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Forest dynamics and climate sensitivity of an endangered Carolina hemlock community in the southern Appalachian Mountains, USA.

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ABSTRACT

During the last century, the eastern United States has functionally lost two major tree species (American chestnut and American elm), two more, eastern and Carolina hemlock, will likely be functionally extinct during much of their ranges by 2050. Carolina hemlock forests are geographically limited to high elevations in the southern Appalachian Mountains and are considered to be endangered. We collected forest stand, composition, and tree age data at the beginning of a hemlock woolly adelgid (HWA) infestation. Prior to the arrival of HWA, Carolina hemlocks were healthy and densely populated in the overstory and understory. While Carolina hemlock regenerated successfully and continuously from 1850 to 2010, the development of this Carolina hemlock forest will be altered by the HWA and may result in an increase in the density of northern red oak, white oak, mountain laurel, and Catawba rhododendron. Carolina hemlocks preferred cool, wet summers with older trees experiencing greater reductions in radial growth than younger trees during droughts. This study demonstrates that dendrochronological techniques can provide critical annual information on Carolina hemlock forest development and tree age-climate response. Our results provide a multi-century perspective for conservation efforts and management of Carolina hemlock forests in the southern Appalachian Mountains.

Keywords: *Tsuga caroliniana*, endangered tree species, dendrochronology, invasive species, hemlock woolly adelgid, old-growth forests

INTRODUCTION

Carolina hemlock (*Tsuga caroliniana* Engelm.) is a long-lived tree species endemic to small, isolated populations in Virginia, Georgia, Tennessee, North Carolina, and South Carolina, USA (James 1943, Rentch et al. 2000). The typical habitat of Carolina hemlock is along exposed ridges in the southern Appalachian Mountains (James 1943). Carolina hemlock can occur in pure or mixed stands at elevations between 600 and 1500 meters. However, Carolina hemlock also occurs streamside along moist, cool ravines (Humphrey 1989). The Carolina hemlock range is limited in the southern United States by high summer temperatures, historically frequent fires, and the limited areas of cliffs and rock outcroppings (Jetton et al. 2008). Conversely, its range to the north is restricted by lower summer precipitation and less frequent fires that lead to increased hardwood competition (Jetton et al. 2008).

Carolina hemlock and eastern hemlock (*Tsuga canadensis* L.) were thought to be closely related species because of range overlap (Szafer 1949). However, LePage (2003) and Orwig and Foster (1998) noted that based on cone shape, cone-scale, and seed morphologies, the two species are very distinct and only distantly related. Carolina hemlock is more closely related to Asian hemlock species and western North America hemlock species than eastern hemlock (LePage 2003).

Carolina hemlock plays an important ecological role in the southern Appalachian Mountains as a foundation species (Ellison et al. 2005, Havill et al. 2008). The Carolina hemlock overstory creates microclimates in the understory that have uniformly low seasonal light level variability and relatively small daily temperature fluctuations

(James 1943, Rentch et al. 2000, Jetton et al. 2008). The ability of Carolina hemlock to modify stand soil conditions and microclimate by depositing acidic litter and maintaining low light levels in the understory influences fundamental community and ecosystem characteristics (Rentch et al. 2000).

Carolina hemlock and eastern hemlock are both susceptible to the hemlock woolly adelgid (HWA; *Adelges tsugae*). The HWA threatens to eliminate Carolina hemlock throughout its limited native range. The invasive insect has spread unimpeded since its initial infestation in Richmond, Virginia during the early 1950s (Morin et al. 2009). HWA causes needle loss, bud mortality, and tree mortality within a decade by defoliating the tree (McClure 1991, Orwig et al. 2002). HWA populations increase rapidly because they are parthenogenetic (all individuals are female and capable of reproduction), complete two generations each year, and have no known natural enemies in eastern North America (Orwig and Foster 1998). They also are capable of rapid dispersal by wind, birds, deer, and human activity such as logging (McClure 1990). It is likely that eastern hemlock and Carolina hemlock species may become functionally extinct during the next 50 years (Beane et al. 2010, Vose et al. 2013).

Land managers have tried multiple HWA control efforts (Jetton et al. 2008). However, eastern hemlock and Carolina hemlock forests have already been impacted by HWA and may suffer a similar fate as the American chestnut (*Castania dentata* (Marsh)) and other functionally extinct forest species (Vose et al. 2013). Fortunately, most of the short-term impacts of HWA-induced mortality appear to be localized and land managers can begin to strategically implement conservation decisions that address changes in ecosystem structure and function on multiple scales (Vose et al. 2013). Carolina hemlock forests should be studied while the research opportunity exists. Research is limited in Carolina hemlock forest ecology (James 1943, Humphrey 1989, Rentch et al. 2000, Jetton et al., 2008). This study augments existing Carolina hemlock ecology research with climate-growth comparisons between younger and older trees. Understanding the dynamics of the Carolina hemlock forest at the site level will provide insight about the anticipated changes across the species' range. By collecting forest information at the beginning of an HWA infestation, this study provides critical information for establishing baseline data of Carolina hemlock forest stand structure, composition, and climate sensitivity that will likely face drastic changes in the near future.

Our primary objectives were to: (1) quantitatively document the current composition, structure, and age of a Carolina hemlock forest at Bluff Mountain, North Carolina, and (2) determine if the climate-growth relationship of Carolina hemlock is influenced by tree age.

