Influence of Elevation on tree species distribution in the southern Appalachian Mountains

by

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Influence of elevation on tree species distribution and growth in the southern Appalachian Mountains.

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(ABSTRACT)

The southern Appalachian Mountains have long been an area of interest for the analysis of forest species growth and composition. Past forest vegetation studies focus on species composition and structure for relatively local scale research areas. Species distribution within this geographic area was compiled from studies published from 1956 to 2006. The distribution of hardwood species within the southern Appalachians decreased as the elevation of the sites increased, but this relationship could not be solely attributed to elevation gradient. In order to better understand the relationship between elevation on the radial growth of tree species within the region, an elevation microsite was selected to explore the relationship between elevation and the radial growth of upland oak. Eight study sites across a 114-meter elevation gradient were selected, and 20 oak tree cores were collected, cross-dated, measured, and a master chronology was created for each site. The correlation between ring width index and Palmer drought severity index (PDSI), precipitation and temperature was calculated with each site's master chronology. There was a significant positive correlation between PDSI and ring width index during the growing season for a majority of the year, and a significant positive correlation between precipitation and ring width index during the growing season. Even though the master chronologies originated from eight separate sites, there were common dendroclimatic responses across seven of the sites.

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Section I. Literature Review

I. INTRODUCTION

Research on forest species distribution has often been used to determine the ecological drivers and the mechanisms of disturbance within a forest ecosystem. Historically, the southern Appalachian Mountains have contained a multitude of diverse species whose distribution was directed by many different ecological variables. Past forest vegetation research on species distribution has focused on the species composition for local scale research areas throughout the southern Appalachian Mountains. The results of these local scale studies have been used to predict species composition throughout much larger regions. Often these small-scale studies include environmental variables, such as elevation, soil type, or topographic position, and these environmental variables are used to model species composition (Day and Monk 1974, Callaway et al. 1987, Stephenson and Mills 1999). For example, Whittaker (1956) related species distribution to elevation and topographic position within the Great Smoky Mountains, while Day and Monk (1974) paralleled this research by investigating the same variables at Coweeta Hydrologic Research Station. These early studies into the distribution of species across an elevation gradient relied upon the assumption that increasing elevation is analogous to decreasing soil moisture, and thus did not investigate any other ecological variables.

The results of these studies indicate a regional variation in species distribution with respect to elevation. The distribution response of species across an elevation gradient is related to the latitudinal location of the study site. For example, *Acer pensylvanicum* L. occurs at high elevations (800+ m) in West Virginia and Virginia, but occurs at middle elevations (400 m to 600 m) in North Carolina and Tennessee (Keever 1953, Whittaker 1956, Woods and Shanks 1959, Golden 1981, Johnson and Ware 1982, Stephenson 1986, Harrison et al. 1989, McNab et al. 1999, Mills and Stephenson 1999, Carter et al. 2000). *Acer rubrum* L. shows a reversal of the pattern, occurring at high elevations (800+ m) in South Carolina, but low to middle (200 m to 600 m) elevations in areas north of South Carolina (Keever 1953, Whittaker 1956, Woods and Shanks 1959, Johnson and Ware 1982, Whitney and Johnson 1984, Harrison et al. 1989, Davis et al. 2004). However, some species show little to no variation in their elevation distribution across a geographic area. For example, *Carya ovalis* (Wagenh.) Sarg. occurs at 200 to 800 m elevations throughout the southern Appalachian Mountains (Fenneman 1938).

Soils and elevation are linked and it is difficult to separate the influence of these two variables on species distribution (Nowacki and Abrams 1992). However, a number of studies have demonstrated a relationship between soil and vegetation distribution. Species are preferentially located on specific parent material or soil type. For example, *Quercus prinus* L. and *Castanea pumila* (L.) Miller has been shown to preferentially locate in soils composed primarily of schists and phyllites and in inceptisol and ultisol soil orders (Strahler 1978, Nowacki and Abrams 1992). Depth and organic matter content of the A-horizon also influenced the distribution of tree species. *Liriodendron tulipifera* L. and *Tsuga canadensis* favor sites with high organic matter and deep A-horizons, while *Quercus coccinea* Muenchh. and *Pinus rigida* Miller were more common in areas with opposite soil characteristics (Elliott et al. 1999). However, several studies have attempted to separate the influence of these variables. In southwestern Virginia, slope, aspect and position affect dominant tree species. *Acer rubrum* and *Nyssa sylvatica* Marshall are more common in coves with southeast aspects and 20% slope, while *Quercus prinus* and *Quercus velutina* Lam. occur on back slopes with southeast aspects and 35-40% slope (McEvoy et al. 1980). There appears to be less regional variation in topographic position in comparison to elevation. *Nyssa sylvatica* occurs in mountain coves and *Quercus prinus* occurs on ridge and slope positions in central Pennsylvania, southwestern Virginia and western North Carolina and Maryland (Strahler 1978, McEvoy et al. 1980, Nowacki and Abrams 1992, Elliott et al. 1999).

The variation in species distribution in localized areas within the southern Appalachian Mountains has been well documented, but little has been done to determine how tree species distribution has been affected on a regional scale for the southern Appalachian Mountains. A thorough investigation of previously conducted research in needed in order to better understand whether elevation alone an influence on species distribution across this large area

II. STUDY OBJECTIVE

The purpose of this literature review was to compile a literature-based assessment of the relationship between tree species distribution and elevation in the southern Appalachian Mountains. This will complement Boerner's (2006) published literature review of the interactions among soils, topographic position and vegetation distribution in the central and southern Appalachian Mountains by examining the influence of elevation on species distribution.

III. STUDY AREA

Physiographic provinces

The area of interest for this study is the southern Appalachian Mountains within the southeastern United States. The states included in this region are Virginia, North Carolina, South Carolina, Tennessee and Georgia. These areas encompass four physiographic provinces: the Piedmont, Blue Ridge, Ridge and Valley, and the Appalachian plateau (Fenneman 1938).

The Piedmont is the non-mountainous region of the Appalachians, sloping from the mountains to the Coastal Plain, with a landscape of gentle slopes surrounded by steep sloped valleys (Braun 1950). Elevation changes within this province are gentle, with an average variation of 213 to 457 m within the study area. The rock underlayer is typically composed of schists and gneisses. The Piedmont is characterized by clay soils from the deep decay of feldspar, and has limited alluvial plains that provide the most fertile areas in the region.

The Blue Ridge Province is along the western border of the Piedmont Province, with the Roanoke River dividing it into two distinct sections (Fenneman 1938). The northern Blue Ridge section reaches north from the Roanoke River, but is never more than 19-23 km in width. All slopes within this section are covered with soil, and there is no uniformity in the height of knobs. Typical elevation ranges from an average of 610 to 1,220 m with deep sags otherwise known as wind gaps. The southern Blue Ridge section stretches south from the Roanoke River and increases to widths up to 113 km. There is a significant increase in height in comparison to the northern section, with 46 peaks above 1,800 m and 288 peaks above 1,500 m. Summits are rounded and higher slopes are less steep than valley sides. A distinct characteristic of the southern Blue Ridge section is the cove geomorphology that occurs along the northwest slop of the Great Smoky Mountains. These coves are oval, flat floored valleys that vary in size from 13 to 26 square kilometers, and are underlain with limestone, which gives these areas an uncharacteristic fertility that is otherwise nonexistent in the southern Blue Ridge section.

The Ridge and Valley Province is series of valley floors surrounded by long, narrow mountain ridges (Fenneman 1938). The topography of this area is a unique composition of limestone and Medina sandstone. Limestone erodes rapidly in the presence of water and oxygen, which forms the valleys and narrow ridges. The upper portions of the ridges are composed of Medina sandstone, which is weather resistant, and provides a stable base in comparison to limestone. Altitude in this province varies from 152 m at the valley floor to more than 732 m in southern Virginia.

The Appalachian Plateau Province, in particular the Cumberland Mountains and Cumberland Plateau sections, is a 241 km long and 40 km wide area in southwest Virginia and southeast Tennessee and Kentucky (Fenneman 1938). The area is characterized by deep angular valleys and high ridges. The plateau is underlain with Pottsville age rocks, in particular shale and sandstone. Altitudes ranging from 762 to 1,067 m are most common, with the higher elevations occurring to the northeast of the plateau.

Forest types

There are three dominant forest types included within the study area: mixed mesophytic, oak-chestnut, and oak-pine (Braun 1950). The mixed mesophytic forest type occurs along the Appalachian Plateau, from north-central West Virginia to the Ridge and Valley province of Virginia, with a western boundary along the Cumberland Plateau (Braun 1950). This forest type is characterized by moist but well drained melanized soils with a mull humus layer. Dominant species within this forest type include *Fagus grandifolia*, *Liriodendron tulipifera*, *Tilia* spp., *Acer saccharum* Marshall, and *Quercus* spp.

The oak-chestnut forest type occurs in the southern Appalachians, ranging from the Blue Ridge Province to the Great Smoky Mountains (Braun 1950). Sites within this forest type can be characterized as moist-slope–and-cove and dry–slope-and-ridge. The mortality of the chestnut (*Castenea dentata*) resulted in the increased growth of intermediate. and shade tolerant species, but has not changed the composition of the forest to another climax forest type, with the exception of *Pinus* spp. dominated forests on west and southwest slopes in the Ridge and Valley province. Dominant species within this forest type include *Quercus* spp., *Betula* spp., *Liriodendron tulipifera*, *Prunus serotina* Ehrh., *Acer* spp., and *Tsuga canadensis*.

The oak-pine forest type occurs in the Piedmont region and along the Great Valley of northwestern Georgian and western Tennessee (Braun 1950). This forest type is often overlapped with the oak-chestnut forest type, and is often identified by the transition from the Chester series of soils to the Cecil series of lateritic soils. Dominant species in this forest type include *Quercus* spp. throughout and *Pinus* spp. in the poor soil nutrient regions.

Land use history

The southern Appalachian Mountains have long been a source of natural resources. Although major extraction of natural resources did not occur until the late nineteenth century, European settlers entered the area in the late 18th century (Eller 1982). The early settlers chose to live on the fertile lands of the hollows, with subsequent settlement occurring further up the slope and eventually onto the ridges (Clarkson 1964). By 1800, settlers began to clear large tracts of land for pasture and cultivation (Eller 1982)(Eller 1982). Early individual farms averaged 81 ha in size, and had on average 45% of their land timbered for cultivation or pasture land. Timber prospecting had been documented in the early 1700's, but large scale timber harvest did not take place until the Reconstruction period following the Civil War (Eller 1982).

Commercial logging began in the 1880's with selective cutting of choice trees along streams and rivers, relying on water as the chief means of timber transportation. Beginning in the 1890's, large tracts of land ranging from 12, 000 to 122,000 ha were purchased by northern timber companies and all marketable species were cut. Railroads permeated the south and became the chief means of transportation for formerly impenetrable areas of southern Appalachia. Railroad logging peaked in the early 1920's, when World War I increased the demand for coal. Eventually, coal surpassed timber as the main natural resource extracted from southern Appalachia. During the Great Depression of the 1930s, many company owned lands reverted to government property for non-payment of taxes and these areas were converted to National Forest lands to be protected for multiple uses, thus providing an opportunity for government oversight of land management (Myers et al. 2004).

Forest disturbance

Another important influence on the forests of the southern Appalachians was the chestnut blight (*Cryphonectria parasitica*). Prior to the blight, the American chestnut (*Castanea dentata*) was found in every state east of the Mississippi River and ranged in elevation from sea level to over 1,500 m (Woods and Shanks 1959, Whittaker 1956, Keever 1953). It was estimated that at its pinnacle in the late 1800's, the chestnut ranged over 80 million hectares, and accounted for 25-40% of all standing timber (Johnson and Ware 1982). Research by Vandermast et al. (2002) identified chestnut's ability to control a majority of the understory growth in the southern Appalachians. The chestnut blight fungus was discovered in 1904 in New York City, and quickly spread south, with full infections occurring in the Blue Ridge Province in 1920 (Keever

1953). By 1930, the chestnut blight had reached full infection levels in North Carolina and other areas in the southeastern United States (Myers et al. 2004). By the 1970's the American chestnut was completely gone from the deciduous forests of the eastern United States, except for the occasional understory sprouts that never reach maturity (Keever 1953, Vandermast et al. 2002, Myers et al. 2004). As a result, co-occurring understory species that were formerly hindered by chestnut growth began to take a more dominant role in the forests. *Acer rubrum*, *Quercus prinus*, *Pinus strobus* L., and *Liriodendron tulipifera* became the important species is most areas of the southern Appalachians, while many shade intolerant species declined because of the lack of large area disturbance (Clinton and Boring 1994).

