VEGETATION CHANGE IN THE DUKE FOREST, 1977 – 2010

Kimberly Anne Israel

A thesis submitted to the faculty of the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the degree of Master of Science in the Department of Biology

Chapel Hill 2011

Approved by:

Robert K. Peet

Alan Weakley

Thomas Wentworth

ABSTRACT

KIMBERLY ISRAEL: Vegetation Change in Duke Forest, 1977 – 2010 (Under the direction of Robert K. Peet)

Herb and sapling vegetation data from permanent plots in Duke Forest were collected and compared with vegetation data from 1977 and 2000 to evaluate compositional change. Declines in herb layer cover and richness indicate likely impacts from white-tailed deer herbivory. Oak regeneration has slowed, and the historical oak-hickory forest may be replaced by dominant maple and beech. The average annual rate of herb layer change is consistently higher for 2000 – 2010 than for 1977 – 2000, indicating acceleration in vegetation shifts, with deer herbivory as a possible contribution. Projections of the 2000 and 2010 successional pine herb layer composition based on a space-for-time substitution of the 1977 data indicate substantial variation from the observed data. Furthermore, MRPP tests indicate grouping of successional pine plots by sampling year and not by age. These factors, combined with the increasing rate of change, suggest that environmental influences may overshadow successional change.

ACKNOWLEDGMENTS

The vegetation plots that provide the basis of this thesis were originally sampled by Robert K. Peet and Norman L. Christensen. The second resurvey (1999-2001) was conducted by Kristin Taverna and Laura Phillips. I wish to thank the Beers family for their generous funding, my field assistant Sarah Brown for assistance with data collection, my committee members Robert K. Peet, Alan S. Weakley and Thomas R. Wentworth for guidance and patience, and lab members Forbes Boyle, Mike Lee, Samantha Tessel, Megan Faestal, Stephanie Seymour, and Kyle Palmquist for invaluable advice.

TABLE OF CONTENTS

List of Tables	V
List of Figures	vi
Introduction	1
Herb layer compositional change	10
Change in invasive species cover	45
Oak-Hickory vs. Maple-Beech changes in sapling basal area	54
Species richness	63
Succession and average annual change	69
Conclusion	
Literature cited	86
Appendix: Full Species List	91

LIST OF TABLES

Table 1: Characteristics of the CCA axis 1 environmental categories	8
Table 2: Direction of change in average herb layer invasive cover by species and data set	48
Table 3: Direction of change in average herb layer invasive cover by species and CCA environmental category	52
Table 4: MRPP groupings based on observed and projected herb layer composition of successional pine plots	76

LIST OF FIGURES

Figure 1: 2-D Constrained NMS Ordination of All Plots by Herb Layer Composition9
Figure 2: Average Cover of Native Herb Species Over All Plots12
Figure 3: Average Cover of Native Herb Species in Hardwood Plots13
Figure 4: Average Cover of Native Herb Species in Pine Plots
Figure 5: Average Cover of Native Herb Species in CCA Type 1 Plots14
Figure 6: Average Cover of Native Herb Species in CCA Type 2 Plots14
Figure 7: Average Cover of Native Herb Species in CCA Type 3 Plots15
Figure 8: Average Cover of Native Herb Species in CCA Type 4 Plots15
Figure 9: Average Cover of Herb Families, Calculated Over Complete Data Set16
Figure 10: Average Cover of Herb Families, Calculated Over Hardwood Plots17
Figure 11: Average Cover of Herb Families, Calculated Over Pine Plots17
Figure 12: Average Cover of Herb Families, Calculated Over CCA Type 1 Plots18
Figure 13: Average Cover of Herb Families, Calculated Over CCA Type 2 Plots19
Figure 14: Average Cover of Herb Families, Calculated Over CCA Type 3 Plots19
Figure 15: Average Cover of Herb Families, Calculated Over CCA Type 4 Plots20
Figure 16: Average Cover of Graminoid Families, Calculated Over Complete Data Set21
Figure 17: Average Cover of Graminoid Families, Calculated Over Hardwood Plots21
Figure 18: Average Cover of Graminoid Families, Calculated Over Pine Plots22
Figure 19: Average Cover of Graminoid Families, Calculated Over CCA Type 1 Plots23
Figure 20: Average Cover of Graminoid Families, Calculated Over CCA Type 2 Plots23
Figure 21: Average Cover of Graminoid Families, Calculated Over CCA Type 3 Plots24

Figure 22: Average Cover of Graminoid Families, Calculated Over CCA Type 4 Plots2	24
Figure 23: Average Herb Layer Cover of Native Woody Species, Calculated Over Complete Data Set	25
Figure 24: Average Herb Layer Cover of Native Woody Species, Calculated Over Hardwood Plots	26
Figure 25: Average Herb Layer Cover of Native Woody Species, Calculated Over Pine Plots	26
Figure 26: Average Herb Layer Cover of Native Woody Species. Calculated Over CCA Type 1 Plots	27
Figure 27: Average Herb Layer Cover of Native Woody Species, Calculated Over CCA Type 2 Plots	28
Figure 28: Average Herb Layer Cover of Native Woody Species, Calculated Over CCA Type 3 Plots	28
Figure 29: Average Herb Layer Cover of Native Woody Species, Calculated Over CCA Type 4 Plots	29
Figure 30: Average Herb Layer Cover of Vine Families, Calculated Over Complete Data Set	30
Figure 31: Average Herb Layer Cover of Vine Families, Calculated Over CCA Type 1 Plots	30
Figure 32: Average Herb Layer Cover of Vine Families, Calculated Over CCA Type 2 Plots	31
Figure 33: Average Herb Layer Cover of Vine Families, Calculated Over CCA Type 3 Plots	31
Figure 34: Average Herb Layer Cover of Vine Families, Calculated Over CCA Type 4 Plots	32
Figure 35: Average Herb Layer Cover of Shrub Families, Calculated Over Complete Data Set	33
Figure 36: Average Herb Layer Cover of Shrub Families, Calculated Over CCA Type 1 Plots	33

Figure 37: Average Herb Layer Cover of Shrub Families, Calculated Over CCA Type 2 Plots	34
Figure 38: Average Herb Layer Cover of Shrub Families, Calculated Over CCA Type 3 Plots	34
Figure 39: Average Herb Layer Cover of Shrub Families, Calculated Over CCA Type 4 Plots	35
Figure 40: Average Herb Layer Cover of Tree Families, Calculated Over Complete Data Set	36
Figure 41: Average Herb Layer Cover of Tree Families, Calculated Over CCA Type 1 Plots	37
Figure 42: Average Herb Layer Cover of Tree Families, Calculated Over CCA Type 2 Plots	37
Figure 43: Average Herb Layer Cover of Tree Families, Calculated Over CCA Type 3 Plots	38
Figure 44: Average Herb Layer Cover of Tree Families, Calculated Over CCA Type 4 Plots	38
Figure 45: Average Herb Layer Cover of Maple/Beech and Oak/Hickory Seedlings, Calculated Over Complete Data Set	
Figure 46: Average Herb Layer Cover of Maple and Beech Seedlings, Displayed by CCA Environmental Category	40
Figure 47: Average Herb Layer Cover of Oak and Hickory Seedlings, Displayed by CCA Environmental Category	40
Figure 48: Average Herb Layer Cover of <i>Lonicera japonica</i> , Displayed by Plot Canopy Composition	47
Figure 49: Average Cover of <i>Microstegium vimineum</i> , Displayed by Plot Canopy Composition	47
Figure 50: Average Herb Layer Cover of Other Invasive Species, Displayed by Plot Canopy Composition	48
Figure 51: Average Herb Layer Cover of <i>Lonicera japonica</i> , Displayed by CCA Environmental Category	50

Figure 52: Average Cover of <i>Microstegium vimineum</i> , Displayed by CCA Environmental Category
Figure 53: Average Herb Layer Cover of Other Invasive Species, Displayed by CCA Environmental Category
Figure 54: Average Percent Change in Sapling Basal Area per Hectare in Hardwood Plots, Comparing Plots by Change in Ratio of Oak-Hickory to Maple-Beech Sapling Basal Area
Figure 55: Average Percent Change in Sapling Basal Area per Hectare in Pine Plots, Comparing Plots by Change in Ratio of Oak-Hickory to Maple-Beech Sapling Basal Area
Figure 56: Average Species Richness at 1000-Square-Meter Scale, Displayed by
Plot Canopy Composition and CCA Environmental Category
Figure 57: Average Annual Change 2000-2010 vs. 1977-2000, Displayed by Plot Canopy Composition
Figure 58: Average Species Richness at 1-Square-Meter Scale, Displayed by
Plot Canopy Composition and CCA Environmental Category
Figure 59: NMS Ordination of Pine Plots by Herb Layer Cover, With
Year-To-Year Vectors
Figure 60: NMS Ordination of Species Herb Layer Cover Class for 1977
Pine Plots, Observed 2000 Pine Plots, and Projected 2000 Pine Plots74
Figure 61: NMS Ordination of Species Herb Layer Cover Class for 1977
Pine Plots, Observed 2010 Pine Plots, and Projected 2010 Pine Plots75
Figure 62: Average Annual Change 2000-2010 vs. 1977-2000, Displayed by
CCA Environmental Category77
Figure 63: Average Annual Change 2000-2010 vs. 1977-2000, Displayed by
Plot Canopy Composition

Figure 64: Average Annual Change for Pine Plots 2000-2010 vs. 1977-2000,	
Displayed by Plot Age in 1977	79
Figure 65:Loss in Canopy Tree Seedling Cover, High-Invasive Plots Compared	
to All Plots	83

INTRODUCTION

The vegetation of eastern North America's temperate forests has experienced forces for change throughout its history, but particularly in recent years. Most forest stands have been cleared and have regrown, sometimes several times, as land has been various cleared for agriculture or timber (Heath et al. 1993, Cowell 1998, Wright and Fridley 2010). Succession, therefore, has been a constant process, and the composition and stability of climax communities is uncertain (Abrams 1998, Taverna et al. 2005, Woods 2007).

Fire suppression has been in effect for almost a century (Abrams and Downs 1990, Shumway et al. 2001), bringing with it the possibility of mesophication and the slow replacement of oaks and hickories with fire-intolerant maples and beeches (Abrams and Downs 1990, Shumway et al. 2001). With the extirpation of predators and the concomitant decrease in hunting pressure, white-tailed deer populations have increased and are changing community composition by their foraging preferences (Stromayer and Warren 1997, Horsely et al. 2003, Cote et al. 2004). Meanwhile, storms such as hurricanes and tornadoes have blown down numerous trees with effects ranging from canopy gaps to catastrophic damage (McNab et al. 2004, Xi et al. 2008). Exotic invasives creep ever further into the forests with as-yet unknown effects on the native species (Wilcove et al. 1998, Mack et al. 2000). Finally, the effects of global climate change could permanently alter vegetation structure and composition.

Duke Forest has long been used as a model system to study and explain succession and other changes occurring in eastern North American temperate forests (see Christensen and Peet 1981). The southeastern Piedmont region of the United States has a substantial and increasing population density of white-tailed deer (Keyser et al. 2005). Many sections of the Duke Forest are adjacent to residential areas, so the spread of invasive plants appears earlier than in more isolated forests (Gavier-Pizarro et al. 2010). The forest includes stands that were abandoned from agricultural use at different times so that successional changes can be observed, and it also experienced disturbances when Hurricanes Hazel (1954) and Fran (1996) impacted the forest (Xi et al. 2008). Signs of mesophication have already been recorded in the forest with a significant increase in red maple abundance and a decline in oak regeneration (McDonald et al. 2002, Taverna et al. 2005). Community composition of the Duke Forest has been sampled twice before, by Peet and Christensen in 1977 (Peet and Christensen 1980, Christensen and Peet 2001) and by Taverna in 1999-2000 (Taverna et al. 2005). Taverna et al. found significant changes in the vegetation composition between 1977 and 2000, indicating that a single stable climax state for the forest may not exist. Instead, changing environmental influences continually affect the forest, bringing about various temporary states. A third sample allows both comparison between the 2010 state and the past two states, and comparison between the 2000-2010 trajectory of change and the 1977-2000 trajectory.