MATERIALS AND METHODS

Study Area

Bluff Mountain Nature Preserve in Ashe County, North Carolina is a high-elevation (1067 to 1550 m) area of ecological significance in the Blue Ridge Mountains (Skeate 2004, van de Gevel et al. 2012) (Figure 1). The Blue Ridge Mountains range in elevation from approximately 300 m to 1800 m above sea level and support some of the highest biodiversity in North America (NCNHP 1999). The preserve, owned and managed by The Nature Conservancy since 1978 (Skeate 2004), is part of a small collection of old-growth forest preserves in the Blue Ridge Mountains (Nash 1999, van de Gevel et al. 2012). Many of the vegetation assemblages characteristic of the Blue Ridge Physiographic Province inhabit Bluff Mountain, including: rock outcrop communities, a Carolina hemlock forest, dwarf oak (*Quercus* spp.) forests, and a southern Appalachian fen (van de Gevel et al. 2012). More than 48 endangered, threatened, or rare vascular plant species have been identified at Bluff Mountain (Tucker 1972, NCNHP 1999, Skeate 2004). Humphrey (1989) identified old Carolina hemlock trees on Bluff Mountain and provided broad baseline population information about a different Carolina hemlock stand from this study.

The climate at Bluff Mountain is classified as Cfb under the Köppen climate classification system (Christopherson 2009). The average January temperature is approximately 0.7°C with average July temperatures of 20°C (PRISM Climate Group 2015). Yearly average temperatures are approximately 10°C and annual precipitation averages 125 cm (PRISM Climate Group 2015). July and August have the highest average monthly precipitation (approximately 12 cm each month) (PRISM Climate Group 2015). Annual snow accumulation averages 71 cm (SCONC 2015). The average growing season length in Ashe County, North Carolina is 139 days (SCONC 2015).

Field Methods

We established five 0.05 ha fixed radius plots at Bluff Mountain, North Carolina. The plots were located in a forest stand with > 50% Carolina hemlock in the canopy (Figure 2). We tallied all tree stems ≥ 5 cm dbh by species in each plot. We recorded tree diameter at breast height (dbh; 1.37m) and crown class for each tree to quantify the vertical and basal area structure of the Carolina hemlock stand. We based crown class categories (overtopped, intermediate, codominant, and dominant) on the amount and direction of intercepted sunlight (Oliver and Larson 1996). We collected two radial cores from every tree below 30 cm height to determine establishment dates, growth rates, and radial growth patterns. We also recorded Global Positioning System (GPS) points from the center of each plot. We established a nested understory 0.01 ha subplot in the center of each overstory plot. Stems ≥ 1m in height and less than 5.0 cm dbh were tallied as saplings and stems <1 m in height were tallied as seedlings. We also visually estimated percentage cover of mountain laurel (*Kalmia latifoli* L.) and Catawba rhododendron (*Rhododendron catawbiense* Michx.) to the nearest 5% in each 0.01 ha subplot.

Laboratory Methods

We calculated density, basal area (dominance), and importance values of each tree species (Cottam and Curtis 1956). Importance values were calculated as the average of the relative density and relative dominance.

We processed increment cores following standard dendroecological techniques

(Stokes and Smiley 1968). We measured annual growth rings from all Carolina hemlock cores to the nearest 0.001 mm with WinDendro image analysis software (version 2009C, Regent Instruments, Canada). We statistically verified crossdating accuracy using the computer program COFECHA and 50-year segments lagged successively by 25 years (Holmes 1983, Grissino-Mayer 2001). We developed two Carolina hemlock tree-ring chronologies from 25 young (44 – 61 years old) and 25 old (103 – 176 years old) trees (Table 1). We wanted to have a minimum 40-year gap in age between the young and old trees in the two chronologies. We detrended each series using the program ARSTAN to remove the influence of tree age, microsite, and local stand dynamics (Cook 1985, Cook and Holmes 1996). We applied a Friedman super smoother to all cores to preserve long-term trends and minimize the effects of suppressed growth or abrupt growth increases. We used a flexible alpha-level or bass enhancement of 3 (Freidman 1984).

Climate Analysis

We analyzed the climate-radial growth relationship of the young and old Carolina hemlock chronologies using Pearson's correlation analysis between the growth index and climate variables: mean monthly maximum temperature, monthly total precipitation, and monthly Palmer Drought Severity Index (PDSI) values. PDSI is often used in dendroclimatic studies (*e.g.,* Copenheaver et al. 2011, Harley et al. 2011, Pederson et al. 2015) because it is a good measure of available soil moisture conditions during the growing season (Alley 1984). We analyzed the climate-growth relationships during the period AD 1895–2010 for the old Carolina hemlock chronology and AD 1951–2010 for the young chronology. This is the first study to explore the differences in Carolina hemlock climate-growth relationships based on tree ages (younger versus older trees). We obtained data for monthly mean maximum temperature and monthly total precipitation from the PRISM Climate Group (2015). The PRISM data represents a grid cell at 36.397 N, - 81.548 W and 981 m elevation. We obtained PDSI data for the northern mountains region of North Carolina (NC02) from the National Climate Data Center (NCDC 2011).

RESULTS

Forest Composition and Structure

Carolina hemlock was the most abundant, dominant species, and important species in the forest canopy (Table 2, Figure 3). Northern red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.) also were important and dominant canopy species. These three species represent over 95% of trees at the study site (Table 2). The next most abundant species were northern red oak and white oak. The most abundant species in the understory stratum was Carolina hemlock, representing 93% of saplings and 41% of seedlings. Catawba rhododendron and mountain laurel covered approximately 50% of the understory layer.

