Forest succession is often conceptualized as resulting in a climax or steady state condition where no net changes in species composition occur (Whittaker, 1975; Connell and Slatyer, 1977; Bormann and Likens, 1979, Runkle, 2000). Runkle (2000) equated this steady state community with the old-growth stage of development, and in part characterized the stage as a state where the understory and overstory have converged in species composition and is at equilibrium in terms of composition and structure. Evidence concerning equilibrium based hypotheses, e.g. niche partitioning, is mixed in the southern Appalachian Mountains (Runkle and Yetter, 1987; Clebsch and Busing, 1989; Busing and White, 1997; Runkle, 1998; Beckage et al. 2000; Markwith and Parker, 2003). Successional pathways, or trajectories, that do not progress in an apparent linear fashion towards a single stable state may be influenced by stochastic processes and chance. As many recognize, including Runkle (2000), equilibrium may never be completely realized, even in forests characterized by low intensity and/or low frequency disturbances.

In the southern Appalachians these non-equilibrium dynamics may be governed by disturbances that include, but are not limited to, drought, wildfire, and canopy gap creation, with drought often initiating conditions conducive to the latter two disturbances. Canopy gaps create variation in resource availability relative to the nongap understory. Light availability, temperature regimes, water and nutrient availability may all be impacted, which in turn affect seed germination and growth of seedlings and saplings (Markwith and Parker, 2003). Although rare over the past century due to suppression, fire is recognized as an important process of forest ecosystems in the southern Appalachians. Native American use of fire in particular may have maintained the extinct oak-American chestnut (Castanea dentata) forest type, and the
dominance of the oaks in general (Abrams, 1992; Delcourt and Delcourt, 1998).

The objectives of the current analysis are to examine potential successional trajectories in a second growth southern Appalachian mixed-hardwood forest, with particular focus on the influence of low-intensity disturbances, such as surface wildfire and gap creation, on the differential success of individual species in the vertical forest strata. The analysis is based on field sampling from 2001 in Blood Mountain Wilderness Area (BMWA) in the southern Appalchians (see Markwith and Parker, 2003), and a restudy of the same sites 5 years later. Specific questions include: 1) is the species composition in the overstory, subcanopy/midstory, and understory following a classical trajectory of dominance of “late successional” species that may indicate a current or future steady state pattern, and 2) what influences have the disturbance agents, fire and canopy gaps, had on individual species regeneration over the 5 year span between sampling?

Study Area

The study plots utilized for this restudy were identical to those used for the original study, and full explanation of the initial identification of study plots can be found in Markwith and Parker (2003). The plots were located within and in proximity to a low-intensity surface wildfire that burned November 16-19, 1999 in BMWA, Chattahoochee National Forest in northern Georgia. The forest is dominated by second growth mixed hardwoods, with stands ranging from 135-77 years of age (Markwith and Parker, 2003). The November 1999 wildfire occurred in the midst of a severe drought, and precipitation remained below normal prior to sampling in May and June, 2001. The years between sampling efforts included a majority of years with above normal precipitation, with the exception of 2002 and the first five months of 2006 (2002 = -18.26 cm, 2003 = +20.04 cm, 2004 = +10.80 cm, 2005 = +9.50 cm, Jan-May 2006 = -9.63 cm) (U. S. Department of Commerce, National Oceanic and Atmospheric Administration, 1999-2006, http://cdo.ncdc.noaa.gov/ancsum/ACS, last accessed May 25, 2009).
Markwith

Sampling

The 2006 sampling protocol followed that of Markwith and Parker (2003), with only minor modification. Study plots consisted of one of 20 canopy gaps and an adjacent nongap sub-plot, and were divided equally among burned and non-burned plots. Gap size was only re-measured in the 2006 study for gaps with edge trees that died between the 2001 and 2006 studies. Size was determined by measuring the longest axis (length) and the longest axis perpendicular to the first axis (width), to the trunk of the gap edge trees. In keeping with Runkle’s (1990) expanded gap method, the area of the gap was calculated based on the equation for an ellipse.

Concentric circular quadrats were located with their centers placed at the approximate center of the gap. Gap centers were not permanently marked during the 2001 study, but were designated as the intersection of the longest axis and longest perpendicular axis of the gap. Due to gap edge tree mortality and other sources of measurement error, some variability in quadrat location resulted between 2001 and 2006. Thus, mortality and growth of specific individuals within the quadrats are not analyzed between the two sampling years. Concentric quadrats of the same size as those in the gap sub-plot were also sampled at a nongap sub-plot located 10 m from a tree on the gap border. These quadrats similarly were not permanently marked in 2001, although the gap border tree to which they were anchored and the direction in degrees from that tree were recorded. For both gap and nongap sub-plots, the area of the outer and inner quadrats each equalled 93 m² (25% of the area of the median gap in 2001).