This study examines forest dynamics by determining how the Duke Forest vegetation composition has changed with changing environmental context. Of particular interest are (1) how the herb layer vegetation has changed since 1977 and what factors most likely caused those changes, (2) which invasive species have expanded or declined and to what degree, (3)

how regeneration of the historically dominant oaks and hickories compares to regeneration of fire-intolerant maples and beeches, (4) how the rate of herb-layer change has varied between sampling periods and what those changes may imply, and (5) to what degree the herb-layer compositional changes are consistent with those expected due to succession as compared to other factors.

METHODS

Study Area

This study was conducted in the Duke Forest located in Durham and Orange counties in the northeastern Piedmont region of North Carolina. During the period covered by the data sets (1977-2010), the average annual temperature in the region was 14.6 $^{\circ}$ C, with January and February the coldest months with the lowest average monthly temperature at -2.6 $^{\circ}$ C, and the warmest months as July and August with the highest average monthly temperature at 27.4 $^{\circ}$ C . The average annual precipitation was 1.16 m. The wettest period in most years was between March and October, but the wettest month in each year varied dramatically (State Climate Office of North Carolina: http://www.nc-climate.ncsu.edu/cronos/normals.php).

Elevation ranges from 85 to 250 m (Palmer 1990). The topography is mainly rolling, though the data set includes plots ranging from flat to 30 degree slopes. Soils are mostly coarse loams at the surface, with clay beneath, over a range of bedrock types that includes mudstones and sandstone in the Triassic Basin and igneous and metamorphic bedrock, such as granite, gneiss, metamorphic rock of the Carolina slate formation and basic igneous intrusives such as diabase, throughout the rest of the forest.

(www.dukeforest.duke.edu/forest/climate.htm, 13 Aug 2011). Weathering of diorite and

diabase produces poorly-drained soils with shrink-swell montmorlinitic clays, while weathering of granite and Carolina slate produces infertile but well-drained soils with abundant kaolinitic clays (Taverna et al. 2005).

Duke Forest consists of a range of pine stands abandoned from agricultural use at various times in the 19th and early- to mid-20th centuries, and hardwood stands, some of which are on sites long abandoned from agriculture, but most of which were variously harvested for timber during the 19th and early 20th century (Christensen and Peet 1984). This study is based on a set of 72 50 x 20 m permanent plots sampled between late May and early August during three different time periods. All plots were originally monumented with 6 thin-wall steel conduit stakes -- 3 at each end of the plot spaced 10 m apart. These are a subset of the plots in the Durham and Korstian Divisions of the forest originally sampled by Peet and Christensen in 1977 (Peet and Christensen 1980). These plots consisted of unevenaged hardwood plots with no evidence of human impacts after 1900 and successional pine plots placed in age categories of 30-50 years, 50-70 years, 70-100 years, and over 100 years post agriculture. Approximately 100 of these permanent plots were resampled by Taverna in 1999-2000 (Taverna et al 2005). Plots were relocated in 2009-2010 using GPS coordinates of the plot origin and/or center recorded in 1999-2000, and the exact location of each plot was confirmed by discovery of at least three remaining stakes, of which at least two had to be at opposite ends of the plot. Furthermore, in order for a plot to be resampled, the bearing had to be recorded or be able to be determined based on whatever data were recorded (such as origin coordinates). The 72 plots sampled in 2009-2010 consisted of 37 in the Durham Division and 35 in the Korstian Division. Of these plots, 30 were in uneven-aged hardwood forest and 42 were in successional pine forests. During the 2009-2010 field seasons,

additional conduit stakes were added every 10 m along the center line of the plot and 10 m to either side perpendicular to the center line at the 10 m and 30 m marks, so as to be consistent with the Carolina Vegetation Survey (CVS) protocol (Peet et al. 1998).

Vegetation data were collected in 2009-2010 for the herb layer and for woody stems using the same protocol as in 1977 and 1999-2000. For the herb layer, a 0.5-m wide transect was established to the right of the center line relative to the origin. This transect was divided into 25 contiguous 0.5 by 2 m subplots. For each subplot, presence and cover were recorded for all plant taxa that had leaf area below 1 m in height. Cover classes used in 1999-2000 and 2009-2010 were those of the CVS protocol (Peet et al. 1998). In 1977, leaf cover was estimated to the nearest percent, and those estimates were converted into CVS cover values by Taverna et al. (2005). Saplings less than 2.5 cm diameter at breast height (dbh; 1.37m) were recorded in a 20% subsample consisting of the area within two meters of the center line. All trees with 2.5 cm or greater dbh were recorded. Sapling size categories were 0-1 cm dbh and 1-2.5 cm dbh, and tree size categories were 2.5-5 cm dbh and then 5-cm increments up to 40 cm dbh. Trees greater than 40 cm dbh had their dbh recorded individually to the nearest centimeter, rounded down. In 2009-2010, woody stem and sapling locations were also recorded by module. Each plot was divided into ten 100 m² modules, five on each side of the center line consistent with the CVS protocol. Trees were recorded separately for the four modules between the 10 and 30 m marks on the center line (modules 2, 3, 8, and 9) to assure full compatibility with other plot data collected using the CVS protocol. In 2009-2010, total plot cover class for each species was estimated at the herb, shrub, and canopy layers, with the herb layer defined as all leaves below 1 meter in height, and the shrub layer defined as all leaves at 1-5 m. In the other sampling years, plot cover below 1 m was also recorded, but the

shrub and canopy cover estimates were added in 2009-2010 for consistency with the CVS protocol and to facilitate comparison with other CVS plot data.

Environmental and site attribute data such as slope, aspect, solar radiation, elevation, exposure, and distance to the nearest permanent water were collected in 1977 and assumed to be constant over time. In addition, soil characteristics such as pH, cation content, organic content, and phosphate content were assumed constant.

Consolidation of the 1977, 2000, and 2010 data sets

Plants from 2009-2010 were identified with expert assistance to the finest resolution possible. Those that could not be identified to at least family, even with expert assistance, were recorded as 'Unknown' in the raw data for 2009-2010. In order to align the data from all years, unknowns were left out of the combined data set. To match the taxonomic standard used for combining the 1977 and 1999-2000 data, species within the following taxonomically difficult genera were lumped to the genus level: Solidago, Viola, Rubus, Sanicula, Ranunculus, Oxalis, Lespedeza, and Eupatorium. In addition, the following pairs of species were lumped in the combined data set (though they were kept separate in the raw data set) because of taxonomic problems in one year or another: Carya ovalis with Carya glabra, Carya carolinae-septentrionalis with Carya ovata, Vaccinium corymbosum with Vaccinium stamineum, Elaeagnus pungens with Elaeagnus umbelleta, and Vitis vulpina and Vitis labrusca with Vitis aestivalis. When this lumping required adding cover values within the same plot, values were converted to the geometric mean of their range and added together and the resulting sum was converted to a CVS cover class value. Taxonomic concepts are based on Weakley 2011. A complete list of taxa recognized is presented in Appendix 1.

Environmental classification of plots

Ordination was used to visualize the relationships among plots based on their herblayer composition. To be consistent with previous work on this system (i.e., Taverna et al. 2005), nonmetric multidimensional scaling (NMS) was used in PC-ORD (version 5.0) with the Sorenson (Bray-Curtis) dissimilarity measure and the whole-plot herb-layer cover class for each species. The algorithm began with six axes and stepped down in dimensionality, using 50 runs with real data and a maximum of 250 iterations. The stability criterion was 0.00001, with 15 iterations to evaluate stability and an initial step length of 0.20. Starting coordinates were random numbers generated by the software. Varimax rotation was used to improve alignment of species abundance vectors with ordination axes (McCune and Grace 2002).

An initial ordination of plots based on total herb-layer cover of each species and overlaid with environmental variable vectors indicated a first axis corresponding to an environmental gradient dependent on a combination of soil pH and distance from permanent water. In order to more clearly define the environmental gradient, I ran a Canonical Correspondence Analysis (CCA) on the 1977 herb layer data, so that the first axis was constrained to be the best single environmental variable, accounting for the effects of moisture, pH, and any other important variables in one number. The 1977 data were used because environmental data for the research plots were collected in 1977. The environmental data were assumed to remain the same through 2010, so that these environmental factors should partially predict vegetation composition from 2000 and 2010 as well.

In order to group the plots by environment, I divided the range of CCA values on the first axis so that each category took up an equal amount of CCA space. Characteristics of

Table 1: Characteristics of the CCA axis 1 environmental categories								
CCA category	CCA range	Number of plots	Average dist. from water	Range of dist. from water	Average pH	Range of pH	Average Ca meq	Range of Ca meq
1	-2.68 to - 1.25	12	849 m	300 m to 999 m	4.05	3.82 to 4.22	0.34	0.13 to 0.74
2	-1.13 to 0.09	37	451 m	10 m to 999 m	4.66	3.86 to 5.84	1.52	0.26 to 6.09
3	0.20 to 1.50	18	165 m	30 m to 600 m	5.36	4.16 to 6.06	3.36	0.31 to 6.33
4	1.70 to 3.10	5	15 m	5 m to 25 m	5.31	4.84 to 5.74	3.91	3.26 to 4.94

each category are summarized in Table 1.

In general, plots that are closer to water have higher pH and cation content, while drier plots also tend to be more acidic and nutrient-poor. I performed a Nonparametric Multidimensional Scaling (NMS) analysis and found that the CCA value strongly correlates with one axis of the ordination of herb-layer composition, both with a three-axis ordination and when the ordination is constrained to two axes (Figure 1). The CCA axis is also strongly correlated with distance from water, pH, and concentrations of calcium, potassium, and magnesium, indicating that these are the major environmental factors affecting herb-layer composition.



Figure 1: 2-D Constrained NMS Ordination of All Plots by Herb Layer Composition

Axis 1

HERB LAYER COMPOSITIONAL CHANGE

Methods

In order to find out how the herb layer vegetation has changed since 1977 and what factors have been involved in those changes, I examined differences in average herb cover of various plant groups. Herbaceous and woody species were distinguished because patterns of deer browse can differ between them and because herb species typically exist only in the herb stratum while woody species grow into the shrub and canopy layers. Herb species were identified as ferns, forbs, or graminoids. Ferns and graminoids are typically less affected by deer browse than herbs (Rooney 2009). Woody species were divided by growth form: vine, shrub, or tree. Shrubs might be more affected by deer browse because individual plants never reach the safety of the canopy. Changes of botanical family abundance were analyzed to look for common traits that may respond to environmental changes. Finally, oak and hickory seedlings were categorized together, as were maple and beech. This final distinction was used to explore the possibility of mesophication, in which maple and beech abundance would be expected to exceed oak and hickory abundance.

To evaluate the changes in herb layer cover of various plant groups, I took the geometric mean of the cover class range for each species in each plot, and then for each group I added the geometric means for all member species in all plots and divided by the number of plots. I repeated this process for subsets of the data based on canopy composition (successional pine or uneven-aged hardwood) and environmental characteristics (CCA types 1 through 4).

