree species in eastern North America. Climate coupled with factors such as disturbance and competition can affect the physiology and growth of trees, including processes such as regeneration and recruitment (Paul et al. 2014). Under various climate change scenarios, one of the most impacted tree species will be northern white cedar (*Thuja occidentalis* L.) (Iverson et al. 2008).

T. occidentalis, also known as arborvitae, is a shade-tolerant coniferous tree species of eastern North America. This slowing growing tree commonly reaches heights of 12–15 m and diameters ranging from 30 to 60 cm (Johnston 1990). Although individuals exceeding 1000 years of age have been documented in Canada, the typical lifespan for *T. occidentalis* is 80–400 years (Larson 2001). The species tolerates a range of substrates, but growth is maximized on moist, well-drained soils derived from calcareous bedrock (Johnston 1990). *T. occidentalis* occurs in mixed to pure stands throughout its contiguous range, which extends across southeastern Canada and the northeastern United States. Isolated, disjunct stands exist beyond the contiguous range margin as far south as North Carolina and Tennessee (Braun 1950; Caplenor and Speir 1975; Walker 1987), but are rare in the central Appalachian Mountains (Fleming 1999; Fleming and Coulling 2001).

It is a common assumption that environmental conditions experienced by marginal or disjunct populations are more stressful or different than those experienced by core populations (Lesica and Allendorf 1995; Hardie and Hutchings 2010; Hart et al. 2010). If marginal populations are adapted to more stressful or different biotic and abiotic conditions, they may have high conservation value as evolutionary legacies or components of biodiversity (Hoffmann and Blows 1994; Allendorf et al. 1997; Hardie and Hutchings 2010). Several studies have examined *T. occidentalis* forest structure and growth in northern portions of the range, including in disjunct populations (e.g. Kelly et al. 1994; Tardif and Stevenson 2001; Kipfmueller et al. 2010; Grotte et al. 2012; Ruel et al. 2014). However, research examining *T. occidentalis* forests south of their contiguous range margin has been limited to examinations of ecological community characteristics and population genetics (Walker 1987; Young 1996; Fleming 1999; Fleming and Coulling 2001).

The overall goal of this research was to document the structural attributes and radial growth dynamics of *T. occidentalis* in disjunct stands south of its contiguous range margin. There were three specific objectives for this research: 1) to quantify stand structural attributes; 2) to reconstruct the history of *T. occidentalis* growth-release events; and 3) to characterize the relationship between *T. occidentals* radial growth and climate.

Study area

This study was conducted in Rockingham County, Virginia (38.6363 N, −78.8502 W) located in the northern Shenandoah Valley, USA (Fig. 1). Rockingham County lies within the Ridge and Valley Physiographic Province, which is characterized by long, linear ridges separated by valleys with a trellis drainage pattern. Bedrock consists of Paleozoic sedimentary rocks (Fenneman 1938). Mean total precipitation in the study area is 852 mm, 61 % of which occurs during the months of May through October. The mean annual temperature is 13 °C (SERCC 2016).

Braun (1950) classified the study area as part of the Ridge and Valley Section of the Oak-Chestnut Forest Region, but the area is a transitional zone with elements of the mixed mesophytic and oak-chestnut regions. More recently the area was classified as the Appalachian Oak Section of the Mesophytic Forest Region with indicator species including *Quercus alba*, *Quercus prinus*, *Liriodendron tulipifera* and *Pinus virginiana* (Dyer 2006). *T. occidentalis* forest stands in the region are typically small (~0.1 to 1.0 ha), isolated, and extremely rare. In Virginia, *T. occidentalis* forests tend to be confined to north-facing slopes and cliffs with calcareous bedrock (Fleming 1999; Fleming and Coulling 2001). The disjunct *T. occidentalis* stands examined in this research are located approximately 440 km south of the contiguous range margin.

Methods

Structural attributes were obtained from 10 0.01 ha circular plots in each of two *T. occidentalis* forest stands ($n = 20$ plots). Plot centroids were established every 10 m along a randomly placed transect in each stand. Each transect was situated at the mid-slope position and parallel to slope contours to avoid forest and environmental transitions. Two transects were adequate for data collection because both stands were oblong in extent and located on steep slopes. In each plot, species, diameter at breast height (dbh = 1.4 m) of all stems ≥ 2.5 cm dbh, and snag abundance were recorded. The