Fire suppression has been another important influence on the forest composition of the southern Appalachians. Prior to European settlement, Native Americans used fire to prepare land for cultivation, clear unwanted vegetation from pasture areas, and to maintain transportation avenues (Rentch and Hicks 2005). European settlement initially reinforced burning practices for land preparation, but once large pockets of civilization were established, fire suppression was implemented (Abrams 2003). Pre-settlement forest composition was dominated by white oak. Fire was an important factor in the dominance of white oak. It allowed more sunlight to penetrate the forest canopy, suppressed competing species of red oak (*Quercus rubra*), red maple (*Acer rubrum*), black birch (*Betula lenta* L.) and white pine (*Pinus strobus*), and allowed white oak seed beds to become established (Abrams 2003, Blankenship and Arthur 2006). In the mid-19th century, white oak was being cut for charcoal production, which allowed red maple, sugar maple (*Acer saccharum*) and red oak to become dominant canopy species throughout much of the southern Appalachians (Blankenship and Arthur 2006, Rentch and Hicks 2005). Charcoal production peaked in the 1850s and the commercial harvest of white oak began. Government regulation of fire regimes began with the establishment of the U.S. Forest Service in 1905. The Forest Service supported a program of fire suppression from 1910 to 1970, and in 1971 began a systematic inspection of its fire suppression methods, instead beginning a program of prescribed burning and fire ecology. The documented benefits of fire have resulted in a policy of fire management by government agencies, allowing fire to reclaim its role in some naturally occurring ecosystems (Pyne 1982). Research by Blankenship and Arthur (2006) has shown that long term prescribed burning reduces competitive species populations in former white oak dominated forests, but has shown that more intensive silvicultural methods are needed to restore forests to pre-settlement composition.

Eastern hemlock (*Tsuga canadensis*) is an important species in the southern Appalachian Mountains. Recent infestation by the hemlock woolly adelgid (*Adelges tsugae*) has resulted in a decline in hemlock populations and a shift in forest understory composition (Eschtruth et al. 2006). Woolly adelgid infestation eventually leads to wholesale defoliation and mortality of infected hemlock stands (Brooks 2004). Pre-emptive logging and salvage logging have been implemented in areas infested with hemlock woolly adelgid, but have done little to curb the rate of infestation (Kizlinski et al. 2002). Research by Eschruth et al. (2006) has shown an increase in understory species in areas that have been infested with hemlock woolly adelgid for nine years or more. Hemlock woolly adelgid infestation is directly correlated to increased light availability in the understory, and an increase in exotic invasive species, such as the tree-of- heaven (*Ailanthus altissima* (Miller) Swingle) (Eschruth et al. 2006, Klizinski et al. 2002). Due to the recentness of hemlock woolly adelgid infestation in the southern Appalachian Mountains, it is difficult to predict the full influence eastern hemlock mortality will have on the forest composition in this geographic area.

IV. VEGETATION OCCURRENCE DATA

This literature review contains vegetation occurrence data from a large array of scientific studies and locations (Figure 1). In general, most of these data were collected using traditional vegetation sampling techniques. To provide an example of the types of techniques used in these studies, I have selected the following studies to demonstrate typical sampling methodology. Day and Monk (1974) sampled vegetation at Coweeta Hydrologic Station, NC. They used a stratified sampling with a total of 25 vegetation plots (25 m x50 m). Within each plot all individuals with a diameter at breast height (dbh) greater than 2.5 cm were recorded by species and diameter. All stems less than 2.5 cm dbh and less than 0.3 m tall were measured in two 5 m x 5 m plots located at the corners of each vegetation plot. Stephenson and Mills (1999) sampled vegetation at Mountain Lake Biological Station, VA. A series of 10 m x 10 m quadrants was subjectively located within a homogeneous region at each topographic position. All species with a dbh greater than 2.5 cm and taller than 1.37 m were recorded by species and diameter. Callaway et al. (1987) used 154 previously established plot locations that had been stratified across topographic positions at Coweeta Hydrologic Laboratory, Otto, NC. Each vegetation plot was 20 m x 50 m and all species with a dbh greater than 1.0 cm were recorded in 1.0 cm classes. These three studies are representative of the vegetation sampling methods used by the other studies used in this literature review. For the purposes of this literature review, species were divided into elevation classes of low (200 m – 400 m), middle (401 m – 800m) and high (greater than 800 m). These elevation ranges represent the lowest documented elevation (200 m) and the defined middle and high elevations described in the literature.

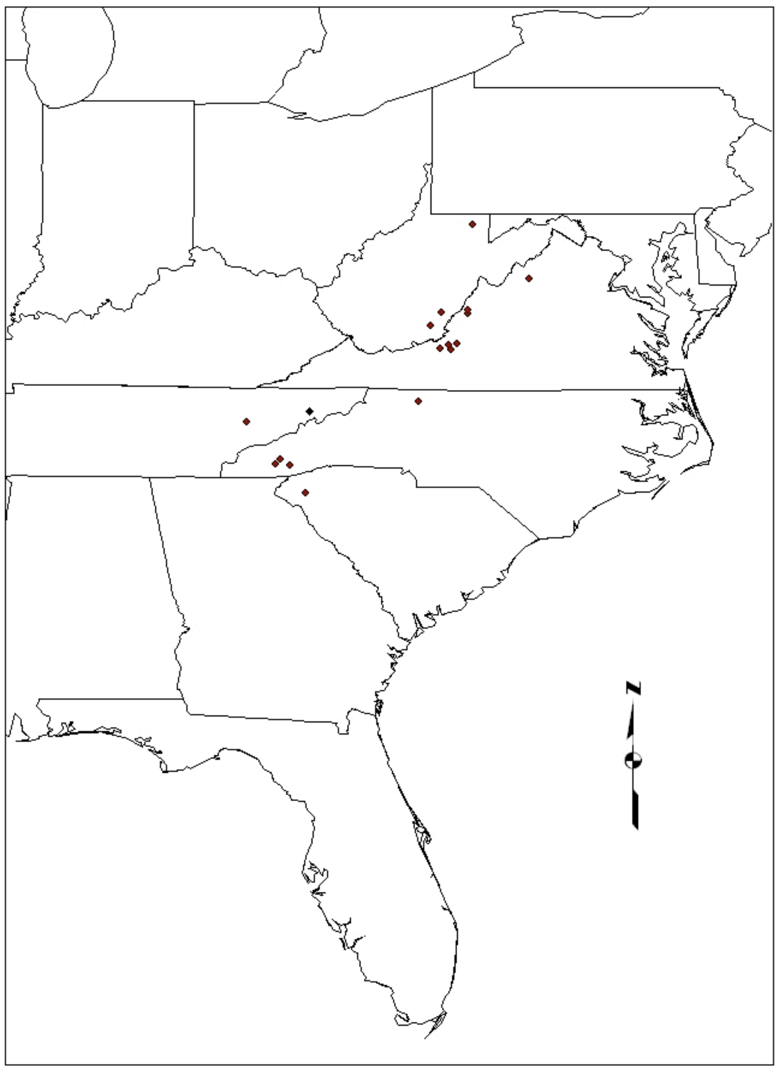

Figure 1. Literature study site locations in the southern Appalachian Mountains.

V. RESULTS AND CONCLUSIONS

This literature review contains elevation-species distribution information for 48 total species from West Virginia, Virginia, North Carolina, Tennessee, and South Carolina (Appendix A). Some of the species were identified as being present only at a single elevation class. For example, *Abies fraseri* and *Quercus muhelenbergii* Engelm. occur only at high elevations. Most of the remaining species occurred at all three elevation classes. The distribution of these species within elevation classes appears to follow a latitudinal trend. In particular, *Quercus*, *Carya* and *Acer* species follow a distribution trend of decreasing elevation with increasing latitude. A causal relationship between elevation and latitude cannot be determined from these data, since multiple studies were located in the same research areas within the southern Appalachian Mountains. However, the data collected from these studies does provide evidence of variation in species distribution with elevation within latitude bands (Figures 2-4). This variation is important to consider when evaluating the growth response of tree species across an elevation gradient and also indicates that few of the species listed in Appendix A are outside of their preferential growing environments.

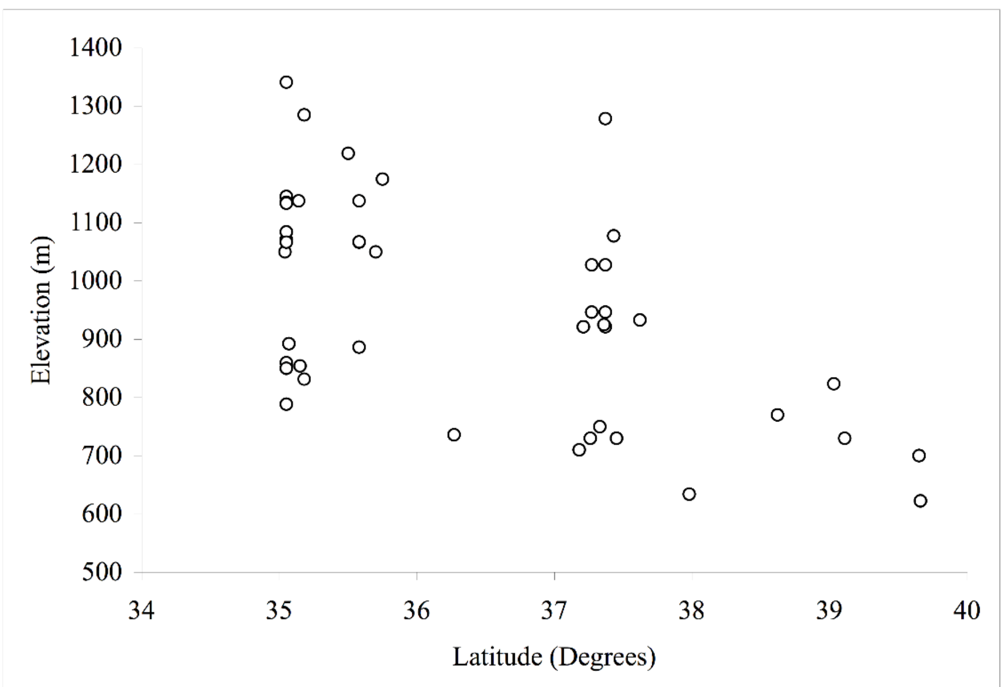

Figure 2. The influence of elevation and latitude on *Quercus* species distribution in the southern Appalachian Mountains.

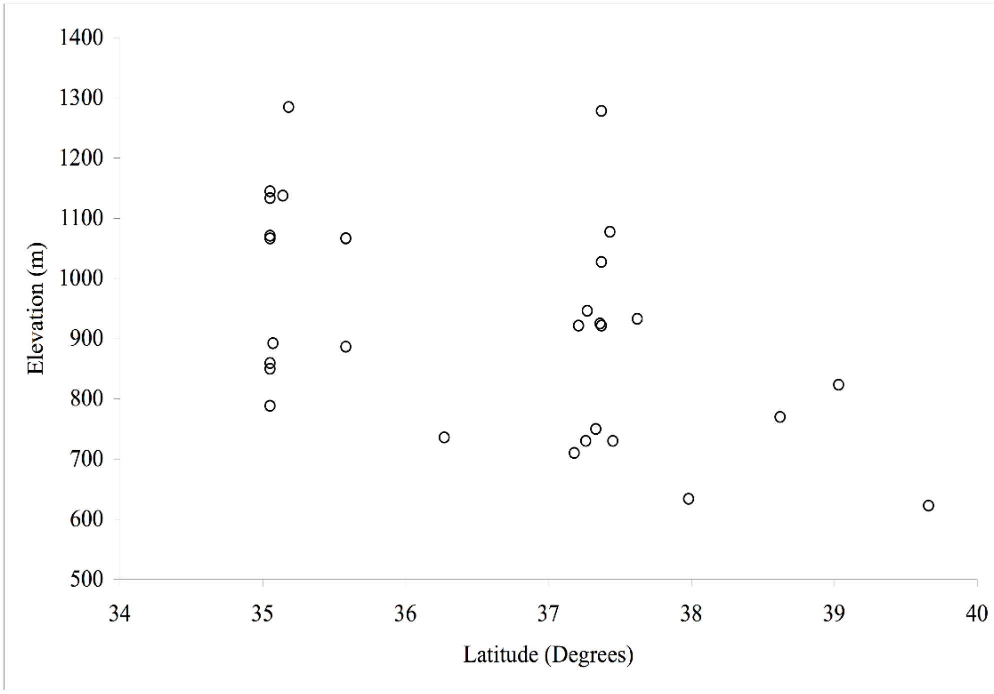

Figure 3. The influence of elevation and latitude on *Carya* species distribution in the southern Appalachian Mountains.