Change in herb-layer species richness was compared between the 1977-2000 period and the 2000-2010 period. In order to capture the most accurate number of species despite difficulties in identification, the raw data from each year were used. Therefore, species listed as unknown were still counted as distinct from known species in a given plot. Average richness was compared across years both for the data set as a whole and for subsets based on CCA environmental category and hardwood or pine composition.

Results

Although the plots showed an average decline in cover of forbs, the cover from ferns and graminoids was relatively constant and was large enough that the total cover of herbs was not significantly changed. The difference between the average herb cover in 1977 and in 2010 was less than the sum of the standard error for each time period, so that one cannot be sure the difference is not due to measurement error. Some variation exists among the different subsets of the data. Pine plots, for example, do show a significant decline in herb cover, though this still appears to result only from decline in forbs, rather than ferns or graminoids (Figures 2-4). Somewhat surprisingly, the greatest stability in the herb cover seems to be found in the most extreme environments: CCA types 1 and 4 show no significant decline in total forbs, ferns, or graminoids (Figures 5-8). The set of hardwood plots and the set of CCA type 2 plots each show an increase in graminoids to balance the decline in forbs. Although the mean value for graminoid cover was higher in 2010 than in 1977 for three of the four environmental categories, only in group 2 was the difference larger than the sum of the standard error for 1977 and 2010. Group 2 also had the lowest graminoid cover in 1977, so its increase nearly doubled the amount of graminoid cover in that subset, even though the average amount of cover added per plot was about 5 square meters(= 0.5%), not dramatically different from the amount gained or lost in the other environmental groups.



Figure 2: Average Cover of Native Herb Species Over All Plots



Figure 3: Average Cover of Native Herb Species in Hardwood Plots



Figure 4: Average Cover of Native Herb Species in Pine Plots



Figure 5: Average Cover of Native Herb Species in CCA Type 1 Plots



Figure 6: Average Cover of Native Herb Species in CCA Type 2 Plots



Figure 7: Average Cover of Native Herb Species in CCA Type 3 Plots





In the data set as a whole, the families of forbs that showed the most decline in cover were Euphorbiacae, Fabaceae, Iridaceae, and Orchidaceae (Figure 9). These losses are offset slightly by an increase in Rubiaceae. Families that were unchanged in cover across all data subsets were Lamiaceae, Caryophyllaceae, Solonaceae, Polygonaceae, Ophioglossaceae, Apocynaceae, Dryopteridaceae, and Juncaceae. Among these, only Lamiaceae and Apocynaceae were present in all data subsets, and only Lamiaceae had a cover of at least 0.05% in all subsets.

The hardwood group shows the same patterns of change as the complete data set, which suggests that hardwood plots, with their larger herb cover, are driving the changes observed in the complete data set (Figure 10). The pine group, which shows a significant decline in herb cover, also has declines in Apiaceae, Asteraceae, and Ranunculaceae, perhaps accounting for that herb cover decline (Figure 11).



Figure 9: Average Cover of Herb Families



Figure 10: Average Cover of Herb Families





Figure 11: Average Cover of Herb Families

The CCA type 1 group, which does not show an average decline in forbs, has an increase in Orchidaceae as well as in Rubiaceae and also does not show a significant decline in Fabaceae (Figure 12). It does, however, share the pine group's decline in Asteraceae cover. The type 2 group does have a decline in cover from forbs and follows the complete data set with decreases in Fabaceae and Orchidaceae, and shares the pine group's decline in Apiaceae and Asteraceae (Figure 13). As in the hardwood data set, Rubiaceae cover is unchanged. CCA group 3 (Figure 14) has an increase in Apiaceae and no decline in Orchidaceae, but this is countered by a decline in Rosaceae and lack of increase in Rubiaceae so that the forb cover still declines on average. Finally, CCA group 4 has declines in Fabaceae and Orchidaceae (Figure 15) but does not show a decline in total forb cover.











Cyperaceae cover has increased on average over the whole data set, but its influence is not enough to significantly change the cover of graminoids since Poaceae cover is unchanged (Figure 16). Likewise, in the hardwood and pine subsets, cover of graminoid families and of graminoids in total is unchanged (Figures 17-18). Although Juncaceae species were present in hardwood plots, they are omitted from the graphs because Juncaceae cover comprises less than 1% of total graminoid cover.





Figure 17: Average Cover of Graminoid Families





CCA groups 1 and 3 show no change in cover of total graminoids or of graminoid families (Figures 19 and 21). CCA group 2 shows an increase in total graminoid cover, which is due to Poaceae increases since Cyperaceae cover is unchanged (Figure 20). CCA group 4 (Figure 22) has an increase in Cyperaceae cover, but the effect on total graminoid cover is negligible since Poaceae cover is much more abundant in this environment.





Figure 20: Average Cover of Graminoid Families







The average cover of woody plants within the herb layer has declined in the complete data set, as well as in both the hardwood and pine subsets. (Figures 23-25). Cover of tree seedlings dropped dramatically from 2000 to 2010, while herb layer cover of shrub species declined both both between 1977 and 2000 and between 2000 and 2010. Cover from woody vines, stayed largely constant.



Figure 23: Average Herb Layer Cover of Native Woody Species Calculated Over Complete Data Set

Figure 24: Average Herb Layer Cover of Native Woody Species Calculated Over Hardwood Plots




Figure 25: Average Herb Layer Cover of Native Woody Species Calculated Over Pine Plots

All four environmental categories show a decline in herb layer cover of woody species (Figures 26-29). All have a decline in herb layer cover of shrubs, while all but type 4 show a decline in tree seedlings. Decline in tree seedlings occurs between 2000 and 2010, while decline in herb layer cover of shrubs happens between 1977 and 2000 in the type 1 group, over both periods in groups 2 and 3, and between 2000 and 2010 in the type 4 group. Herb layer cover from vines varies the most strongly with environment: cover from vines stays constant in group 1, increases in group 2, and declines in groups 3 and 4.



Figure 26: Average Herb Layer Cover of Native Woody Species Calculated Over CCA Type 1 Plots

Figure 27: Average Herb Layer Cover of Native Woody Species Calculated Over CCA Type 2 Plots





Figure 28: Average Herb Layer Cover of Native Woody Species Calculated Over CCA Type 3 Plots

Figure 29: Average Herb Layer Cover of Native Woody Species Calculated Over CCA Type 4 Plots



Although the herb layer cover of native vines has stayed constant, the total herb layer cover of vines has declined, mainly due to declines in the invasive species *Lonicera japonica* (Figure 30). At first glance, the decline of *L. japonica* appears to drive the decline of vines in the herb layer of CCA groups 3 and 4, in which it previously made up the majority of the herb layer vine cover (Figures 33-34). In fact, however, all vine families in those groups have shown declines. Although the drier, more acidic CCA groups also show declines in *L. japonica*, the total cover of vine species in the herb layer remains nearly constant (Figures 31-32). This is partly because *L. japonica* was never as prevalent in these plots, so its decline has had less impact, and partly because most other vine families have stayed constant or increased. (The exception is *Toxicodendron radicans*, which has declined in CCA group 2, though it has remained constant in group 1.)

Figure 30: Average Herb Layer Cover of Vine Families Calculated Over Complete Data Set













Figure 33: Average Herb Layer Cover of Vine Families





Over the whole data set, the decline in herb layer cover of shrubs appears to be due primarily to decline in Adoxaceae cover, since this has shown the largest change (Figure 35). Ericaceae cover has remained constant, while Rosaceae cover has declined some, but not as dramatically as Adoxaceae. Differences among environmental categories are slight. CCA group 1 does not show a decline in woody Rosaceae cover (Figure 36) and also has a much higher cover of Ericaceae than the other groups, which is consistent with the ability of Ericaceae species to thrive in more acidic soils. Groups 2 and 4 follow the same trends as the complete data set (Figures 37 and 39), while group 3 shows a decline in all shrub families, including Ericaceae (Figure 38).



Figure 35: Average Herb Layer Cover of Shrub Families

Figure 36: Average Herb Layer Cover of Shrub Families Calculated Over CCA Type 1 Plots





Figure 37: Average Herb Layer Cover of Shrub Families Calculated Over CCA Type 2 Plots

Figure 38: Average Herb Layer Cover of Shrub Families Calculated Over CCA Type 3 Plots





Figure 39: Average Herb Layer Cover of Shrub Families Calculated Over CCA Type 4 Plots

Tree seedling cover has declined over the complete data set and over most subsets. Learning which families contribute most to the decline can improve understanding of the causal factors and the role of environmental variation. Over the complete data set, almost all tree families show decline in herb layer cover. The exceptions are Fagaceae, which is about the same in 1977 and 2010, and Aquifoliaceae, which shows an increase (Figure 40). The lack of change in Fagaceae is surprising since oak leaves are a preferred food of white-tailed deer. It does seem to indicate, however, that the mature oaks are producing abundant seed. The temporary increase in Fagaceae that appears in 2000 is likely due to release resulting from canopy gaps formed by Hurricane Fran in 1996. The declines in tree seedling cover occur mainly between 2000 and 2010, perhaps indicating large-scale environmental change. The same pattern of decline in all families except Fagaceae and Aquifoliaceae occurs in CCA groups 1 through 3 (Figures 41-43), with the decline again occurring between 2000 and 2010. Group 4, the wettest and highest-nutrient group, does not show declines in tree seedling cover except in the Cornaceae (Figure 44). This group, however, is also the smallest in the data set, which would tend to make changes more difficult to detect.



Figure 40: Average Herb Layer Cover of Tree Families



Figure 41: Average Herb Layer Cover of Tree Families Calculated Over CCA Type 1 Plots







Figure 43: Average Herb Layer Cover of Tree Families Calculated Over CCA Type 3 Plots



The overall data set and most subsets show a decline in herb layer cover of both

maples and beeches as a group and oaks and hickories as a group (Figure 45). The maple/beech decline, however, is generally larger than the oak/hickory decline, resulting in a larger percent cover from oaks and hickories than maples and beeches in 2010. The exceptions to this trend are that CCA groups 3 and 4 show no change in oak/hickory seedling cover (Figure 47). CCA group 4, also shows no change in maple/beech cover in the herb layer (Figure 46).

Figure 45: Average Herb Layer Cover of Maple/Beech and Oak/Hickory Seedlings Calculated Over Complete Data Set





Figure 46: Average Herb Layer Cover of Maple and Beech Seedlings Displayed by CCA Environmental Category

Figure 47: Average Herb Layer Cover of Oak and Hickory Seedlings Displayed by CCA Environmental Category



Discussion

The analysis of Taverna et. al. (2005) revealed a decline in herb species richness and an increase in woody seedling species richness between 1977 and 2000. Those findings are slightly different from, though not inconsistent with, the pattern of cover change found in this analysis -- between 1977 and 2000 cover of both herbs and woody seedlings stayed relatively constant, but there was a significant increase specifically in tree seedling cover. Between 2000 and 2010, however, herb layer cover of woody species declined dramatically. Maple and beech seedlings suffered substantially more loss of cover than oak and hickory seedlings. Ericaceae cover was unchanged, while several other families, such as Pinaceae, Oleaceae, and Ulmaceae spiked in cover in 2000 but dropped below 1977 levels in 2010. Taverna pointed out that the increase in woody seedlings from 1977 to 2000 was evidence of successful reproduction, while the declines were apparently due to inability of the plants to survive as they got older. By 2010, then, reproductive success itself had declined for many woody species.

