

# American chestnut (*Castanea dentata*) to northern red oak (*Quercus rubra*): forest dynamics of an old-growth forest in the Blue Ridge Mountains, USA

Saskia L. van de Gevel, Justin L. Hart, Mark D. Spond, Philip B. White, Megan N. Sutton, and Henri D. Grissino-Mayer

**Abstract:** We analyzed tree species composition and age structure in a rare, old-growth *Quercus rubra* L. (northern red oak) forest at Bluff Mountain Preserve, North Carolina, to assess potential changes associated with *Cryphonectria parasitica* (Murrill) M.E. Barr (chestnut blight), selective logging, livestock grazing, ice storms, wind events, and fire history. We established forest inventory plots to determine the forest composition, vertical structure, and age of the high-elevation *Q. rubra* dominated forest. We developed the longest *Q. rubra* dendroecological history (1671–2009) in North America. Several living *Q. rubra* individuals were more than 250 years old. The frequency, magnitude, and spatial extent of canopy disturbance events were shown in radial growth trends in *Q. rubra* samples. We also examined *Q. rubra* climate – radial growth relationships to compare high-elevation *Q. rubra* climate response patterns with results from lower elevation *Quercus* dendroclimatological studies. Stand-wide release events corresponded with the loss of *Castanea dentata* (Marsh.) Borkh. (American chestnut) during the 1930s and frequent ice storms or wind events. Although we observed fire scars on living hardwood trees, we did not find fire scars on the remnant logs. The lack of fire scars on the remnant logs indicates that the observed fires likely occurred during the second half of the 20th century. *Quercus rubra* were most climatically sensitive to cool March temperatures. *Quercus rubra* sampled at higher elevations were more sensitive to temperature than lower elevation *Quercus* spp. trees, which may indicate higher sensitivity to March frosts. *Quercus rubra* has been a dominant species at Bluff Mountain for the past 300 years; however, our data indicate that the forest will transition to support a much stronger *Acer saccharum* Marsh. (sugar maple) component during the next 50 years. This study provides a multcentury perspective to guide conservation efforts and forest management in high-elevation *Quercus* spp. forests in the southern Appalachian Mountains.

**Key words:** succession, fire, ice storms, dendroecology, high elevation, southern Appalachian Mountains.

**Résumé :** L'auteur a analysé la composition en espèces ligneuses et la structure de l'âge dans une rare forêt surannée de *Quercus rubra* L. (chêne rouge du nord) dans la réserve de Bluff Mountain, en Caroline du Nord, dans le but d'évaluer les changements potentiels associés au *Cryptomeria parasitica* (Murrill) M. E. Barr (brûlure du châtaignier), à la coupe sélective, au broutage animal, aux tempêtes de verglas et de vents et à l'histoire des feux. Ayant établi des parcelles d'inventaire forestier il a déterminé la composition de la forêt, la structure verticale et l'âge des forêts en haute élévation dominées par les *Quercus*. Il a développé l'histoire dendrochronologique la plus étendue (1671–2009) en Amérique du Nord. On y trouve plusieurs individus vivants de plus de 250 ans. La fréquence, la grandeur et l'étendue spatiale des événements de perturbation de la canopée se manifestent dans les tendances de la croissance radiale chez les échantillons de *Quercus*. L'auteur a également examiné les relations climat – croissance radiale du *Q. rubra* afin de comparer les patrons de réaction au climat des *Q. rubra* venant en altitude avec les résultats provenant d'études dendroclimatologiques de *Quercus* en plus faible élévation. Des événements à l'échelle des peuplements ont coïncidé avec la perte des *Castanea dentata* (Marsh.) Borkh. (noisetier américain) au cours des années 1930 ainsi que des tempêtes de verglas et de vent. Bien que l'auteur ait observé des marques de brûlures sur des arbres décidus vivants, il n'a pas trouvé de telles marques sur les billes restantes. Ce manque de brûlures sur les billes restantes indique que les feux observés sont survenus vraisemblablement au cours de la deuxième moitié du 20<sup>e</sup> siècle. Les *Q. rubra* se sont montrés sensibles au climat, surtout aux fraîches températures de mars. Les *Q. rubra* échantillonnés aux plus hautes altitudes se sont montrés plus sensibles à la température que les arbres du genre *Quercus* de faible élévation, ce qui pourrait indiquer une forte sensibilité aux gels de mars. Le *Q. rubra* a constitué une espèce dominante dans la réserve de Bluff Mountain au cours des 300 dernières

Received 22 June 2012. Accepted 7 September 2012. Published at [www.nrcresearchpress.com/cjb](http://www.nrcresearchpress.com/cjb) on 22 November 2012.

**S.L. van de Gevel, M.D. Spond, and P.B. White.** Department of Geography and Planning, Appalachian State University, Boone, NC 28608, USA.

**J.L. Hart.** Department of Geography, The University of Alabama, Tuscaloosa, AL 35487, USA.

**M.N. Sutton.** Mountains Stewardship Program Manager, The Nature Conservancy, Asheville, NC 28806, USA.

**H.D. Grissino-Mayer.** Department of Geography, The University of Tennessee, Knoxville, TN 37916, USA.

**Corresponding author:** Saskia van de Gevel (e-mail: [gevelsv@appstate.edu](mailto:gevelsv@appstate.edu)).

années. Cependant, les données indiquent que la forêt subira une transition pour supporter une composante beaucoup plus importante d'*Acer saccharum* Marsh. (érable à sucre) au cours des 50 prochaines années. Cette étude fournit une perspective multicentenaire pour guider les efforts de conservation et l'aménagement des forêts de *Quercus* spp., dans la partie sud des montagnes Appalaches.

*Mots-clés* : succession, feu, tempête de verglas, dendroécologie, haute élévation, montagnes appalachiennes méridionales.

[Traduit par la Rédaction]

## Introduction

Changes in disturbance regimes since European settlement are relevant to modern forest development and management (Nowacki and Abrams 2008). Southern Appalachian forests have been altered by a broad range of disturbances, including logging, ice storms, wind events, fire, and species loss (Delcourt and Delcourt 1998; Ellsworth and McComb 2003). Ice storms and wind events are common in southern Appalachian Mountain forests and may change the rate and trajectory of forest succession (Lafon and Speer 2002; Copenheaver et al. 2006). The introduction of exotic species during the 20th century, especially the chestnut blight (*Cryphonectria parasitica* (Murrill) M.E. Barr), has led to the loss of key forest components and the conversion of low-density American chestnut (*Castanea dentata* (Marsh.) Borkh.) stands into dense hardwood forests (Keever 1953; Woods and Shanks 1959; Whigham 1969; Stephenson and Adams 1986; Turner et al. 2003). Northern red oak (*Quercus rubra* L.) has filled the niche of a dominant canopy species once occupied by *C. dentata* in high-elevation southern Appalachian forest communities (Braun 1950; Nelson 1955; Woods and Shanks 1959; Stephenson and Adams 1986).

Dendroecological research has shown the prevalence of fire in pine–oak (*Pinus* spp. – *Quercus* spp.) communities in the Appalachian region during the last several centuries, prior to the implementation of fire suppression policies during the 20th century (Schuler and McClain 2003; McEwan et al. 2007; Hoss et al. 2008; Aldrich et al. 2010; Brose and Waldrop 2010). Soil and sediment charcoal records further indicate the presence of fire in *Pinus*–*Quercus* and mixed hardwood forests in the southern Appalachian Mountains during the last 4000 years (Delcourt and Delcourt 1998; Fesenmyer and Christensen 2010). However, existing *Quercus* spp. dendroecological studies are limited to the northern and central Appalachian Mountains and have not addressed the role of fire in high-elevation *Quercus*-dominated forests in the southern Appalachian Mountains.

Long-term climate change associated with increased temperatures and alterations to precipitation regimes could dramatically impact southern Appalachian forests (Dale et al. 2001). Twenty-first century climate predictions for the southeastern United States suggest increasing temperatures and possible alterations to precipitation regimes, which could dramatically impact the structure and composition of southern Appalachian forests (Dale et al. 2001). However, the impact of climate change on southern Appalachian forests remains uncertain (Ford et al. 2011). If climate in the southern United States becomes more erratic during the 21st century, weather events such as ice storms, droughts, and high winds may occur more frequently, further altering high-elevation southern

Appalachian forests (Bachelet et al. 2003; Hanson and Weltzin 2000; Greenberg et al. 2011).

Our objectives were to (i) quantitatively describe the species composition and structure of a high-elevation old-growth *Quercus* spp. forest after the introduction of *C. parasitica*, (ii) document the role of selective logging, grazing, fire history, wind events, and ice storms on the successional pathway of a high-elevation *Q. rubra* forest in the Blue Ridge Mountains, and (iii) examine the response of high-elevation *Q. rubra* to climate during the 20th century.

## Materials and methods

### Study area

Bluff Mountain is a high-elevation area of ecological significance in western North Carolina (Whigham 1969; Skeate 2004). The mountain is part of a small collection of old-growth forest preserves in the Blue Ridge Mountains (Nash 1999). Many of the vegetation assemblages characteristic of the Blue Ridge Province are present at Bluff Mountain, including rock outcrop communities, *Tsuga caroliniana* Engelm. (Carolina hemlock) forests, dwarf *Quercus* spp. forests, and a southern Appalachian fen (Whigham 1969; Tucker 1972; Lynch and Fields 2002). More than 48 endangered, threatened, or rare vascular plant species have been identified on Bluff Mountain (Tucker 1972; North Carolina Natural Heritage Program (NCNHP) 1999; Skeate 2004).

Bluff Mountain is a component of the Amphibolite Mountains of the Blue Ridge Province in the southern Appalachian Mountains (Mowbray and Schlesinger 1988; Lynch and Fields 2002). Elevation in the southern Appalachian Mountains ranges between ca. 300 and 2000 m. The region supports some of the highest species richness in North America (NCNHP 1999). Located in Ashe County, North Carolina, Bluff Mountain rises from an elevation of approximately 1000 m to a central peak of 1546 m (36°23'27"N, 81°34'18"W; Lynch and Fields 2002). Local soils formed from amphibolite (metamorphosed basalt) contain high levels of calcium, magnesium, and iron (Mowbray and Schlesinger 1988; NCNHP 1999). Much of the exposed rock at Bluff Mountain is composed of hornblende and gneiss (Lynch and Fields 2002). Average January temperature for the area is approximately –7 °C, with average July temperatures of 21 °C (State Climate Office of North Carolina (SCONC), <http://www.nc-climate.ncsu.edu/cronos/normals.php?station=313455>, accessed March 2011). Yearly average temperatures are approximately 10 °C. Total annual precipitation averages 100 cm. March and October have the highest average monthly precipitation (approximately 9 cm each month). Annual snow accumulation in Ashe County averages 71 cm (SCONC, <http://www.nc-climate.ncsu.edu/cronos/normals.php?station=313455>, accessed March 2011). The average grow-

ing season in Ashe County is 139 days (SCONC, <http://www.nc-climate.ncsu.edu/cronos/normals.php?station=313455>, accessed March 2011). The growing season of high-elevation hardwood forests ( $\geq 1350$  m) typically begins in late April and ends in October.