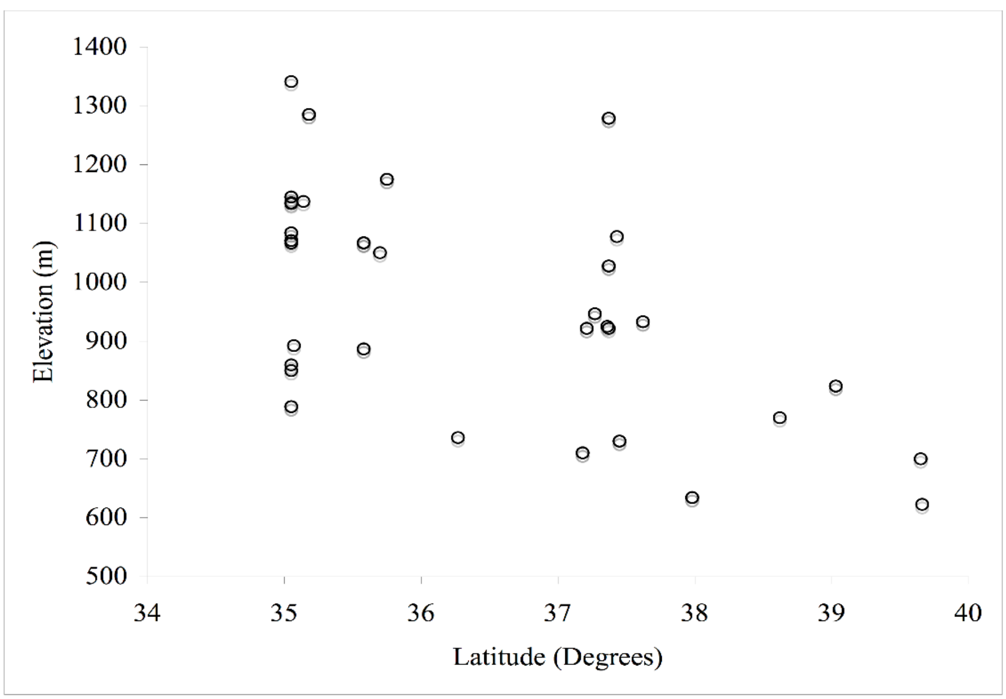

Figure 4. The influence of elevation and latitude on *Acer* species distribution in the southern Appalachian Mountains.

VI. LITERATURE CITED

Abella, S. R., V. B. Shelburne, and N. W. MacDonald. 2003. Multifactor classification of forest landscape ecosystems of Jocassee Gorges, southern Appalachian Mountains, South Carolina. Canadian Journal of Forest Research **33**:1933-1946.

Abrams, M. D. 2003. Where has all the white oak gone? Bioscience **53**:927-939.

Abrams, M. D., D. A. Orwig, and T. E. Demeo. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white-pine mixed-oak forest in the southern Appalachians, USA. Journal of Ecology **83**:123-133.

Adams, H. S., and S. L. Stephenson. 1983. A description of the vegetation on the south slopes of Peters Mountain, southwestern Virginia. Bulletin of the Torrey Botanical Club **110**:18-22.

Barden, L. S. 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. Oikos **35**:16-19.

Blankenship, B. A., and M. A. Arthur. 2006. Stand structure over 9 years in burned and fire-excluded oak stands on the Cumberland Plateau, Kentucky. Forest Ecology and Management **225**:134-145.

Boerner, R. E. J. 2006. Unraveling the Gordian Knot: Interactions among vegetation, topography, and soil properties in the central and southern Appalachians. Journal of the Torrey Botanical Society **133**:321-361.

Bolstad, P. V., W. Swank, and J. Vose. 1998. Predicting Southern Appalachian overstory vegetation with digital terrain data. Landscape Ecology **13**:271-283.

Bolstad, P. V., J. M. Vose, and S. G. McNulty. 2001. Forest productivity, leaf area, and terrain in southern Appalachian deciduous forests. Forest Science **47**:419-427.

Braun, E. L. 1950. Deciduous Forests of Eastern North America. The Blakiston Company, Philadelphia.

Brooks, R. T. 2004. Early regeneration following the presalvage cutting of hemlock from hemlock-dominated stands. Northern Journal of Applied Forestry **21**:12-18.

Busing, R. T. 1995. Disturbance and the population-dynamics of *Liriodendron tulipifera* - simulations with a spatial model of forest succession. Journal of Ecology **83**:45-53.

Callaway, R. M., E. E. C. Clebsch, and P. S. White. 1987. A multivariate-analysis of forest communities in the western Great Smoky Mountains National-Park. American Midland Naturalist **118**:107-120.

Carter, R. E., N. J. Myers, V. B. Shelburne, and S. M. Jones. 2000. Ecological land classification in the high rainfall belt of the southern Appalachian Mountains. Castanea **65**:258-272.

Clark, T. D. 1984. The Greening of the South. The University Press of Kentucky, Lexington.

Clarkson, R. B. 1964. Tumult in the Mountains:Lumbering in West Virginia, 1770-1920. McClain Publishing Company, Parsons.

Clinton, B. D., and L. R. Boring. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the southern Appalachians -influences of topographic position and evergreen understory. American Midland Naturalist **132**:308-319.

Cogbill, C. V., and P. S. White. 1991. The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian mountain chain. Vegetatio **94**:153-175.

Collins, R. J., and W. P. Carson. 2004. The effects of environment and life stage on *Quercus* abundance in the eastern deciduous forest, USA: are sapling densities most responsive to environmental gradients? Forest Ecology and Management **201**:241-258.

Davis, J. P., B. Haines, D. Coleman, and R. Hendrick. 2004. Fine root dynamics along an elevational gradient in the southern Appalachian Mountains, USA. Forest Ecology and Management **187**:19-34.

Day, F. P., and C. D. Monk. 1974. Vegetation patterns on a southern Appalachian watershed. Ecology **55**:1064-1074.

Desta, F., J. J. Colbert, J. S. Rentch, and K. W. Gottschalk. 2004. Aspect induced differences in vegetation, soil, and microclimatic characteristics of an Appalachian watershed. Castanea **69**:92-108.

Doolittle, W. T. 1957. Site index of scarlet and black oak in relation to southern Appalachian soil and topography. Forest Science **3**:114-124.

Eller, R. D. 1982. Miners, Millhands, and Mountaineers. University of Tennessee, Knoxville.

Elliott, K. J., L. R. Boring, W. T. Swank, and B. R. Haines. 1997. Successional changes in plant species diversity and composition after clearcutting a Southern Appalachian watershed. Forest Ecology and Management **92**:67-85.

Elliott, K. J., J. M. Vose, W. T. Swank, and P. V. Bolstad. 1999. Long-term patterns in vegetation-site relationships in a southern Appalachian forest. Journal of the Torrey Botanical Society **126**:320-334.

Eschtruth, A. K., N. L. Cleavitt, J. J. Battles, R. A. Evans, and T. J. Fahey. 2006. Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Canadian Journal of Forest Research **36**:1435-1450.

Fenneman, N. M. 1938. Physiography of Eastern United States. McGraw-Hill New York.

Golden, M. S. 1981. An integrated multivariate-analysis of forest communities of the central Great Smoky Mountains. American Midland Naturalist **106**:37-53.

Grigal, D. F., and R. A. Goldstein. 1971. An integrated ordination-classification analysis of an intensively sampled oak-hickory forest. Journal of Ecology **59**:481-492.

Harrison, E. A., B. M. McIntyre, and R. D. Dueser. 1989. Community dynamics and topographic controls on forest pattern in Shenandoah National Park, Virginia. Bulletin of the Torrey Botanical Club **116**:1-14.

Hicks, R. R., and P. S. Frank. 1984. Relationship of aspect to soil nutrients, species importance and biomass in a forested watershed in West Virginia. Forest Ecology and Management **8**:281-291.

Johnson, G. G., and S. Ware. 1982. Post chestnut forests in the central Blue Ridge of Virginia. Castanea **47**:329-343.

Keever, C. 1953. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains. Ecology **34**:44-54.

Kizlinski, M. L., D. A. Orwig, R. C. Cobb, and D. R. Foster. 2002. Direct and indirect ecosystem consequences of an invasive pest on forests dominated by eastern hemlock. Journal of Biogeography **29**:1489-1503.

Madgwick, H. A. I., and P. A. Desrochers. 1972. Association-analysis and the classification of forest vegetation of the Jefferson National Forest. Journal of Ecology **60**:285-292.

McCormick, J. F., and R. B. Platt. 1980. Recovery of an Appalachian forest following the chestnut blight or Keever,Catherine - you were right. American Midland Naturalist **104**:264-273.

McEvoy, T. J., T. L. Sharik, and D. W. Smith. 1980. Vegetative structure of an Appalachian oak forest in southwestern Virginia. American Midland Naturalist **103**:96-105.

McNab, W. H. 1993. A topographic index to quantify the effect of mesoscale landform on site productivity. Canadian Journal of Forest Research **23**:1100-1107.

McNab, W. H., S. A. Browning, S. A. Simon, and P. E. Fouts. 1999. An unconventional approach to ecosystem unit classification in western North Carolina, USA. Forest Ecology and Management **114**:405-420.

Meiners, T. M., D. W. Smith, T. L. Sharik, and D. E. Beck. 1984. Soil and plant water stress in an Appalachian oak forest in relation to topography and stand age. Plant and Soil **80**:171-179.

Mills, H. H., and S. L. Stephenson. 1999. Forest vegetation and boulder streams in the central Appalachian Valley and Ridge province, southwestern Virginia. Journal of the Torrey Botanical Society **126**:188-196.

Monk, C. D., and F. P. Day. 1985. Vegetation analysis, primary production and selected nutrient budgets for a southern Appalachian oak forest - a synthesis of IBP studies at Coweeta. Forest Ecology and Management **10**:87-113.

Mou, P., and M. P. Warrillow. 2000. Ice storm damage to a mixed hardwood forest and its impacts on forest regeneration in the ridge and valley region of southwestern Virginia. Journal of the Torrey Botanical Society **127**:66-82.

Myers, B. R., J. L. Walck, and K. E. Blum. 2004. Vegetation change in a former chestnut stand on the Cumberland Plateau of Tennessee during an 80-year period (1921-2000). Castanea **69**:81-91.

Nowacki, G.J., and M.D. Abrams. 1992. Community, edaphic, and historical-analysis of mixed oak forests of the Ridge and Valley Province in central Pennsylvania. Canadian Journal of Forest Research **22**: 790-800.

Oosting, H. J., and W. D. Billings. 1939. Edapho-vegetational relations in Ravenel's Woods, a virgin hemlock forest near Highlands, North Carolina. American Midland Naturalist **22**:333-350.

Parker, G. R., and W. T. Swank. 1982. Tree species response to clear-cutting a southern Appalachian watershed. American Midland Naturalist **108**:304-310.

Pyne, S. J. 1982. The Forester's Policy: A History of Fire Policy in the U.S. Forest Service. Fire in America: a Cultural History of Wildland and Rural Fire. Princeton University Press, Princeton.

Racine, C. H. 1971. Reproduction of three species of oak in relation to vegetational and environmental gradients in the southern Blue Ridge. Bulletin of the Torrey Botanical Club **98**:297-310.

Rentch, J. S., R. H. Fortney, S. L. Stephenson, W. N. Adams, W. N. Grafton, R. B. Coxe, and H. H. Mills. 2005. Vegetation patterns within the lower Bluestone River Gorge in southern West Virginia. Castanea **70**:184-203.

Rentch, J. S., and R. R. Hicks. 2005. Changes in presettlement forest composition for five areas in the central hardwood forest, 1784-1990. Natural Areas Journal **25**:228-238.

Schuler, T. M., and A. R. Gillespie. 2000. Temporal patterns of woody species diversity in a central Appalachian forest from 1856 to 1997. Journal of the Torrey Botanical Society **127**:149-161.

Stephenson, S. L. 1974. Ecological composition of some former oak-chestnut communities in western Virginia. Castanea **39**:278-286.

Stephenson, S. L. 1986. Changes in a former chestnut dominated forest after a half century of succession. American Midland Naturalist **116**:173-179.

Stephenson, S. L., H. S. Adams, and M. L. Lipford. 1991. The present distribution of chestnut in the upland forest communities of Virginia. Bulletin of the Torrey Botanical Club **118**:24-32.

Stephenson, S. L., and H. H. Mills. 1999. Contrasting vegetation of noses and hollows in the Valley and Ridge province, southwestern Virginia. Journal of the Torrey Botanical Society **126**:197-212.

Stephenson, S. L., and A. K. Saxena. 1994. A comparative study of oak-dominated forests in the mid-Appalachians of the Eastern United-States and the Kumaun Himalaya of Northern India. Bulletin of the Torrey Botanical Club **121**:369-376.

Strahler, A.H. 1978. Response of woody species to site factors of slope angle, rock type, and topographic position in Maryland as evaluated by binary discriminate-analysis. Journal of Biogeography **5**:403-423.

Tainter, F. H., S. W. Fraedrich, and D. M. Benson. 1984. The effect of climate on growth, decline, and death of northern red oaks in the western North Carolina Nantahala mountains. Castanea **49**:127-137.

Vandermast, D. B., D. H. Van Lear, and B. D. Clinton. 2002. American chestnut as an allelopath in the southern Appalachians. Forest Ecology and Management **165**:173-181.

Whitney, H. E., and W. C. Johnson. 1984. Ice storms and forest succession in southwestern Virginia. Bulletin of the Torrey Botanical Club **111**:429-437.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs **26**:1-80.

Williams, R. M., and H. J. Oosting. 1944. The vegetation of Pilot Mountain, North Carolina: A community analysis. Bulletin of the Torrey Botanical Club **71**:23-45.