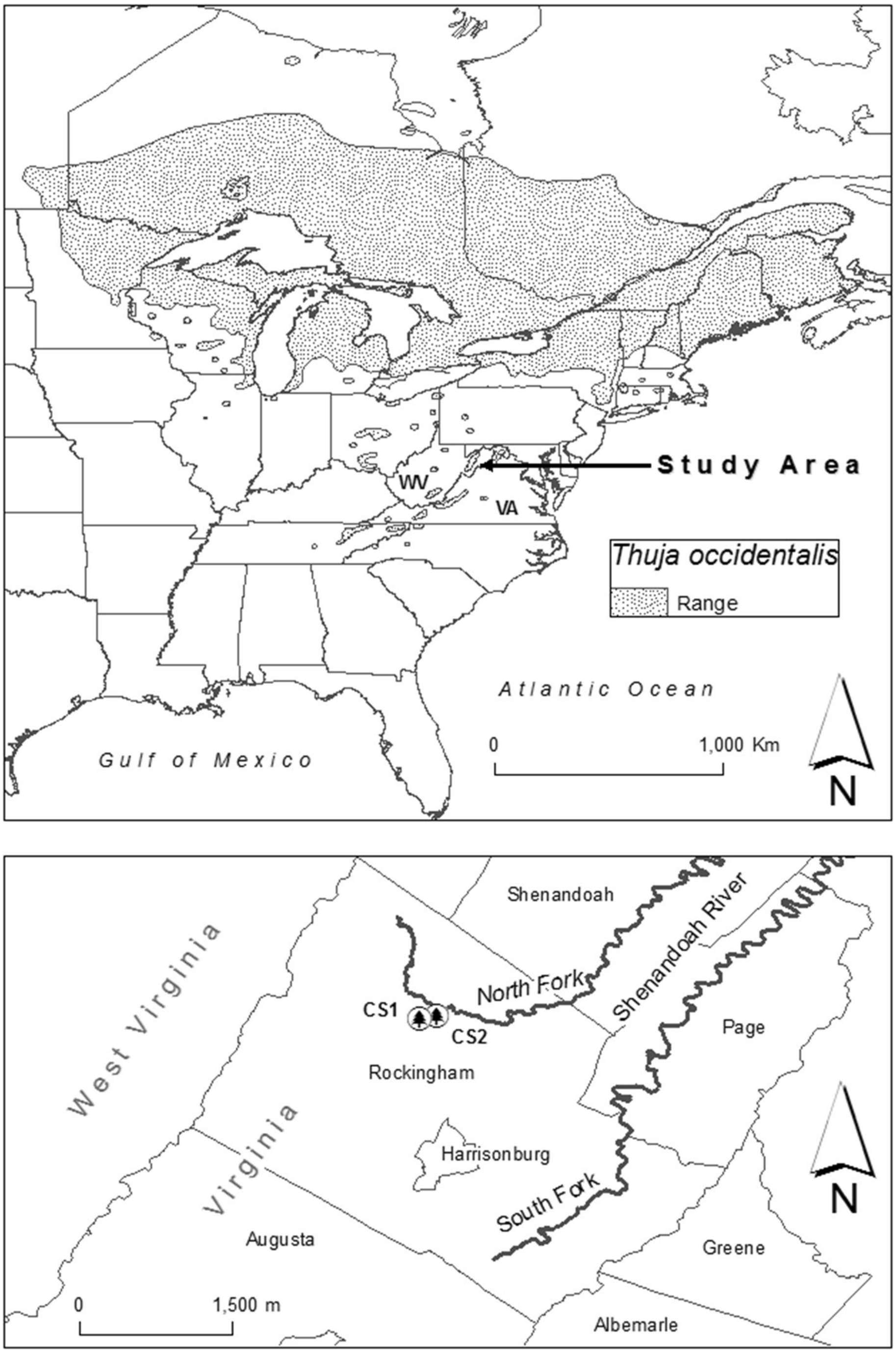

Fig. 1 Map showing the range of *Thuja occidentalis* and study area (see Additional file 1 for high resolution)

point-quarter method was used at plot centroids to systematically select canopy trees for the collection of increment cores (Cottam and Curtis 1956). In some cases steep terrain restricted sampling to trees that could be safely cored at breast height. A total of 42 trees were examined in this research.

In the laboratory, all increment 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 inspected and crossdated using the list method (Yamaguchi 1991). Ring-widths were measured to the nearest 0.001 mm using a Velmex measuring stage and Measure J2X software. The visually crossdated measurement series were statistically verified using the computer program COFECHA (Holmes 1983; Grissino-Mayer 2001).