*Quercus rubra* is a common canopy species that occurs throughout the Appalachian *Quercus* spp. forest region of eastern North America (Braun 1950; Stephenson and Adams 1986). However, tree species composition within *Q. rubra* forests varies greatly with topographic position (Whittaker 1956; Day et al. 1988; Bolstad et al. 1998). *Quercus rubra* typically grows at low- to mid-elevation sites but can live at elevations as high as 1680 m in the southern Appalachian Mountains (Burns and Honkala 1990). In most *Quercus* spp. communities, *Q. rubra* shares dominance with a number of other tree species. However, in high-elevation *Q. rubra* communities, the species is the overwhelming dominant (Whittaker 1956; Whigham 1969; Racine 1971).

The first botanist to visit Bluff Mountain was Asa Gray during July 1841 (Sargent 1889; Tucker 1972). Gray noted the dominance of *C. dentata*, *Quercus alba* L. (white oak), *Liriodendron tulipifera* L. (tulip-poplar), *Magnolia acuminata* L. (cucumber tree), and *Acer saccharum* Marsh. (sugar maple) on Bluff Mountain (Sargent 1889). Gray also documented cattle grazing in the Bluff Mountain forest communities. However, the extent of grazing and the impact of grazing on Bluff Mountain forest dynamics are not known. Old home sites and roads are present in the Bluff Mountain Preserve and suggest a history of selective logging (Tucker 1972). The contemporary forests of Bluff Mountain have been impacted by anthropogenic disturbances such as selective logging and grazing and by natural disturbances such as high wind events and ice storms (Sargent 1889; Tucker 1972). The Nature Conservancy has owned and managed  $>520$  ha of Bluff Mountain since 1978. The high-elevation ( $>1350$  m) *Q. rubra* forest community is only found on the ridgeline of Bluff Mountain and is approximately 10 ha in size ( $<2\%$  of the Bluff Mountain Preserve). High-elevation *Q. rubra* dominated communities exist in only a few disjunct, island populations in the southern Appalachian Mountains. Forest managers are currently conducting environmental education management and using prescribed burning to retain *Quercus* spp. and other mast trees in the forest canopy and to limit competition from mixed-mesophytic species.

## Methods

Forest composition and age-structure data were collected within eight *Q. rubra* dominated 0.05 ha fixed-radius (radius = 12.66 m) plots on the ridge of Bluff Mountain. Plots were located on the ridge of Bluff Mountain in close proximity to an area with large hardwood logs ( $\geq 60$  cm diameter) on the forest floor. Hardwood remnant logs were an indicator of disturbance and were sampled to add annual resolution data to the multicentury forest history. Our sample size was appropriate for the relatively small size of the high-elevation *Q. rubra* dominated forest ( $<2\%$  of Bluff Mountain Preserve).

We tallied all trees by species and recorded diameter at breast height (DBH; height = 1.37 m) of all trees  $\geq 10.0$  cm DBH within each plot. Relative importance values were calculated for each species as the average of the relative density (number of individuals) and relative dominance (basal area)

(Cottam and Curtis 1956; Abrams et al. 2001). Importance values combined with age–diameter data can show patterns in past and current forest composition as a function of tree species' density and tree size (dominance) (Abrams et al. 1997, 2001; Ruffner and Abrams 1998). Importance values were calculated as the average of relative density and relative dominance for each species. Dominance values are particularly useful for projecting future overstory composition after stand-wide disturbances. Canopy class structure was also analyzed for species composition in the dominant, codominant, intermediate, and suppressed canopy classes (Oliver and Larson 1996).

Dendroecological techniques and analyses were used to provide temporally precise information on the forest disturbances and climate sensitivity of the *Q. rubra* dominated forest (Stahle and Chaney 1994; Stokes and Smiley 1996; Hart et al. 2008; Pederson 2010). We sampled all living trees ( $\geq 10.0$  cm DBH) in each plot using increment borers. All cores intersected or very nearly intersected the tree's pith and were taken at or below 30 cm above the root collar and along the contour of the slope to minimize the effects of reaction wood on the growth patterns in each sample (Fritts 1976). We also collected 20 cross sections from large remnant logs ( $\geq 60$  cm diameter) to extend the tree-ring information obtained from the cores further into the past (Fig. 1). A stem disk (ca. 2–4 cm in thickness) was sawn from within 30 cm of the base of the logs. Cross sections were collected to determine the occurrence and temporal frequency of fire scars. All cross sections had missing bark and decayed sapwood. We visually examined each log and cross section in the field and noted the presence or absence of fire scars.

Cores were allowed to air-dry completely and then were glued to wooden core mounts with cells vertically aligned to ensure a transverse view of the wood surface (Stokes and Smiley 1996). Cross sections were given an initial flat surface using a band saw to remove deep chain saw cuts prior to sanding. The cross sections and core samples were progressively sanded using a belt sander. The sanding process produced a wood surface with cellular features clearly defined under  $10\times$  magnification for clear ring identification (Stokes and Smiley 1996). Remnant wood species identification was determined after sanding (Hoadley 1990). After cross sections were sanded, we visually crossdated the cross sections and examined the samples for fire scars, discoloration, healing wood, and charcoal following methods described in Smith and Sutherland (1999).

We measured the ring widths on all *Q. rubra* cores and cross sections to 0.001 mm precision. We confirmed the graphical crossdating and relative placements of all tree-ring series using COFECHA, which uses segmented time-series correlation techniques to confirm the previously assigned temporal placements of all tree rings to the exact year that each was formed (Holmes 1983; Stokes and Smiley 1996; Grissino-Mayer 2001a). The cores from all living *Q. rubra* were used to date the cross sections from the remnant logs. Crossdating was verified when the correlation coefficient for each tested segment exceeded 0.36 ( $p < 0.01$ ), although coefficients were usually much higher. The final suggested placement made by COFECHA had to be convincing both graphically (similar patterns in wide and narrow rings) and statistically (correlation significant at  $p < 0.001$ ) (Grissino-Mayer 2001a).



**Fig. 1.** Large remnant logs on the forest floor of Bluff Mountain Preserve, North Carolina (Philip White (co-author) appears in this picture taken by S. van de Gevel).



We standardized all *Q. rubra* series in a chronology to remove effects from age-related growth trends that could add noise to the series unrelated to the climate signal desired in chronology development (Fritts 1976). We developed a *Q. rubra* chronology because *Q. rubra* were the oldest trees at the study site. We removed the age-related growth trend of each sample using the program ARSTAN (Cook 1985), which fits a negative exponential trend line to the growth of the sample using the least squares technique. ARSTAN then creates an index for that year by dividing the actual ring width by the value predicted by the regression (Fritts 1976; Cook 1985). The indices were then averaged for each year across all series to create a single *Q. rubra* chronology (Fritts 1976).

We documented the frequency, magnitude, and spatial extent of canopy disturbance events by analyzing radial growth trends (raw ring widths) in all dated *Q. rubra* samples. The identification of release episodes (i.e., periods of anomalous increased growth) is a widely used technique to develop forest canopy disturbance chronologies (Nowacki and Abrams 1997; Rubino and McCarthy 2004). Percent growth change equations are commonly used to reconstruct canopy disturbance history in *Quercus*-dominated forests of the eastern United States (Rentch et al. 2002; Copenheaver et al. 2009). In our study, releases were defined as periods when raw ring width of individual trees exceeded the mean of the previous and subsequent 10 years (i.e., a 20-year window) by 25% (minor) or 50% (major) (Nowacki and Abrams 1997). In addition, we required that the increased radial growth be sustained for a minimum of three years (Hart and Grissino-Mayer 2008; Hart et al. 2008, 2010, 2012). This release detection method has

been validated in mature *Quercus* stands, and empirical tests revealed that a raw ring width increase of at least 25% over the 10-year running mean directly corresponds to a 25%–40% increase in photosynthetically active radiation for the tree crown. The three-year duration criterion required that the tree crown was exposed to increased insolation for at least three years (Buchanan and Hart 2012). We did not analyze the first 10 years of each tree-ring series to avoid juvenile growth.

We classified stand-wide disturbance events as episodes when a minimum of 25% of living *Q. rubra* trees from at least 30% of our study plots with trees living at that time recorded simultaneous release events (Nowacki and Abrams 1997; Rubino and McCarthy 2004; Hart and Grissino-Mayer 2008). Portions of our tree-ring record had relatively low sample depth, and by establishing minimum percentages for trees and plots recording concurrent releases, we attempted to avoid classification of isolated events as stand-wide disturbances. Stand-wide releases indicate that overstory trees were removed or severely damaged throughout the entire stand during a short period. In this region, natural disturbances capable of removing trees from a broad area include ice storms and high wind events. Release initiation dates and durations were entered into the computer program FHX2 to display spatiotemporal characteristics of the disturbance chronology (Grissino-Mayer 2001b; Hart et al. 2008).

The climate – radial growth relationships for *Q. rubra* were analyzed using divisional climate data obtained from the National Climatic Data Center (NCDC; <http://www.ncdc.noaa.gov>, accessed December 2010). We used climate data from the NCDC North Carolina 2 (Northwestern) Division (Asheville, North Carolina; <ftp://ftp.ncdc.noaa.gov/pub/data/cirs/>, accessed

**Table 1.** Density (number of trees·ha<sup>-1</sup>), dominance (basal area; m<sup>2</sup>·ha<sup>-1</sup>), and importance of trees (mean of relative density and relative dominance) by species at Bluff Mountain Preserve, North Carolina.