Woods, F. W., and R. E. Shanks. 1959. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. Ecology **40**:349-361.
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Section II: Manuscript

Dendroclimatic relationships of upland oak across an elevation gradient in the southern Appalachian Mountains

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Abstract

Comparing climatic response by trees across an elevation gradient is a useful technique for understanding patterns of radial growth with relation to small scale variation in topography. The objective of this research was to sample trees from eight different topographic positions across a range of elevation from 582 m to 719 m on a single mountain in the southern Appalachian Mountains and investigate the relationship between ring width index and climate events. We constructed eight different master tree-ring chronologies from upland oak species including *Quercus alba*, *Quercus coccinea*, *Quercus prinus*, *Quercus rubra* and *Quercus velutina*. Ring width indices (RWI) from the master chronologies were tested for correlations with regional temperature, precipitation and Palmer drought severity index (PDSI) from 1919 to 2001. Seven of the sites showed significant correlations between RWI and climatic variables for growing season months. Palmer drought severity index exhibited significant positive correlations with RWI at all upland sites. Precipitation was significantly positively correlated with RWI in July at all upland sites and the same pattern was also observed for June precipitation at six of the upland sites. Temperature at all seven sites was significantly correlated with RWI. Canonical correspondence analysis of site characteristics and RWI indicate that six of the study sites showed very similar tree ring response and these sites could be combined into a single master chronology. However, two of the sites were identified as showing unique tree ring response and thus would not be considered for a single chronology. The results indicate that, in the southern Appalachian Mountains, water availability may be a limiting factor to radial growth in upland oak species. Trees respond to climate in unique ways that reflect the microtopography of their environment, even over small variations in elevation.

Keywords: Dendrochronology; Tree rings; *Quercus*; Topographic position

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I. INTRODUCTION

Much of the current understanding of plant species distribution is based on tracing the relationship between species presence, soils and topography (Oosting and Billings 1939, Williams and Oosting 1944, Keever 1953, Madgwick and Desrochers 1972, McEvoy et al. 1980, Cogbill and White 1991, Burgi et al. 2000). A classic example of this type of research is Whittaker's (1956) investigation of species distributions in the Great Smoky Mountains. Whittaker observed that red oak-hickory forest type dominated the 450 to 750 m elevation range on the flats and draws, while Eastern hemlock and white oak dominated the 1,000 to 1,600 m elevation range on the sheltered and open slopes. Pine species were dominant from 400 to 1,200 m on the ridges and peaks (Whittaker 1956). The correlation of topographic position to vegetation distribution has been applied in many ecosystems, resulting in the better understanding of species distribution within the landscape (Guarin and Taylor 2005, Abella and Covington 2006, Rehfeldt et al. 2006, Zier and Baker 2006). Later studies used the same sampling methods, but examined the influence of other environmental factors or disturbance events such as aspect, rainfall, disease, and fire (Grimm 1984, Clark 1990, Bergeron 1991, Everett et al. 2000, Wolf 2004). For example, Boerner (2006) found that mixed oak forests in Ohio occur on southwest and northeast facing midslope positions in sandstone colluvium parent material, while in Kentucky the same forest type may occur in northeast facing coves and footslopes in sandstone or shale parent material (Boerner 2006). While many studies link species presence with environmental characteristics, recent attempts to account for the impact of multiple environmental variables, including land use history, on species distribution have also emerged within the literature. However, while reconstruction of historical land use has added to our understanding of species distribution patterns across the landscape, these techniques (correlations between species occurrence and environmental factors and connecting land-use history with species presence) fail to relate dendroclimatic response with species location on the landscape.

Recent investigations into climatic response by trees at different topographic positions indicate that dendroclimatology may be a useful technique for elucidating patterns of tree growth rates with relation to species presence on the landscape (Jacobi and Tainter 1988, Tardiff and Bergeron 1997). Dendroclimatology provides a means of studying year to year variations in tree growth and allows investigators to correlate climatic influence on radial growth rates from trees at different sites (Fritts et al. 1965, Oberhuber et al. 1998). Comparing these dendroclimatic relationships from a species across a range of topographic positions will show patterns in the variation of growth patterns across that range. The objective of this study was to identify localized differences in oak dendroclimatic relationships from eight different topographic positions. In addition to the standard site variables of slope, aspect, site index and elevation, the depth of the A-horizon and depth to bedrock were added as additional site variables.

II. METHODS

Study area

The study area for this study was Virginia Polytechnic Institute and State University's Fishburn Forest located in the Ridge and Valley section of southwest Virginia (37° 11' N, 80° 29' W) and ranged in elevation from 561 m to 675 m (Figure 1). The Fishburn Forest is a 500 ha educational and research forest that is comprised mainly of second-growth broadleaved deciduous stands with mixed pine stands on some of the ridge tops.

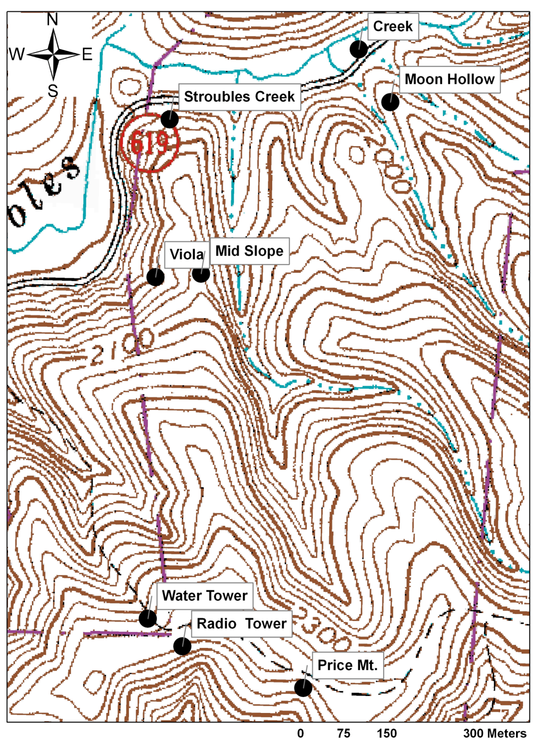

Figure 1. Location of study sites Fishburn Forest, Montgomery County, Virginia on a USGS 7.5 minute series topographic map. Elevations indicate feet above sea level with a 20-foot contour interval.

Field methods

The eight study sites selected for this project represented a range in topographic positions and elevations along Price Mountain, the tallest ridge in the Fishburn Forest (Table 1). The elevation range of this study site is similar to dendroclimatic studies performed in the central Appalachian Mountains of northern West Virginia (Pan et al. 1997). Within each study site, twenty of the largest upland oaks were cored at 0.5 m above the ground. Site index was calculated by the Baker and Broadfoot (1979) method, which involves measuring soil depth, soil texture, current vegetation, slope, aspect, and topographic position to evaluate site quality. Site characteristics were gathered from the field and a previously conducted study that outlined the influence of land use history on forest stand development (Copenheaver et al. 2006). Soil data were gathered at the center of each site and slope was measured by clinometer in multiple areas to determine the average slope within each site. Elevation for each study site was determined based upon GPS locations on a USGS 7.5 minute series a topographic map.

Table 1. Characteristics of the eight sites sampled within the Fishburn Forest, Montgomery County, VA.

Location	Elevation (m)	Site Index	Depth of A horizon (cm)	Depth to Bedrock (cm)	Aspect	Slope (%)
Creek	582	80	44	88	-	-
Stroubles	597	50	10	48	N	32
Moon Hollow	597	62	5	70	SW	28
Viola	613	50	0	> 150	W	35
Midslope	658	71	6	54	NE	32
Water Tower	713	74	14	62	NNW	32
Price Mountain	716	70	13	64	SSW	27
Radio Tower	719	51	8	40	SSE	33

Laboratory methods

Tree cores were air dried, mounted and sanded in preparation for crossdating. Cores from within each study site were visually crossdated using the list year technique which matches patterns of narrow years (Yamaguchi 1991). Although the study sites were within the same region, some differences were noted in list years used to cross date across the study sites. Crossdated cores were measured to the nearest 0.002 mm using a Velmex TA Tree Ring System (Velmex, Bloomfield, NY). Visual crossdating was verified with the computer dating verification program COFECHA (available through the Dendrochronology Program Library http://www.ltrr.arizona.edu/pub/dpl). Any errors detected with COFECHA were examined and corrected. The eight crossdated series were detrended with a spline 30% the length of the series (Cook and Peters 1981) using the ARSTAN program (also available in the Dendrochronology Program Library). These procedures resulted in eight standardized master chronologies- one for each site (Table 2).

Data analysis

Autocorrelation of ring width indices can occur due to the influence of environmental variables from the previous growing season (Fritts 1976). Significant first order autocorrelation occurred in the standard chronologies for all sites except Moon Hollow. Residual chronologies were used for each of these sites, which removed the significant autocorrelation (Table 2). The ring width indices (RWI) for the seven residual chronologies and the Moon Hollow standard chronology were tested for correlation to average monthly regional temperature, precipitation and Palmer drought severity index (PDSI) data available for 1919 to 2006 from the National Oceanic and Atmospheric Administration's southwest region of Virginia regional weather stations (http://www.ncdc.noaa.gov/oa/climate/climatedata.html). Palmer drought severity index is a widely used method to classify longitudinal drought. Weather conditions are typically classified in increments from -4.00 (extreme drought) to +4.00 (extremely wet) (Alley 1984). The relationship between environmental variables, site characteristics and RWI were analyzed by canonical correspondence analysis (CANOCO). Aspect was mathematically transformed into eastness and northness variables. Northness ranges from +1 (due north) and -1 (due south), while eastness ranges from +1 (due east) and -1 (due west) (Roberts 1986). In addition to aspect, site index, depth to bedrock and depth of A-horizon were used in the CCA.

Table 2. First-order autocorrelation values for the standard and residual chronologies for the eight sites in Fishburn Forest.

Site	Standard first- order autocorrelation	Standard p-value	Residual first- order autocorrelation	Residual p-value
Creek	0.35	<0.0001	0.24	0.0002
Stroubles	0.50	<0.0001	0.09	0.03
Moon Hollow	0.03	0.2753	0.14	<0.0001
Viola	0.88	<0.0001	0.07	0.1981
Midslope	0.31	<0.0001	-0.14	0.9757
Water Tower	0.27	0.0002	0.03	0.3393
Price Mtn.	0.42	<0.0001	0.00	0.2266
Radio Tower	0.24	<0.0001	-0.02	0.5974

III. RESULTS

Chronology characteristics

Mean sensitivity, chronology length and interseries correlations were calculated for each site (Table 3). Mean sensitivity is a method used to determine the environmental variance of the vegetation at a site. A high mean sensitivity value indicates a greater sensitivity to environmental variables. The interseries correlations of a site is the response of the individual chronologies of a stand to environmental variables. Low interseries correlations are indicative of individual tree climate responses rather than stand wide response to climatic events (Fritts 1976). The Water Tower site had the oldest chronology, while the Creek site had the youngest. The Viola site had the lowest mean sensitivity, while the Creek site had the highest. The Radio Tower site had the highest interseries correlation and the Stroubles site had the lowest interseries correlation. Master chronologies for each site were spline transformed. There was a decrease in ring width during drought years occurring in 1929, 1966 in all stands, and all stands had a growth release in the decades following both drought events (Figure 2). The Moon Hollow and Price Mountain sites had the longest prolonged growth release following the 1966 drought event, while the Stroubles, Viola and Water Tower sites had the shortest temporal growth release.

Table 3. Chronology length, mean sensitivity, and interseries correlation for each study site in Fishburn Forest.

Location	Number of Trees	Chronology Length	Mean Sensitivity	Interseries Correlation
Creek	20	1919-2006	0.29	0.48
Viola	20	1902-2001	0.18	0.45
Stroubles	20	1883-2003	0.21	0.43
Moon Hollow	20	1900-2002	0.25	0.49
Midslope	20	1872-2006	0.25	0.45
Radio Tower	20	1885-2003	0.25	0.62
Price Mountain	20	1828-2003	0.24	0.44
Water Tower	20	1802-2003	0.25	0.49

Dendroclimatic relationships

The growing season for the study area occurs from May to September, with signs of oak leaf emergence in late April to early May and the start of leaf fall in mid-October. No significant (non-zero) correlations were observed between the Creek site RWI and temperature (Figure 3). Significant negative relationships occurred between temperature and RWI during July of the current growing season for the Viola, Midslope, Water Tower, Price Mountain and Radio Tower sites. Water Tower, Price Mountain and Radio Tower were the sites with an observed significant positive relationship between RWI and temperature during the winter preceding the growing season. Significant, negative correlations between precipitation and RWI were observed during May of the previous growing season for the Midslope and Water Tower sites, and May and June of the previous growing season for the Creek site (Figure 4). A significant, positive relationship was observed between precipitation and RWI during May and June of the current growing season. Significant positive correlations were observed in a portion of the previous growing season for Moon Hollow, Viola, Midslope, Water Tower and Radio Tower. A significant positive relationship between RWI and PDSI was observed for the current growing season (Figure 5). Viola, Price Mountain and Radio Tower had significant, positive correlation between RWI and PDSI for the winter following the current growing season, and Moon Hollow had a significant positive relationship between RWI and PDSI for the preceding winter.