I used standard dendroecological techniques to reconstruct the history of *T. occidentalis* growth-release events in each stand (Lorimer and Frelich 1989; Nowacki and Abrams 1997; Rubino and McCarthy 2004). Raw tree-ring measurements were analyzed using a 10-year running median and percent-increase equation (Nowacki and Abrams 1997; Rubino and McCarthy 2004). Minor release events were defined as median growth increases between 25 % and 49.9 %. Major releases were defined as median growth increases of ≥ 50 %. The temporal distribution of growth-release events detected using the ≥ 50 % growth threshold was not significantly different ($t = 1.36$; $p = 0.20$) than the distribution observed using the absolute increase threshold (≥0.41 mm) of Fraver and White (2005). Only growth-release events sustained for a minimum of 3 years were recorded in this research (Rubino and McCarthy 2004). The growth-release data were used to construct a decadal disturbance chronology detailing the history of *T. occidentalis* growth-release events in each stand.

In preparation for the analysis of *T. occidentalis* growth-climate interactions, I used the computer program ARSTAN to standardize the raw tree-ring measurements with a 30-year cubic smoothing spline. Standardization removes the effects of tree age and forest disturbance and allows for the comparison of trees with different growth rates (Cook 1985). Pearson correlation analysis was used to examine the relationship between climate and the *T. occidentalis* standard chronology. Climate data for Virginia Climate Division 5 were retrieved from the National Climate Data Center (NCDC 2015). Division 5 data were interpolated from stations using a 5 km grid resolution to ensure adequate spatial sampling. The climate variables examined in this research included monthly mean temperature, monthly total precipitation, and monthly Palmer Drought Severity Index (PDSI) for the current and previous year. The PDSI is commonly used in climate-tree growth research because it integrates measures of soil water, precipitation, and temperature, and more closely reflects the conditions required for tree growth than a single variable alone (Henderson and Grissino-Mayer 2009). The *T. occidentalis* radial growth-climate relationship was analyzed using a 17-month window extending from 1895–2010.

Results

Forest structural attributes

The *T. occidentalis* forest stands contained a total of 13 tree species with a mean stand density of 915 ± 219.2 stems/ha (Table 1). Total stand basal area averaged 54.3 ± 12.4 m^2/ha with *T. occidentalis* contributing substantially to the basal area of the sites. The importance values for *T. occidentalis* at CS1 and CS2 were 82.2 % and 52.5 %, respectively. *Tilia americana* comprised a distinct second tier at CS2 where the relative dominance of the species was 21.7 %. Species of tertiary importance at CS1 and CS2 included *Liriodendron tulipifera*, *Fraxinus americana*, *Ailanthus altissima* and *Pinus strobus*.

Table 1 Compositional characteristics by forest stand

Site	Species	*D*	BA	IV
CS1	*Thuja occidentalis* L.	830	54.8	82.2
	Quercus muehlenbergi Engelm.	40	0.5	2.3
	Liriodendron tulipifera L.	40	3.6	4.7
	Ostrya virginiana (Mill.) K. Koch	50	0.2	2.5
	Cercis canadensis L.	20	0.1	1.0
	Acer saccharum Marshall	10	0.5	0.9
	Pinus strobus L.	50	2.3	4.2
	Fraxinus americana L.	30	1.1	2.3
CS2	*Thuja occidentalis* L.	310	29.2	52.5
	Tilia americana L.	60	9.9	14.8
	Cercis canadensis L.	110	0.2	7.5
	Ostrya virginiana (Mill.) K. Koch	140	1.5	10.9
	Cornus florida L.	10	0	0.7
	Hamamelis virginiana L.	20	0	1.3
	Ailanthus altissima (Mill.) Swingle	20	1.9	3.3
	Juglans nigra L.	10	0	0.7
	Acer saccharum Marshall	20	0.9	2.3
	Fraxinus americana L.	60	1.9	6.0

Columns refer to density (*D*, stems/ha), basal area (BA, m^2/ha), and importance value [IV = (relative density + relative basal area)/2]

The size distribution of stems within the stands varied from unimodal or bimodal to multimodal structures (Fig. 2). At CS1 the size distribution approximated a unimodal structure with the number of *T. occidentalis* stems peaking in the 20–25 cm size class. No *T. occidentalis* stems were present in the smallest size class. *L. tulipifera*, *P. strobus*, and the "other hardwood" group exhibited a bimodal structure of stems at CS1. *F. americana* occupied the intermediate size classes from 10–30 cm at both sites. The size distribution of *T. americana* was distinctly multimodal, while *A. altissima* exhibited a bimodal distribution of stems at CS2. *T. occidentalis* peaked in the largest size class at CS2, but was absent from the smallest class. The number of "other hardwood" stems was greatest in the smallest size classes at both sites.