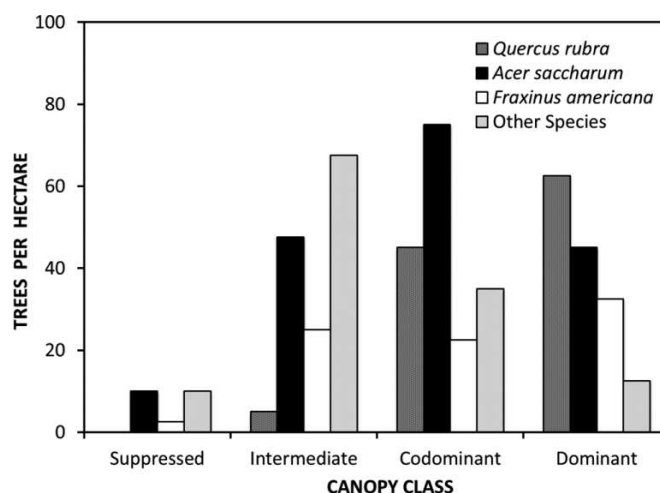
Species	Density	Relative density	Dominance	Relative dominance	Relative importance
<i>Quercus rubra</i>	112.5	22.61	18.50	45.70	34.16
<i>Acer saccharum</i>	177.5	35.68	11.88	29.36	32.52
<i>Fraxinus Americana</i>	82.5	16.58	4.94	12.22	14.4
<i>Betula alleghaniensis</i>	27.5	5.53	2.44	6.04	5.78
<i>Ostrya virginiana</i>	40.0	8.04	0.96	2.37	5.20
<i>Quercus alba</i>	22.5	4.52	0.95	2.34	3.43
<i>Carya glabra</i>	10.0	2.01	0.36	0.88	1.45
<i>Acer rubrum</i>	7.5	1.51	0.10	0.24	0.87
<i>Prunus serotina</i>	5.0	1.01	0.17	0.42	0.71
<i>Fagus grandifolia</i>	5.0	1.01	0.08	0.20	0.60
<i>Tilia americana</i>	5.0	1.01	0.06	0.15	0.58
<i>Acer pensylvanicum</i>	2.5	0.50	0.03	0.08	0.29
Total	497.5	100.0	40.47	100.0	100.0

July 2011) between 1930 and 2009. The climate variables used in the climate response analysis included monthly average temperature, monthly total precipitation, and monthly Palmer drought severity index (PDSI). PDSI is used by the National Weather Service to monitor drought and wetness conditions in the United States and is a measure of the moisture conditions during the growing season. PDSI incorporates temperature, precipitation, and evapotranspiration as an estimate of soil moisture availability as a monthly index (Palmer 1965). Correlation analysis was used to statistically determine the strength of association between climate and *Q. rubra* annual radial growth (ARSTAN index values). Correlation coefficients were calculated between growth indices and climate variables (temperature, precipitation, and PDSI) for a 24-month period from previous January to current December. Seasons were determined for each climate variable based on sequences of months during which the climatic variable exhibited statistically significant ( $p < 0.05$ ) relationships to *Q. rubra* radial growth. Seasonalizing climate data was important because seasons illustrate the longer period over which a climatic signal has the greatest effect on tree radial growth.

## Results

The dominant species in the high-elevation hardwood forest were *Q. rubra*, *A. saccharum*, and *Fraxinus Americana* L. (white ash) (Table 1). Living *Q. rubra* were the most dominant trees in the forest canopy. *Quercus rubra* at Bluff Mountain contributed 22% of the tree density and 45.7% of the total basal area (m<sup>2</sup>·ha<sup>-1</sup>). Basal area for *Q. rubra* was 18.5 m<sup>2</sup>·ha<sup>-1</sup>, and *A. saccharum* had the second highest basal area of 11.88 m<sup>2</sup>·ha<sup>-1</sup>. *Quercus alba* was present in the forest but had a relatively low density (22.5 trees·ha<sup>-1</sup>) and low basal area (0.95 m<sup>2</sup>·ha<sup>-1</sup>). The most abundant species in the tree layer (based on relative density) were *A. saccharum*, *Q. rubra*, and *F. americana*. We found low relative densities of *A. rubrum*, *F. grandifolia*, and *P. serotina*. Forest species were also grouped by canopy class, and values were standardized at the hectare level to reveal canopy class distribution (Fig. 2). *Acer saccharum* and *Q. rubra* were the most abundant species in the

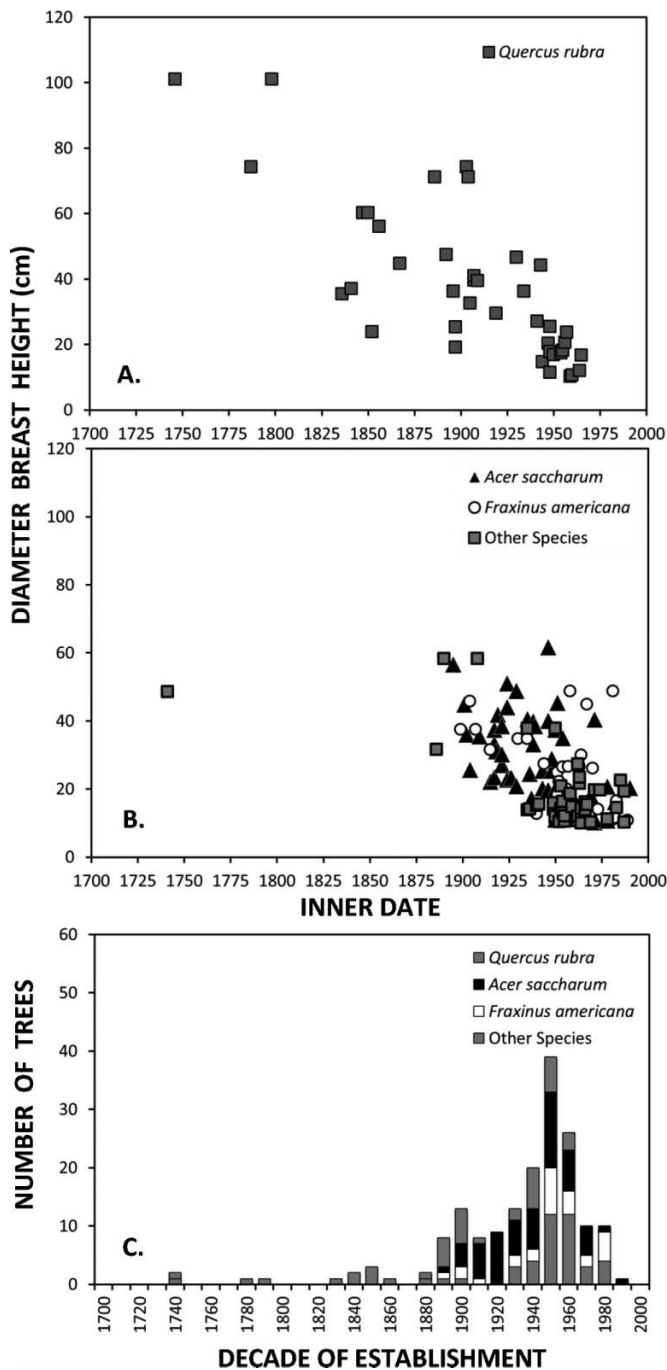
**Fig. 2.** Canopy class distributions for the three most important species on the Bluff Mountain Preserve, North Carolina. Other species: *Betula alleghaniensis*, *Ostrya virginiana*, *Quercus alba*, *Carya glabra*, *Acer rubrum*, *Prunus serotina*, *Fagus grandifolia*, *Tilia Americana*, and *Acer pensylvanicum*. Categories are based on the amount and direction of intercepted light (Oliver and Larson 1996).



canopy classes. Although *Q. rubra* was an important species in dominant and codominant canopy positions, the number of *Q. rubra* per hectare was very low compared with other species in the intermediate and suppressed canopy classes.

We identified 170 living trees that established between 1741 and 1990 in the high-elevation hardwood forest (Fig. 3). The oldest living trees were *Q. rubra* and one *Q. alba* that established during the 1700s. The youngest *Q. rubra* tree established during 1965. *Acer saccharum*, *F. americana*, and other species established from the 1890s to the 1990s. We found two distinct pulses of tree establishment during the last 250 years. *Quercus* spp. established continuously between 1741 and 1900. The establishment of a cohort of *Q. rubra* occurred

**Fig. 3.** Age–diameter patterns and establishment periods of living trees: (A) *Q. rubra*, (B) *A. saccharum*, *F. americana*, and other species of the 170 living trees dated at Bluff Mountain Preserve, North Carolina. (C) Establishment decades of all living trees. Other species: *Betula alleghaniensis*, *Ostrya virginiana*, *Quercus alba*, *Carya glabra*, *Acer rubrum*, *Prunus serotina*, *Fagus grandifolia*, *Tilia Americana*, and *Acer pensylvanicum*.



during the 1930s–1950s. A large cohort of *A. saccharum*, *F. americana*, and other hardwood individuals also established during the 1930s–1950s.

Cross sections taken from remnant logs in the study area were identified as *Q. rubra*, not *C. dentata* or other *Quercus* species

(Fig. 4). The wood anatomy feature that helped distinguish *Quercus* spp. from *C. dentata* was the multiseriate rays. The size and distribution of rays on a cross section are unique for many species (Hoadley 1990). *Quercus rubra* and *Q. alba* have multiseriate rays that are easily seen without a hand lens, but *C. dentata* has numerous and extremely narrow rays (uniseriate) that can only be seen with magnification (Hoadley 1990). *Quercus rubra* and *Q. alba* were distinguished by the absence of tyloses in the earlywood of *Q. rubra* (Hoadley 1990). After we determined that the logs were *Q. rubra*, we extended the *Q. rubra* chronology further back in time.