Canonical correspondence analysis

The relationship between site characteristics and RWI was evaluated using canonical correspondence analysis (Figure 6). Site index and eastness were the most influential on all sites and slope was the least influential. The depth of the A-horizon, depth to bedrock, elevation and northness appear to have the same influence on all study sites.

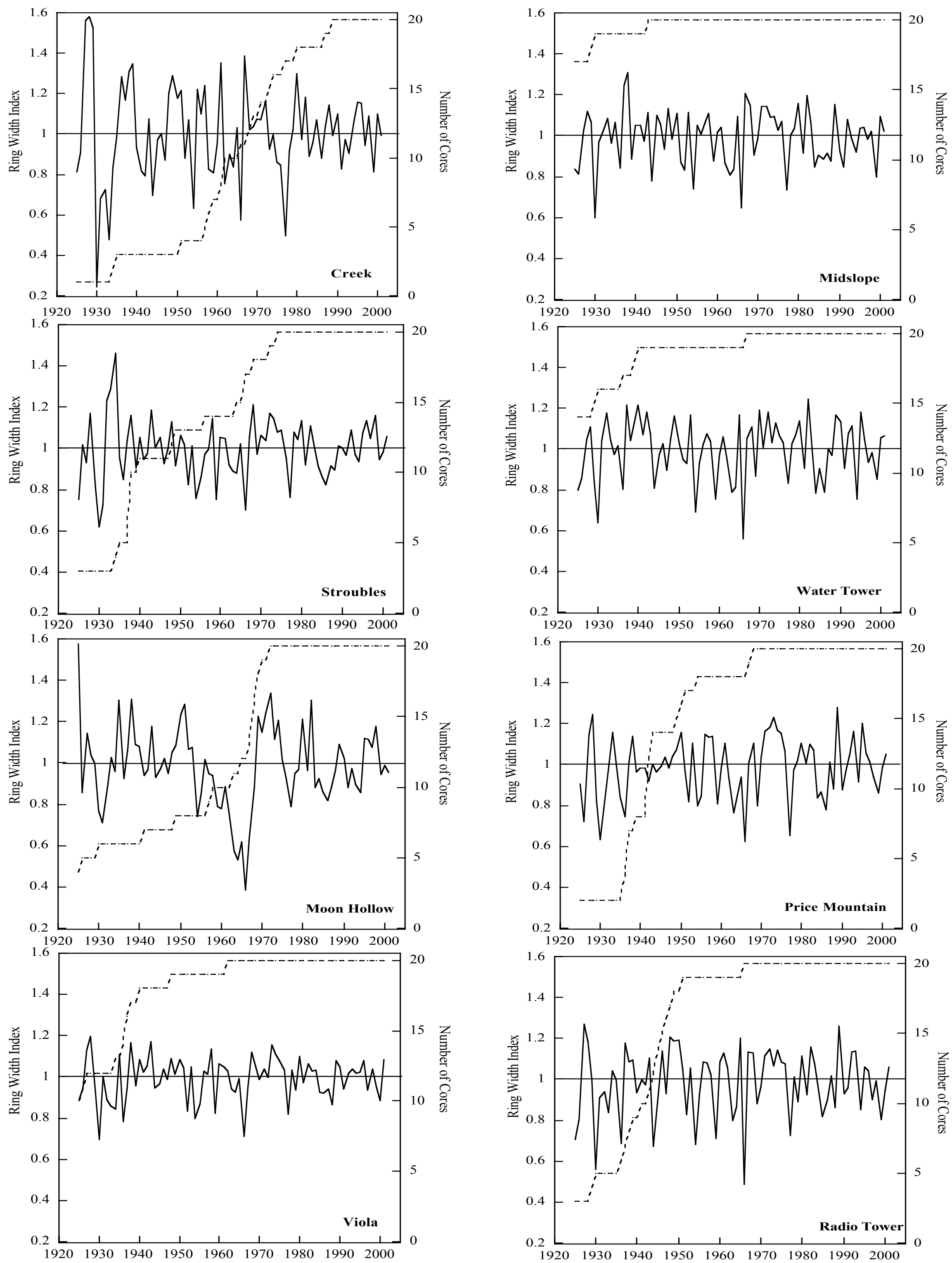

Figure 2. Master chronologies from 1925- 2001 for upland oaks cored in Fishburn Forest, VA.

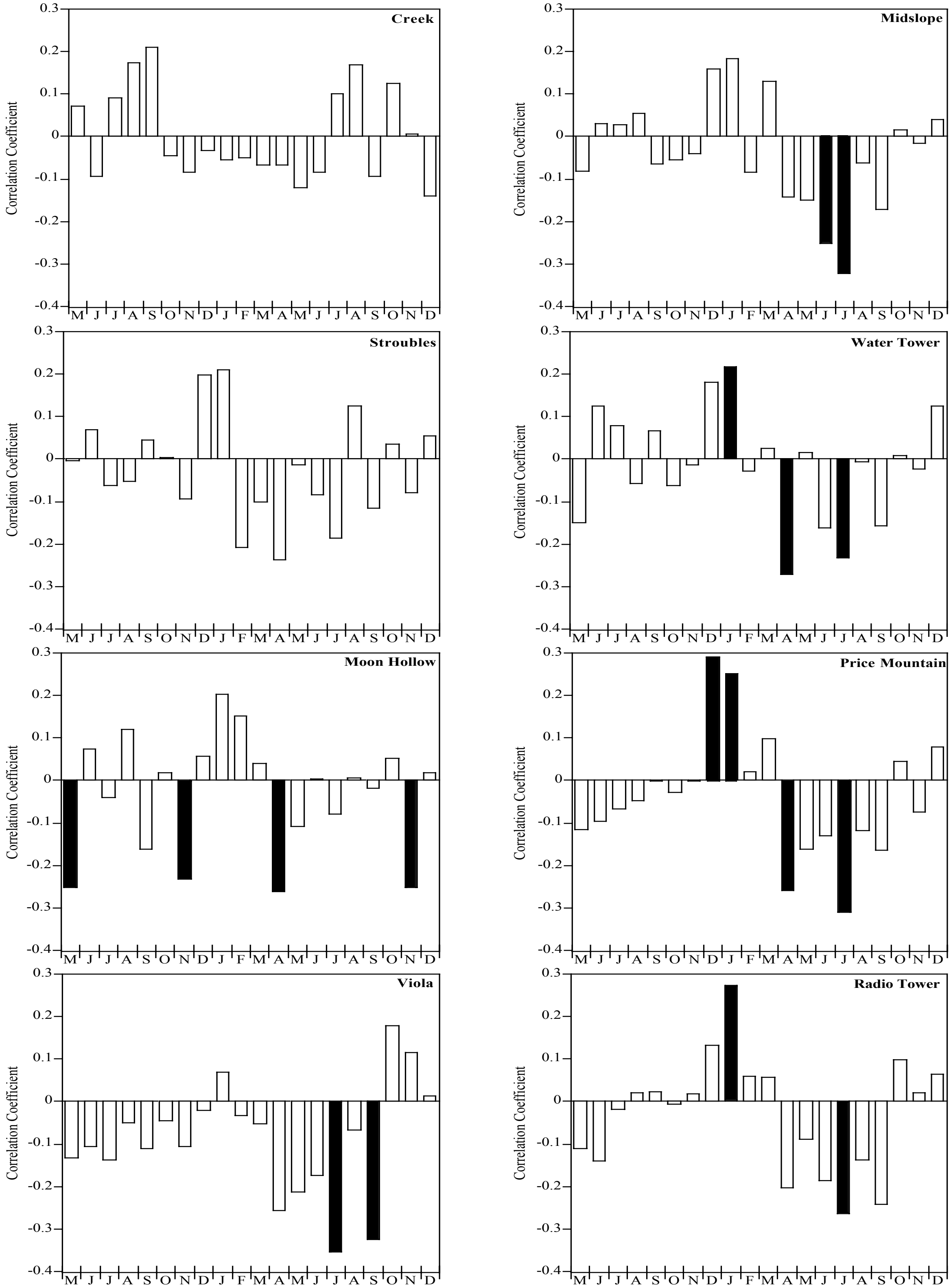

Figure 3. Ring width index and temperature correlations for the dendroclimatic year for 1919 to 2001. Dark columns are statistically significant at the α = 0.05 level.

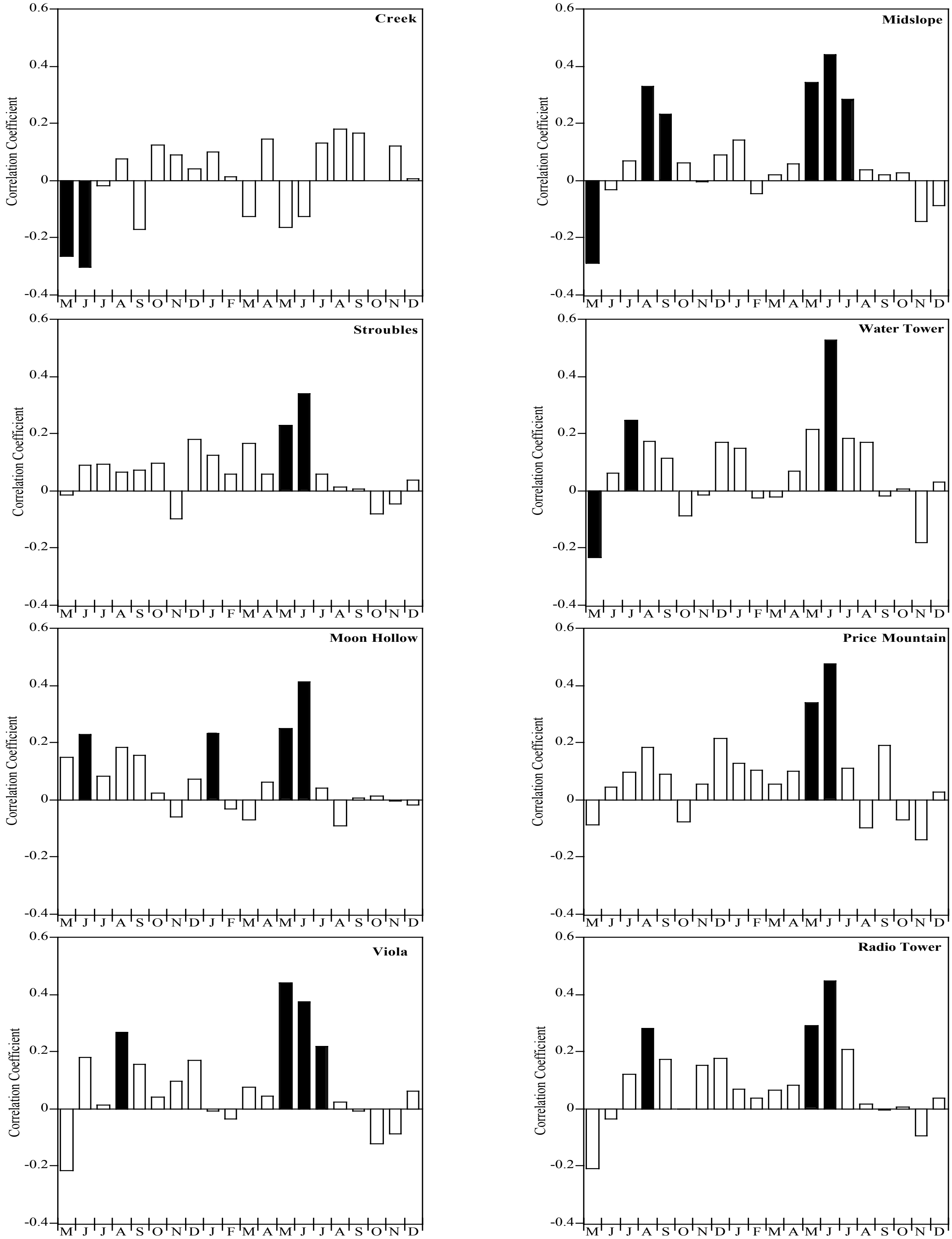

Figure 4. Ring width index and precipitation correlations for the dendroclimatic year for 1919 to 2001. Dark columns are statistically significant at the α = 0.05 level.