The absence of *T. occidentalis* stems in the smallest size class at both sites was reflected in the age distribution of the species. The number of *T. occidentalis* stems peaked in the 90–110 year age-classes, while stems less than 70 years old were absent from the stands. Aside from sapling snags, there was no evidence of recent *T. occidentalis* establishment and recruitment in the understories of CS1 or CS2 (Fig. 3).

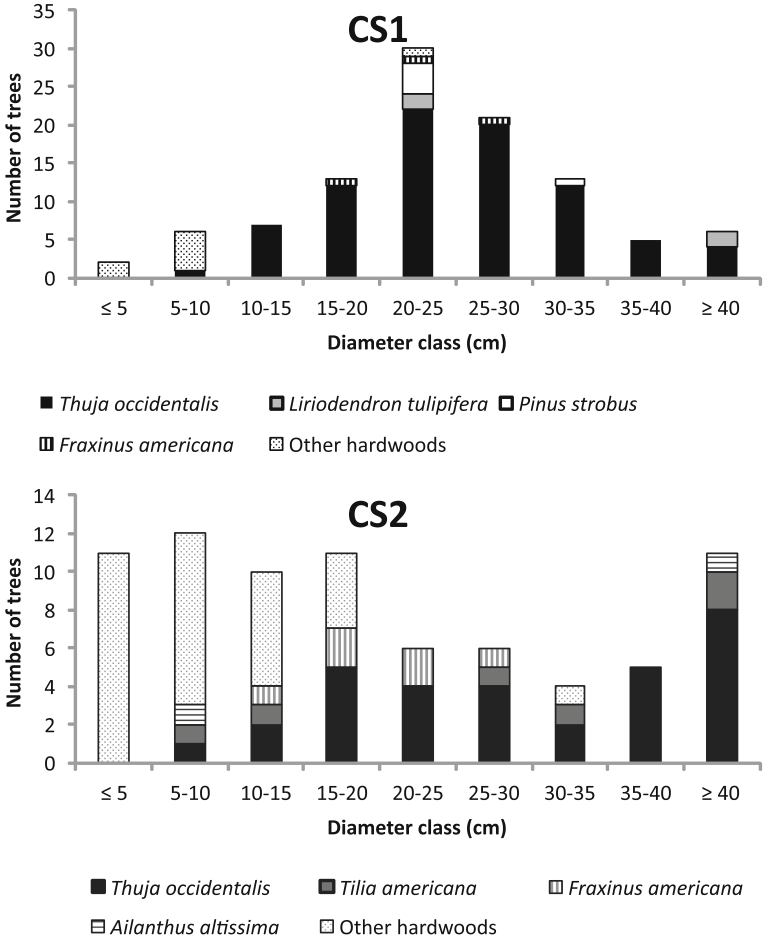

Fig. 2 Diameter class distributions for tree species in each forest stand. Note that *y*-scale varies (see Additional file 1 for high resolution)

A total of 57 snags representing four different species were identified in this research (Table 2; Fig. 4). Seven percent of the snags ($n = 4$) were identified only as "hardwood." Mean snag dbh for all stems was 11.3 ± 4.0 cm with a maximum of 36.5 cm for a single *Tsuga canadensis* stem. Total snag density averaged 280 ± 212.1 stems/ha within stands. The basal area of all snags was similar (~3.0 m^2/ha) for both stands. *T. occidentalis* represented 71.9 % of all snags, but *T. canadensis* snags were dominant (76.9 % of snags) at CS2.

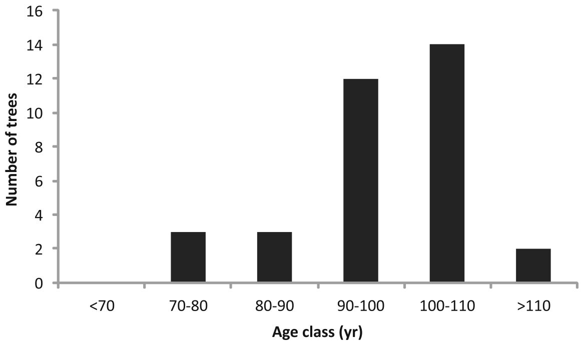

Fig. 3 Age class distribution of *Thuja occidentalis* in the study area (see Additional file 1 for high resolution)

Radial growth-release events

Of the 42 *T. occidentalis* individuals examined in this research, 59.5 % ($n = 25$) experienced growth release events (Fig. 5). All 25 of these trees exhibited at least one growth increase between 25 % and 49.9 % over the 10-year running median. Major events resulting in a ≥ 50 % growth increase were detected in 28.6 % ($n = 12$) of the trees. One *T. occidentalis* individual experienced four minor release