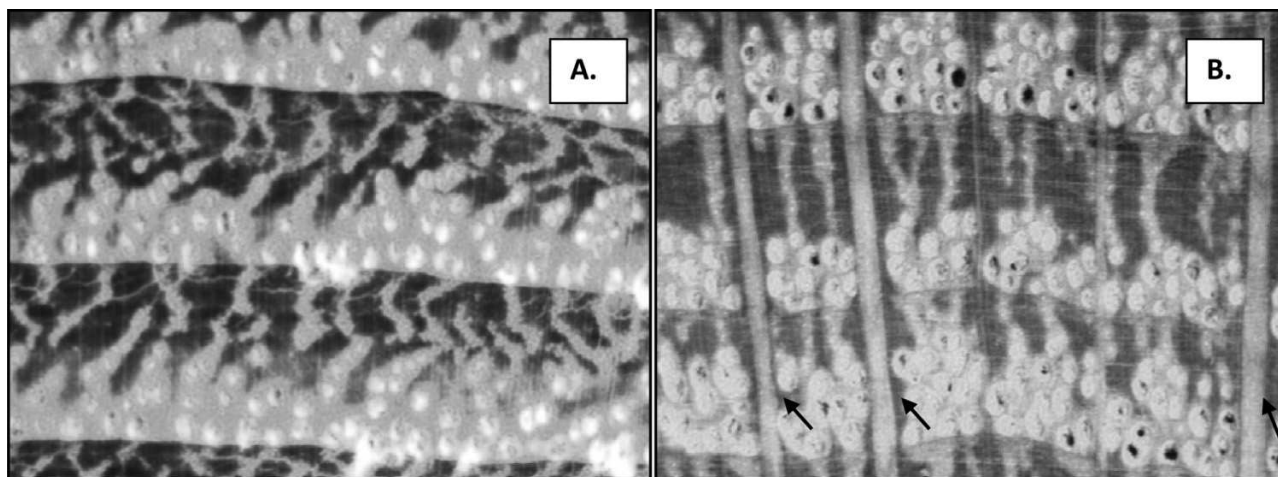
*Quercus* spp. trees have thick bark and do not exhibit scars from all fires (Guyette and Stambaugh 2004). After careful examination of the intact wood in the 20 *Q. rubra* cross sections, we did not find any fire scars, discoloration, healing wood, or woundwood (Smith and Sutherland 1999). However, fire scars were present at the base of several living trees in the study area. The lack of scars in the cross sections does not indicate the absence of fire in the study area (Guyette and Stambaugh 2004). Decayed bark and sapwood may have included recent fire scars and fire injuries (after 1950). The decayed outer rings prevented us from the determining mortality dates of the *Q. rubra* logs. However, the outermost dates of the cross sections were clustered during the 1940s and 1950s.

The Bluff Mountain *Q. rubra* chronology (1671–2009) of 47 series (cross sections and cores) is the oldest and highest elevation *Q. rubra* chronology in North America (Fig. 5) (Speer et al. 2009; International Tree-Ring Data Bank 2010; White et al. 2011). The interseries correlation and mean sensitivity of the *Q. rubra* chronology were consistent with other *Quercus* spp. chronologies from the region (Speer et al. 2009; White et al. 2011). The average interseries correlation for the *Q. rubra* chronology was 0.53, with a mean sensitivity of 0.19. Approximately 5% of the 40-year segments by the program COFECHA were flagged for possible dating errors. We visually checked the flagged time segments in the cores and cross sections to ensure proper dating. Periods of reduced growth and narrow rings in the *Q. rubra* chronology were formed during 1700–1718, 1780–1804, 1811–1820, 1867–1878, 1967–1982, and 1990–2000 (although the actual magnitudes of the indices varied) and served as marker rings for crossdating. Larger tree rings during 1672, 1740, 1766, 1833, 1851, 1951, 1957, 1960, 1964, and 2005–2008 were also used in the crossdating process. We also noted the frequency of ice storms, tornadoes, and tropical storms recorded between 1907 and 2008 in this region of the Blue Ridge Mountains (Table 2).

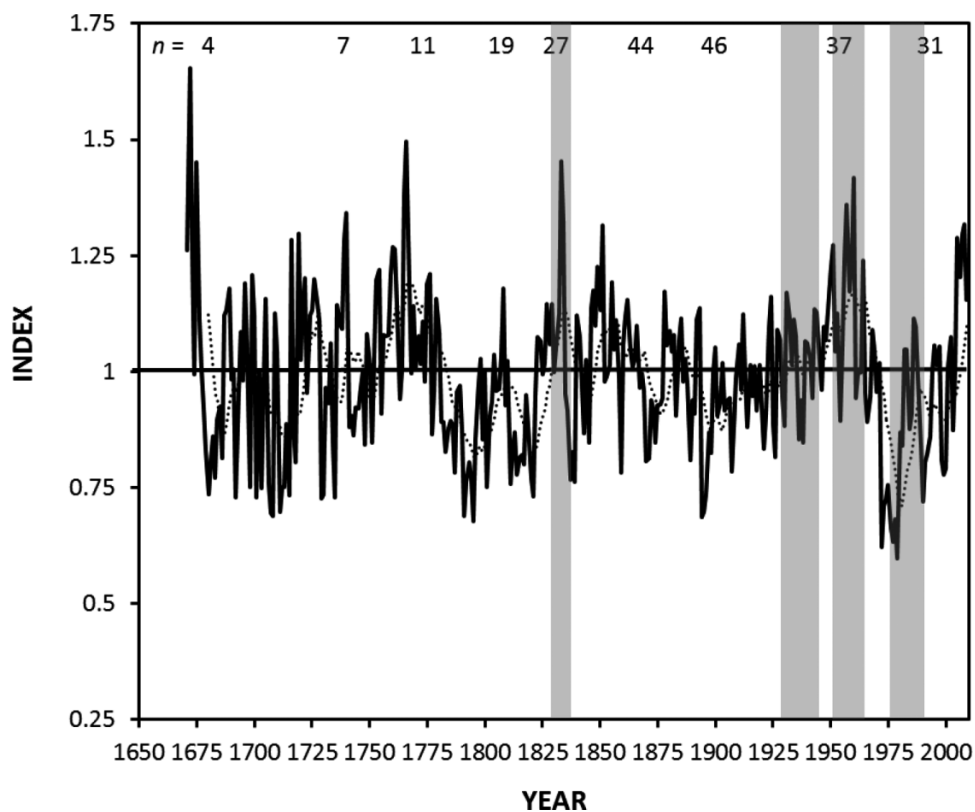
A total of 68 release events were detected from the 31 *Q. rubra* individuals analyzed (Fig. 6). Of these 68 releases, 58 (85%) were minor and 10 (15%) were major. The greatest growth change increase over the 10-year running mean was 111%, recorded in 1902 for a single individual. Only three trees (9%) did not exhibit at least one release episode during their life span. Notably, 23 (74%) of the 31 series analyzed exhibited multiple releases. The maximum number of releases recorded in a single tree was four, but this pattern occurred in three individuals. The mean release duration was 4.42 years  $\pm$  0.18 (SE). The longest release episode lasted 9 years (1885–1893) and was classified as a minor event. The mean duration between release initiation years was 7.07 years  $\pm$  1.33 (SE). However, throughout the record, consecutive release initia-



**Fig. 4.** Radial view of (A) *Castanea dentata* and (B) *Quercus rubra*. Note the multiseriate rays (marked with black arrows) in the *Q. rubra* and the lack of rays in the *C. dentata*.



**Fig. 5.** Ring-width index chronology generated from *Quercus rubra* series sampled at Bluff Mountain Preserve (AD 1671–2009), the oldest *Q. rubra* chronology (340 years) in North America. The mean radial growth is standardized to 1.0 ( $n$  = number of series at that time). The dotted line is the 10-year moving average of the *Q. rubra* chronology. Gray vertical bars indicate stand-wide release episodes.



tions occurred approximately every 12 years. *Quercus rubra* trees experienced frequent releases from the late 1920s to the early 1930s, throughout the 1950s, the late 1960s, and the early 1980s. Notably, no trees released between 1986 and 2005 (19 years), representing the longest release-free period since the early 1800s. The site experienced four stand-wide release events, with more release episodes initiated during the

1980s than in any other decade. Notably, no stand-wide disturbances occurred between the 1830s and the 1920s.

The climate correlation analysis showed the strongest relationship between *Q. rubra* radial growth and temperature (Fig. 7). *Quercus rubra* responded positively to cool March temperatures. The negative correlations during the previous summer indicate an increase in temperature in the previous

**Table 2.** Ice storms, tornado damage, and tropical storm history in northwestern North Carolina.

Ice storm dates (1960–2008)	Tornado damage (1950–2002)	Tropical storm year and type (1907–2004)	Tropical storm wind speed (km/h)
March 1960	October 1950	1907 (ES)	56
December 1962	November 1954	1920 (TD)	40
January 1968	April 1956	1940 (ES)	56
January 1982	September 1959	1949 (TS)	64
December 1989	September 1960	1959 (ES Gracie)	72
March 1993	September 1963	1989 (TS Hugo)	88
February 1994	September 1964	2003 (ES)	32
June 1995	October 1965	2004 (TD)	32
December 1995	October 1969		
February 1996	May 1973		
December 2000	April 1974		
December 2003	March 1975		
February 2005	May 1976		
February 2008	April 1977		
	June 1978		
	July 1979		
	May 1980		
	June 1981		
	September 1982		
	May 1983		
	March 1984		
	June 1986		
	May 1989		
	June 1990		
	March 1991		
	July 1992		
	August 1993		
	June 1994		
	May 1995		
	April 1996		
	October 1997		
	March 1998		
	September 1999		
	April 2000		
	September 2002		

**Note:** Ice storm data (NCDC, <ftp://ftp.ncdc.noaa.gov/pub/data/cirs/>, accessed July 2011); tornado damage in Ashe County, North Carolina (Storm Prediction Center (SPC), NOAA, <http://www.spc.noaa.gov/wcm/#data>, accessed July 2012); and tropical storm data for mountainous areas within 80 km of Bluff Mountain (SCONC, <http://www.nc-climate.ncsu.edu/lsrcdb/index.php>, accessed July 2012); ES, extratropical storm; TS, tropical storm; TD, tropical depression.

year's summer results in decreased radial growth. We also found a strong negative relationship with *Q. rubra* growth and temperature during July and November. *Quercus rubra* had a strong negative correlation to previous January and current May precipitation. However, we found positive correlations between *Q. rubra* radial growth and previous July precipitation and current July precipitation. We also found negative correlations between *Q. rubra* radial growth and PDSI during the previous January and previous July.