Within all quadrats, species of seedlings and saplings <2.5 cm diameter at breast height (dbh) were identified, and their heights were measured in five 30 cm classes, with a sixth class >150 cm. All stems >2.5 cm dbh were also identified and dbh measured, the same is true for trees of canopy height constituting the gap border.

Statistical Analysis

Based on the existing methodology the gap border trees constitute the only vegetation parameter with individuals that can be measured repeatedly. Thus, they were analyzed for mortality between
sampling periods. Overstory changes were analyzed by calculating the total number of stems for each species represented in the gap edge. The number of individuals of each species in the gap edge that died between 2001 and 2006 was determined, and the percent mortality per year for each species in the overstory calculated.

The sub-canopy and midstory layers were examined concurrently for potential gap filling individuals. Although growth and mortality of sub-canopy and midstory trees between sampling periods cannot be confidently addressed due to the lack of permanent quadrat locations, the composition within these quadrats is very similar between sampling periods. Thus, only the 2006 gap quadrat data is considered herein. The minimum size for analysis was defined as trees >15 cm dbh sampled within the inner and outer quadrats of each gap sub-plot (none of the individuals sampled in the quadrats of the gap sub-plots exceeded 30 cm dbh). Exceptions to the minimum were made for two gaps with no trees >15 cm, but with one tree each >13 cm dbh, and whose size was clearly distinguishable from the rest of the trees in those plots. One or more potential gap filling individuals was identified for each gap, with the exception of two plots that did not contain any trees with a measured dbh with the potential of reaching canopy height, i.e. only flowering dogwood (Cornus florida) present. The percentage of stems contributed by each species was calculated. The same methodology was also used to identify sub-canopy and midstory individuals in the nongap sub-plots, with a dbh range limited to 15-30 cm.

Seedlings and saplings <2.5 cm dbh were analyzed by first calculating density of stems/ha of individual species for each size class individually and for the sum of all size classes. Paired t-tests were then used to test for significant differences among samples in 2001 and 2006 for all plots together, burned plots, non-burned plots, gap sub-plots, and nongap sub-plots. Also, the proportion of 2006 understory density contributed by the oaks (Quercus spp.), hickories (Carya spp.), tulip poplar (Liriodendron tulipifera), and red maple (Acer rubrum) were analyzed in the smallest and largest size classes, 0-30 cm and >150 cm.
Results

Canopy Edge Mortality

Mortality of canopy trees along gap edges between 2001 and 2006 affected 10 out of the 20 sampled gaps. In turn, the size of canopy gaps with dead edge trees nearly significantly differed between sampling periods (2001 = 0.0379 ha vs. 2006 = 0.0435 ha, p = 0.072). Of the 219 gap edge trees sampled in 2001, 13 of those individuals died by 2006, for an annual mortality rate of 1.19%. The greatest loss in terms of both number of stems and basal area was found for northern red oak (Quercus rubra), 6 and 130.0 dm², respectively, for an annual mortality rate of 2.1%. However, the proportion of stems lost per year for northern red oak was largely consistent with other dominant species due to its high relative dominance (Figure 1). Other gap edge species with recorded mortality included chestnut oak (Quercus prinus) (0.7%), tulip poplar (0.6%), and red maple (2%). Scrub pine (Pinus virginiana) demonstrated the highest rate of annual mortality, 15%, with 3 of the 4 sampled individuals dying between 2001 and 2006. All sampled scrub pine were found in one gap sub-plot, so the high mortality rate may have resulted from a localized wind event or pests.