Table 2 Snag characteristics by forest stand. Columns refer to density (*D*, stems/ha) and basal area (BA, m^2/ha)

Site	Species	*D*	BA
CS1	*Thuja occidentalis* L.	380	2.63
	Pinus strobus L.	10	0.27
	Hardwood	40	0.06
CS2	*Thuja occidentalis* L.	30	0.45
	Tsuga canadensis (L.) Carr.	100	2.51

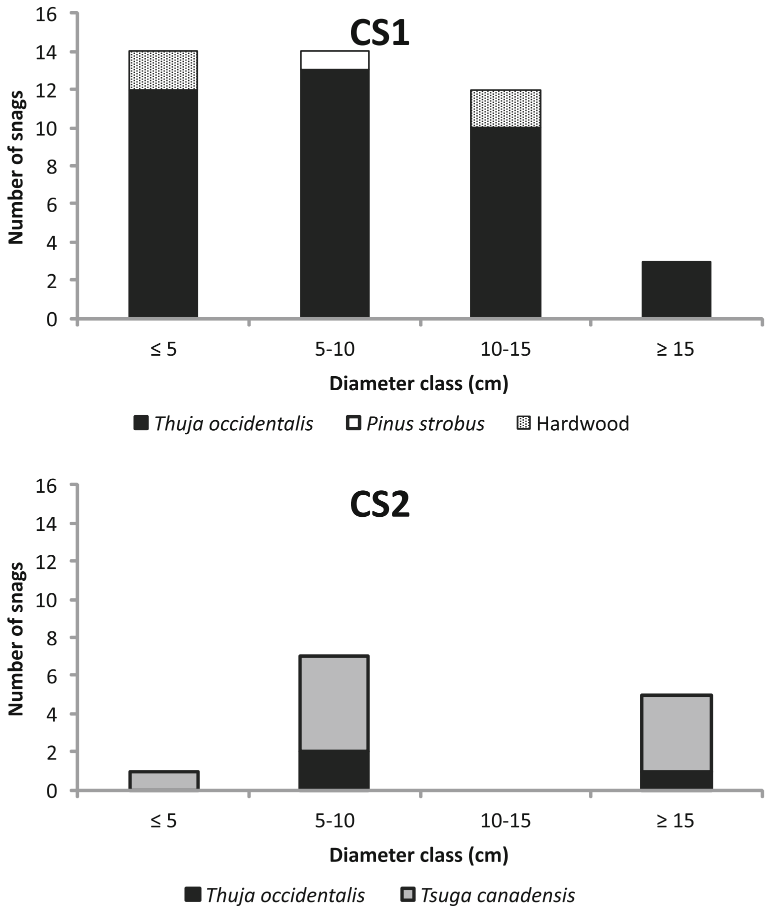

Fig. 4 Diameter class distributions for snags in each forest stand (see Additional file 1 for high resolution)

events, while an additional five individuals experienced 2 to 3 minor growth release events. Only three individuals experienced a growth increase ≥ 100 % over the 10-year running median, with the increase in one tree peaking at 165.3 %. Growth release events were generally distributed across the chronology, but there was a conspicuous increase in major events during the 1950s and 1960s. The mean release duration was 7.1 ± 1.0 years.

Radial growth-climate interactions

The 42 *T. occidentalis* measurement series composing the chronology possessed an interseries correlation of 0.62 ($p < 0.01$) and mean sensitivity of 0.25. Mean sensitivity is a measure of the year-to-year variability in tree-ring widths and is a standard COFECHA metric (Speer 2010). Sustained periods of above mean radial growth occurred during the 1940s and late 1960s to mid-1970s. Notable peaks in mean growth occurred in 1906 and 1995. Prolonged periods of below mean radial growth occurred in the late 1910s to mid-1920s and late 1940s to late 1950s.

Examination of the standard chronology revealed significant correlations ($p < 0.05$) between *T. occidentalis* radial growth and climate variables (Fig. 6). The relationship between mean temperature and *T. occidentalis* growth was the weakest among all climate variables examined in this research. Only previous August (+) and current July (–) mean temperature were significantly correlated with *T. occidentalis* growth. The relationship between *T. occidentalis* growth and precipitation was predominantly positive, with previous October, current June and August-September precipitation being significantly correlated with the chronology. The positive correlation between *T. occidentalis* growth and PDSI was generally stronger and more persistent than the association between growth and temperature or precipitation alone.