## Discussion

### Forest composition

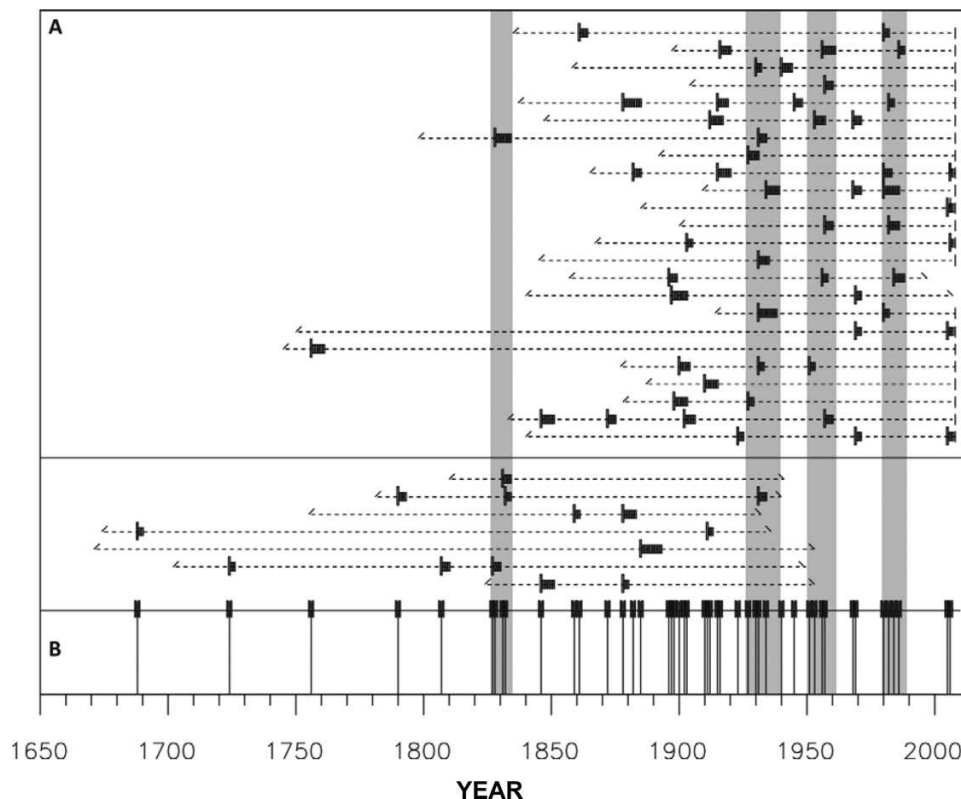
High-elevation hardwood forests in the Appalachian Mountains were historically dominated by *C. dentata*, comprising between 25% and 75% of southern Appalachian forests (Holmes 1911; Braun 1950; Kuhlman 1978). *Castanea*

*dentata* was in the dominant and codominant canopy classes, similar to the current dominance of *Q. rubra*. In 1905, *C. dentata* was the most important tree species in the high-elevation hardwood forests of northwestern North Carolina (Reed 1905; Braun 1950). *Castanea dentata* contributed 45%–47% of the tree density, with *Q. rubra* second in abundance (Reed 1905; Braun 1950). In Ashe County, North Carolina, *C. dentata* contributed to approximately 27% of all standing trees and 20% of cut lumber (Holmes 1911). Although we do not have *C. dentata* density data specifically for Bluff Mountain from the early 20th century, we saw *C. dentata* stump regeneration and Asa Gray identified the dominance of *C. dentata* on Bluff Mountain (Sargent 1889).

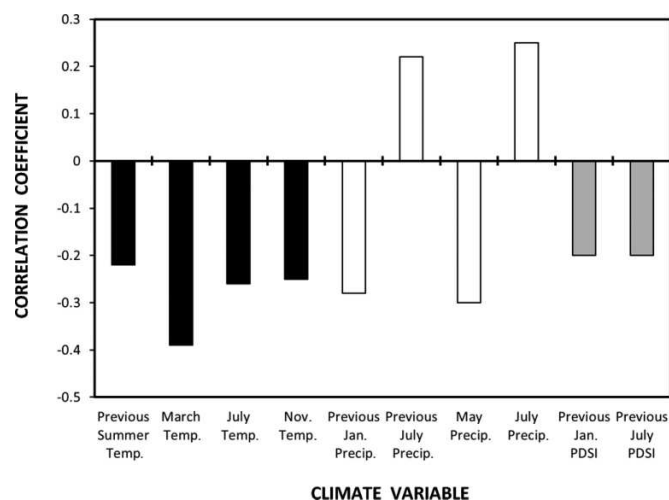
In southern Appalachian Mountain forests, the disappearance of *C. dentata* from the canopy during the 1930s provided a period of unusually high recruitment of new individuals of *Q. rubra* and



**Fig. 6.** (A) Release events using the 10-year running mean method for 31 *Quercus rubra* individuals sampled from Bluff Mountain Preserve, North Carolina. Each horizontal line represents the record from one individual tree, long vertical bars indicate release initiation, and short vertical bars indicate release duration. Gray vertical bars indicate release episodes that occurred in 25% or more of the living trees across 30% or more of our study plots with living trees at that time. The series above the break are tree cores and beneath the break are cross sections. (B) A composite of release events for all stands.



**Fig. 7.** Significant ( $r = \pm 2.0$ ,  $p \leq 0.05$ ) relationships between *Quercus rubra* and temperature (Temp.), precipitation (Precip.), and Palmer drought severity index (PDSI) at Bluff Mountain Preserve, North Carolina.



other species into the canopy (Keever 1953; Woods and Shanks 1959; Stephenson and Adams 1986; Turner et al. 2003). The *C. parasitica* fungus caused the functional extinction of *C. dentata* (Ellison et al. 2005), which created large gaps in the

forest canopy. We found an increase in abundance of several *Quercus* spp. trees after the introduction of *C. parasitica* during the 1930s. The loss of *C. dentata* contributed towards *Q. rubra* dominance in the forest canopy. We also found tree establishment patterns between the 1930s and 1950s that correspond with the decline of *C. dentata* in the forest.

The ability to study multicentury forest dynamics within high-elevation *Q. rubra* communities of the southern Appalachian Mountains is restricted by a lack of old-growth stands (Lorimer 1980; Loehle 1988; Blozan 1994). Old-growth characteristics are abundant throughout the Bluff Mountain forest, including features found in other studies such as large-diameter trees, a variety of diameter classes and canopy layers, canopy gaps, and coarse woody debris on the forest floor (Stahle and Chaney 1994; Abrams and Copenheaver 1999; Abrams et al. 2001; Pederson 2010). The Bluff Mountain forest has been heavily influenced by natural and anthropogenic disturbances. Asa Gray observed the presence of cattle grazing on Bluff Mountain during the mid-19th century (Sargent 1889). Cattle and sheep grazing was noted as “extensive” in Ashe County, North Carolina (Holmes 1911). Overstory trees showed signs of disturbance, including broken branches and abundant canopy gaps. We observed canopy disturbance evidence from ice storms, windthrow events, and past fires at the study site.

Importance values, canopy class distributions, and age-diameter results show the future trajectory of the historically

*C. dentata* dominated forest. The forest canopy was dominated by *Q. rubra*, *A. saccharum*, and *F. americana*. However, stem density was highest for *A. saccharum*. Shade-tolerant species will likely increase in dominance as intermediate and suppressed individuals are recruited to larger size and canopy classes. Juvenile *Q. rubra* are outcompeted by shade-tolerant tree species that remain suppressed until the formation of canopy gaps. *Acer saccharum* is a shade-tolerant species that can competitively exclude *Quercus* spp. in the lower canopy classes (Lorimer et al. 1994). As more trees in the suppressed and intermediate canopy positions reach codominant and dominant positions, the forest will likely change from a *Q. rubra* dominated forest to a forest with more shade-tolerant mesophytic species, specifically *A. saccharum*. Canopy gaps historically assisted *Q. rubra* and *C. dentata* establishment. The establishment of *A. saccharum* and other mesophytic species prohibits *Q. rubra* from establishing in emergent forest gaps and recruiting to larger size classes. *Quercus rubra* is moderately shade tolerant but less tolerant than the competing *Acer* spp. (Abrams 1990, 1992). Therefore, understory *Q. rubra* may be competitively excluded under the current disturbance regime from recruitment into larger canopy classes by *A. saccharum* and other shade-tolerant species.

### Fire history

Previous studies have proposed that the *Quercus*-to-*Acer* successional shift was caused by active fire suppression that began during the early 20th century (Abrams 1992; McEwan et al. 2007; Nowacki and Abrams 2008). *Quercus rubra* is considered tolerant of fire, but *A. saccharum* and other mesophytic species are fire sensitive. It has been widely hypothesized that frequent, low-intensity fires historically inhibited *A. saccharum* establishment and facilitated *Quercus* spp. recruitment (Abrams 1992; Brose et al. 2001; Nowacki and Abrams 2008). Fire suppression may contribute towards the *Quercus*-to-*Acer* succession pattern on some high-elevation *Quercus* sites. However, fires may not have directly impacted the establishment of *Q. rubra* at Bluff Mountain during the past 250 years. Furthermore, the lack of fire scars and fire injuries prior to ca. 1950 in the *Q. rubra* cross sections suggests that fire was not a disturbance that inhibited establishment of *A. saccharum* on this site. Fire scars were present on several living hardwood trees in the study area but were not present in the *Q. rubra* cross sections. Although not all fires scar trees and it is possible that fire scars may have been present in the decayed sapwood and bark of the *Q. rubra* cross sections, we propose that fires were rare or did not scar *Q. rubra* trees in the stand prior to 1950. Frequent, low-intensity fires did not inhibit *A. saccharum* establishment. The majority of the trees sampled in our study established between 1935 and 1990. We suggest that tree establishment from the 1930s to the 1950s was a function of the introduction of *C. parasitica* and unrelated to a change in the fire regime (i.e., fire suppression). Our results indicate that factors other than fire suppression may explain the transition from *Quercus* to *Acer* forests at Bluff Mountain (e.g., Hart et al. 2008; McEwan et al. 2011).