We cored and dated 357 trees. The oldest trees (> 250 years old) were white oaks and northern red oaks, while the oldest Carolina hemlock was 189 years old. The age of the forest and the strong relationship between tree age and diameter is indicative of an old-growth stand (Tyrell and Crow 1994, Pederson 2010, Hart et al. 2012). Tree size generally increased with age for all species (Figure 4). The largest tree was a 176 year-old Carolina hemlock with a dbh of 50.5 cm (Figure 4a). Tree establishment was continuous for Carolina hemlock, white oak, and northern red oak after 1820 and more abundant from 1935 to 1980 (Figure 4). Carolina hemlocks have been regenerating successfully during the last 150 years.

Radial Growth and Climate Response

The temporal pattern of radial growth of Carolina hemlock is absent of any long-term trends (Figure 5). While the old and young chronologies are closely related ($r = 0.549$, $p < 0.001$), there is greater variance evident in the older trees during their concurrent growth period.

Both the young and old trees respond negatively to spring and summer maximum temperatures (Figure 6). The strongest relationships between the young chronology and temperature were with July temperature and average summer temperature. The old chronology had a significant relationship with both May temperature and average summer temperature. Overall, younger trees were more responsive to maximum temperatures than the older trees. The negative response of young and old trees to spring and summer temperatures with a positive response to precipitation during the same months is a function of available moisture.

The old chronology was more sensitive to precipitation and PDSI than the young chronology (Figure 6). There was a weak positive response between radial growth and growing season precipitation, with the strongest relationship in May for older trees and July for the younger trees (Figure 6). As the PDSI is a water balance-based measure of drought severity (Alley 1984), positive summer values are generally reflective of cooler, wetter conditions and negative values warmer and drier. There was a consistently strong and positive relationship between radial growth and moisture availability throughout the growing season, peaking in August (Figure 6). However, there were differences in response by tree age, with the older trees consistently recording stronger relationships with PDSI values.

DISCUSSION

Carolina hemlock forest development and succession

Carolina hemlock has a narrow geographic range and only establishes along ridges and rock outcroppings (Humphrey 1989, Rentch et al. 2000, Jetton et al. 2008), thus their populations are relatively small compared to the extensive areas dominated by eastern hemlock (Levy and Walker 2014) and are more likely to become endangered from HWA. While the disjunct locations of Carolina hemlock populations may allow more protection from the transmission of HWA from other Carolina hemlock forests, once HWA is established, small population dynamics may lead to increased infestation (Levy and Walker 2014).

Although HWA has been present at Bluff Mountain since 2006, measures of forest composition and structure (basal area, density, and importance values) are similar to those recorded for a healthy Carolina hemlock forest in Virginia (Rentch et al. 2000) and a healthy eastern hemlock forest in Delaware (Eschtruth et al. 2006). The Bluff Mountain Carolina hemlock forest and the Delaware eastern hemlock forest (Eschtruth et al. 2006) had a high density of hemlock reported in the understory both before and after HWA infestation. In the absence of HWA, Carolina hemlock would continue to outcompete hardwood species in the understory and forest canopy (Eschtruth et al. 2006).

The absence of oak species in the understory indicates that oaks are currently not successfully regenerating. However, the forest composition is likely to change as Carolina hemlock continues to be affected by the HWA. The codominant oak species will claim the canopy space created by HWA-induced hemlock mortality. A transition from a hemlock-dominated forest to a hardwood forest has been reported in New England (Orwig et al. 2002, Eschtruth et al. 2006, Orwig et al. 2008, Orwig et al. 2013) and is likely to occur at Bluff Mountain with the removal of Carolina hemlock by HWA.

We observed several traits indicative of gap-phase dynamics. A large increase in tree establishment between 1935-1980 was likely caused by gaps formed from American chestnut tree death due to chestnut blight (*Cryphonectria parasitica* (Murrill), frequent ice storms, tornado damage, and tropical storms (van de Gevel et al. 2012). Although the tree ages and basal area at Bluff Mountain are within the range reported for old-growth hemlock forests, the high stem density at Bluff Mountain is similar to those reported in younger stands (Tyrell and Crow 1994, Hart et al. 2012). The exposed nature of Bluff

Mountain makes trees prone to extreme storms, which likely limits the frequency of trees reaching larger diameter classes but creates ideal conditions for tree establishment.

Dendroclimatology

The climate-growth relationships of older Carolina hemlock at Bluff Mountain are similar to those found in eastern hemlock (Abrams et al. 2000, D'Arrigo et al. 2001, Hart et al. 2010, Pederson et al. 2015, Saladyga and Maxwell 2015). Carolina and eastern hemlock respond to cool, wet summers despite differences in their habitat types and species genetics. Specifically, the Carolina hemlock at Bluff Mountain are located on the edge of a cliff at a high elevation (1550 m), while eastern hemlock are often found in low-elevation (0-730 m) cove forests between 33ºN and 48ºN latitude (Cook and Jacoby 1977, Abrams et al. 2000, D'Arrigo et al. 2001, Hart et al. 2010, Saladyga and Maxwell 2015). One factor that contributes to age-related difference in climate response is the ability of Carolina hemlock trees to respond to early summer conditions. Older trees respond to available moisture earlier in the growing season than younger trees (Copenheaver et al. 2011). During May (spring), moisture availability is more important for the growth of the old trees compared to the young. Conversely, during July (summer) moisture availability is more important for growth of the young trees compared to the old (Ford and Vose 2007). The old chronology had significant relationships with May temperature, precipitation, and PDSI. The young chronology was less responsive to May temperature. The difference in summer temperature response between the young and old trees may be a function of differences in canopy structure. Dominant trees intercept more incoming solar radiation than younger subcanopy trees, thus creating a lag between canopy and subcanopy temperatures.