Discussion

Forest structures and dynamics

T. occidentalis was the leading canopy dominant at CS1 and CS2, but was not well-represented in the smallest size classes. The age distribution of *T. occidentalis* indicated a wave of establishment between 1900 and 1920, with successful recruitment lacking after 1940. Heitzman et al. (1997) documented a comparable timeline of *T. occidentalis* establishment and recruitment in Michigan, which they ascribed to stand initiating disturbances between 1870 and 1935, followed by stem exclusion in the

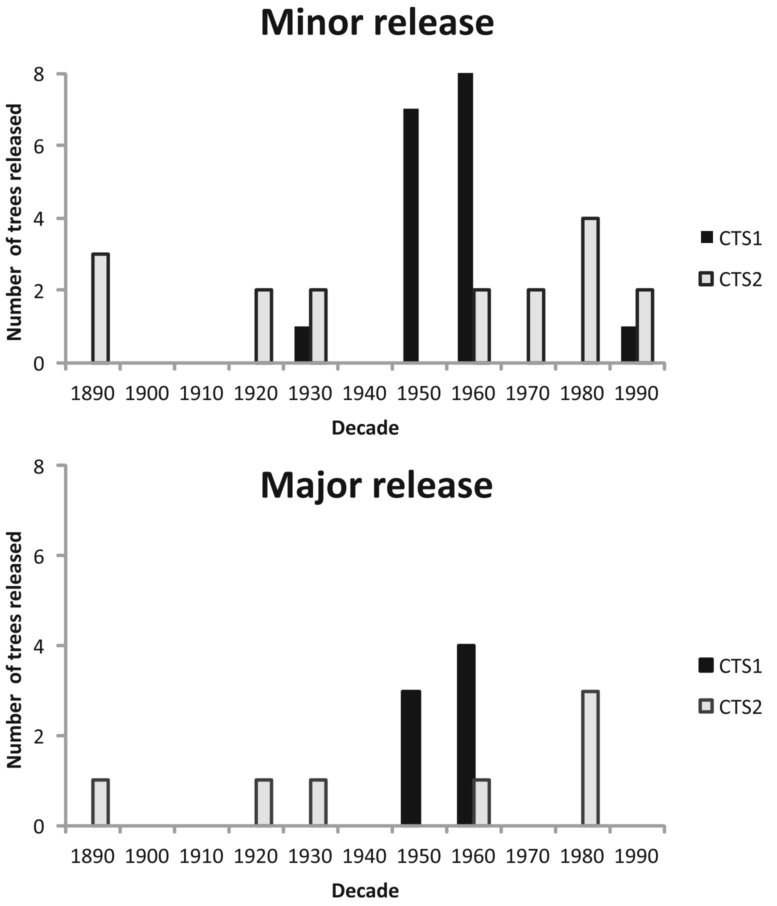

Fig. 5 Disturbance chronologies for *Thuja occidentalis* in each forest stand. Minor releases are events eliciting median growth increases between 25 and 49.9 %. Major releases are events eliciting median growth increases of ≥ 50 % (see Additional file 1 for high resolution)

1940s. The abundance of snags, indicative of self-thinning in the past, and the presence of hardwood species in the smallest size classes suggests CS1 and CS2 are in the early phases of the understory reinitiation stage during which herbs, shrubs, and advance regeneration invade the forest (Oliver and Larson 1996). As the understory reinitiation stage progresses, stand densities should decline to levels at which the regeneration of *T. occidentalis* is more likely to occur (Lamy et al. 1999).

The presence of *A. altissima* in the understory and overstory at CS2 is cause for concern. *A. altissima* is an introduced species from China that frequently spreads into forests by aggressively colonizing canopy gaps (Knapp and Canham 2000; Espenschied-Reilly and Runkle 2008; Martin et al. 2010). In addition to outcompeting native species in canopy gaps, *A. altissima* is associated with changes in ecosystem processes and soil nutrient cycling, which may change the relative abundance of native trees to favor other, more competitive species (Gomez-Aparicio and Canham 2008). Using herbicides to control *A. altissima* is probably the most effective approach at this time, although landowners with limited budgets can remove the species with physical approaches such as pulling, cutting, digging, or girdling (Virginia 2009).