Sub-canopy and Midstory

Chestnut oak had the most sub-canopy and midstory stems in gap sub-plots, followed by tulip poplar, red maple, hickory species, and sourwood (Oxydendrum arboreum) in equal numbers (Figure 1). Although northern red oak had the second greatest relative dominance in the canopy, only one individual of this species reached sub-canopy or midstory status in gap sub-plots. Both white oak (Quercus alba) and scarlet oak (Quercus coccinea) also only contributed one individual each to this size class. The nongap sub-plots exhibited a similar pattern as gap sub-plots, with chestnut oak having the highest proportion of stems, followed by tulip poplar, then the hickory species. Red maple and sourwood were not as strongly represented, but northern red oak and white oak had a higher proportion than in gap sub-plots. Red maple did not have a single sub-canopy/midstory individual in the burned plots in either the gap or nongap sub-plots. Three of the oaks, northern red, scarlet, and white, were present in the burned but not the nonburned
Figure 1: Relative dominance of overstory gap edge species and proportion of stems by species in the subcanopy/midstory, i.e. 15-30 cm dbh size range, found in gap and nongap sub-plots. Species abbreviations: CO = chestnut oak, NRO = northern red oak, TP = tulip poplar, WO = white oak, HICK = hickory species, RM = red maple, SW = sourwood, SO = scarlet oak, BG = black gum, BO = black oak.

Source: Author

plots, while chestnut oak was represented equally in burned and non-burned areas.

Seedlings and Saplings

Comparing density of the 10 most common understory species indicates that northern red oak, chestnut oak, and black oak (Quercus velutina) significantly decreased from 2001 to 2006 among all plot types except non-burned plots for chestnut oak (Table 1). White oak did not have significant differences for any category, but did exhibit consistent mean decreases from 2001 to 2006. Scarlet oak displayed significant
Table 1: Paired t-tests comparing 2001 and 2006 density of stems/ha for individual species of seedlings and saplings in all size classes combined.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Red Maple</td>
<td>6256.1</td>
<td>6122.6</td>
<td>8248.0</td>
<td>7719.7</td>
<td>4264.2</td>
<td>4525.6</td>
<td>6396.2</td>
<td>5735.8</td>
<td>6115.9</td>
</tr>
<tr>
<td>Tulip Poplar</td>
<td>4404.3</td>
<td>3629.4</td>
<td>6924.5</td>
<td>5711.6</td>
<td>1864.1</td>
<td>1547.2</td>
<td>5350.4</td>
<td>4558.0</td>
<td>3458.2</td>
</tr>
<tr>
<td>Northern Red Oak</td>
<td>2885.4</td>
<td>1896.2</td>
<td>2827.5</td>
<td>1838.3</td>
<td>2943.4</td>
<td>1954.2</td>
<td>3528.3</td>
<td>2186.0</td>
<td>2242.6</td>
</tr>
<tr>
<td>Chestnut Oak</td>
<td>1529.6</td>
<td>963.6</td>
<td>2245.3</td>
<td>1215.6</td>
<td>814.0</td>
<td>711.6</td>
<td>994.8</td>
<td>665.8</td>
<td>2064.7</td>
</tr>
<tr>
<td>White Oak</td>
<td>920.5</td>
<td>867.9</td>
<td>1420.5</td>
<td>1372.0</td>
<td>420.5</td>
<td>393.9</td>
<td>849.4</td>
<td>819.4</td>
<td>946.1</td>
</tr>
<tr>
<td>Sassafras</td>
<td>796.5</td>
<td>859.8</td>
<td>1102.4</td>
<td>1307.3</td>
<td>490.6</td>
<td>412.4</td>
<td>706.2</td>
<td>857.1</td>
<td>856.8</td>
</tr>
<tr>
<td>Hickory</td>
<td>739.9</td>
<td>625.3</td>
<td>711.6</td>
<td>539.1</td>
<td>768.2</td>
<td>711.6</td>
<td>743.9</td>
<td>593.0</td>
<td>735.8</td>
</tr>
<tr>
<td>Black Locust</td>
<td>636.1</td>
<td>347.7</td>
<td>1172.5</td>
<td>622.6</td>
<td>99.7</td>
<td>72.8</td>
<td>719.7</td>
<td>404.3</td>
<td>552.6</td>
</tr>
<tr>
<td>Black Oak</td>
<td>483.8</td>
<td>339.6</td>
<td>752.0</td>
<td>568.7</td>
<td>215.6</td>
<td>110.5</td>
<td>420.5</td>
<td>277.6</td>
<td>547.2</td>
</tr>
<tr>
<td>Scarlet Oak</td>
<td>394.9</td>
<td>408.4</td>
<td>469.0</td>
<td>598.4</td>
<td>328.8</td>
<td>218.3</td>
<td>420.5</td>
<td>439.4</td>
<td>369.3</td>
</tr>
</tbody>
</table>

Source: Author

decreases in non-burned plots, but showed non-significant increases across all other plots types. In addition to the oaks, black locust (Robinia pseudoacacia) showed significant decreases from 2001 to 2006 in all but the non-burned plots. Tulip poplar significantly decreased only for the combined plots category, although a non-significant decrease in the mean density was apparent in the other categories. Red maple decreased in 3 out of 5 categories from 2001 to 2006, but increased in the non-burned plots and nongap sub-plots. However, none of the differences were significant, and red maple continued to dominate stem density in all categories in 2006.