Another factor that may cause age-related differences in climate response is root biomass. Older Carolina hemlocks with established root systems at deeper soil levels have been shown to be more sensitive to soil moisture availability (measured by the PDSI) (Copenheaver et al. 2011). PDSI incorporates a modeled measure of moisture availability in the lower soil levels that is similar to the conditions experienced by old trees with extensive root networks (Copenheaver et al. 2011). Younger trees typically have less biomass and less developed root systems (Copenheaver et al. 2011, Walker et al. 2014).

CONCLUSIONS

Forest inventory and dendroecological analyses allowed us to determine the establishment sequence of an old-growth Carolina hemlock forest in the southern Appalachian Mountains. Prior to the arrival of HWA, Carolina hemlock were healthy and densely populated in the overstory and understory. While Carolina hemlock regenerated successfully and continuously from 1850 to 2010, the development of this Carolina hemlock forest will be altered by the HWA and may result in an increase in the density of northern red oak, white oak, mountain laurel, and Catawba rhododendron.

The small range of Carolina hemlock makes the species particularly vulnerable to HWA and climate shifts. Because Carolina hemlocks prefer cool, wet summers (Berdanier and Clark 2015), projected climate change in the Appalachian Mountains (i.e., increased warming) will create more stress, especially for those trees infested with HWA. Further, there will likely be differential impacts from drought, with older Carolina hemlock trees experiencing greater reductions in radial growth than younger trees. This is the first dendroclimatic study to explore the differences in Carolina hemlock climate-growth relationships based on tree ages (younger versus older trees).

This study demonstrates that dendrochronological techniques can provide critical annual information on dynamic forest development and climate shifts and provides a multi-century perspective for conservation efforts and management of Carolina hemlock forests in the southern Appalachian Mountains. Given the continuing threats to forest health from HWA, Carolina hemlock forests in the southern Appalachian Mountains should be continuously monitored to record changes in successional patterns and forest health.

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Table 1. Characteristics of the young (44–61 years old) and old (103–176 years old) *Tsuga caroliniana* chronologies from Bluff Mountain, North Carolina.

Chronology	Number of trees	Maximum age	Mean age	Minimum age	Series Intercorrelation	Mean Sensitivity
Old	25	176	135	103	0.581	0.247
Young	25	61	54	44	0.515	0.205

Table 2. Density (number of trees ha^{-1}), dominance (basal area; m^2ha^{-1}), and importance of trees (mean of relative density and relative dominance) by species at Bluff Mountain, North Carolina.

Species	**Density (stems/ha)**	**Relative Density (%)**	**Dominance (m^2/ha)**	**Relative Dominance (%)**	**Relative Importance (%)**
Tsuga caroliniana	1048	65	21	49	57.3
Quercus rubra	220	14	11	25	19.4
Quercus alba	176	11	9	21	15.8
Acer rubrum	92	6	1	3	4.5
Carpinus caroliniana	36	2	0	1	1.5
Betulla lenta	12	1	0	0	0.4
Castanea dentata	12	1	0	0	0.4
Acer pensylvanicum	8	0	0	0	0.3
Prunus serotina	4	0	0	0	0.4
Total	1608	100	43	100	100

Figure 1. Map of the natural range of Carolina hemlock (blue) and eastern hemlock (green) in the southeastern United States. This study was conducted at Bluff Mountain Nature Preserve, North Carolina (36.397 N, -81.548 W, red circle). Map source data was collected from the U.S. Census Bureau and the U.S. Department of Agriculture. Map was created in ArcMap 10.3.1 by Tina Ball.