Disturbance and radial growth

T. occidentalis growth-release events were distributed across the disturbance chronology and generally affected a small number of trees, which is characteristic of forest gap dynamics. Canopy gap-scale processes involving the death of a tree or group of trees are often necessary for the persistence of shade tolerant tree species in forests (Runkle and Yetter 1987; Runkle 1998; Frelich 2002; Kincaid 2012). Increased light availability has been reported to enhance *T. occidentalis* seedling survival and abundance in northern portions of the range (Cornett et al. 2000; Rooney et al. 2002). Moreover, Scott and Murphy (1987) observed most *T. occidentalis* regeneration in their study area in Michigan was associated with a large patch of windthrown trees, not small, single-tree gaps. Despite evidence of ongoing canopy gap-scale processes within the forest stands, both structural attributes and field observations suggested a lack of successful *T.*

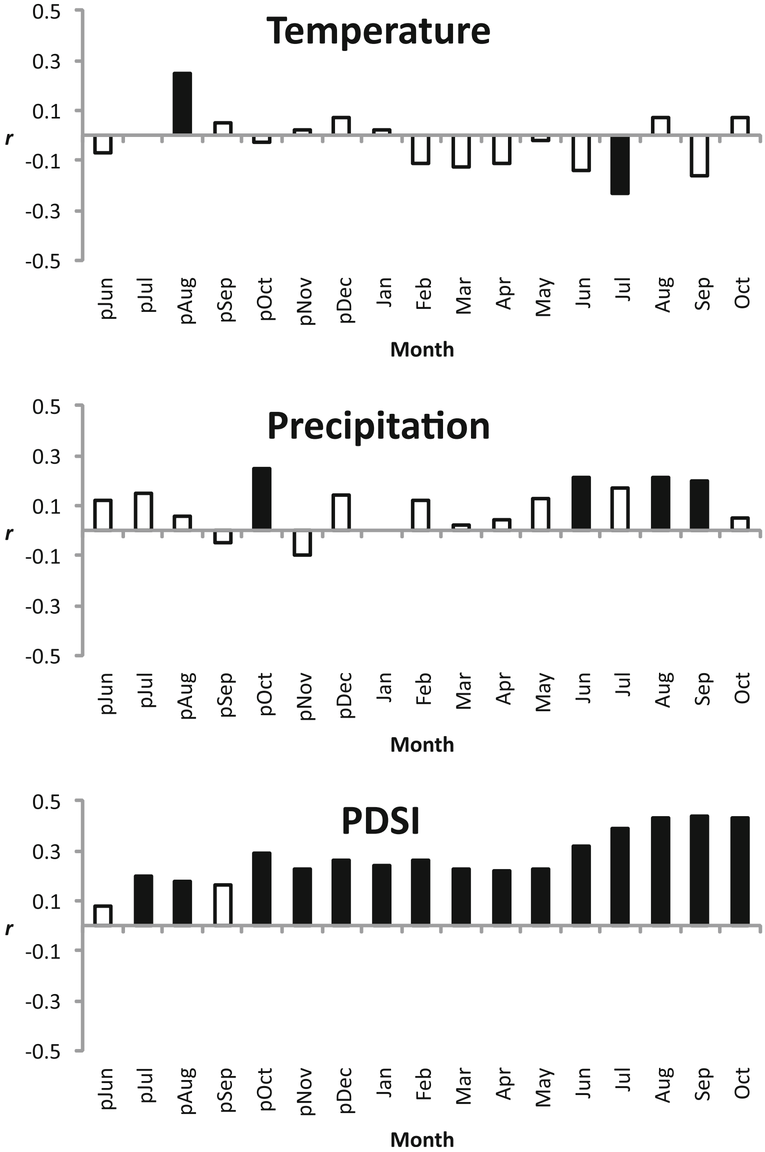

Fig. 6 Correlation between the standardized tree-ring chronology and climate variables. Solid bars indicate significant values ($p < 0.05$) (see Additional file 1 for high resolution)

occidentalis establishment during the last 70 years. This research was limited to the examination of radial growth-release events and stand structures, but I speculate single tree gaps are insufficient for *T. occidentalis* regeneration because adjacent canopy trees rapidly expand to occupy the space (Oliver and Larson 1996).

Climate and radial growth

The interseries correlation for all 42 *T. occidentalis* measurement series was statistically significant and compared well with the coefficient (0.66 versus 0.62, $p < 0.01$) reported by Kipfmueller et al. (2010) for a chronology developed in Minnesota, USA. Mean sensitivity of the *T. occidentalis* chronology also was within the range of variation reported for other chronologies developed in northern portions of the range (Kelly et al. 1994; Tardif and Bergeron 1997; Tardif and Stevenson 2001; Kipfmueller et al. 2010). The mean sensitivity of the chronology was nearly identical (0.25 versus 0.24) to the sensitivity of another disjunct shade tolerant conifer at its southern range margin in the Appalachian Mountains, USA (Hart et al. 2010). Although the sensitivity of *T. occidentalis* to climate is similar throughout its range, there appears to be geographical variation in the growth response of the species to climate factors such as temperature and precipitation, a phenomenon also observed in other tree species (Cook and Cole 1991; Hart et al. 2010).