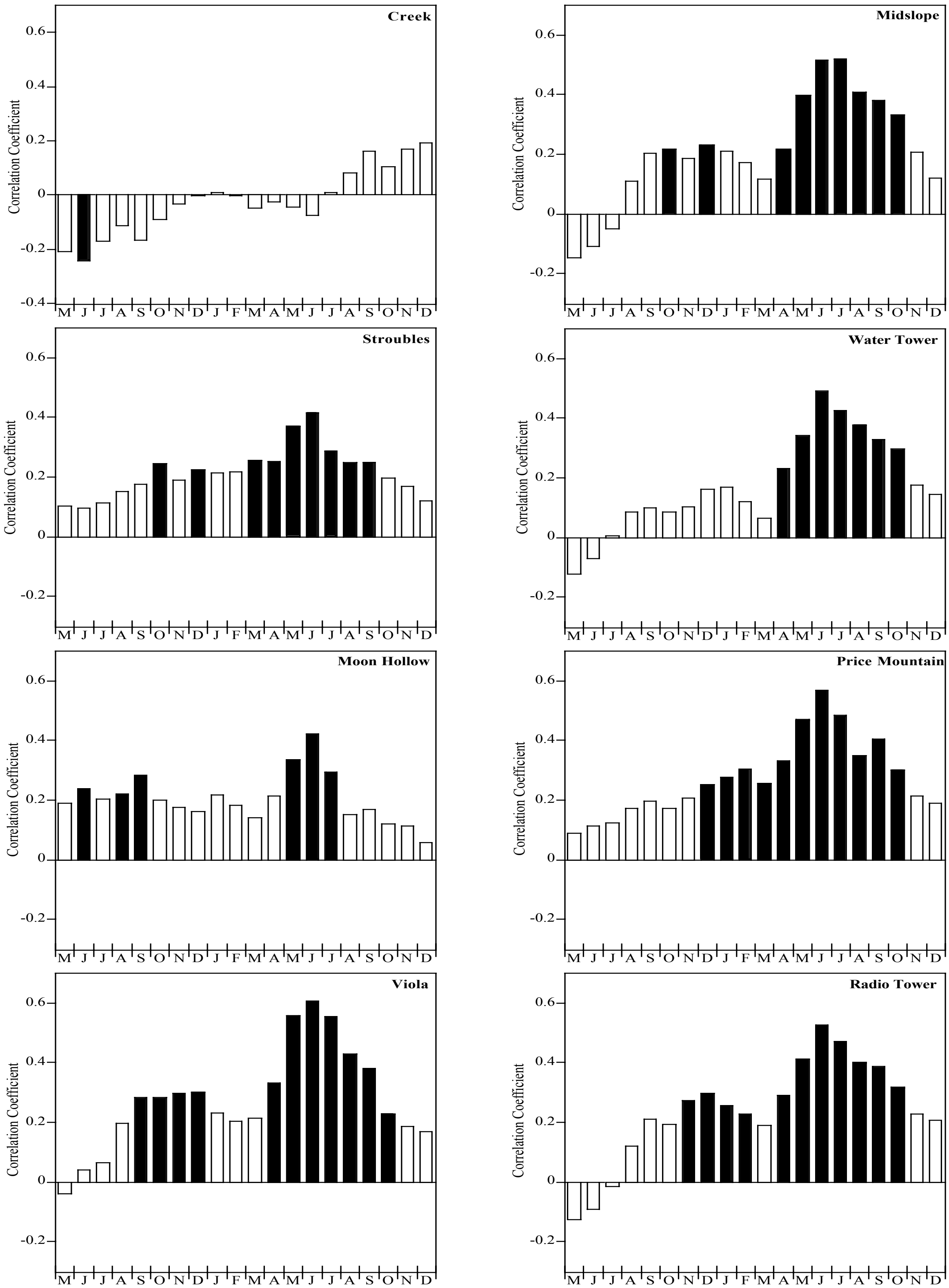

Figure 5. Ring width index and PDSI correlations for the dendroclimatic year for 1919 to 2001. Dark columns are statistically significant at the $\alpha = 0.05$ level.

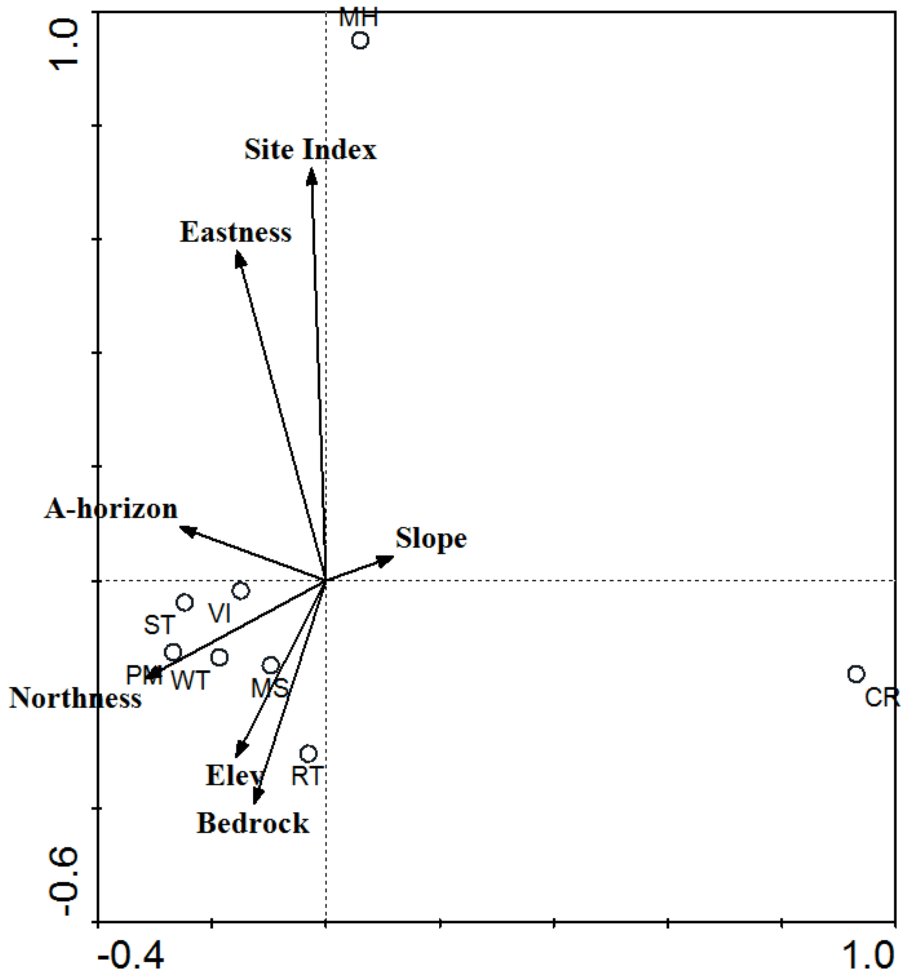

Figure 6. CCA analysis of the relationship between site characteristics and RWI for study sites located in Fishburn Forest, VA. (Note: Bedrock refers to depth to bedrock, Elev refers to elevation, ST refers to Stroubles, VI refers to Viola, WT refers to Water Tower, MS refers to Midslope, RT refers to Radio Tower, MH refers to Moon Hollow, CR refers to Creek and PM refers to Price Mountain).

IV. DISCUSSION

This study compliments other dendroclimatological analyses of *Quercus* spp. from the eastern United States. Oak has served as a valuable species for dendroclimatic reconstructions because of its long lifespan coupled with climate sensitivity (Duvick and Blasing 1981, Blasing et al. 1988). The species has also proven valuable in the analysis of the effect of pollution on tree growth (McClenahen and Dochinger 1985, LeBlanc 1993). *Quercus* species has also been shown to be a proxy species for analyzing the response to climate events at varying topographic positions (Jacobi and Tainter 1988, Jenkins and Pallardy 1995, Pan et al. 1997, Rubino and

McCarthy 2000) (Figures 3-5). Although many of these studies only evaluated dendroclimatic relationships from a single master chronology, the relationships between RWI and climatic variables are very similar to the results from this study. For example, Rubino and McCarthy's (2000) study from southeastern Ohio identified the significant correlations between PDSI and precipitation during the growing season that are similar the results from Price Mountain (Figures 4 and 5), while Jacobi and Tainter's (1988) study on *Quercus alba* from South Carolina observed more significant relationships between RWI and temperature than we found in our study (Figure 3). This is most likely explained by the difference in geographic range and elevation between the two study sites with Jacobi and Tainter's (1988) study located in the Piedmont of South Carolina, which has less topographic variation and higher temperatures compared to where our study sites were located. In addition, Pan, et al. (1997) identified significant, positive relationships between growth and precipitation during the preceding growing season for red oak in the central Appalachian Mountains of West Virginia, which is similar to what was observed in our study. The comparison to these studies highlights the similarities between *Quercus* response to climate in the southern Appalachian Mountain region but also demonstrates that small regional variations exist that may impact species response to climate.

The differences in dendroclimatic response between the Creek site and the other sites are not reflected in the mean sensitivity values (Table 3). Mean sensitivity values have traditionally been viewed as an indication of a species climatic sensitivity; however, our results indicate that mean sensitivity may be best used to augment other climatological analyses (Fritts 1976). Previous work has shown the limitations of PDSI (LeBlanc 1998), however, we observed strong correlations using this variable (Figure 5). However, it is important to keep Leblanc's (1998) comments regarding the slow response of PDSI as an index of water availability in mind when viewing dendroclimatic responses. For example, the time period associated with significant precipitation influence on RWI is shorter in duration than the significant PDSI period, thus indicating a lag effect in the PDSI data that is not reflected by the precipitation data (Figure 4).

The influence of site characteristics on RWI was analyzed by canonical correspondence analysis (Figure 6). The master chronologies of the eight sites can be separated into three separate master chronologies based upon the influence of site characteristics. The Creek site did not have an aspect or slope and appears to be most influenced by a combination of elevation, depth of the A-horizon, depth to bedrock and site index. Site index and elevation appear to more heavily influence the Moon Hollow site, while the remaining six sites appear to be similarly influenced by all of the site characteristics. These sites had similar tree ring response to climate and could be grouped together into a single chronology. The Moon Hollow and Creek site responses were not analogous to any of the other sites and thus would remain as separate master chronologies.

This study illustrates the importance of climate to radial growth rates in *Quercus* in the southern Appalachian Mountains. Although climate alters growth, it does not have a limiting effect on *Quercus* distribution, and the species appears to survive under a wide variety of environmental conditions. Although the eight sites had similar responses to climatic events, the results of the canonical correspondence analysis indicate that the chronologies could be grouped into three separate groups based upon tree ring response and site characteristics.

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V. LITERATURE CITED

Abella, S. R., and W. W. Covington. 2006. Forest ecosystems of an Arizona *Pinus ponderosa* landscape: multifactor classification and implications for ecological restoration. Journal of Biogeography **33**:1368-1383.

Alley, W. M. 1984. The Palmer Drought Severity Index: limitations and assumptions. Journal of Climate and Applied Meteorology **23**:1100-1109.

Baker, J. B., and W. M. Broadfoot. 1979. A practical field method for commercially important southern hardwoods. Pages 1-51 General Technical Report SO-26. United States Department of Agriculture, Forest Service, Southern Forest Experiment Station.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology **72**:1980-1992.

Blasing, T. J., D. W. Stahle, and D. N. Duvick. 1988. Tree ring-based reconstruction of annual precipitation in the south-central United States from 1750 to 1980. Water Resources Research **24**:163-171.

Boerner, R. E. J. 2006. Unraveling the Gordian Knot: Interactions among vegetation, topography, and soil properties in the central and southern Appalachians. Journal of the Torrey Botanical Society **133**:321-361.

Burgi, M., E. W. B. Russell, and G. Motzkin. 2000. Effects of postsettlement human activities on forest composition in the north-eastern United States: a comparative approach. Journal of Biogeography **27**:1123-1138.

Clark, J. S. 1990. Fire and climate change during the last 750 yr in northwestern Minnesota. Ecological Monographs **60**:135-159.

Cogbill, C. V., and P. S. White. 1991. The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian mountain chain. Vegetatio **94**:153-175.

Cook, E. R., and K. Peters. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-Ring Bulletin **41**:45-53.

Copenheaver, C. A., J. M. Matthews, J. M. Showalter, and W. E. Auch. 2006. Forest stand development patterns in the southern Appalachians. Northeastern Naturalist **13**:477-494.

Duvick, D. N., and T. J. Blasing. 1981. A dendroclimatic reconstruction of annual precipitation amounts in Iowa since 1680. Water Resources Research **17**:1183-1189.

Eller, R. D. 1982. Miners, Millhands, and Mountaineers. University of Tennessee, Knoxville.

Everett, R. L., R. Schellhaas, D. Keenum, D. Spurbeck, and P. Ohlson. 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. Forest Ecology and Management **129**:207-225.

Fenneman, N. M. 1938. Physiography of Eastern United States. McGraw-Hill New York.

Fritts, H. C. 1976. Tree Rings and Climate. Academic Press, New York.

Fritts, H. C., D. G. Smith, J. W. Cardis, and C. A. Budelsky. 1965. Tree-ring characteristics along a vegetation gradient in northern Arizona. Ecology **46**:393-401.

Grimm, E. C. 1984. Fire and other factors controlling the big woods vegetation of Minnesota in the mid-nineteenth century. Ecological Monographs **54**:291-311.

Guarin, A., and A. H. Taylor. 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. Forest Ecology and Management **218**:229-244.

Jacobi, J. C., and F. H. Tainter. 1988. Dendroclimatic examination of white oak along an environmental gradient in the Piedmont of South Carolina. Castanea **53**:252-262.