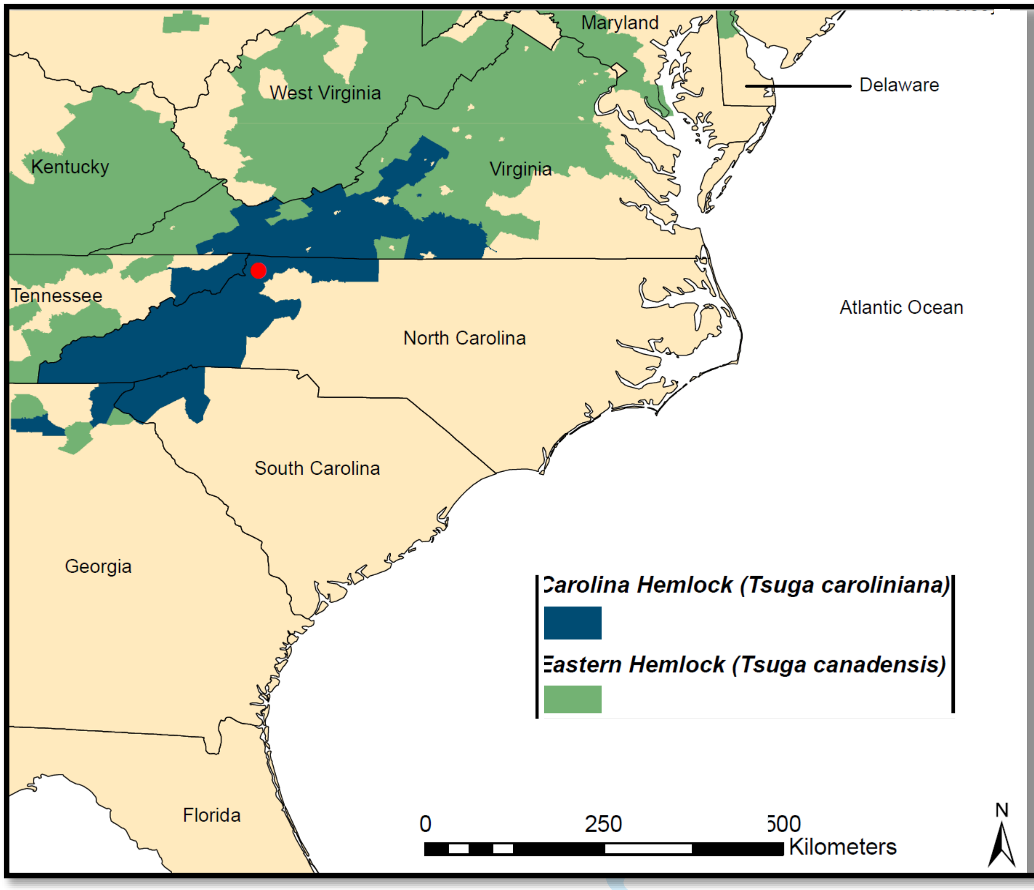
Figure 2. Carolina hemlock forest at Bluff Mountain, North Carolina. Carolina hemlocks are found in disjunct populations along exposed ridges in the southern Appalachian Mountains. Photograph taken by David Austin.

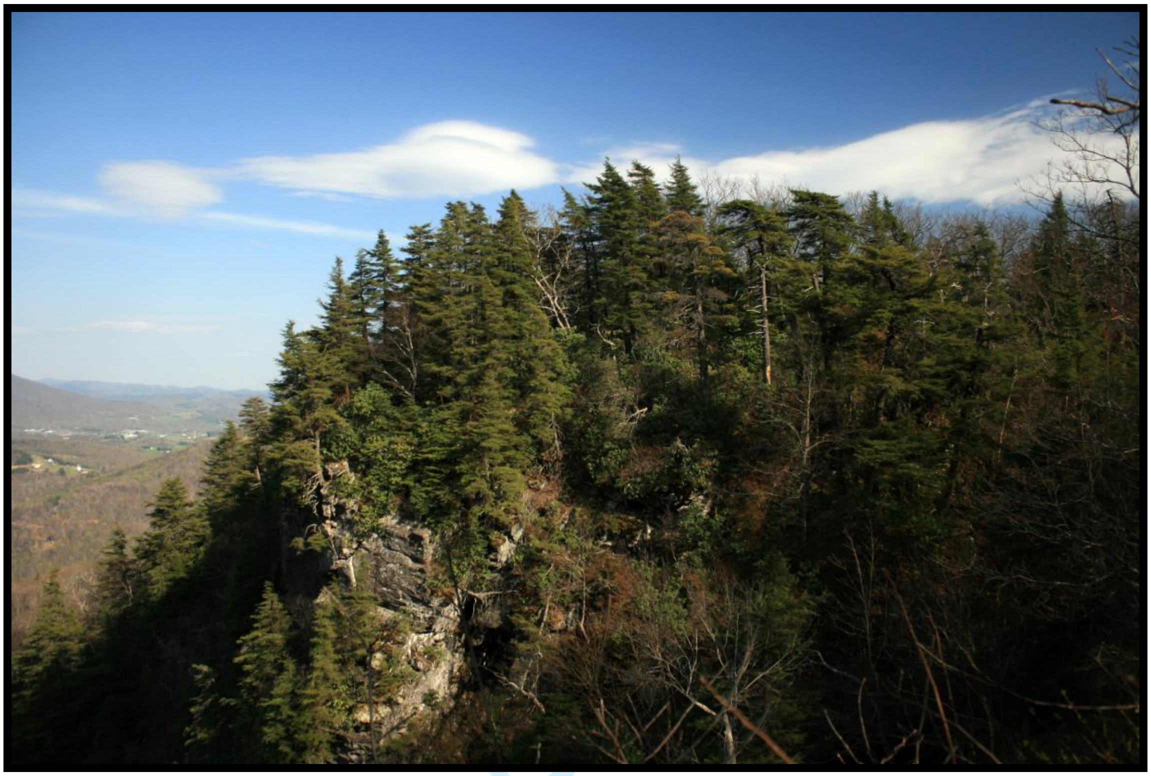
Figure 3. Canopy class distributions per hectare of Carolina hemlock (*Tsuga caroliniana*), red oak (*Quercus rubra*), white oak (*Quercus alba*). Canopy class categories are based on the amount and direction of intercepted light. Other species included *Acer rubrum*, *Carpinus caroliniana*, *Betula lenta*, *Castanea dentata*, *Acer pensylvancium*, and *Prunus serotina* and represented less than 10% of the forest canopy structure.