The proportion of understory density contributed by the oaks, hickories, tulip poplar, and red maple in 2001 showed species based variation among plot types and among the smallest and largest size classes, 0-30 cm and >150 cm, respectively (Figure 2). The most striking differences among plot types in the 0-30 cm size class were the variation in tulip poplar and red maple among burned and non-burned plots. Substantial variation was also found among burned and non-burned plots within the >150 cm size class, with tulip poplar and the hickories exhibiting a greater proportion of density in non-burned plots and the opposite pattern in red maple. Tulip poplar also had a greater proportion in gap sub-plots as opposed to nongap sub-plots. The oaks together maintained a relatively consistent proportion of density across
Figure 2: Proportion of understory density in the 0-30 cm and >150 cm seedling and sapling height classes represented by the dominant oaks, red maple, tulip poplar, and hickory species. Species abbreviations follow that of Figure 1

Source: Author
Markwith

all plot types within both size classes; however, there was visible variation among size classes in the oaks, tulip poplar, and red maple. The oaks together constituted approximately 1/3 of the density in the 0-30 cm size class, but only represented approximately 1/8 of the density in the >150 cm size class. Red maple had a greater proportion of density in the >150 cm size class compared to the 0-30 cm size class in burned plots and gap and nongap sub-plots, with approximately 3/4 of the density in burned plots and nongap sub-plots in the >150 cm class.

Discussion

As with much of the southern Appalachian woodlands, BMWA is a relatively youthful second growth forest historically influenced by logging and changes in the canopy species pool, e.g. the effects of the chestnut blight. Along with the natural disturbance regime, these and other anthropogenic disturbances have imposed an environmental context recently dominated by non-equilibrium processes. However, comparison of the relative abundance, dominance, and density of species in the overstory, sub-canopy/midstory, and understory indicates that a trajectory of classical succession toward more shade tolerant species is apparent with minor exceptions. Oaks range from very intolerant to intermediate shade tolerance (Burns and Honkala, 1990), and are currently dominant in the overstory, constituting greater than half of the overstory, but the younger cohorts generally support greater abundances of more shade tolerant species. Northern red oak in particular, and to a lesser extent white oak, are not proportionately maintaining the cohort of potential recruits from the sub-canopy/midstory and understory to continue their dominance into the foreseeable future. On the other hand, based on the number of trees with gap filling potential, chestnut oak, perhaps the most tolerant of the dominant oaks in BMWA, apparently has the capacity to maintain its overstory dominance. More tolerant species, such as hickory, red maple, and sourwood, may experience a period of ascendancy in dominance through time as their relatively high proportion of sub-canopy/midstory stems recruit into the overstory. Somewhat antithetical to this successional trend is the apparent ability of the pioneer and shade intolerant tulip poplar to maintain its dominant position as the forest changes.
Although northern red oak mortality was slightly higher than the other dominant species, mortality rates in BMWA between 2001 and 2006 are very similar to those estimated by Wyckoff and Clark (2002) for red maple, tulip poplar, chestnut oak, and northern red oak at Coweeta Hydrologic Laboratory in North Carolina. Also at Coweeta, Clinton et al. (1993) found that drought increased scarlet oak and northern red oak mortality, while Elliott and Swank (1994) found that red maple had lower drought mortality than oaks. Drought was not a particularly important issue between 2001 and 2006, so differential mortality based on this effect may be less evident in the current analysis.

In the understory many of the most abundant species showed some density decreases between the 2001 and 2006 sampling periods, but the occurrence of significant decreases was concentrated within the oaks. This is consistent with other studies, where closure of the understory 4-6 years after disturbance resulted in decreases in seedling germination and understory production (Shure et al., 2006). Clinton and Vose (2000) concluded that most species decrease in density after an initial fire induced pulse of regeneration due to density-dependent mortality. Red maple, considered shade tolerant, did have non-significant decreases in disturbed sites, but actually had moderate increases in density in non-burned plots and nongap sub-plots where competition for light is generally expected to be consistently high. Interestingly, northern red, chestnut, and black oak all showed significant density decreases, while the least shade tolerant oak, scarlet oak, slightly increased density in some plots between sampling periods. Some of the other intolerant species that are expected to be negatively affected by increased competitors, i.e. tulip poplar and sassafras, did not exhibit significant decreases like the more tolerant oaks.