Jenkins, M. A., and S. G. Pallardy. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. Canadian Journal of Forest Research **25**:1119-1127.

Keever, C. 1953. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge mountains. Ecology **34**:44-54.

LeBlanc, D. C. 1993. Temporal and spatial variation of oak growth- climate relationships along a pollution gradient in the midwestern United States. Canadian Journal of Forest Research **23**:772-782.

LeBlanc, D. C. 1998. Interactive effects of acidic deposition, drought, and insect attack on oak populations in the midwestern United States. Canadian Journal of Forest Research **28**:1184-1197.

Madgwick, H. A. I., and P. A. Desrochers. 1972. Association-analysis and the classification of forest vegetation of the Jefferson National Forest. Journal of Ecology **60**:285-292.

McClenahen, J. R., and L. S. Dochinger. 1985. Tree ring response of white oak to climate and air pollution near the Ohio River Valley. Journal of Environmental Quality **14**:274-280.

McEvoy, T. J., T. L. Sharik, and D. W. Smith. 1980. Vegetative structure of an Appalachian oak forest in southwestern Virginia. American Midland Naturalist **103**:96-105.

Oberhuber, W., M. Stumbock, and W. Kofler. 1998. Climate-tree-growth relationships of Scots pine stands (*Pinus sylvestris* L.) exposed to soil dryness. Trees **13**:19-27.

Oosting, H. J., and W. D. Billings. 1939. Edapho-vegetational relations in Ravenel's Woods, a virgin hemlock forest near Highlands, North Carolina. American Midland Naturalist **22**:333-350.

Pan, C., S. J. Tajchman, and J. N. Kochenderfer. 1997. Dendroclimatological analysis of major forest species of the central Appalachians. Forest Ecology and Management **98**:77-87.

Rehfeldt, G. E., N. L. Crookston, M. V. Warwell, and J. S. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Sciences **167**:1123-1150.

Roberts, D. W. 1986. Ordination on the basis of fuzzy set theory. Vegetatio **66**:123-131.

Rubino, D. L., and B. C. McCarthy. 2000. Dendroclimatological analysis of white oak (*Quercus alba* L., Fagaceae) from an old-growth forest in southeastern Ohio, USA. Journal of the Torrey Botanical Society **127**:240-250.

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

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs **26**:1-80.

Williams, R. M., and H. J. Oosting. 1944. The vegetation of Pilot Mountain, North Carolina: A community analysis. Bulletin of the Torrey Botanical Club **71**:23-45.

Wolf, J. 2004. A 200-year fire history in a remnant oak savanna in southeastern Wisconsin. American Midland Naturalist **152**:201-213.

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

Zier, J. L., and W. L. Baker. 2006. A century of vegetation change in the San Juan Mountains, Colorado: An analysis using repeat photography. Forest Ecology and Management **228**:251-262.

APPENDIX A

Table 1. Species occurrence by elevation according to study site location. Elevation ranges are defined as: low elevation range (200-400m), middle elevation (401- 800m) and high elevation (800+m). Middle-high elevations span the middle and high elevations.

Species	Elevation	Study Site	State	Reference
Abies fraseri	high	Great Smoky Mountains National Park	NC/TN	Cogbill and White, 1991
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
Acer pensylvanicum	high	Bedford County	VA	Johnson and Ware, 1982
		Mountain Lake, Giles County	VA	Mills and Stephenson, 1999
		Salt Pond Mountain	VA	Stephenson, 1986
		Nantahala National Forest	NC	Carter, et al., 2000
		Nantahala National Forest	NC	McNab, et al., 1999
	middle-high	Shenandoah National Park	VA	Harrison, et al., 1989
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Highlands	NC	Keever, 1953
Acer rubrum	high	Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Mountain Lake, Giles County	VA	Mills and Stephenson, 1999
		Salt Pond Mountain	VA	Stephenson, 1986
		Shenandoah National Park	VA	Harrison, et al., 1989
		Montgomery County	VA	Mou and Warrillow, 2000

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Acer rubrum (cont.)	middle-high	Giles County	VA	Stephenson and Mills, 1999
		Giles County	VA	Stephenson and Saxena, 1994
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Coweeta Hydrologic Laboratory	NC	Clinton and Boring, 1994
		Nantahala National Forest	NC	McNab, et al., 1999
		Nantahala National Forest	NC	Carter, et al., 2000
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1999
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Coweeta Hydrologic Laboratory	NC	Davis, et al., 2004
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Coweeta Hydrologic Laboratory	NC	Day and Monk, 1974
		Highlands	NC	Keever, 1953
		Highlands	NC	Oosting and Billings, 1939
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
		Little Laurel Run	WV	Hicks and Frank, 1984
		Peters Mountain	VA	Adams and Stephenson, 1983

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Acer rubrum (cont.)	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Acer saccharum	high	Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
	middle-high	Little Laurel Run	WV	Desta, et al., 2004
		Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Potts Mountain	VA	McEvoy, et al., 1980
		Giles County	VA	Stephenson and Mills, 1999
		Salt Pond Mountain	VA	Stephenson, 1986
		Montgomery County	VA	Mou and Warrillow, 2000
		Giles County	VA	Stephenson and Saxena, 1994
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Davis, et al., 2004
		Nantahala National Forest	NC	McNab, et al., 1999
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Acer spicatum	high	Bedford County	VA	Johnson and Ware, 1982
		Potts Mountain	VA	McEvoy, et al., 1980
		Salt Pond Mountain	VA	Stephenson, 1986
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
	middle-high	Montgomery County	VA	Mou and Warrillow, 2000
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
Aesculus octandra	high	Potts Mountain	VA	McEvoy, et al., 1980
		Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
	middle-high	Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
Amelanchier arborea	high	Peters Mountain	VA	Adams and Stephenson, 1983
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Mountain Lake, Giles County	VA	Mills and Stephenson, 1999
		Salt Pond Mountain	VA	Stephenson, 1986
		Nantahala National Forest	NC	McNab, et al., 1999
	middle-high	Montgomery County	VA	Mou and Warrillow, 2000
		Giles County	VA	Stephenson and Mills, 1999
		Giles County	VA	Stephenson and Saxena, 1994
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Amelanchier arborea (cont)	middle-high	Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
Amelanchier laevis	middle-high	Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Highlands	NC	Oosting and Billings, 1939
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
Betula allegheniensis	high	Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Nantahala National Forest	NC	McNab, et al., 1999
	middle-high	Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
Betula lenta	high	Shenandoah National Park	VA	Harrison, et al., 1999
		Mountain Lake, Giles County	VA	Mills and Stephenson, 1999
		Giles County	VA	Stephenson and Mills, 1999
		Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Golden, 1981

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Betual lenta (cont)	high	Nantahala National Forest	NC	McNab, et al., 1999
	middle-high	Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Shenandoah National Park	VA	Harrison, et al., 1989
		Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Giles County	VA	Stephenson and Saxena, 1994
		Salt Pond Mountain	VA	Stephenson, 1986
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Nantahala National Forest	NC	Carter, et al., 2000
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Highlands	NC	Oosting and Billings, 1939
		Highlands	NC	Keever, 1953
	middle	Little Laurel Run	WV	Hicks and Frank, 1984
		Bedford County	VA	Johnson and Ware, 1982
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
	low-middle	Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Jocassee Gorge	SC	Abella, et al., 2003
Betula lutea	high	Bedford County	VA	Johnson and Ware, 1982
		Giles County	VA	Stephenson and Mills, 1999
		Giles County	VA	Stephenson and Saxena, 1994
		Salt Pond Mountain	VA	Stephenson, 1986
	middle-high	Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Highlands	NC	Keever, 1953

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Betual lutea (cont.)	middle	Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
Carya cordiformis	high	Montgomery County	VA	Whitney and Johnson, 1984
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
	middle-high	Shenandoah National Park	VA	Harrison, et al., 1989
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
Carya glabra	high	Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Peters Mountain	VA	Adams and Stephenson, 1983
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Potts Mountain	VA	McEvoy, et al., 1980
		Mountain Lake, Giles County	VA	Mills and Stephenson, 1999
		Montgomery County	VA	Whitney and Johnson, 1984
	middle-high	Giles County	VA	Stephenson and Mills, 1999
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Day and Monk, 1974
		Highlands	NC	Keever, 1953
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
Carya ovalis	high	Montgomery County	VA	Whitney and Johnson, 1984

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Carya ovalis (cont.)	middle-high	Shenandoah National Park	VA	Harrison, et al., 1989
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Davis, et al., 2004
		Highlands	NC	Keever, 1953
	middle	Bedford County	VA	Johnson and Ware, 1982
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
Carya ovata	high	Little Laurel Run	WV	Desta, et al., 2004
		Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Salt Pond Mountain	VA	Stephenson, 1986
	middle-high	Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
Carya tomentosa	high	Montgomery County	VA	Mou and Warrillow, 2000
		Montgomery County	VA	Whitney and Johnson, 1984
		Nantahala National Forest	NC	McNab, et al., 1999
	middle-high	Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
Carya spp.	high	Giles County	VA	Stephenson and Saxena, 1994
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Jefferson National Forest	VA	Madgwick and Desrochers, 1972

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Carya spp. (cont.)	middle-high	Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Nantahala National Forest	NC	Carter, et al., 2000
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1999
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Cornus florida	high	Peters Mountain	VA	Adams and Stephenson, 1983
	middle-high	Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Montgomery County	VA	Mou and Warrillow, 2000
		Montgomery County	VA	Whitney and Johnson, 1984
		Shenandoah National Park	VA	Harrison, et al., 1989
		Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Giles County	VA	Stephenson and Mills, 1999
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Clinton and Boring, 1994

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	**Elevation**	**Study Site**	**State**	**Reference**
Cornus florida (cont.)	middle-high	Pilot Mountain	NC	Williams and Oosting, 1944
		Nantahala National Forest	NC	Carter, et al., 2000
		Coweeta Hydrologic Laboratory	NC	Day and Monk, 1974
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Highlands	NC	Keever, 1953
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
Fagus grandifolia	high	Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Nantahala National Forest	NC	McNab, et al., 1999
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Fagus grandifolia (cont.)	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
Fraxinus americana	high	Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Bedford County	VA	Johnson and Ware, 1982
		Montgomery County	VA	Mou and Warrillow, 2000
		Salt Pond Mountain	VA	Stephenson, 1986
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Nantahala National Forest	NC	McNab, et al., 1999
		Pilot Mountain	NC	Williams and Oosting, 1944
	middle-high	Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Shenandoah National Park	VA	Harrison, et al., 1989
		Giles County	VA	Stephenson and Mills, 1999
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Highlands	NC	Keever, 1953
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
	low-middle	Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Halesia carolina	high	Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Nantahala National Forest	NC	McNab, et al., 1999
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Nantahala National Forest	NC	Carter, et al., 2000
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Highlands	NC	Keever, 1953
		Highlands	NC	Oosting and Billings, 1939
Hamamelis virginiana	high	Bedford County	VA	Johnson and Ware, 1982
		Mountain Lake, Giles County	VA	Mills and Stephenson, 1999
		Montgomery County	VA	Mou and Warrillow, 2000
		Salt Pond Mountain	VA	Stephenson, 1986
		Nantahala National Forest	NC	Carter, et al., 2000
		Pilot Mountain	NC	Williams and Oosting, 1944
	middle-high	Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Giles County	VA	Stephenson and Mills, 1999
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Highlands	NC	Keever, 1953
		Highlands	NC	Oosting and Billings, 1939

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Ilex spp.	high	Bedford County	VA	Johnson and Ware, 1982
		Salt Pond Mountain	VA	Stephenson, 1986
	middle-high	Giles County	VA	Stephenson and Mills, 1999
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Highlands	NC	Keever, 1953
		Highlands	NC	Oosting and Billings, 1939
Liriodendron tulipifera	high	Little Laurel Run	WV	Desta, et al., 2004
		Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Montgomery County	VA	Mou and Warrillow, 2000
		Montgomery County	VA	Whitney and Johnson, 1984
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Bent Creek Experimental Forest	NC	McNab, 1993
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Shenandoah National Park	VA	Harrison, et al., 1989
		Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Golden, 1981

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Liriodendron tulipifera (cont.)	middle-high (cont.)	Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Nantahala National Forest	NC	Carter, et al., 2000
		Coweeta Hydrologic Laboratory	NC	Clinton and Boring, 1994
		Coweeta Hydrologic Laboratory	NC	Davis, et al., 2004
		Coweeta Hydrologic Laboratory	NC	Day and Monk, 1974
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1999
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Highlands	NC	Keever, 1953
		Highlands	NC	Oosting and Billings, 1939
	middle	Little Laurel Run	WV	Hicks and Frank, 1984
		Bedford County	VA	Johnson and Ware, 1982
		Giles County	VA	Stephenson and Mills, 1999
		Great Smoky Mountains National Park	NC/TN	Busing, 1995
	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Magnolia acuminata	high	Little Laurel Run	WV	Desta, et al., 2004
		Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Mountain Lake, Giles County	VA	Mills and Stephenson, 1999
		Giles County	VA	Stephenson and Saxena, 1994
		Salt Pond Mountain	VA	Stephenson, 1986