### Canopy disturbance history

Previous forest studies in the Appalachian Mountains documented radial growth increases in *Quercus* spp. caused by the decline of *C. dentata* and tree damage from ice storms and

high-speed wind events (Keever 1953; Woods and Shanks 1959; Stephenson and Adams 1986; Lafon and Speer 2002; Hart et al. 2008). Bluff Mountain *Q. rubra* trees experienced stand-wide disturbances between the 1930s and 1950s that corresponded with *C. dentata* decline. Large disturbances also occurred during the late 1960s and the early 1980s that favorably affected radial growth in the *Q. rubra* chronology. We hypothesize that the large disturbances during the late 1960s and the early 1980s were ice storms or high-speed wind events that impacted high elevations in the southern Appalachians (Cseke 2003; NCDC, <ftp://ftp.ncdc.noaa.gov/pub/data/cirs/>, accessed July 2011). The *Q. rubra* trees showed a period of radial growth suppression between 1967 and 1982 that could have been caused by damage to tree canopies from ice storms or high winds. Ice storm and wind damage in *Q. rubra* forests can facilitate the formation of tree cavities, which may predispose the affected trees to windthrow during storms (Whitney and Johnson 1984; Rebertus et al. 1997; Bragg et al. 2003). Large broken branches and canopy gaps on Bluff Mountain suggested recent ice or wind damage. Ice storms and high winds are common in the Blue Ridge Province, which influences frequency and scale of gap formation, coarse woody debris loadings, and forest succession in *Quercus* forests (Rebertus et al. 1997; Copenheaver et al. 2006). Tree-ring evidence of ice storms or wind events included periods of suppression and release in the *Q. rubra* samples (Lafon and Speer 2002). *Quercus rubra* radial growth during 1986–2005 was average and did not show suppressions or releases related to disturbance events. The lack of *Q. rubra* releases between 1986 and 2005 could indicate that the ice storms or wind events during this period were not strong enough to cause canopy damage.

The occurrence of four stand-wide disturbances during the 250-year forest record indicates that the return interval of stand-wide disturbance events in the study area is within the range of what has been reported elsewhere in the eastern United States. The 90-year stand-wide release gap between the 1830s and the 1920s was unexpected. We expected to see a stand-wide release during this period from selective logging, but perhaps logging did not impact this high-elevation site compared with lower elevation forests. Disturbance events did not occur in every *Q. rubra* tree, yet many release episodes occurred in a single tree. Therefore, we hypothesize that the introduction of *C. parasitica*, wind events, and ice storms were the primary disturbance events that influenced forest dynamics in the Bluff Mountain Preserve during the 19th and 20th centuries. These release events likely resulted from canopy disturbances that involved the partial or total death of canopy individuals (Nowacki and Abrams 1997; Rubino and McCarthy 2004).

### Climate response

The climatic response of high-elevation *Q. rubra* at Bluff Mountain was not consistent with relationships identified in previous *Quercus* spp. dendroclimatological studies in the eastern United States. Radial growth in *Quercus* spp. at lower elevations is typically associated with cool, moist summers (Cook and Jacoby 1977; Stahle and Hehr 1984; Bortolot et al. 2001; D'Arrigo et al. 2001; Speer et al. 2009; White et al. 2011). Unlike other *Quercus* spp. climate studies, we found a weak relationship between summer conditions and *Q. rubra* radial growth (Speer et al. 2009; White et al. 2011; Crawford

2012). We identified spring temperatures to be most associated with *Q. rubra* radial growth on Bluff Mountain. Specifically, radial growth in sampled *Q. rubra* responded positively to cool March temperatures. Warm March temperatures can lead to early budbreak and leafing that increases risk of exposure to freezing temperatures (Lopez et al. 2008). The risk of freezing temperatures during March is high in southern Appalachian hardwood forests (Lopez et al. 2008). *Quercus rubra* trees damaged by freezing temperatures allocate resources to replace nutrients lost in damaged leaves (Givnish 2002). Thus, *Q. rubra* may favor cool March temperatures that delay budbreak and leafing in high-elevation forests. Relationships between radial growth and previous and current July precipitation, coupled with inverse relationships with temperature, indicate that July moisture availability also influenced *Q. rubra* radial growth at Bluff Mountain. The *Q. rubra* radial growth and July temperature and precipitation relationships were weaker than in other studies (Cook and Jacoby 1977; Stahle and Hehr 1984; Bortolot et al. 2001; D'Arrigo et al. 2001; Speer et al. 2009; White et al. 2011; Crawford 2012).

An improved knowledge of how *Q. rubra* responds to climate factors, especially drought, may provide a better understanding of maturing *Quercus* spp. forests at high elevations (Voelker et al. 2008). *Quercus rubra* is a drought-tolerant species (Abrams 1990; Kolb et al. 1990; Abrams and Copenheaver 1999; Olano and Palmer 2003) and is an important species on mesic and xeric sites in southern Appalachian forests. Drought and root rot fungi (e.g., *Armillaria mellea* Vahl ex Fr.) are important contributing factors to the mortality of *Q. rubra* (Biocca et al. 1993; Jenkins and Pallardy 1995; Oak et al. 1996; Bruhn et al. 2000; Clinton et al. 2003; Voelker et al. 2008). Drought can directly affect *Q. rubra* by reducing growth or inducing mortality (Fahey 1998; Condit et al. 1999). Drought can also indirectly affect vitality by predisposing trees to damage from other abiotic (e.g., fire and wind events) or biotic (e.g., disease and pathogens) factors (Olano and Palmer 2003; Klos et al. 2009). The observed drought tolerance of high-elevation *Q. rubra* may favor *Quercus*-dominated forests more than mixed mesophytic forests if drought episodes increase in frequency and intensity during the 21st century (Klos et al. 2009).

## Conclusions

Forest inventory and dendroecological analyses allowed us to determine the establishment sequence of *Q. rubra*, *A. saccharum*, and other hardwood species. Tree species composition and age structure have changed as a consequence of *C. parasitica*, wind events, and ice storms in an old-growth *Q. rubra* forest in the Blue Ridge Mountains. In this study, we crossdated remnant logs with old-growth *Q. rubra* trees to develop a forest disturbance history that spans 340 years and created the oldest *Q. rubra* chronology in North America. Although fire scars were present in living hardwood trees, we did not find fire scars in the *Q. rubra* remnant logs. The lack of fire scars and fire injuries in remnant logs indicates that fires occurred after 1950 but may have been rare prior to this time. Major release events in *Q. rubra* trees corresponded to the loss of *C. dentata* during the 1930s and to ice storms and wind events. Understory *A. saccharum* and other mesophytic species may respond to ice storm and wind damage in the *Q. rubra* dominated overstory (De Steven et al. 1991; Rebertus

et al. 1997). Although *Q. rubra* has been a dominant species at this site during the past 300 years, the forest will likely transition to support a much stronger *A. saccharum* component during the 21st century. The species establishment pattern that we identified at Bluff Mountain is consistent with those of other studies throughout the eastern United States where *Quercus*-dominated forests will transition to mixed mesophytic species (Fralish et al. 1991; Abrams 1992; Ruffner and Abrams 1998; Hart et al. 2008). Fire may not have historically maintained *Q. rubra* dominance in this forest, but forest managers may consider manipulating stand structure through prescribed burning to decrease the density of *A. saccharum* and other mesophytic species in the understory. High-elevation *Q. rubra* were less sensitive to summer drought than lower elevation *Quercus* spp. forests. As temperatures increase, drought-tolerant *Q. rubra* may have a successional advantage over *A. saccharum* and other species that are more drought sensitive. This study provides a multicentury perspective for forest conservation and management in high-elevation *Quercus* spp. forests in the southern Appalachian Mountains.

## Acknowledgments

This study was supported by a research grant from The Nature Conservancy and a University Research Council grant from Appalachian State University. Margit Bucher, Doug Sprouse, and Jordan Holcolm assisted with dendroecological data collection. Carolyn Copenheaver and Audrey Zink-Sharp assisted with remnant wood identification. John L'Heureux assisted with obtaining information from weather databases.

## References

- Abrams, M.D. 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiol.* **7**(1–2–3–4): 227–238. PMID:14972920.
- Abrams, M.D. 1992. Fire and the development of oak forests. *Bio-science*, **42**(5): 346–353. doi:10.2307/1311781.
- Abrams, M.D., and Copenheaver, C.A. 1999. Temporal variation in species recruitment and dendroecology of an old-growth white oak forest in the Virginia Piedmont, USA. *For. Ecol. Manage.* **124**(2-3): 275–284. doi:10.1016/S0378-1127(99)00071-7.
- Abrams, M.D., Orwig, D.A., and Dockry, M.J. 1997. Dendroecology and successional status of two contrasting old-growth oak forests in the Blue Ridge Mountains, USA. *Can. J. For. Res.* **27**(7): 994–1002. doi:10.1139/x97-042.
- Abrams, M.D., Copenheaver, C.A., Black, B.A., and van de Gevel, S.L. 2001. Dendroecology and climatic impacts for a relict, old-growth, bog forest in the Ridge and Valley Province of central Pennsylvania. *Can. J. Bot.* **79**(1): 58–69.
- Aldrich, S.R., Lafon, C.W., Grissino-Mayer, H.D., DeWeese, G.G., and Hoss, J.A. 2010. Three centuries of fire in montane pine oak stands on a temperate forest landscape. *Appl. Veg. Sci.* **13**(1): 36–46. doi:10.1111/j.1654-109X.2009.01047.x.
- Bachelet, D., Neilson, R.P., Hickler, T., Drapek, R.J., Lenihan, J.M., Sykes, M.T., Smith, B., Sitch, S., and Thonicke, K. 2003. Simulating past and future dynamics of natural ecosystems in the United States. *Global Biogeochemistry Cycles*, **17**: 1045. doi:10.1029/2001GB001508.
- Biocca, M., Tainter, F.H., Starkey, D.A., Oak, S.W., and Williams, J.G. 1993. The persistence of oak decline in the western North Carolina Nantahala Mountains. *Castanea*, **58**(3): 178–184.
- Blozan, W. 1994. The importance of core samples and disturbance