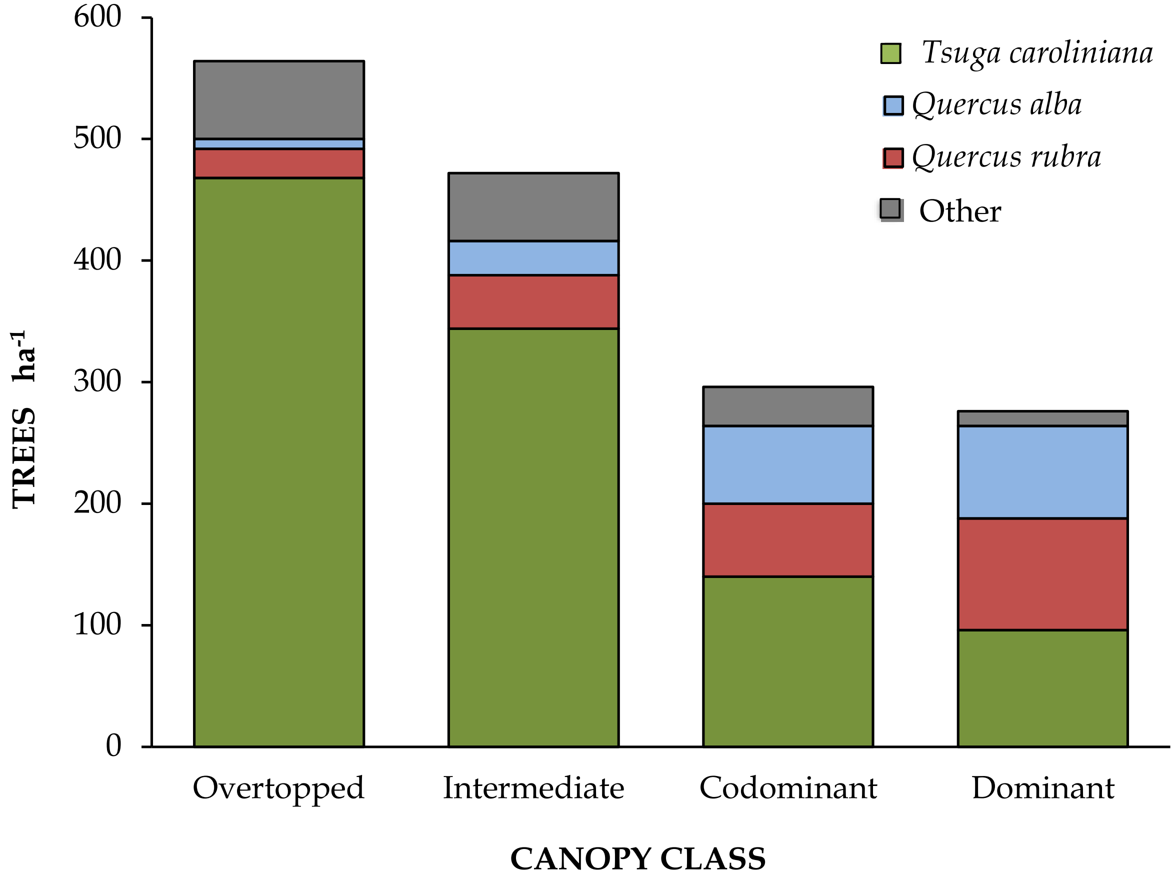
Figure 4. Diameter-age relationships of 357 trees at Bluff Mountain, North Carolina. Carolina hemlock (*Tsuga caroliniana*) (A.), red oak (*Quercus rubra*), and white oak (*Quercus alba*) had significant relationships ($r^2 = 0.45 - 0.55$, $p < 0.001$) between size and age of the trees (B.). Other species included *Acer rubrum*, *Carpinus caroliniana*, *Betula lenta*, *Castanea dentata*, *Acer pensylvancium*, and *Prunus serotina.*