The herb layer trends also indicate a decline in herb layer cover due to loss of cover from forbs. Cover from ferns and graminoids, however, is unchanged over the data set as a whole. The decline in forb cover without a decline in ferns or graminoids may be due to deer herbivory. Rooney (2009) found greater cover of grasses and sedges outside of deer exclosure plots, which makes sense given that grasses are better able to survive herbivory than other herbs (Ferraro and Oesterheld 2002). Rooney (2009) points out that ferns are also relatively unpalatable to deer. Taverna et al. (2005) also suggest deer herbivory as a likely explanation for loss of herb species from 1977 to 2010.

42

The patterns of change that are common to the whole data set and to all the subsets also seem to indicate deer browse effects, combined with successional changes and some possibility of disease (dogwood Anthracnose) also playing a role in the decline of Cornaceae herb layer cover. The decline in cover of woody species, particularly shrubs, is consistent with deer browse, as deer forage preferentially on many woody species, and shrubs and saplings are within the height range that a deer can reach while browsing. Waller and Alverson (1997) reports that deer can have profound effects on tree and shrub abundance. The decline of these species in the herb layer may be due to deer eating the seedlings directly, or it may be a result of herbivory on the established plants, reducing their reproductive capacity. Lamiaceae cover did not change significantly in any of the data subsets, possibly because the pungent oils of plants in the mint family are unpalatable to deer. The dramatic decline in Caprifoliaceae is probably also a result of herbivory since deer will preferentially forage on Lonicera japonica (Sotala and Kirkpatrick 1973). The herb layer cover of Smilacaceae did not change significantly in any of the data subsets, despite *Smilax* being known as a preferred forage species for deer Fabaceae herb cover also declined in the data set as a whole and in all subsets except CCA group 1, which is also consistent with deer browse since legume plants are particularly rich in nitrogen. The cover from Adoxaceae species has also declined dramatically, and deer browse seems the most likely explanation since *Viburnum* species are shade tolerant; successional change would not affect them. Regardless of the 1977 Adoxaceae cover, the 2010 cover in each data subset was about 0.5%. The areas with the highest cover, therefore, experienced the most decline, similar to the pattern of decline McDonald et al. (2002) observed with oaks.

Ericaceae cover has also not changed significantly in any of the data sets from 1977 to 2010. Perhaps their protective allelochemicals provide some defense against herbivory, as found in studies of moose browsing in Canada (Thompson 1989).. Herb layer cover of Pinaceae species, on the other hand, has declined in all plots, possibly because of successional change. The youngest successional pine plots were 30-50 years old in 1977, making them 63-83 years old by 2010. Tthis would put them all past the peak of maximum pine growth and into the period of at least starting to be overtaken by hardwoods, an effect that would be seen first in the herb layer (Peet and Christensen 1987). In addition, early successional pines are shade-intolerant (Cain et al. 2001) so the establishment of broad-leaved trees would make it more difficult for pine seedlings to survive.

Interpretation of the differences in plant group changes between data sets is difficult and must be done cautiously. Smaller data sets mean more risk of trying to explain a variation that is purely coincidental on one hand or of failing to detect a change because of noise in the data on the other hand. The best I can do here is suggest possible hypotheses for some changes and encourage further research on Piedmont forests with larger numbers of plots representing each data subset.

The pine plots, but not the hardwood plots, showed an average decline in herb layer cover of oak and hickory seedlings. One possible explanation is that the hardwood plots, with a greater number of large, canopy-height oaks and hickories, have more consistent seed production from year to year, such that seedlings remain relatively common in the herb layer, even if they do not establish as saplings.

Among the CCA environmental types, significant decline in cover of forbs was not

44

found in group 1 and group 4, but only in the middle groups. The type 1 group includes the driest, most acidic environments. The cover from forbs is lowest in this group out of all the CCA groups, but the forbs that are there might be those that are able to tolerate these harsher conditions and are resistant to herbivory, rather like Grime's stress-tolerant plants (Grime 1977, 2002). The type 4 group, on the other hand, consists of moist plots, close to water and also high in nutrients. The closeness to water gives these sites continual access to propagules, and the richer soil leads to higher herb cover than in the other CCA groups. With high-nutrient soil and a constant influx of new competitors, loss of cover may be less likely, even if the species composition changes. The cover of graminoids, meanwhile, stayed nearly constant among all CCA categories, consistent with the observations of Kirkpatrick (2004) that perennial graminoids in Australia showed no variation in abundance based on moisture.

It is also important, however, to be aware of the limitations of sample size, particularly in CCA group 4, which consists of only five plots. Little change was detected in herb layer cover of tree species in this group, and several families did not show the declines found in other subsets of the data. With such a small sample, however, the standard error is so large that it is hard to tell whether the change is truly absent or simply undetectable because of noise in the data. Further studies with more plots from this kind of environment would be helpful to truly discover what is and is not changing.

CHANGE IN INVASIVE SPECIES COVER

Methods

Invasive species were identified according to the list published by the North Carolina Native Plant Society (<u>http://www.ncwildflower.org/invasives/list.htm</u>). Invasive taxa present in at least one plot during at least one sampling period were: *Ailanthus altissima, Albizia julibrissin, Broussonetia papyrifera, Cirsium vulgare, Elaeagnus sp. (E. pungens* and *E. umbelleta* considered together), *Glechoma hederacea, Hedera helix, Ligustrum japonicum, Ligustrum sinense, Lonicera japonica, Mahonia bealei, Microstegium vimineum, Nandina domestica, Paulownia tomentosa, Stellaria media, Wisteria sinensis, and Youngia japonica.*

For each invasive species, average herb-layer cover was calculated at each time point (1977, 2000, and 2010), and standard error was used to evaluate significance of differences between one year and another; if the difference between the two means was greater than the sum of their standard errors, the difference was likely to be real and not a result of measurement error. One plot was dropped from the *Microstegium vimineum* average because of probable flood damage in 2000. The invasive species with the highest average cover were *Lonicera japonica* and *Microstegium vimineum*. In order to evaluate the overall change in emerging invasive species, average total invasive herb layer cover was calculated with *L. japonica* and *M vimineum* excluded. In addition to the tendency of their larger cover values to drive the average invasive cover value when they were included, *L. japonica* also exhibited a pattern of change unlike those of other invasive species in that its average cover

dramatically declined between each sampling year, while other species increased.

Results

Over the data set as a whole, *Lonicera japonica* showed a dramatic decline (Figure 48), while *Microstegium vimineum* increased significantly: the difference between the average cover in 1977 and in 2010 was greater than the sum of the standard error of the mean for those two years. (Figure 49). Consideration of all other invasives together shows a significant increase in herb layer invasive cover between 1977 and 2000, continuing into 2010 (Figure 50). Individual species that show significant increase from their 1977 levels are *Glechoma hederacea*, which becomes significant in the complete data set in 2000, and *Ailanthus altissima, Elaeagnus sp*, and *Nandina domestica*, which increase significantly beyond 1977 levels in 2010 (Table 2).



Figure 49: Average Cover of Microstegium vimineum Displayed by Plot Canopy Composition





Figure 50: Average Herb Layer Cover of Other Invasive Species Displayed by Plot Canopy Composition

Table 2: Direction of Change in average herb layer invasive cover by species and data set					
Species	All Plots	Hardwood Plots	Pine Plots		
Ailanthus altissima	Positive 2000-2010	Positive 2000-2010	Not present		
Albizia julibrissin	Not significant	Not significant	Positive 2000-2010		
Elaeagnus sp.	Positive 2000-2010	Positive 1977-2010	Positive 1977-2000, 2000-2010		
Glechoma hederacea	Positive 1977-2000	Positive 1977-2000	Not significant		
Nandina domestica	Positive 2000-2010	Not significant	Positive 2000-2010		

The pine and hardwood data sets both show increases in *Elaeagnus sp*, but differ in which other invasive species have increased. The pine plots show increases in *A. julibrissin* and *N. domestica*, whereas the hardwood plots had increases in *G. hederacea* and in *A. altissima*, which is not present in any of the pine plots. (See Table 2).

The environmental gradient categories were formed using CCA values such that type 1 tends to be dry, acidic, and nutrient-poor, whereas type 4 is close to water and has a higher pH and higher mineral cation concentration. All four types showed the same pattern of decline in *L. japonica* that was found in the data set as a whole (Figure 51). *M. vimineum* was not present in the type 1 subset in 1977 or 2010, though it did appear in two plots in 2000 (Figure 52). In the type 2 and 3 environments, *M. vimineum* reached significant cover levels in 2000. The cover values presented for *M. vimineum* in category 4 are artificially low because the plot that was discarded from the average for each year due to flooding in 2000 was also the plot with the highest *M. vimineum* cover. That single plot would raise the category average to at least 2% in all years.



Figure 51: Average Herb Layer Cover of Lonicera japonica Displayed by CCA Environmental Category

Figure 52: Average Cover of Microstegium vimineum Displayed by CCA Environmental Category



No other invasives were found in the type 1 plots, so this subset shows a pattern of decline in invasive cover, driven by the decline in *L. japonica*. Groups 2 and 3 show an increase in herb layer cover of other invasive species from 1977 to 2000 (Figure 53). The cover increase in the type 2 group is primarily due to the establishment of *Elaeagnus* in a few plots. The pattern of invasive species cover change in the type 3 group is complex. The main invasive species in 2010 are *Albizia julibrissin, Elaeagnus sp, and Glechoma hederacea* (Table 3). These species, however, do not become significant in 2000, even though the total invasive cover for 2000 is significant. Instead, *Paulonia tomentosa, Cirsium vulgaris,* and *Ligustrum sinense* appear in a handful of plots in 2000 but decline in 2010 as other invasive species increase. The type 4 subset does not shows an increase in invasive cover, but the fact that only five plots fit into the category means that the variation among them produces a particularly high standard error. These plots do, however, show a significant increase in *M. bealei* and *G. hederacea* (Table 3).



Figure 53: Average Herb Layer Cover of Other Invasive Species Displayed by CCA Environmental Category

Table 3: Direction of change in average herb layer invasive coverby species and CCA environmental category						
Species	Group 1	Group 2	Group 3	Group 4		
Ailanthus altissima	Not present	Not significant	Not significant	Not present		
Albizia julibrissin	Not present	Not significant	Positive 2000- 2010	Not present		
Elaeagnus sp.	Not present	Positive 1977-2000	Increase 1977- 2010	Not significant		
Glechoma hederacea	Not present	Not present	Positive 2000- 2010	Positive 1977-2000		
Ligustrum sinense	Not present	Not significant	Not significant	Not significant		
Mahonia bealei	Not present	Not present	Not present	Positive 1977-2010		

Discussion

The complex patterns of invasive species change in the Duke Forest lend themselves to a variety of possible explanations. The decline in *Lonicera japonica* is consistent across all variations in plot composition and plot environment, suggesting that the reason for the decline is common to the whole forest. A likely explanation is deer browse, since *L. japonica* is a preferred forage source for white-tailed deer (Sotala and Kirkpatrick 1973). This is also supported by the fact that *Toxicodendron radicans*, another deer forage source (Sotala and Kirkpatrick, 1973), has shown a similar pattern of decline in the Duke Forest.

Although *Microstegium vimineum* has increased in both the pine and hardwood subset, that increase is confined to the middle two environmental subsets.-It may be that the

M. vimineum population has saturated the wetter regions but is only beginning to encroach on some of the drier areas. Since it is an annual, and since these encroaching populations are currently small, it may be possible to restrict its spread by using volunteers to remove as many plants as possible before they set seed for the year.