Some investigators conclude that regeneration of oaks may be experiencing a widespread failure in mesic forests of the eastern U.S. (Loftis and McGee, 1993; McDonald et al., 2002; Shure et al., 2006). Shure et al. (2006) concluded that reestablishment of oaks as canopy dominants was doubtful following a 78% decline in abundance of young stems due to two major droughts in the 80s and 90s that caused substantial oak mortality (Clinton et al., 1993). Annual seed crop failures are higher in large seeded trees, such as oaks, than in small
seeded trees (Godman and Mattson, 1976), and oaks do not compensate for seed crop failure with a buried seed bank (Canham and Marks, 1985). The Georgia Department of Natural Resources, Wildlife Resource Division, conducts yearly acorn mast surveys and ratings (good > 3.00, fair = 2.01-3.00, poor = 0.00-2.00) (Georgia Department of Natural Resources, (http://georgiawildlife.dnr.state.ga.us/content/displaycontent.asp?txtDocument=211&txtPage=1, last accessed May 25, 2009). Acorn production in the Appalachian Mountain region in 2005, the mast event prior to sampling in spring 2006, was poor for white oaks and chestnut oaks (1.09 and 1.72, respectively) and good for red oaks (3.02), for a total region rating of 2.07. The mast survey for the year 2000 shows a similar overall regional rating of 1.88, with white and chestnut oaks rated 0.78 and 0.15, respectively, and red oaks 3.50 (Scott Frazier, Georgia DNR, personal communication). Because these ratings are so similar between years immediately preceding the sampling periods, and high mast variability was found in the intervening years, it is not evident that reproductive output is the major determining factor in density decline over the sampling period. Other factors such as density dependent effects and disturbance may be equally or more important.

Many of the plants present at a site soon after a disturbance generally will not reach reproductive size. Thus, differential growth rates should be important in competition during the early stages of biomass recovery (Canham and Marks, 1985). As pioneer species, shade-intolerant species typically have a growth rate advantage that allows them to avoid intense competition for light. Beckage and Clark (2003) concluded that northern red oak may out survive red maple and tulip poplar, but that tulip poplar and red maple will grow more quickly than northern red oak when competition for resources is removed from the overstory or understory, i.e. wildfire or canopy gaps. They found that gap creation was especially advantageous for tulip poplar growth, but also gave red maple a nonsignificant advantage over northern red oak. Although survival and growth could not be directly analyzed in the understory and sub-canopy/midstory in BWMA, the evidence indicates that both red maple and tulip poplar may out grow and out survive northern red oak in gaps based on changes in understory density from 2001 to 2006 and the proportion of sub-canopy/midstory stems.
towards more shade tolerant species may be best achieved by increasing mortality rates of fire sensitive species as they recruit into the midstory instead of the seedling and sapling cohorts.

**Conclusion**

Humanized landscapes, like BMWA, are subjected to numerous non-equilibrial processes and anomalous historical disturbance regimes, and it can be difficult to determine whether successional patterns will ultimately prove to be a steady state or dynamic equilibrium, or these disturbances will contribute to non-equilibrium of community dynamics. Our temporally constrained understanding of the systems makes the prediction of future trajectories difficult, but even on a five year timeline, indicators suggest progression towards a forest with oaks becoming a minority and more shade tolerant species dominant. The effects of management techniques such as prescribed fire may only be transitory for less shade tolerant species, e.g. oak species, while more competitive species out grow, reproduce, or survive the management targets. A small window of opportunity may be available to many species following disturbance as competition for resources amplifies over the pre-disturbance environment, and only a few species like red maple appear to be selected for success throughout the shifting mosaic of disturbed, recovering, and undisturbed environments.

**References**


Arthur, M. A., Paratley, R. D., and Blankenship, B. A. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous...


Clebsch, E. E. C., and Busing, R. T. 1989. Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. in Moser, W. K. and Moser, C. F. eds. Fire and forest ecology:
innovative silviculture and vegetation management. Tall Timbers Fire Ecology Conference Proceedings, No. 21. Tall Timbers Research Station, Tallahassee, FL.


The Florida Geographer


Markwith