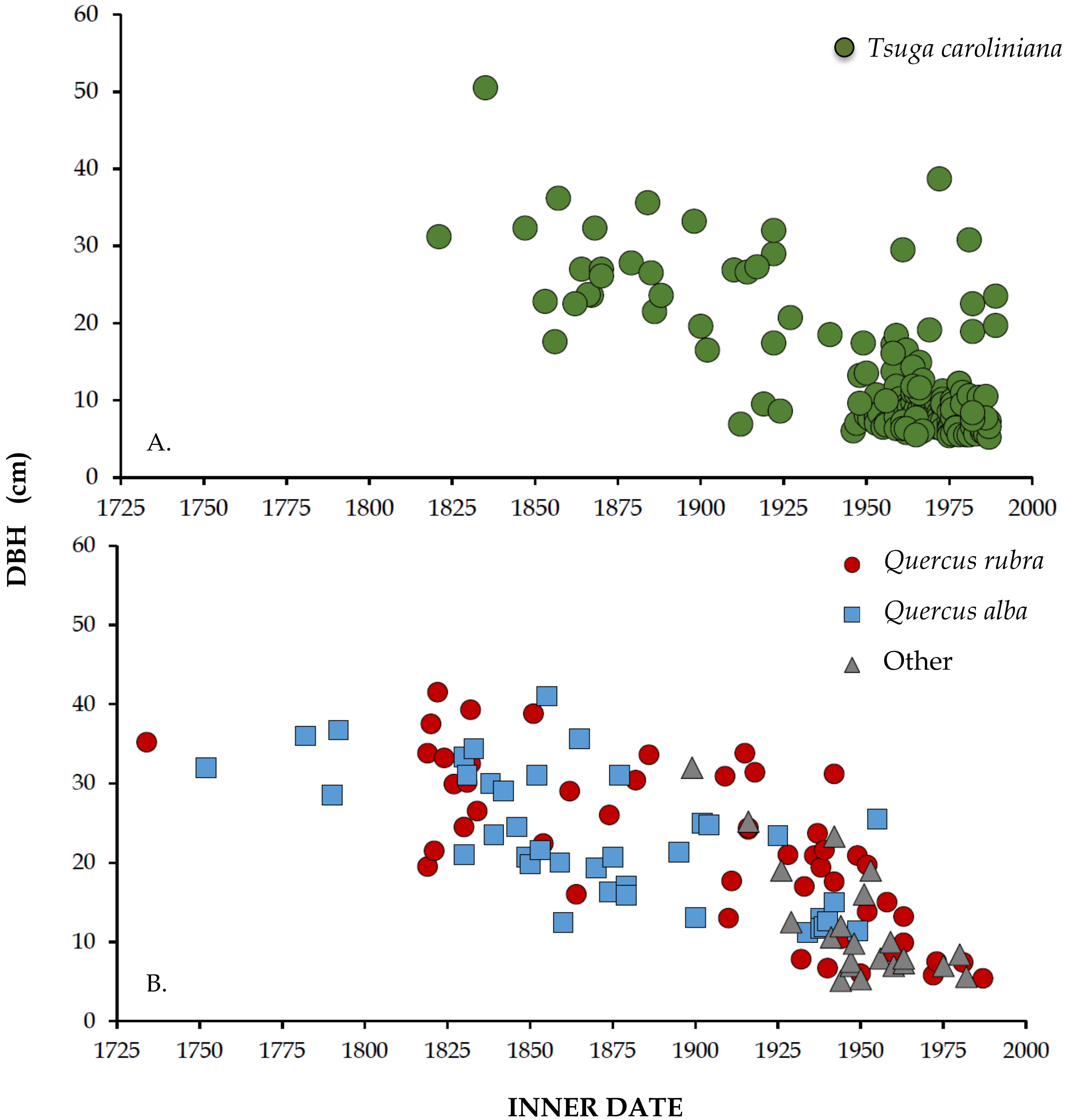
Figure 5. Radial growth chronologies (index) from Carolina hemlock (*Tsuga caroliniana*) trees at Bluff Mountain, North Carolina. Carolina hemlock is divided into two chronologies, young (AD 1950-2010) and old (AD 1847-2010). The mean radial growth is standardized to 1.0 (black line).

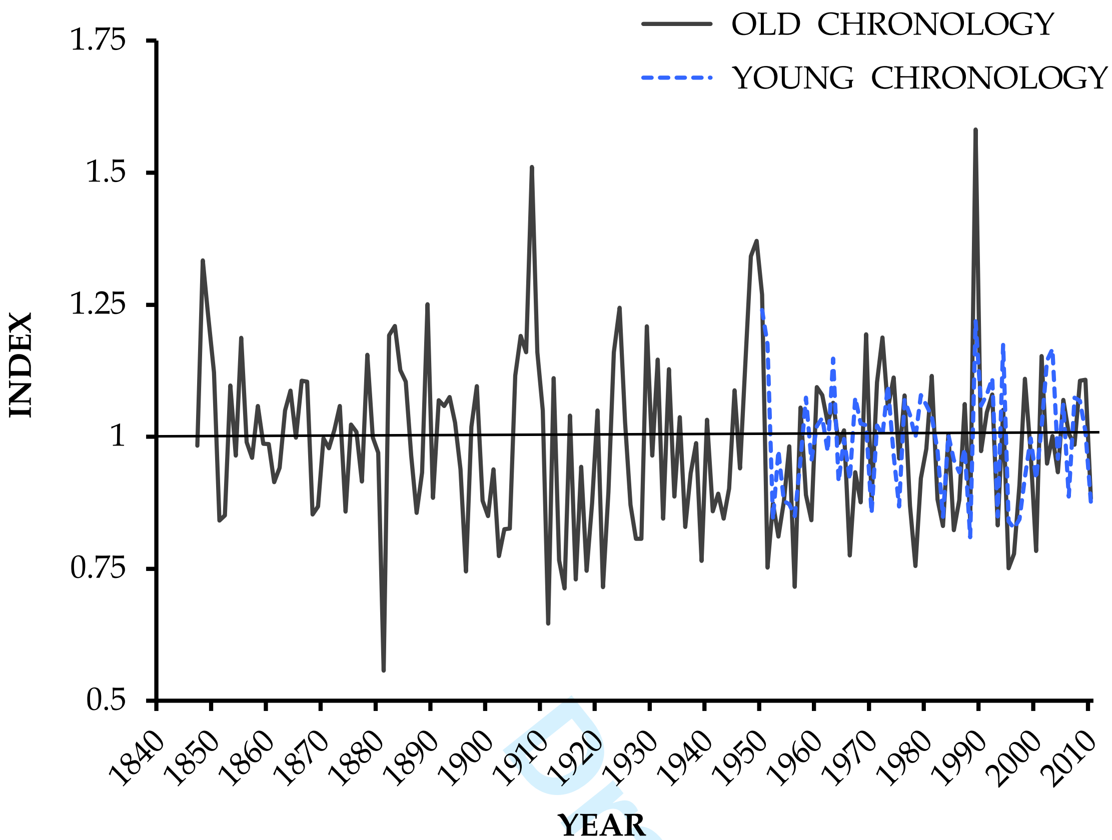
Figure 6. Significant relationships ($r = \pm 0.2$, $p < 0.05$, dashed lines) between Carolina hemlock (*Tsuga caroliniana*) and maximum temperature (A.), precipitation (B.), and Palmer Drought Severity Index (C.) at Bluff Mountain, North Carolina. Carolina hemlock is divided into two age classes, young (44–61 years old) and old (103–176 years old). The growing season is from April-September. The monthly variables are listed on the x-axis, with variables preceded by “p” representing months from the previous year.