Elaeagnus sp. may become a major concern in the future, as it already is in Piedmont and Coastal Plain riparian areas (Matthews et al. 2011, Faestal 2012). *Elaeagnus* is the next most abundant invasive in the herb layer, after *L. japonica* and *M. vimineum*. As with *M. vimineum*, its herb layer cover has increased significantly since 1977 in the middle two environmental subsets, though the largest average cover values are in the CCA type 4 subset. It may be that *Elaeagnus* is more established in the moist areas while newly encroaching into some of the drier sites. Particularly noteworthy is the fact that *Elaeagnus* was not reported at all in the pine subset or in the CCA type 2 subset (the second driest / second most acidic overall) in 1977; it is now present in about 18% of pine plots and 13% of type 2 plots, up from about 8% and 5% when it appeared in 2000. *Elaeagnus*, is likely to be a future cause for concern in the Duke Forest.

Leaving out *L. japonica* and *M. vimineum* to examine the change in herb layer cover of the remaining invasives shows a significant increase from 1977 to 2010, both within the data set as a whole and within both the hardwood and pine subsets, as well the two environmental subsets with middle levels of moisture and pH. The cover from other invasives is already higher in the type 4 group, with its high moisture and pH, than in the other environmental categories. The trend seems to be a pattern of increased encroachment of invasive species in all but the driest sites.

OAK-HICKORY VS. MAPLE-BEECH CHANGES IN SAPLING BASAL AREA

Methods

Previous work on eastern North American oak-hickory forests has indicated a decline in regeneration of oak and hickory trees and an increase in mesophytic species like maples and beeches (Abrams and Down 1990, Abrams 1998; Nowacki and Abrams 2008). In order to determine whether that pattern applied in the Duke Forest, I compared change in basal area of oak, hickory, maple, and beech saplings._

For each plot-year combination, I calculated the basal area per hectare for all maple and beech saplings up to the 2.5-5 cm dbh size class and for all oak and hickory saplings of the same size class. In using basal area rather than stem density, I hoped to account for changes in size as the saplings grew over the 33-year study period. As saplings grow, some thinning is to be expected, which could appear as a steep decline in stem density, but not show up as a significant drop in basal area since the remaining saplings will grow larger when competitors are eliminated. I calculated the ratio of oak-hickory basal area to maplebeech basal area and examined the change in ratio between each sampling period (1977-2000, 2000-2010, and 1977-2010). In addition to finding the total change in the ratio, I also divided by the number of years in each sampling period to find the average change in ratio per year. For most plots, the oak-hickory sapling basal area declined relative to the maplebeech basal area between 1977 and 2010, but there were twelve plots in which it increased. I explored the oak-hickory to maple-beech ratio change by graphing change vs. plot variables for each plot and by comparing group averages of data subset by oak-hickory to maple-beech ratio as well as plot composition and CCA environmental category. Possible factors considered for affecting the change in the oak-hickory to maple-beech ratio were environmental conditions (which were proxied with pH and distance to water), increased light availability due to hurricane damage (tested using total basal area change of all tree species and size categories as the independent variable), successional state in pine communities (proxied by total pine basal area change in those plots), and the role of oaks and hickories compared to maples and beeches in driving the change in ratio (tested by comparing the percent changes in basal area within each group).

Results

Although my data set from 1977 and 2010 contained 72 plots, 2 of these were not resampled in 2000 and consequently could not be used for year-to-year comparisons. Of the 70 plots analyzed, 4 showed no significant change in the ratio of oak-hickory to maple-beech sapling basal area per hectare. Of the rest, 54 showed a decrease in oak-hickory sapling basal area relative to maple-beech, and 12 showed an increase. In most cases (36 of the oak-hickory decline plots and 8 of the oak-hickory increase plots), the average annual rate of change in the ratio was higher from 1977 to 2000 than from 2000 to 2010. The average change in ratio is 0.008 per year from 1977 to 2010. The positive number means that on

average, oak and hickory sapling basal area increased over maple and beech sapling basal area between 1977 and 2010. As noted above, however, this average is skewed by a few plots with a large increase in the ratio; in most cases the ratio decreased, indicating that oak and hickory sapling basal area was declining compared to maple and beech sapling basal area.

The group of twelve plots with the increase in the oak-hickory to maple-beech sapling basal area ratio does not differ significantly from the full set of plots in terms of pH, distance from water, or total tree basal area change. Eight of the twelve plots with a ratio increase were successional pine plots, and that group of eight does not differ significantly from the group of all pine plots in terms of total pine basal area change.

Of the plots with an increase in the oak-hickory to maple-beech ratio (OH/MB), 8.3 % were in CCA environmental category 1, 75.0% in category 2, and 16.7% in category 3. For the set of all plots, 17.3% were in category 1, 51.4% in category 2, 15.7% in category 3, and 7.1% in category 4. This means that the distribution of plots with OH/MB increase is somewhat skewed towards drier, more acidic plots, though no direct correlation was found between OH/MB change and pH or distance from water. No variation was found in the patterns of difference between plots with OH/MB increase and decrease in different CCA categories.

The plots with an increase in the OH/MB ratio consisted of 66.7% successional pine plots and 33.3% uneven-aged hardwood plots. Among the plots that had a decrease or no change in OH/MB ratio, 53.4% were successional pine plots and 46.6% were uneven-aged hardwood plots. Both the group of hardwood plots with an OH/MB increase and that without showed an average decrease in oak-hickory sapling basal area, with no significant variation

between the two groups (Figure 54). The maple-beech saplings, on the other hand, showed a large average increase in basal area in the plots with OH/MB decrease and a moderate decrease in basal area in the plots with OH/MB increase. This seems to indicate that the maple-beech sapling basal area is driving the OH/MB ratio in the hardwood plots. Oak-hickory sapling basal area is declining overall, but in some areas maple-beech sapling basal area had declined even more, while in other areas it has increased, affecting the OH/MB ratio accordingly. The groups of pine plots, on the other hand, show a large average increase in oak-hickory sapling basal area in the plots with OH/MB increase, and a moderate average decrease in oak-hickory sapling basal area in the plots with OH/MB increase (Figure 55). The average maple-beech sapling basal area, meanwhile, shows a moderate decrease in the plots with OH/MB increase, and no significant change in the plots with OH/MB increase or decrease or decrease in oak-hickory sapling basal area.





Figure 55: Average Percent Change in Sapling Basal Area per Hectare in Pine Plots Comparing Plots by Change in Ratio of Oak-Hickory to Maple-Beech Sapling Basal Area



Discussion

Although a few plots show an increase in the ratio of oak-hickory sapling basal area to that of maples and beeches, in most plots, oak-hickory sapling basal area has decreased relative to maple-beech. This may be a precursor to change in the canopy structure if oak and hickory trees are not regenerated at a rate equal to their loss or if maple and beech trees replace them in the canopy. Nowacki and Abrams (2008) argue that fire suppression in eastern North American forests is leading to mesophication and the replacement of oaks and hickories with shade tolerant maples and beeches. Abrams (1998) describes red maple as a "super-generalist," able to compete effectively in varied conditions. Fire tolerance is one of the few areas in which red maple is not able to compete at least moderately well. The decline in oaks and hickories relative to maples and beeches supports the hypothesis that the forest is becoming more mesic, perhaps due to fire suppression. Deer herbivory may also play a role, as white-tailed deer forage preferentially on oak (Waller and Alverson1997, Wakeland and Swihart, 2009).

In hardwood plots, oak and hickory sapling basal area has declined about the same percentage in plots with oak-hickory to maple-beech (OH/MB) ratio increase and plots where the OH/MB ratio has decreased or is unchanged. Oak and hickory are relatively shadeintolerant (Robison and McCarthy 1999, McDonald et al. 2002), which might partially explain their decline in hardwood plots. Maple-beech sapling basal area, on the other hand, has increased where the OH/MB ratio has decreased, and vice versa. This indicates that increase in maple-beech competitiveness is likely the cause of decrease in the OH/MB ratio. McDonald et al. (2002) found larger increases in red maple in Duke Forest plots with higher soil moisture. *Acer rubrum* is known to be a superior competitor on mesic soils in the absence of fire. Furthermore, it has a tendency, once well-established, to alter soil chemistry to its own benefit and to the detriment of historical canopy dominants like oaks and hickories (Nowacki and Abrams 2008). Fire suppression, then, may be partially responsible for the increase in maple-beech sapling basal area in hardwood plots with a decrease in OH/MB ratio. Although fire has been suppressed in the Duke Forest for many decades (ca 1920 for most of the region), it may have taken time for mesic species such as maples and beeches to become well-established and produce enough seed rain to outcompete the dominant oaks and hickories. In addition,, deer browse may be responsible for decline in oak and hickory sapling basal area for hardwood plots in general.

In successional pine plots, the difference between plots with OH/MB increase and OH/MB decrease is pronounced for both maple-beech and oak-hickory sapling basal area. Maple-beech sapling basal area has declined in the pine plots with an increase in OH/MB ratio, but is not significantly changed in those plots with OH/MB decrease. In addition, oak-hickory sapling basal area is increased with OH/MB increase, and vice versa. Therefore, the plots with an increase in OH/MB ratio are affected by both the increase in oak-hickory basal area and the decrease in maple-beech basal area, but the plots with a decrease in OH/MB ratio are affected only by the decrease in oak-hickory basal area. This is consistent with McDonald et al.'s (2002) observation that oak abundance increased in successional pine plots, with declines in hardwood plots. The pine plots with an increase in OH/MB ratio have a slightly higher average nutrient concentration (measured as calcium ion meq) than those with an OH/MB ratio decrease but no other appreciable environmental differences. It seems

unlikely that the nutrient concentration alone would have such an effect, especially considering that both increases and decreases in OH/MB ratio are also seen in hardwood plots with a much higher soil nutrient content. Further study will be needed to completely resolve the causes of OH/MB ratio change in successional pine forests.

Total basal area change was plotted against change in OH/MB ratio in order to examine the role of increased light availability due to hurricane damage. No correlation between total basal area change and oak-hickory to maple-beech ratio was found, which was unexpected, considering past work done on canopy gaps. Other researchers have found correlations between canopy gaps and herb layer diversity (Schumann et al. 2003, Taverna et al. 2005) and woody species regeneration (Clinton et al. 1994, Holladay et al. 2006), so it was expected that basal area loss would be correlated with increased seedling cover. It was also hypothesized that the additional light availability caused by canopy gaps would allow for greater regeneration of oaks and hickories, since they are less shade-tolerant than maples (Robison and McCarthy 1999, McDonald et al. 2002), but no relationship was found between total basal area change and change in sapling basal area of oaks and hickories compared to maples and beeches. Other studies have mostly dealt with changes in vegetation right at the site of measured canopy gaps compared to non-gap areas, while this study looked at the degree of basal area loss in each plot, with the assumption that basal area loss was a good proxy for canopy cover loss. Perhaps the effect of gaps was diluted by measuring change over the whole plot rather than just directly in gaps, or perhaps basal area loss was not as effective a proxy for canopy cover loss as expected. It is also possible that any canopy gap effects were short-lived: Cain and Shelton (2001) found an increase in herb cover one year
after the creation of artificial gaps, but a decrease as time passed, up to 17 years, as the canopy closed again. Since Hurricane Fran was fourteen years ago, it is possible that any temporary changes have disappeared, though one might expect a legacy in the form of an increase in small saplings. It is also possible that there was no significant effect. Collins and Pickett (1988) found no clear effect from artificial gap creation, so it is also possible that there simply was no significant effect.

SPECIES RICHNESS

Methods

Change in herb-layer species richness was compared between the 1977-2000 period and the 2000-2010 period at the 1000 square meter, 25 square meter, and 1 square meter levels. In order to capture the most accurate number of species despite difficulties in identification, the raw data from each year were used. Specifically, species listed as unknown were still counted as distinct from known species in a given plot. Average richness at each level was compared across years, both for the data set as a whole and for subsets based on CCA environmental category and hardwood or pine composition.