- history in the evaluation of old-growth forests in the Great Smoky Mountain National Park. *Nat. Areas J.* **14**(2): 140–142.
- Bolstad, P.V., Swank, W., and Vose, J. 1998. Predicting Southern Appalachian overstory vegetation with digital terrain data. *Landsc. Ecol.* **13**(5): 271–283. doi:10.1023/A:1008060508762.
- Bortolot, Z.J., Copenheaver, C.A., Longe, R.L., and Van Aardt, J.A.N. 2001. Development of a white oak chronology using live trees and a post-Civil War cabin in south-central Virginia. *Tree-Ring Res.* **57**: 197–203.
- Bragg, D.C., Shelton, M.G., and Zeide, B. 2003. Impacts and management implications of ice storms on forests in the southern United States. *For. Ecol. Manage.* **186**(1-3): 99–123. doi:10.1016/S0378-1127(03)00230-5.
- Braun, E.L. 1950. Eastern deciduous forests of North America. Blakiston Publishing, Philadelphia, Pennsylvania.
- Brose, P.H., and Waldrop, T.A. 2010. A dendrochronological analysis of a disturbance–succession model for oak–pine forests of the Appalachian Mountains, USA. *Can. J. For. Res.* **40**(7): 1373–1385. doi:10.1139/X10-077.
- Brose, P., Schuler, T., van Lear, D., and Berst, J. 2001. Bringing fire back: the changing regimes of the Appalachian mixed oak forests. *J. For.* **99**(11): 30–35.
- Brubaker, L.B., and Cook, E.R. 1983. Tree-ring studies of Holocene environments. *In* Late-Quaternary environments of the United States. Edited by J.H.E. Wright. University of Minnesota Press, Minneapolis, Minnesota. pp. 222–235.
- Bruhn, J.N., Wetteroff, J.J., Mihail, J.D., Kabrick, J.M., and Pickens, J.B. 2000. Distribution of *Armillaria* species in upland Ozark Mountain forests with respect to site, overstory species composition and oak decline. *For. Pathol.* **30**(1): 43–60. doi:10.1046/j.1439-0329.2000.00185.x.
- Buchanan, M.L., and Hart, J.L. 2012. Canopy disturbance history of old-growth *Quercus alba* sites in the eastern United States: examination of long-term trends and broad-scale patterns. *For. Ecol. Manage.* **267**: 28–39. doi:10.1016/j.foreco.2011.11.034.
- Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. Vol. 2. Hardwoods. USDA Forest Service, Washington, DC, Agriculture Handbook No. 654.
- Clinton, B.D., Boring, L.R., and Swank, W.T. 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. *Ecology*, **74**(5): 1551–1558. doi:10.2307/1940082.
- Clinton, B.D., Yeakley, J.A., and Apsley, D.K. 2003. Tree growth and mortality in a southern Appalachian deciduous forest following extended wet and dry periods. *Castanea*, **68**: 189–200.
- Condit, R., Ashton, P.S., Manokaran, N., LaFrankie, J.V., Hubbell, S.P., and Foster, R.B. 1999. Dynamics of the forest communities at Pasoh and Barro, Colorado: comparing two 50 ha plots. *Philos. Trans. R. Soc. Lond. Ser. B*, **354**: 1739–1748.
- Cook, E.R. 1985. A time series analysis approach to tree-ring standardization. Ph.D. dissertation, University of Arizona, Tucson, Arizona.
- Cook, E.R. 1987. The decomposition of tree-ring series for environmental studies. *Tree-Ring Bull.* **47**: 37–59.
- Cook, E.R., and Jacoby, G.C., Jr. 1977. Tree-ring-drought relationships in the Hudson Valley, New York. *Science*, **198**(4315): 399–401. doi:10.1126/science.198.4315.399. PMID:17809441.
- Copenheaver, C.A., Matthews, J.M., Showalter, J.M., and Auch, W.E. 2006. Forest stand development patterns in the Southern Appalachians. *Northeast. Nat.* **13**(4): 477–494. doi:10.1656/1092-6194(2006)13[477:FSDPIT]2.0.CO;2.
- Copenheaver, C.A., Black, B.A., Stine, M.B., McManamay, R.H., and Bartens, J. 2009. Identifying dendroecological growth releases in American beech, jack pine, and white oak: within-tree sampling strategy. *For. Ecol. Manage.* **257**: 2235–2240.
- Cottam, G., and Curtis, J.T. 1956. The use of distance measures in phytosociological sampling. *Ecology*, **37**(3): 451–460. doi:10.2307/1930167.
- Crawford, C.J. 2012. Do high-elevation northern red oak tree-rings share a common climate-driven growth signal? *Arct. Antarct. Alp. Res.* **44**(1): 26–35. doi:10.1657/1938-4246-44.1.26.
- Cseke, J.J. 2003. A dendroecological approach for dating individual small-scale canopy disturbance events, Great Smoky Mountains National Park, Tennessee, USA. M.S. thesis, University of Tennessee, Knoxville, Tennessee.
- D'Arrigo, R.D., Schuster, W.S.F., Lawrence, D.M., Cook, E.R., Wiljanen, M., and Thetford, R.D. 2001. Climate–growth relationships of eastern hemlock and chestnut oak from Black Rock Forest in the highlands of southeastern New York. *Tree-Ring Res.* **57**: 183–190.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., and Wotton, B.M. 2001. Climate change and forest disturbances. *Bioscience*, **51**: 723–734. doi:10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2.
- Dale, V.H., Tharp, M.L., Lannom, K.O., and Hodges, D.G. 2010. Modeling transient response of forests to climate change. *Sci. Total Environ.* **408**(8): 1888–1901. doi:10.1016/j.scitotenv.2009.11.050. PMID:20163827.
- Day, F.P., Phillips, D.L., and Monk, C.D. 1988. Forest communities and patterns. *In* Forest hydrology and ecology at Coweeta. Edited by W.T. Swank and D.A. Crossley. Springer-Verlag, New York.
- De Steven, D., Kline, J., and Matthiae, P.E. 1991. Long-term changes in a Wisconsin *Fagus-Acer* forest in relation to glaze storm disturbance. *J. Veg. Sci.* **2**(2): 201–208. doi:10.2307/3235952.
- Delcourt, P.A., and Delcourt, H.R. 1998. Paleoeological insights on conservation of biodiversity: a focus on species, ecosystems, and landscapes. *Ecol. Appl.* **8**: 921–934.
- Elliott, K.J., and Swank, W.T. 2008. Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). *Plant Ecol.* **197**(2): 155–172. doi:10.1007/s11258-007-9352-3.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloepfel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., and Webster, J.R. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* **3**(9): 479–486. doi:10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.
- Ellsworth, J.W., and McComb, B.C. 2003. Potential effects of passenger pigeon flocks on the structure and composition of pre-settlement forests of eastern North America. *Conserv. Biol.* **17**(6): 1548–1558. doi:10.1111/j.1523-1739.2003.00230.x.
- Fahey, T.J. 1998. Recent changes in an upland forest in southcentral New York. *J. Torrey Bot. Soc.* **125**: 51–59.
- Fesenmyer, K.A., and Christensen, N.L., Jr. 2010. Reconstructing Holocene fire history in a southern Appalachian forest using soil charcoal. *Ecology*, **91**(3): 662–670. doi:10.1890/09-0230.1. PMID:20426326.
- Ford, C.R., Laseter, S.H., Swank, W.T., and Vose, J.M. 2011. Can forest management be used to sustain water-based ecosystem services in the face of climate change? *Ecol. Appl.* **21**(6): 2049–2067.

- Foster, D.R. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. *J. Ecol.* **80**(4): 753–772. doi:10.2307/2260864.
- Foster, D.R., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., and Knapp, A. 2003. The importance of land-use legacies to ecology and conservation. *Bioscience*, **53**(1): 77–88. doi:10.1641/0006-3568(2003)053[0077:TIOLUL]2.0.CO;2.
- Fralish, J.S., Crooks, F.B., Chambers, J.L., and Harty, F.M. 1991. Comparison of presettlement, second-growth and old-growth forests on six site types in the Illinois Shawnee Hills. *Am. Midl. Nat.* **125**(2): 294–309. doi:10.2307/2426234.
- Fritts, H.C. 1976. *Tree rings and climate*. Academic Press, New York.
- Givnish, T.J. 2002. Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fenn.* **36**: 703–743.
- Greenberg, C.H., Keyser, T.L., and Speer, J.H. 2011. Temporal patterns of oak mortality in a southern Appalachian forest (1991–2006). *Nat. Areas J.* **31**(2): 131–137. doi:10.3375/043.031.0205.
- Grissino-Mayer, H.D. 2001a. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res.* **57**(2): 205–221.
- Grissino-Mayer, H.D. 2001b. FHX2 — software for analyzing temporal and spatial patterns in fire regimes from tree rings. *Tree-Ring Res.* **57**: 115–124.
- Guyette, R.P., and Stambaugh, M.C. 2004. Post-oak fire scars as a function of diameter, growth, and tree age. *For. Ecol. Manage.* **198**(1–3): 183–192. doi:10.1016/j.foreco.2004.04.016.
- Hanson, P.J., and Weltzin, J.F. 2000. Drought disturbance from climate change: response of United States forests. *Sci. Total Environ.* **262**: 205–220.
- Hart, J.L., and Grissino-Mayer, H.D. 2008. Vegetation patterns and dendroecology of a mixed hardwood forest on the Cumberland Plateau: implications for stand development. *For. Ecol. Manage.* **255**(5–6): 1960–1975. doi:10.1016/j.foreco.2007.12.018.
- Hart, J.L., van de Gevel, S.L., and Grissino-Mayer, H.D. 2008. Disturbance dynamics in a natural area of the southern Ridge and Valley, Tennessee. *Nat. Areas J.* **28**(3): 275–289. doi:10.3375/0885-8608(2008)28[275:FDIANA]2.0.CO;2.
- Hart, J.L., van de Gevel, S.L., Sakulich, J., and Grissino-Mayer, H.D. 2010. Influence of climate and disturbance on the growth of *Tsuga canadensis* at its southern limit in eastern North America. *Trees Structure and Function*, **24**(4): 621–633. doi:10.1007/s00468-010-0432-y.
- Hart, J.L., Clark, S.L., Torreano, S.J., and Buchanan, M.L. 2012. Composition, structure, and dendroecology of an old-growth *Quercus* forest on the tablelands of the Cumberland Plateau, U.S.A. *For. Ecol. Manage.* **266**: 11–24. doi:10.1016/j.foreco.2011.11.001.
- Hoadley, R.B. 1990. *Identifying wood: accurate results with simple tools*. The Taunton Press, Newtown, Connecticut.
- Holmes, J.S. 1911. *Forest conditions in western North Carolina*. The North Carolina Geological and Economic Survey, Raleigh, North Carolina, Bulletin 23.
- Holmes, R.L. 1983. Computer assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* **43**: 69–78.
- Hoss, J.A., Lafon, C.W., Grissino-Mayer, H.D., Aldrich, S.R., and DeWeese, G.G. 2008. Fire history of a temperate forest with an endemic fire-dependent herb. *Phys. Geogr.* **29**(5): 424–441. doi:10.2747/0272-3646.29.5.424.
- International Tree-Ring Data Bank. 2010. Median COFECHA chronology statistics by species. Available at <http://www.ncdc.noaa.gov/paleo/treering/cofecha/speciesdata.html> [accessed November 2010].
- Jenkins, M.A., and Pallardy, S.G. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. *Can. J. For. Res.* **25**(7): 1119–1127. doi:10.1139/x95-124.
- Keever, C. 1953. Present composition of some stands of the former oak–chestnut forest in the southern Blue Ridge Mountains. *Ecology*, **34**(1): 44–54. doi:10.2307/1930307.
- Kloeppel, B.D., Clinton, B.D., Vose, J.M., and Cooper, A.R. 2003. Drought impacts on tree growth and mortality of southern Appalachian forests. In *Climate variability and ecosystem response at long-term ecological research sites*. Edited by D. Greenland, D.G. Goodin, and R.C. Smith. Oxford University Press, New York. pp. 43–55.
- Klos, R.J., Wang, G.G., Bauerle, W.L., and Rieck, J.R. 2009. Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. *Ecol. Appl.* **19**(3): 699–708. doi:10.1890/08-0330.1. PMID:19425432.
- Kolb, T.E., Steiner, K.C., McCormick, L.H., and Bowersox, T.W. 1990. Growth response of northern red oak and yellow-poplar seedlings to light, soil moisture, and nutrients in relation to ecological strategy. *For. Ecol. Manage.* **38**(1–2): 65–78. doi:10.1016/0378-1127(90)90086-Q.
- Kuhlman, E.G. 1978. The devastation of American chestnut by blight. In *Proceedings of the American Chestnut Symposium*. Edited by W.L. MacDonald. West Virginia University Press, Morgantown, West Virginia.
- Lafon, C.W., and Speer, J.H. 2002. Using dendrochronology to identify major ice storm events in oak forests of southwestern Virginia. *Clim. Res.* **20**: 41–54. doi:10.3354/cr020041.
- Loehle, C. 1988. Tree life history strategies: the roles of defenses. *Can. J. For. Res.* **18**(2): 209–222. doi:10.1139/x88-032.
- Lopez, O.R., Farris-Lopez, K., Montgomery, R.A., and Givnish, T.J. 2008. Leaf phenology in relation to canopy closure in southern Appalachian trees. *Am. J. Bot.* **95**(11): 1395–1407. doi:10.3732/ajb.0800104. PMID:21628147.
- Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology*, **61**(5): 1169–1184. doi:10.2307/1936836.
- Lorimer, C.G., and Frelich, L.E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Can. J. For. Res.* **19**(5): 651–663. doi:10.1139/x89-102.
- Lorimer, C.G., Chapman, J.W., and Lambert, W.D. 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* **82**: 227–237.
- Lynch, I.P., and Fields, M. 2002. *North Carolina afield: a guide to the Nature Conservancy projects in North Carolina*. The Nature Conservancy, North Carolina Chapter, Durham, North Carolina.
- McCormick, J.F., and Platt, R.B. 1980. Recovery of an Appalachian forest following the chestnut blight or Catherine Keever—you were right! *Am. Midl. Nat.* **104**(2): 264–273. doi:10.2307/2424865.
- McEwan, R.W., Hutchinson, T.F., Long, R.P., Ford, R.D., and McCarthy, B.C. 2007. Temporal and spatial patterns of fire occurrence during the establishment of mixed-oak forests in eastern North America. *J. Veg. Sci.* **18**(5): 655–664. doi:10.1111/j.1654-1103.2007.tb02579.x.
- McEwan, R.W., Dyer, J.M., and Pederson, N. 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography*, **34**(2): 244–256. doi:10.1111/j.1600-0587.2010.06390.x.
- Mowbray, T., and Schlesinger, W.H. 1988. The buffer capacity of organic soils of the Bluff Mountain fen, North Carolina. *Soil Sci.* **146**(2): 73–79. doi:10.1097/00010694-198808000-00003.