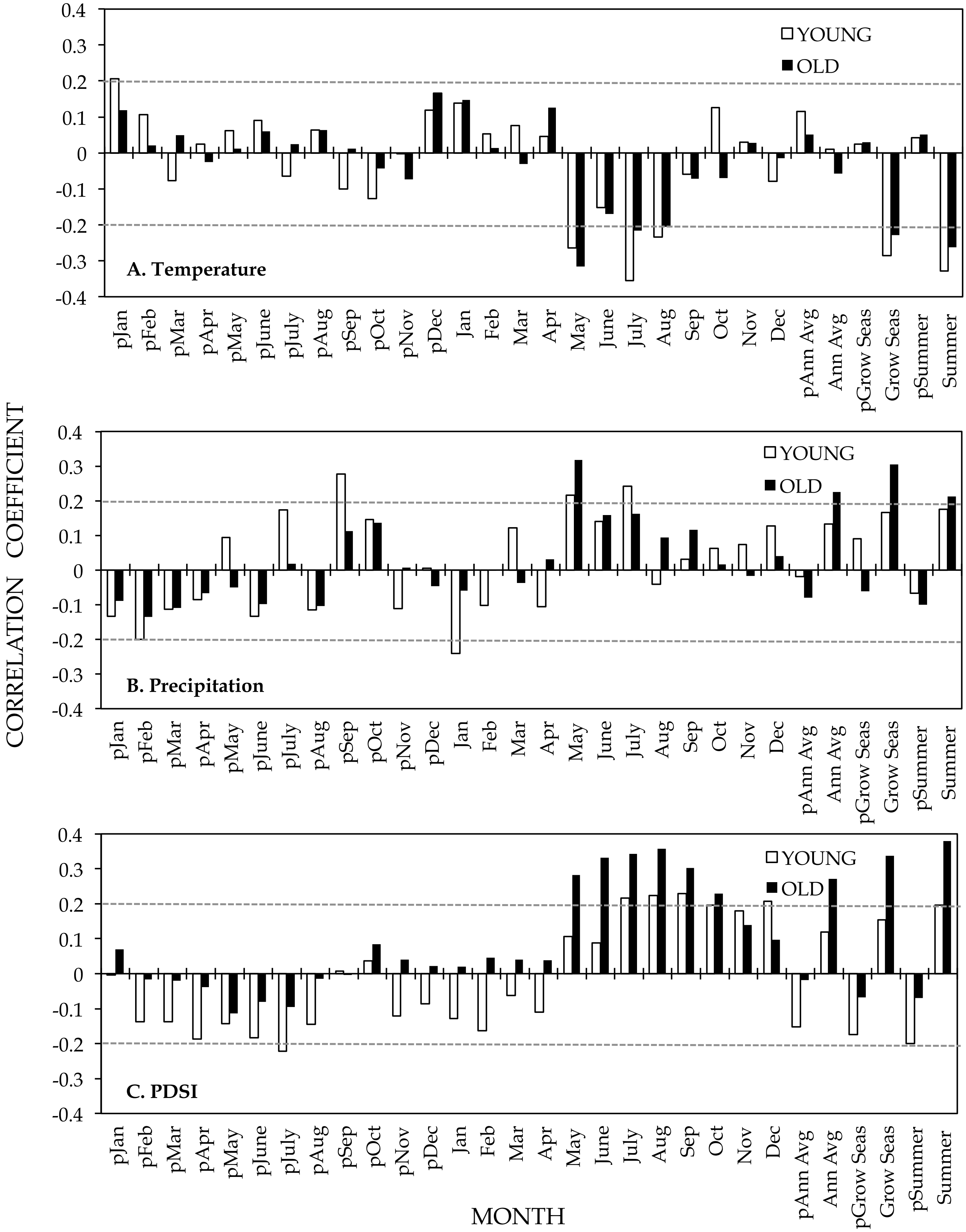

Maryland
Delaware
West Virginia
Kentucky
Virginia
Tennessee
North Carolina
Atlantic Ocean
South Carolina
Georgia
Florida
Carolina Hemlock (Tsuga caroliniana)
Eastern Hemlock (Tsuga canadensis)
0
250
500
Kilometers
N




600
500
400
300
200
100
0
TREES ha-1
Tsuga caroliniana
Quercus alba
Quercus rubra
Other
Overtopped
Intermediate
Codominant
Dominant
CANOPY CLASS


Tsuga caroliniana
A.
Quercus rubra
Quercus alba
Other
B.
DBH (cm)
INNER DATE
0
10
20
30
40
50
60
1725
1750
1775
1800
1825
1850
1875
1900
1925
1950
1975
2000


OLD CHRONOLOGY
YOUNG CHRONOLOGY
INDEX
1.75
1.5
1.25
1
0.75
0.5
1840
1850
1860
1870
1880
1890
1900
1910
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010
YEAR


CORRELATION COEFFICIENT
A. Temperature
B. Precipitation
C. PDSI
YOUNG
OLD
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
pJan pFeb pMar pApr pMay pJune pJuly pAug pSep pOct pNov pDec Jan Feb Mar Apr May June July Aug Sep Oct Nov Dec pAnn Avg Ann Avg pGrow Seas Grow Seas pSummer Summer
MONTH