Results

Average species richness was calculated at the 1000-square-meter, 25-square-meter, and 1-square meter level for each sampling year over all plots, over each CCA environmental category, and over hardwood and pine plots. For the most part, species richness at the 1000-square meter level stayed nearly constant over all sampling years. Over the full data set, there was a small but significant increase between 1977 and 2000, but by 2010 the average richness had dropped to a level between the 1977 and 2000 levels, indicating a lack of long-term change (Figure 56). Average species richness was higher in hardwood plots than in pine

plots in 1977 and 2000, but not significantly so in 2010. Species richness did not change significantly in the hardwood plots, but it did increase significantly in pine plots from 1977 to 2000 and in 2010 remained higher than the 1977 level. Species richness rises consistently with CCA category, tracking pH, nutrient content, and closeness to water. Richness is unchanged over each CCA category between 1977 and 2010. In 2010, the species richness is not significantly different between the two driest and most acidic CCA categories.



Figure 56: Average Species Richness at 1000-Square-Meter Scale

The 25-square-meter scale showed at least a modest decline in species richness from 2000 to 2010 for all subsets of the dataset. There was a significant decline for the complete dataset (Figure 57). The significant decline was also present in the pine subset but not in the hardwood subset. The hardwood plots had a higher 25-square-meter richness than the pine plots in all years. Species richness declined significantly in the two driest and most acidic CCA categories, but not in the other two. Richness consistently rose along the CCA gradient, tracking moisture and nutrient content.



Figure 57: Average Species Richness at 25-Square-Meter Scale Displayed by Plot Canopy Composition and CCA Environmental Category

The 1-square-meter scale (Figure 58) shows an increase in species richness between 1977 and 2000, followed by a drop below 1977 levels between 2000 and 2010. This pattern occurs both in the complete dataset and in the pine and hardwood datasets separately, as well as in CCA group 3. CCA groups 1 and 2 show a decline in richness between 2000 and 2010 but no change from 1977 to 2000, and CCA group 4 shows an increase in richness between 1977 and 2000, but no change between 2000 and 2010. As at the 1-square-meter scale, the species richness is higher in the hardwood group than in the pine group and increases with CCA category from drier and more acidic groups to more moist and less acidic groups.



Figure 58: Average Species Richness at the 1-Square-Meter Scale

Discussion

Although cover declined for forbs and woody species from 1977 to 2010, the average total species richness per plot stayed relatively constant. The average richness per plot was highest in the CCA category 4 subset and lowest in the CCA category 1 subset, consistent with the observation of Peet and Christensen (1980) that species richness increased with pH in the Duke Forest_a Although Peet (1988, 1992) observed that species richness in successional pine forests was not dependent on age, the hardwood plots did have higher richness than the pine plots until 2010, and species richness increased over time for the pine plots. Perhaps the transition from pine dominant to hardwood dominant brings in additional species. Since even the youngest pine plots were over 60 years old by 2010, they should all have started being overtaken by hardwoods (Christensen and Peet 1981)

The species richness at the 25-square-meter level did decline between 2000 and 2010,

both over the complete data set, and in the pine subset and the CCA type 2 subset, as well as declining between 1977 and 2010 in the CCA type 1 subset. This finding is consistent with the loss of herb layer cover reported earlier. Even though the number of species per plot has not changed appreciably, the decline in cover means that many species that have not disappeared have become more sparse, reducing their chance of being found in any given 1 m2 subplot area. The decline in richness at the 25-square-meter level but not the 1000-square-meter level is consistent with the findings of Schwartz (2007), which showed a greater loss of species over all plots at the 25-square-meter scale than at the 1000-square-meter scale. The decline in species richness occurs within those groups that are consistently lowest in species richness at each year: the pine group and the driest two CCA groups. These groups also have lower cover of both herb and woody species from 1977 on, which likely indicates that any given species is more sparsely distributed in those groups, and therefore more vulnerable to being lost.

The 1-square-meter scale shows an increase in species richness between 1977 and 2000 in both the pine and hardwood groups, as well as in the complete data set, followed by a drop below 1977 levels between 2000 and 2010. The two less acidic, more water and nutrient rich CCA categories also show an increase in species richness between 1977 and 2000; those are probably the plots causing the average increase in richness in the pine and hardwood groups. In CCA group 3, the species that have the largest number of subplot presence increases between 1977 and 2010 are *Carpinus caroliniana, Fraxinus sp, Acer floridanum, Acer rubrum*, and *Ostrya virginiana*. In CCA group 4, the highest subplot increases were in *Carpinus caroliniana, Acer floridanum, Carex sp, Euonymus americanus, Fraxinus sp,*

Liriodendron tulipifera, and *Ostrya virginiana*.. This is consistent with the pattern of increase in cover followed by greater decrease which occurs with the herb layer cover of some woody families, and also with the increase in woody species richness in the herb layer found by Taverna et al. (2005) between 1977 and 2000. The drop in species richness between 2000 and 2010 for both the pine and hardwood groups, as well as for all but the most moist CCA group, is consistent with the findings on larger scales. As the measurement scale gets smaller, the impact of reduced herb-layer cover on species richness becomes greater; it is simply more likely that removing a given percentage of the vegetation will entirely remove a species from a smaller area than from a larger one. If herb-layer cover continues to vanish at the same rate, declines in species richness will likely start to appear at the 1000-square-meter or larger scales.

SUCCESSION AND AVERAGE ANNUAL CHANGE

Methods

NMS ordinations using Bray-Curtis dissimilarity of herb-layer cover by species were conducted for successional pine plots from 1977, 2000, and 2010. All three sampling years were included in order to capture changes over time. The plots were ordinated together and also in groups based on the 1977 age classes of 50-70 years, 70-100 years, and over 100 years. Year-to-year vectors were produced by connecting the points for the 1977, 2000, and 2010 samples of each plot in the 2-D ordination graph. These year-to-year vectors were examined for the successional pine plots, both grouped together and subdivided by age to evaluate the similarity of patterns of change among plots. MRPP tests were used to determine whether groups based on sampling year, age class, or both formed groups that were statistically distinct.

The 1977 successional pine data with its range of age classes was also used in a space-for-time substitution to create a projection of species gain, loss, and change for 2000 and 2010. If a species was present in two consecutive age classes, the average cover of that species within each age class was used to calculate an estimated change in cover for that species as a given plot aged into the next class. For example, if a species has an average cover of 1% in the 50-year age class and 2% in the 70-year age class, it was projected that

each plot in the 50-year age class would double its cover of that particular species, provided the species was present to start with.

The probabilities of species gain were calculated for those species that were present in a lower percentage of plots for a given age class than for the next consecutive class. Species gain probability was calculated as: (% present in class 2 - % present in class 1)/(1 - % present in class 1). For example, a species that was present in 50% of the 70-year plots and 25% of the 50-year plots would have a 33.33 chance of being gained in a 50-year plot as it aged into the 70-year class, provided the species was not already present in a given plot. A series of random numbers between 0 and 1 was then generated, one number for each plot-species combination that had a chance of species gain, using the Research Randomizer generator at http://www.randomizer.org. Each random number was compared to the appropriate speciesage-class gain probability, and in cases where the random number was less than the species gain probability, the plot was projected to have gained that species as it passed into the next age class, with a starting cover value of the average for that species in the new age class. In the example above, a random number below 0.333 would mean that the species in question had been projected to be gained in that plot. Obviously, this does not mean that a plot with a given random number assigned to it is actually assumed to be more likely to gain a given species. Rather, the purpose is to produce a realistic estimate of possible combinations of composition change for the whole data set. For the purposes of this projection, species gain probability was calculated once as the plot moved to the next age class rather than as a function of annual rate of change.

Probability of species loss was calculated similarly, with a chance of loss for each

71

species that was present in a high percentage of plots for a given-age class rather than for the next consecutive class. Species loss probability was calculated as: (% present in class 1 - % present in class 2) / (% present in class 1). A species present in 50% of the 50-year plots but only 25% of the 70-year plots would have a 50% chance of being lost from any 50-year p lot in which it was present. As with species gain, a collection of random numbers was generated, one for each plot in which a species was present, repeating the procedure for each species, and if the number for a given species in a plot was less than the probability of loss for that species-age class combination, for example, less than 0.5 for the hypothetical species above, the species was projected to be lost from the plot and given a new cover class of 0. As with species gain, species loss probability was calculated once as the plot moved to the next age class.

To finish the projection for 2000, the average annual rate of change for each species in each age class was applied for three more years. This calculation was performed as a separate step because many of the age classes have a span of 20 years. A plot in the 50-70 year class in 1977 would therefore be in the 70-100 year class in 1997, so the 70-100 year annual rates of change would need to be applied to the last three years of the projection. (The plots that began in the 70-100 year class simply have the 70-100 year annual rate of change applied for the entire projection. This also means that the 70-100 year annual rate of change is actually used to project 33 years of change; there are no data available to create a projection starting with the over-100-year age class.) For the 2010 projection, the annual rates of change were simply applied to the 2000 projection for another 10 years. No changes in age class occurred during this time, so the same annual rate of change could be used as was applied for the previous three years. No further estimates of species gains and losses were produced because those estimates depend on a shift from one age class to the next; there are no data to indicate probability of species gain or loss within an age class. Once all calculations were completed, the values were used to populate a plot-by-species matrix with projected herb cover values for 2000 and 2010, based on the 1977 pine age class data. NMS ordinations using a Bray-Curtis dissimilarity matrix were then conducted using a matrix that contained the projections as well as the 1977 data and the actual 2000 and 2010 data. Two ordination diagrams were produced: one showing the 1977 values and the projected and actual 2010 values. In addition to visual inspection, MRPP tests were used to evaluate the differences between the projected and actual groups for both 2000 and 2010.

Average amount of change per year was then quantified by finding the Bray-Curtis dissimilarity between sampling periods for each plot. The dissimilarity was then divided by the number of years between sampling periods (i.e., the dissimilarity between a given plot in 1977 and the same plot in 2000 was divided by 23, and the dissimilarity between the plot in 2000 and in 2010 was divided by 10). For every plot, the average annual increase in dissimilarity was higher between 2000 and 2010 than between 1977 and 2000. In other words, the rate of change increased in the more recent sampling period for every plot.

Results

NMS ordination of the pine plot herb layers with year-to-year vectors shows a high degree of consistency in the vector directions (Figure 59). This indicates that the herb layers

of the pine plots have changed in similar ways since 1977. Furthermore, both the 1977 to 2000 interval and the 2000 to 2010 intervals are consistent, which means that change has been occurring in the same general pattern throughout the entire sampling interval.



Figure 59: NMS Ordination of Pine Plots by Herb Layer Cover, With Year-to-Year Vectors

Projections of the 2000 and 2010 herb layers based on the 1977 data for successional pine plots give results very different from the observed data (Figures 60-61). In ordinations of the 1977 data, the projected data from 2000 or 2010, and the observed data from 2000 or 2010, the overlap between the 1977 points and the projected points is much larger than the overlap between either of those and the observed points. The difference is most pronounced for the 2010 data, in which the observed points have essentially no overlap with the projected points.

Figure 60: NMS ordination of species herb-layer cover class for 1977 pine plots, observed 2000 pine plots, and projected 2000 pine plots. Lines connect 1977 points to projected and observed 2000 points.



Figure 61: NMS ordination of species herb-layer cover class for 1977 pine plots, observed 2010 pine plots, and projected 2010 pine plots. Lines connect 1977 points to projected and observed 2010 points.



MRPP tests show that the projected points do not form a distinct group from the 1977 points for either the 2000 or the 2010 projection (Table 4). The set of observed points, however, does form a distinct group in both the 2000 case and the 2010 case. The difference is more pronounced for the 2010 points.