In northern portions of the range, *T. occidentalis* radial growth is inversely related to previous summer temperatures (Kelly et al. 1994; Tardif and Bergeron 1997; Tardif and Stevenson 2001; Kipfmueller et al. 2010). The current study found a positive association between previous August mean temperature and *T. occidentalis* growth. The positive relationship between previous summer temperatures and growth has been observed in other conifers, including *Chamaecyparis thyoides* L. (Atlantic white cedar) (Hopton and Pederson 2003; Henderson and Grissino-Mayer 2009). Moderate temperatures and abundant precipitation late in the growing season may be favorable for *T. occidentalis* growth in the central Appalachian Mountains; however, the association between growth and temperature is not constant throughout the year. The temperature-growth association turns negative during the spring and summer of the current year, which is a period of phloem expansion in *T. occidentalis* (Bannan 1955). Phloem tissue is essential for the translocation of photosynthates from leaves to other parts of the tree. An inverse growth response to summer temperatures is common in trees because higher temperatures tend to facilitate internal water deficits and increased respiration over carbon fixation (Edwards and Dixon 1995; Henderson and Grissino-Mayer 2009). Although some researchers have suggested *T. occidentalis* growth is not limited by climate, particularly by temperature in northern portions of the range, climate could influence the regeneration and growth of the species (Tardif and Stevenson 2001; Paul et al. 2014) in disjunct stands south of the contiguous range margin.

In contrast to the relationship between *T. occidentalis* radial growth and temperature, the relationship between radial growth and moisture variables was more consistently positive. The positive associations between spring and summer precipitation of the current year and *T. occidentalis* growth are consistent with relationships reported in northern portions of the range, including the northwestern range margin (Tardif and Stevenson 2001; Kipfmueller et al. 2010). The significant positive association between previous October precipitation and *T. occidentalis* growth is unique to this study. Hart et al. (2010) found a positive association between precipitation in October of the previous year and the growth of *T. canadensis* in disjunct stands near its southern range margin in the Appalachian Mountains. The authors speculated that October precipitation influences autumn phenology. It also is possible precipitation during the fall of the previous year facilitates ongoing carbohydrate storage, which is necessary for renewed growth in the following spring (Henderson and Grissino-Mayer 2009). The consistently positive association between *T. occidentalis* growth and PDSI has been observed in other southern conifers and is at least partly the result of autocorrelation in the index because values from previous months are used to calculate current values (Grissino-Mayer and Butler 1993; Henderson and Grissino-Mayer 2009; Hart et al. 2010). Despite the autocorrelation in the index values, the positive relationship between PDSI and *T. occidentalis* growth may reflect the sensitivity of the species to moisture conditions in disjunct stands south of its contiguous range margin. The positive association between growth and PDSI is particularly strong from late summer to fall of the current year, which indicates that moisture conditions during this period are important to the growth of *T. occidentalis* in the study area.

Conclusion

This research has characterized the structural attributes and radial growth dynamics of disjunct *T. occidentalis* forests in the central Appalachian Mountains, USA. Structural attributes indicate the forest stands are in the understory reinitiation stage of forest development (Oliver and Larson 1996). Silvicultural manipulations such as thinning may be necessary to stimulate the understory and promote *T. occidentalis* establishment. It also may be necessary to utilize chemical and physical approaches to reduce *A. altissima* in order to prevent the species from colonizing canopy gaps and outcompeting native species such as *T. occidentalis* (Knapp and Canham 2000; Espenschied-Reilly and Runkle 2008; Virginia 2009; Martin et al. 2010).

The sensitivity of *T. occidentalis* radial growth to climate appears similar throughout its range, including at disjunct sites beyond its contiguous range margin. However, geographical variation in the growth response of the species to climate factors is apparent (Cook and Cole 1991; Hart et al. 2010). The response of *T. occidentalis* growth to moisture conditions is predominately positive throughout the year, while the relationship between growth and temperature is much more irregular.

The current study has documented geographical variation in the growth of *T. occidentalis* in disjunct forest stands south of its contiguous range margin. Most studies examining *T. occidentalis* ecology and growth come from northern portions of the range, so more research is necessary to increase the geographical and ecological scope of our knowledge, particularly at more southern and disjunct sites. Indeed, current research could be overlooking important local or regional biotic and abiotic factors that can significantly affect *T. occidentalis* ecology and growth.

Additional file

Additional file 1: All figures in high resolution. (ZIP 3.57 mb)

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Author's contribution

Joshua Kincaid is the sole author of this manuscript.

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Competing interests

There are no financial or non-financial competing interests with regard to this manuscript.

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