- Nash, S. 1999. Blue Ridge 2020 — an owner's manual. The University of North Carolina Press, Chapel Hill, North Carolina.
- Nelson, T.C. 1955. Chestnut replacement in the southern highlands. *Ecology*, **36**(2): 352–353. doi:10.2307/1933248.
- North Carolina Natural Heritage Program. 1999. An inventory of the significant natural areas of Ashe County, North Carolina. Available at <http://www.ncnhp.org/Images/Ashe10-10-2005.pdf> [accessed May 2011].
- Nowacki, G.J., and Abrams, M.D. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecol. Monogr.* **67**: 225–249.
- Nowacki, G.J., and Abrams, M.D. 2008. The demise of fire and “mesophication” of forests in the eastern United States. *Bioscience*, **58**(2): 123–138. doi:10.1641/B580207.
- Oak, S.W., Tainter, F., Williams, J., and Starkey, D. 1996. Oak decline risk rating for the southeastern United States. *Ann. For. Sci.* **53**(2–3): 721–730. doi:10.1051/forest:19960248.
- Olano, J.M., and Palmer, M.W. 2003. Stand dynamics of an Appalachian old-growth forest during a severe drought episode. *For. Ecol. Manage.* **174**: 139–148.
- Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley & Sons, Ltd., New York.
- Palmer, W.C. 1965. Meteorological drought. U.S. Weather Bureau, Washington, D.C., Research Paper 45.
- Pederson, N. 2010. External characteristics of old trees in the eastern deciduous forest. *Nat. Areas J.* **30**(4): 396–407. doi:10.3375/043.030.0405.
- Pederson, N., Cook, E.R., Jacoby, G.C., Peteet, D.M., and Griffin, K.L. 2004. The influence of winter temperatures on the annual radial growth of six northern range margin tree species. *Dendrochronologia*, **22**(1): 7–29. doi:10.1016/j.dendro.2004.09.005.
- Racine, C.H. 1971. Reproduction of three species of oak in relation to vegetational and environmental gradients in the southern Blue Ridge. *Bull. Tor. Bot. Club*, **98**: 297–310.
- Rebertus, A.J., Shirley, S.R., Richards, R.H., and Roovers, L.M. 1997. Ice storm damage to an old-growth oak–hickory forest in Missouri. *Am. Midl. Nat.* **137**(1): 48–61. doi:10.2307/2426754.
- Reed, F.W. 1905. Report on the examination of a forest tract in western North Carolina. US Bureau of Forestry Bulletin 60.
- Rentch, J.S., Fekedulegn, D., and Miller, G.W. 2002. Climate, canopy disturbance, and radial growth averaging in a second-growth, mixed-oak stand in West Virginia, USA. *Can. J. For. Res.* **32**: 915–927. doi:10.1139/x02-016.
- Rubino, D.L., and McCarthy, B.C. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia*, **21**(3): 97–115. doi:10.1078/1125.7865.00047.
- Ruffner, C.M., and Abrams, M.D. 1998. Relating land-use history and climate to the dendroecology of a 326-year-old *Quercus prinus* talus slope forest. *Can. J. For. Res.* **28**(3): 347–358. doi:10.1139/x97-220.
- Sargent, C.S. 1889. Scientific papers of Asa Gray. Vol. II. 1841–1886. Houghton, Mifflin, and Company, Boston, Massachusetts.
- Schuler, T.M., and McClain, W.R. 2003. Fire history of a Ridge and Valley oak forest. USDA Forest Service, Northeastern Research Station, Pennsylvania, Research Paper NE-724.
- Skeate, S. 2004. A nature guide to northwest North Carolina. Parkway Publishers, Boone, North Carolina.
- Smith, K., and Sutherland, E.K. 1999. Fire scar formation and compartmentalization in oak. *Can. J. For. Res.* **29**(2): 166–171. doi:10.1139/x98-194.
- Speer, J.H., Grissino-Mayer, H.D., Orvis, K.H., and Greenberg, C.H. 2009. Climate response of five oak species in the eastern deciduous forest of the southern Appalachian Mountains, USA. *Can. J. For. Res.* **39**(3): 507–518. doi:10.1139/X08-194.
- Stahle, D.W., and Chaney, P.L. 1994. A predictive model for the location of ancient forests. *Nat. Areas J.* **14**(3): 151–158.
- Stahle, D.W., and Hehr, J.G. 1984. Dendroclimatic relationships of post oak across a precipitation gradient in the southcentral United States. *Ann. Assoc. Am. Geogr.* **74**(4): 561–573. doi:10.1111/j.1467-8306.1984.tb01474.x.
- Stephenson, S.L., and Adams, H.S. 1986. Changes in a former chestnut-dominated forest after a half century of succession. *Am. Midl. Nat.* **116**(1): 173–179. doi:10.2307/2425949.
- Stephenson, S.L., Ash, A.N., and Stauffer, D.F. 1993. Appalachian oak forests. In Biodiversity of the southeastern United States: upland terrestrial communities. Edited by W.H. Martin, S.G. Boyce, and A.C. Echternacht. John Wiley & Sons, Ltd., New York.
- Stokes, M.A., and Smiley, T.L. 1996. An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois.
- Tucker, G.E. 1972. The vascular flora of Bluff Mountain, Ashe County, North Carolina. *Castanea*, **37**(1): 2–26.
- Turner, M.G., Pearson, S.M., Bolstad, P., and Wear, D.N. 2003. Effects of land-cover change on spatial pattern of forest communities in the Southern Appalachian Mountains (USA). *Landsc. Ecol.* **18**(5): 449–464. doi:10.1023/A:1026033116193.
- Voelker, S.J., Muzika, R.M., and Guyette, R.P. 2008. Individual tree and stand level influences on the growth, vigor, and decline of red oaks in the Ozarks. *For. Sci.* **54**(1): 8–20.
- Vose, J.M., Swank, W.T., Clinton, B.D., Knoepp, J.D., and Swift, L.W. 1999. Using stand replacement fires to restore southern Appalachian pine–hardwood ecosystems: effects on mass, carbon, and nutrient pools. *For. Ecol. Manage.* **114**(2–3): 215–226. doi:10.1016/S0378-1127(98)00352-1.
- Whigham, D.F. 1969. Vegetation patterns on the north slopes of Bluff Mountain, Ashe County, North Carolina. *J. Elisha Mitchell Sci. Soc.* **85**: 1–15.
- White, P.B., Van de Gevel, S.L., Grissino-Mayer, H.D., and LaForest, L.B. 2011. Climatic response of oak species across an environmental gradient in the southern Appalachian Mountains, USA. *Tree-Ring Res.* **67**(1): 27–37.
- Whitney, H.E., and Johnson, W.C. 1984. Ice storms and forest succession in southwestern Virginia. *Bull. Torrey Bot. Club*, **111**(4): 429–437. doi:10.2307/2995892.
- Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* **26**(1): 1–80. doi:10.2307/1943577.
- Woods, F.W., and Shanks, R.E. 1959. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. *Ecology*, **40**(3): 349–361. doi:10.2307/1929751.