Table 4: MRPP groupings based on observed and projected herb layer compositionof successional pine plots						
Ordination	Comparison	A (effect size)	p-value			
2000 projection	1977 vs. projected 2000	0.0030	0.148			
	1977 vs. observed 2000	0.037	<1.0E-8			
	Projected 2000 vs. observed 2000	0.038	<1.0E-8			
2010 projection	1977 vs. projected 2010	0.0039	0.090			
	1977 vs. observed 2010	0.057	<1.0E-8			
	Projected 2010 vs. observed 2010	0.077	<1.0E-8			

Average amount of change per year was quantified by finding the Bray-Curtis dissimilarity between sampling periods for each plot. The dissimilarity was then divided by the number of years between sampling periods (i.e., the dissimilarity between a given plot in 1977 and the same plot in 2000 was divided by 23, and the dissimilarity between the plot in 2000 and in 2010 was divided by 10). For every plot, the average annual increase in dissimilarity was higher between 2000 and 2010 than between 1977 and 2000. In other words, the rate of change increased in the more recent sampling period for every plot.

Graphing the average annual change in dissimilarity of herb layer composition for each plot between 2000 and 2010 against the average annual change between 1977 and 2000 shows that for all plots, the average annual change is larger between 2000 and 2010 than between 1977 and 2000 (Figure 62). Most of the herb layer cover losses between 2000 and 2010 have been woody seedlings, so their loss appears to be driving this increase in average annual change. Annual loss of self-similarity during the more recent sampling period ranges from about 1.62 times as much as between 1977 and 2000 to about 4.92 times as much. As shown (Figs. 62-64), the average amount of annual change does not appear to be correlated with environment, hardwood vs. pine composition, or pine successional age.



Change Per Year, 1977-2000



Figure 63: Average Annual Change 2000-2010 vs. 1977-2000 Displayed by Plot Canopy Composition



Figure 64: Average Annual Change for Pine Plots 2000-2010 vs. 1977-2000 Displayed by Plot Age in 1977

Discussion

The projection developed from the 1977 pine data provides some insight into how the pine plots may have changed in the absence of environmental factors that have been altered since 1977. It does, however, have some significant weaknesses. The projection was developed using a space-for-time substitution: plots in, for example, the 70-year age class were used as models for compositional change over time of plots in the 50-year age class.

The model took the 1977 composition of each plot as a starting point so that changes in cover value were calculated based on the cover that was already present. It did not, however, take site conditions into account when calculating probable rates of gain, loss, and change. Because the number of plots used for calculations was already small (3 in the 30-year class, 15 in each of the 50-year and 70-year classes, and 7 in the 100-year class), subdividing them further by site conditions ran the risk of subjecting the model to the chance unique characteristics of a single plot. The trade-off is that, since the model does not consider the effects of site conditions, the projections may tend towards predicting more homogeneity in vegetation composition than is actually warranted. A better projection could possibly be developed by using data from all successional pine plots sampled in 1977. The larger number of plots would allow for an attempt to predict separate trajectories based on site conditions as well as age class. Although comparison data would only be available for a subset of those plots (the ones resampled in 2000 and 2010), the additional starting data could provide a more nuanced projection better able to support or reject the findings presented here.

The data we do have suggest that non-successional changes are occurring in the pine plots and that these changes are larger than the successional changes that are presumably continuing. The point-to-point time vectors for the pine plots indicate the same general magnitude and direction of change, regardless of successional age class. Furthermore, the difference between the observed and projected composition in pine plots for 2010 is greater than the difference for 2000. Some of this discrepancy is obviously due to the fact that the 2010 data reflects another ten years of time to deviate from the projection, but the effect size for comparing 2010 projected to observed is just over twice the effect size for comparing 2000 projected to observed, despite the fact that the first sampling period is just over twice as long as the second In addition, Furthermore, the average annual amount of change in the herb layer is not correlated with pine stand age category. Rather, the rate of change in the herb layer has accelerated for all plots. The calculated average annual change between 2000 and 2010 is greater than that between 1977 and 2000 for every plot in the data set. Something must be happening to increase the rate of change so dramatically.

Species whose cover values are associated with the year vector on the NMS ordination of herb-layer cover include: Andropogon sp, Desmodium sp, Juniperus virginianus, Lespedeza sp, Ouercus phellos, and Euphorbia corrollata, All these species are negatively correlated with year, meaning that they have declined in herb-layer cover since 1977. When only plots from 1977 and 2000 are ordinated, the year has only a weak correlation with an ordination axis (r = 0.24 for axis 1.) The species most strongly correlated with axis 1 in a direct correlation are *Liquidambar styraciflua* and *Oxydendrum* arboreum. The species with the strongest inverse correlation with axis 1 are Symphotricum unudlatum, Viburnum rafinesqueanum, Viburnum rufidulum, Carex sp (red fibrous base subtype), Cheilanthes lanosa, Ruellia caroliniensis, and Endodeca serpentaria. These species likely had some of the largest gains and losses in the herb layer between 1977 and 2000, though it is hard to be sure since year is only weakly correlated with axis 1 and with cover value for these species. When only plots from 2000 and 2010 are ordinated, year has a strong correlation (r = -0.65) with axis 1. Several woody species are inversely correlated with the year vector: Juniperus virginiana, Quercus rubra, Nyssa sylvatica, Quercus phellos, Oxydendrum arboreum, Quercus stellata, Carya ovata, Quercus falacata, Acer rubrum, and

Prunus serotina. No herbaceous species are correlated with the year vector either positively or negatively, and no woody species are positively correlated with the year vector. Our picture, then, is of a decline in some herb and shrub cover between 1977 and 2000, as well as increases in cover from a few trees, followed by a dramatic decline in canopy tree seedling cover between 2000 and 2010. This pattern of woody seedling loss in consistent with the effect of deer herbivory.

Although Oswalt et al. (2007) and Flory and Clay (2009) found that Microstegium invasion inhibited the establishment of woody seedlings, in my data set the six plots with 2000-2010 increase in invasive cover 25% or more above average actually had less of a decline in canopy tree seedling cover than did the whole data set considered together (Figure 65). It seems unlikely, then, that increases in invasive cover are responsible for the rapid change in herb layer composition between 2000 and 2010. Since we know from other analyses that cover of forbs and woody species has declined in the herb layer, particularly since 2000, it is likely that deer browse is a major contributing factor in this accelerated change.



CONCLUSION

The changes in Duke Forest continue to call into question the idea of stable climax communities in eastern North American temperate forests, a concept challenged by Abrams (1998), Christensen and Peet (1984) and Taverna et al. (2005). Instead of settling into stability, Duke Forest has shown accelerating change in the herb layer composition since 1977. Succession can account for some of the change, but the clear difference between sampling years and the universal increase in rate of change indicates that forest-wide environmental factors are also playing a large role. Cover from forbs and woody species has declined in the herb layer. Deer herbivory has likely played a major role in these declines as many of the declining taxa are those preferentially foraged by deer (Sotala and Kirkpatrick 1973, Waller and Alverson 1997, Wakeland and Swihart 2009) and deer herbivory on other plant species tends to benefit graminoids (Rooney 2009), which have not declined. Oaks and hickories are decreasing in importance in the sapling layer, with maples and beeches taking their place, as predicted by Nowacki and Abrams (2008) for North American temperate forests under fire suppression. Deer browse may play a role here too, as oaks are a preferred source of forage. Finally, exotic species have increased in diversity and abundance; the longterm effect of these invasions is unknown, but exotic species are well known to threaten biodiversity outside their native habitats (Chorensky and Randall 2003). Preserving biodiversity within Duke Forest and maintaining the historical oak-hickory canopy will

present a challenge for forest management. At a minimum, forest managers will need to consider reduction of the deer population, increasing use of fire, and active removal of invasive woody species.

APPENDIX: FULL SPECIES LIST

Nomenclature follows Weakley 2011.

Taxon	Woody?	Growth- form	Tree category	Family
Acalypha sp.	Herb	Forb		Euphorbiaceae
Acer floridanum	Woody	Tree	Canopy	Sapindaceae
Acer rubrum	Woody	Tree	Canopy	Sapindaceae
Actaea racemosa	Herb	Forb		Ranunculaceae
Adiantum pedatum	Herb	Fern		Pteridaceae
Aesculus sylvatica	Woody	Tree	Understory	Sapindaceae
Ageritina altissima	Herb	Forb		Asteraceae
Agrimonia microcarpa	Herb	Forb		Rosaceae
Agrimonia pubescens	Herb	Forb		Rosaceae
Ailanthus altissima	Woody	Tree	Understory	Simaroubaceae
Albizia julibrissin	Woody	Tree	Understory	Fabaceae
Allium canadense	Herb	Forb		Alliaceae
Allium cernuum	Herb	Forb		Alliaceae
Allium sp.	Herb	Forb		Alliaceae
Alnus serrulata	Woody	Shrub	Understory	Betulaceae
Amelanchier arborea	Woody	Tree	Understory	Rosaceae
Amphacarpaea bracteata	Herb	Forb		Fabaceae
Amsonia ultramontane	Herb	Forb		Apocynaceae
Andropogon sp.	Herb	Graminoid		Poaceae
Anemone americana	Herb	Forb		Ranunculaceae
Anemonella	Herb	Forb		Ranunculaceae

thalictroides			
Anemone virginiana	Herb	Forb	Ranunculaceae
Angelica venenosa	Herb	Forb	Apiaceae
Antennaria plantaginifolia	Herb	Forb	Asteraceae
Apiaceae sp.	Herb	Forb	Apiaceae
Aplectrum hyemale	Herb	Forb	Orchidaceae
Apocynum cannabinum	Herb	Forb	Apocynaceae
Boechera canadensis	Herb	Forb	Brassicaceae
Arisaema dracontium	Herb	Forb	Araceae
Arisaema triphyllum	Herb	Forb	Araceae
Arnoglossum atriplicifolium	Herb	Forb	Asteraceae
Asclepias amplexicaulis	Herb	Forb	Apocynaceae
Ascelpias sp.	Herb	Forb	Apocynaceae
Asclepias tuberosa	Herb	Forb	Apocynaceae
Asclepias variegata	Herb	Forb	Apocynaceae
Asclepias verticillata	Herb	Forb	Apocynaceae
Asclepias viridiflora	Herb	Forb	Apocynaceae
Asimina parviflora	Woody	Shrub	Annonaceae
Asimina triloba	Woody	Shrub	Annonaceae
Asplenium platyneuron	Herb	Fern	Aspleniaceae
Asteraceae sp.	Herb	Forb	Asteraceae
Aster sp.	Herb	Forb	Asteraceae

Athyrium angustum	Herb	Fern		Dryopteridaceae
Aureolaria flava	Herb	Forb		Orobanchace
Aureolaria sp,	Herb	Forb		Orobanchace
Aureolaria virginica	Herb	Forb		Orobanchace
Baptisia sp.	Herb	Forb		Fabaceae
Betula nigra	Woody	Tree	Canopy	Betulaceae
Boehmeria cylindrica	Herb	Forb		Urticaceae
Boraginaceae sp.	Herb	Forb		Boraginaceae
Botrychium lanceolatum	Herb	Fern		Ophioglossaceae
Botrypus virginianus	Herb	Fern		Ophioglossaceae
Brachyelytrum erectum	Herb	Graminoid		Poaceae
Bromus pubescens	Herb	Graminoid		Poaceae
Broussonetia papyrifera	Woody	Tree	Understory	Moraceae
Campsis radicans	Woody	Vine		Bignoniaceae
Campanula rapunculoides	Herb	Forb		Campanulaceae
Carex cephalophora	Herb	Graminoid		Cyperaceae
Carex complanata	Herb	Graminoid		Cyperaceae
Carex digitalis	Herb	Graminoid		Cyperaceae
Carex laxiflora	Herb	Graminoid		Cyperaceae
Carex muhlenbergii	Herb	Graminoid		Cyperaceae
Carex nigromarginata	Herb	Graminoid		Cyperaceae
Carex oxylepis	Herb	Graminoid		Cyperaceae
Carex (red fibrous base) sp.	Herb	Graminoid		Cyperaceae