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Magnolia acuminata (cont.)	high (cont.)	Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Nantahala National Forest	NC	McNab, et al., 1999
	middle-high	Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Giles County	VA	Stephenson and Mills, 1999
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Highlands	NC	Keever, 1953
		Highlands	NC	Oosting and Billings, 1939
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
Magnolia fraseri	high	Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Highlands	NC	Oosting and Billings, 1939

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Nyssa sylvatica	high	Little Laurel Run	WV	Desta, et al., 2004
		Peters Mountain	VA	Adams and Stephenson, 1983
		Mountain Lake, Giles County	VA	Mills and Stephenson, 1999
		Montgomery County	VA	Mou and Warrillow, 2000
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Shenandoah National Park	VA	Harrison, et al., 1989
		Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Nantahala National Forest	NC	Carter, et al., 2000
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Highlands	NC	Keever, 1953
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
		Potts Mountain	VA	McEvoy, et al., 1980
		Giles County	VA	Stephenson and Mills, 1999
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Nyssa sylvatica (cont.)	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Ostrya virginiana	high	Montgomery County	VA	Mou and Warrillow, 2000
	middle-high	Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
Oxydendrum arboreum	high	Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Peters Mountain	VA	Adams and Stephenson, 1983
		Montgomery County	VA	Mou and Warrillow, 2000
		Giles County	VA	Stephenson and Mills, 1999
		Giles County	VA	Stephenson and Saxena, 1994
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Nantahala National Forest	NC	McNab, et al., 1999
		Pilot Mountain	NC	Williams and Oosting, 1944
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	**Elevation**	**Study Site**	**State**	**Reference**
Oxydendrum arboretum (cont.)	middle-high (cont.)	Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Nantahala National Forest	NC	Carter, et al., 2000
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Highlands	NC	Keever, 1953
	middle	Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
Picea rubens	high	Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Great Smoky Mountains National Park	NC/TN	Cogbill and White, 1991
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
	middle-high	Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
Pinus pungens	high	Montgomery County	VA	Whitney and Johnson, 1984
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
	middle-high	Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Pinus pungens (cont.)	middle	Bedford County	VA	Johnson and Ware, 1982
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Pinus rigida	high	Peters Mountain	VA	Adams and Stephenson, 1983
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
	middle-high	Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Potts Mountain	VA	McEvoy, et al., 1980
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Nantahala National Forest	NC	Carter, et al., 2000
		Coweeta Hydrologic Laboratory	NC	Davis, et al., 2004
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1999
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
	middle	Bedford County	VA	Johnson and Ware, 1982
	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Pinus strobus	high	Lower Bluestone River Gorge	WV	Rentch, et al., 2005

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Pinus strobus (cont.)	middle-high	Shenandoah National Park	VA	Harrison, et al., 1989
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Highlands	NC	Keever, 1953
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
Pinus virginiana	high	Montgomery County	VA	Mou and Warrillow, 2000
		Montgomery County	VA	Whitney and Johnson, 1984
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
	middle-high	Shenandoah National Park	VA	Harrison, et al., 1989
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Plantus occidentalis	high	Montgomery County	VA	Mou and Warrillow, 2000
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
Prunus pensylvanicum	high	Nantahala National Forest	NC	Carter, et al., 2000
		Great Smoky Mountains National Park	NC/TN	Golden, 1981

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	**Elevation**	**Study Site**	**State**	**Reference**
Prunus pensylvanicum (cont.)	middle-high	Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
Prunus serotina	high	Montgomery County	VA	Mou and Warrillow, 2000
		Giles County	VA	Stephenson and Mills, 1999
		Salt Pond Mountain	VA	Stephenson, 1986
		Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Nantahala National Forest	NC	McNab, et al., 1999
		Pilot Mountain	NC	Williams and Oosting, 1944
	middle-high	Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Highlands	NC	Oosting and Billings, 1939
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
		Little Laurel Run	WV	Hicks and Frank, 1984
		Bedford County	VA	Johnson and Ware, 1982
Quercus alba	high	Monongahela National Forest	WV	Collins and Carson, 2004
		Little Laurel Run	WV	Desta, et al., 2004
		Lower Bluestone River Gorge	WV	Rentch, et al., 2005

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	**Elevation**	**Study Site**	**State**	**Reference**
Quercus alba (cont.)	high (cont.)	Peters Mountain	VA	Adams and Stephenson, 1983
		Montgomery County	VA	Mou and Warrillow, 2000
		Giles County	VA	Stephenson and Mills, 1999
		Giles County	VA	Stephenson and Saxena, 1994
		Salt Pond Mountain	VA	Stephenson, 1986
		Montgomery County	VA	Whitney and Johnson, 1984
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Nantahala National Forest	NC	McNab, et al., 1999
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Coweeta Hydrologic Laboratory	NC	Davis, et al., 2004
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1999
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Nantahala National Forest	NC	Tainter, et al., 1984
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Highlands	NC	Keever, 1953

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Quercus alba (cont.)	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
		Little Laurel Run	WV	Hicks and Frank, 1984
	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Quercus coccinea	high	Peters Mountain	VA	Adams and Stephenson, 1983
		Montgomery County	VA	Mou and Warrillow, 2000
		Montgomery County	VA	Whitney and Johnson, 1984
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Nantahala National Forest	NC	McNab, et al., 1999
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Shenandoah National Park	VA	Harrison, et al., 1989
		Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Potts Mountain	VA	McEvoy, et al., 1980
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Potts Mtn, Craig County	VA	Meiners, et al., 1984
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Coweeta Hydrologic Laboratory	NC	Clinton and Boring, 1994
		Coweeta Hydrologic Laboratory	NC	Davis, et al., 2004

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Quercus coccinea (cont.)	middle-high (cont.)	Coweeta Hydrologic Laboratory	NC	Day and Monk, 1974
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1999
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Thompson River Gorge	NC	Racine, 1971
		Highlands	NC	Keever, 1953
	middle	Bedford County	VA	Johnson and Ware, 1982
		Giles County	VA	Stephenson and Mills, 1999
	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Quercus muehlenbergii	high	Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
Quercus prinus	high	Monongahela National Forest	WV	Collins and Carson, 2004
		Little Laurel Run	WV	Desta, et al., 2004
		Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Peters Mountain	VA	Adams and Stephenson, 1983
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Mountain Lake, Giles County	VA	Mills and Stephenson, 1999
		Montgomery County	VA	Mou and Warrillow, 2000
		Giles County	VA	Stephenson and Saxena, 1994
		Montgomery County	VA	Whitney and Johnson, 1984
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Quercus prinus (cont.)	high (cont.)	Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Potts Mountain	VA	McEvoy, et al., 1980
		Giles County	VA	Stephenson and Mills, 1999
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Potts Mtn, Craig County	VA	Meiners, et al., 1984
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Nantahala National Forest	NC	Carter, et al., 2000
		Coweeta Hydrologic Laboratory	NC	Davis, et al., 2004
		Coweeta Hydrologic Laboratory	NC	Day and Monk, 1974
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1999
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Thompson River Gorge	NC	Racine, 1971
		Highlands	NC	Keever, 1953
	middle	Little Laurel Run	WV	Hicks and Frank, 1984
		Bedford County	VA	Johnson and Ware, 1982

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Quercus rubra	high	Monongahela National Forest	WV	Collins and Carson, 2004
		Little Laurel Run	WV	Desta, et al., 2004
		Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Peters Mountain	VA	Adams and Stephenson, 1983
		Bedford County	VA	Johnson and Ware, 1982
		Mountain Lake, Giles County	VA	Mills and Stephenson, 1999
		Giles County	VA	Stephenson and Saxena, 1994
		Salt Pond Mountain	VA	Stephenson, 1986
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Nantahala National Forest	NC	McNab, et al., 1999
	middle-high	Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Shenandoah National Park	VA	Harrison, et al., 1989
		Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Giles County	VA	Stephenson and Mills, 1999
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Coweeta Hydrologic Laboratory	NC	Clinton and Boring, 1994
		Coweeta Hydrologic Laboratory	NC	Davis, et al., 2004
		Coweeta Hydrologic Laboratory	NC	Day and Monk, 1974
		Bent Creek Experimental Forest	NC	Doolittle, 1957
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Quercus rubra (cont.)	middle-high (cont.)	Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1999
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Thompson River Gorge	NC	Racine, 1971
		Highlands	NC	Keever, 1953
		Highlands	NC	Oosting and Billings, 1939
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
		Little Laurel Run	WV	Hicks and Frank, 1984
Quercus velutina	high	Little Laurel Run	WV	Desta, et al., 2004
		Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Peters Mountain	VA	Adams and Stephenson, 1983
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Montgomery County	VA	Mou and Warrillow, 2000
		Giles County	VA	Stephenson and Saxena, 1994
		Montgomery County	VA	Whitney and Johnson, 1984
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Nantahala National Forest	NC	Carter, et al., 2000
		Nantahala National Forest	NC	McNab, et al., 1999
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Shenandoah National Park	VA	Harrison, et al., 1989
		Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Potts Mountain	VA	McEvoy, et al., 1980
		Giles County	VA	Stephenson and Mills, 1999
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Quercus velutina (cont.)	middle-high (cont.)	Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Coweeta Hydrologic Laboratory	NC	Clinton and Boring, 1994
		Coweeta Hydrologic Laboratory	NC	Day and Monk, 1974
		Bent Creek Experimental Forest	NC	Doolittle, 1957
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1999
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Highlands	NC	Keever, 1953
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
		Little Laurel Run	WV	Hicks and Frank, 1984
	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Robinia pseudoacacia	high	Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Nantahala National Forest	NC	McNab, et al., 1999
		Montgomery County	VA	Mou and Warrillow, 2000
		Giles County	VA	Stephenson and Saxena, 1994
		Salt Pond Mountain	VA	Stephenson, 1986

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Robinia pseudoacacia (cont.)	middle-high	Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Shenandoah National Park	VA	Harrison, et al., 1989
		Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Nantahala National Forest	NC	Carter, et al., 2000
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Highlands	NC	Keever, 1953
	middle	Bedford County	VA	Johnson and Ware, 1982
	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Sassafras albidum	high	Little Laurel Run	WV	Desta, et al., 2004
		Peters Mountain	VA	Adams and Stephenson, 1983
		Montgomery County	VA	Mou and Warrillow, 2000
		Walker Branch Watershed	TN	Grigal and Goldstein, 1971
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Nantahala National Forest	NC	Carter, et al., 2000
		Nantahala National Forest	NC	McNab, et al., 1999

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Sassafras albidum (cont.)	middle-high	Jefferson National Forest	VA	Madgwick and Desrochers, 1972
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Potts Mtn, Craig County	VA	Meiners, et al., 1984
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Highlands	NC	Keever, 1953
	middle	North Fork of Anthony Creek	WV	Abrams, et al., 1995
		Giles County	VA	Stephenson and Mills, 1999
	low-middle	Pilot Mountain	NC	Williams and Oosting, 1944
Tilia americana	high	Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Giles County	VA	Stephenson and Mills, 1999
	middle-high	Fernow Experimental Forest	WV	Schuler and Gillespie, 2000
		Shenandoah National Park	VA	Harrison, et al., 1989
		Beanfield Mtn, Giles County	VA	McCormick and Platt, 1980
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
	middle	Bedford County	VA	Johnson and Ware, 1982
Tilia heterophylla	high	Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Tilia heterophylla (cont.)	high (cont.)	Great Smoky Mountains National Park	NC/TN	Golden, 1981
	middle-high	Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1997
		Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
Tsuga canadensis	high	Lower Bluestone River Gorge	WV	Rentch, et al., 2005
		Montgomery County	VA	Mou and Warrillow, 2000
		Great Smoky Mountains National Park	NC/TN	Barden, 1980
		Great Smoky Mountains National Park	NC/TN	Callaway, et al., 1987
		Great Smoky Mountains National Park	NC/TN	Golden, 1981
		Nantahala National Forest	NC	McNab, et al., 1999
		Jocassee Gorge	SC	Abella, et al., 2003
	middle-high	Shenandoah National Park	VA	Harrison, et al., 1989
		Giles and Allegheny Counties	VA	Stephenson, et al., 1991
		Great Smoky Mountains National Park	NC/TN	Whittaker, 1956
		Great Smoky Mountains National Park	NC/TN	Woods and Shanks, 1959
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 1998
		Coweeta Hydrologic Laboratory	NC	Bolstad, et al., 2001
		Nantahala National Forest	NC	Carter, et al., 2000
		Coweeta Hydrologic Laboratory	NC	Day and Monk, 1974
		Coweeta Hydrologic Laboratory	NC	Elliott, et al., 1999

Table 1 (cont.) Species occurrence by elevation according to study site locations.

Species	Elevation	Study Site	State	Reference
Tsuga canadensis (cont.)	middle-high (cont.)	Coweeta Hydrologic Laboratory	NC	Parker and Swank, 1982
		Coweeta Hydrologic Laboratory	NC	Monk and Day, 1985
		Highlands	NC	Keever, 1953

VITA

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