Carex rosea	Herb	Graminoid		Cyperaceae
Carex sp.	Herb	Graminoid		Cyperaceae
Carex styloflexa	Herb	Graminoid		Cyperaceae
Carex wildenowii	Herb	Graminoid		Cyperaceae
Carpinus caroliniana	Woody	Tree	Understory	Betulaceae
Carya alba	Woody	Tree	Canopy	Juglandaceae
Carya cordiformis	Woody	Tree	Canopy	Juglandaceae
Carya glabra (including C. ovalis)	Woody	Tree	Canopy	Juglandaceae
Carya ovata (including C. carolinae- septentrionalis)	Woody	Tree	Canopy	Juglandaceae
Carya pallida	Woody	Tree	Canopy	Juglandaceae
Castanea dentata	Woody	Tree	Understory	Fagaceae
Castanea pumila	Woody	Shrub		Fagaceae
Ceanothus americanus	Herb	Shrub		Rhamnaceae
Celtis laevigata	Woody	Tree	Canopy	Cannabaceae
Celtis occidentalis	Woody	Tree	Understory	Cannabaceae
Centrosema virginianum	Herb	Forb	Canopy	Fabaceae
Cercis canadensis	Woody	Tree	Understory	Fabaceae
Chamaecrista fasiculata	Herb	Forb		Fabaceae
Chamaelirium luteum	Herb	Forb		Melanthiaceae
Chasmanthium latifolium	Herb	Graminoid		Poaceae
Chasmanthium laxum	Herb	Graminoid		Poaceae
Cheilanthes lanosa	Herb	Fern		Pteridaceae
Chimaphila	Woody	Subshrub		Ericaceae

maculata				
Chimaphila umbellata	Woody	Subshrub		Ericaceae
Chionanthus virginicus	Woody	Shrub		Oleaceae
Chrysopsis mariana	Herb	Forb		Asteraceae
Chrysogonum virginianum	Herb	Forb		Asteraceae
Circaea lutetiana	Herb	Forb		Onagraceae
Cirsium vulgare	Herb	Forb		Asteraceae
Clematis viorna	Herb	Forb		Ranunculaceae
Clematis virginiana	Herb	Forb		Ranunculaceae
Clitoria mariana	Herb	Forb		Fabaceae
Commelina communis	Herb	Forb		Commelidaceae
Conopholis americana	Herb	Forb		Orobanchaceae
Conyza canadensis	Herb	Forb		Asteraceae
Corallorhiza odontorhiza	Herb	Forb		Orchidaceae
Coreopsis major	Herb	Forb		Asteraceae
Coreopsis verticillata	Herb	Forb		Asteraceae
Cornus amomum	Woody	Shrub		Cornaceae
Cornus florida	Woody	Tree	Understory	Cornaceae
Cornus foemina	Woody	Shrub		Cornaceae
Corylus americana	Woody	Shrub		Betulaceae
Crataegus flava	Woody	Tree	Understory	Rosaceae
Crataegus marshallii	Woody	Tree	Understory	Rosaceae
Crataegus sp.	Woody	Tree	Understory	Rosaceae
Crataegus uniflora	Woody	Tree	Understory	Rosaceae

Cryptotaenia canadensis	Herb	Forb		Apiaceae
Cunila origanoides	Herb	Forb		Lamiaceae
Cynoglossum virginianum	Herb	Forb		Boraginaceae
Danthonia spicata	Herb	Graminoid		Poaceae
Dennstaedia punctulobula	Herb	Fern		Dennsteadiaceae
Desmodium paniculatum	Herb	Forb		Fabaceae
Desmodium spp.	Herb	Forb		Fabaceae
Desmodium rotundifolia	Herb	Forb		Fabaceae
Dichanthelium boscii	Herb	Graminoid		Poaceae
Dichanthelium commutatum	Herb	Graminoid		Poaceae
Dichanthelium dichotonum	Herb	Graminoid		Poaceae
Dichanthelium laxiflorum	Herb	Graminoid		Poaceae
Dichanthelium sp.	Herb	Graminoid		Poaceae
Dichanthelium villosissimum	Herb	Graminoid		Poaceae
Dioscorea villosa	Herb	Forb		Dioscoreaceae
Disopyros virginiana	Woody	Tree	Canopy	Ebenaceae
Diphasiastrum digitatum	Herb	Fern		Lycopodiaceae
Elaeagnus umbelleta (including E. pungens)	Woody	Shrub		Elaeagnaceae
Elephantopus carolinianus	Herb	Forb		Asteraceae
Elephantopus sp.	Herb	Forb		Asteraceae

Elephantopus tomentosus	Herb	Forb		Asteraceae
Elymus hystrix	Herb	Graminoid		Poaceae
Elymus sp.	Herb	Graminoid		Poaceae
Elymus villosus	Herb	Graminoid		Poaceae
Elymus virginicus	Herb	Graminoid		Poaceae
Endodeca serpentaria	Herb	Forb		Aristolochiaceae
Epifagus virginiana	Herb	Forb		Orobanchaceae
Epigea repens	Woody	Subshrub		Ericaceae
Erectites hieraciifolia	Herb	Forb		Asteraceae
Erigeron annuus	Herb	Forb		Asteraceae
Erigeron pulchellus	Herb	Forb		Asteraceae
Erythronium umbillicatum	Herb	Forb		Liliaceae
Euonymus americanus	Woody	Shrub		Celastraceae
Eupatorium sp.	Herb	Forb		Asteraceae
Euphorbia corollata	Herb	Forb		Euphorbiaceae
Eurybia divaricata	Herb	Forb		Asteraceae
Fagus grandifolia	Woody	Tree	Canopy	Fagaceae
Festuca subverticillata	Herb	Graminoid		Poaceae
Fragaria virginiana	Herb	Forb		Rosaceae
Fraxinus americana (includes F. pennsylvanica)	Woody	Tree	Canopy	Oleaceae
Galactia volubilis	Herb	Forb		Fabaceae
Galium aparine	Herb	Forb		Rubiaceae
Galium circaezans	Herb	Forb		Rubiaceae

Galium sp,	Herb	Forb		Rubiaceae
Galium triflorum	Herb	Forb		Rubiaceae
Galium uniflorum	Herb	Forb		Rubiaceae
Gamochaeta sp.	Herb	Forb		Asteraceae
Gaylussacia baccata	Woody	Shrub		Ericaceae
Gaylussacia sp.	Woody	Shrub		Ericaceae
Gelsemium sempervirens	Woody	Vine		Loganiaceae
Gentiana sp.	Herb	Forb		Gentianaceae
Gentiana villosa	Herb	Forb		Gentianaceae
Geum canadense	Herb	Forb		Rosaceae
Geum virginianum	Herb	Forb		Rosaceae
Glechoma hedera	Herb	Forb		Lamiaceae
Gleditsia triacanthos	Woody	Tree	Canopy	Fabaceae
Goodyera pubescens	Herb	Forb		Orchidaceae
Hamamelis virginiana	Woody	Shrub		Hamamelidaceae
Hedera helix	Woody	Vine		Araliaceae
Hedeoma pulcherrima	Herb	Forb		Lamiaceae
Heliopsis helianthoides	Herb	Forb		Asteraceae
Heuchera americana	Herb	Forb		Saxifragaceae
Heuchera caroliniana	Herb	Forb		Saxifragaceae
Hexastylis arifolia	Herb	Forb		Aristolochiaceae
Hexastylis minor	Herb	Forb		Aristolochiaceae
Hieracium gronovii	Herb	Forb		Asteraceae
Hieracium venosum	Herb	Forb		Asteraceae

Houstonia caerulea	Herb	Forb		Rubiaceae
Houstonia purpurea	Herb	Forb		Rubiaceae
Huperzia lucidula	Herb	Fern		Lycopodiaceae
Hydrangea arborea	Woody	Shrub		Hydrangeaceae
Hylodesmum nudiflorum	Herb	Forb		Fabaceae
Hypericum gentianoides	Herb	Forb		Clusiaceae
Hypericum hypericoides	Woody	Subshrub		Clusiaceae
Hypericum nudiflorum	Woody	Subshrub		Clusiaceae
Hypericum prolificum	Woody	Subshrub		Clusiaceae
Hypericum punctatum	Herb	Forb		Clusiaceae
Hypericum sp.	Herb	Forb		Clusiaceae
Hypoxis hirsuta	Herb	Forb		Hypoxidaceae
Ilex ambigua	Woody	Shrub		Aquifoliaceae
Ilex decidua	Woody	Shrub		Aquifoliaceae
Ilex opaca	Woody	Tree	Understory	Aquifoliaceae
Ilex verticillata	Woody	Shrub		Aquifoliaceae
Impatiens capensis	Herb	Forb		Balsaminaceae
Impatiens pallida	Herb	Forb		Balsaminaceae
Ipomoea pandurata	Herb	Forb		Convolvulaceae
Iris cristata	Herb	Forb		Iridaceae
Iris sp.	Herb	Forb		Iridaceae
Iris verna	Herb	Forb		Iridaceae
Itea virginica	Woody	Shrub		Grossulariaceae
Juglans nigra	Woody	Tree	Canopy	Juglandaceae
Juncus acuminatus	Herb	Graminoid		Juncaceae

Juncus coriaceous	Herb	Graminoid		Juncaceae
Juniperus virginiana	Woody	Tree	Understory	Cupressaceae
Krigia sp.	Herb	Forb		Asteraceae
Lactuca canadensis	Herb	Forb		Asteraceae
Lactuca sp.	Herb	Forb		Asteraceae
Lamiaceae sp.	Herb	Forb		Lamiaceae
Lamium sp.	Herb	Forb		Lamiaceae
Laportea canadensis	Herb	Forb		Urticaceae
Lathyrus venetus	Herb	Forb		Fabaceae
Leersia virginica	Herb	Graminoid		Poaceae
Lespedeza sp.	Herb	Forb		Fabaceae
Liatris pilosa	Herb	Forb		Asteraceae
Ligusticum canadense	Herb	Forb		Apiaceae
Ligustrum japonicum	Woody	Shrub		Oleaceae
Ligustrum sinense	Woody	Shrub		Oleaceae
Lilium michauxii	Herb	Forb		Liliaceae
Lindera benzoin	Woody	Shrub		Lauraceae
Liparis liliifolia	Herb	Forb		Orchidaceae
Liquidambar styraciflua	Woody	Tree	Canopy	Altingiaceae
Liriodendron tulipifera	Woody	Tree	Canopy	Magnoliaceae
Lobelia inflata	Herb	Forb		Campanulaceae
Lobelia sp.	Herb	Forb		Campanulaceae
Lonicera japonica	Woody	Vine		Caprifoliaceae
Lonicera sempervirens	Woody	Vine		Caprifoliaceae
Luzula acuminata	Herb	Graminoid		Juncaceae
Luzula sp.	Herb	Graminoid		Juncaceae

Lycopus virginicus	Herb	Forb		Lamiaceae
Lysimachia ciliata	Herb	Graminoid		Poaceae
Magnolia tripetala	Woody	Tree	Subcanopy	Magnoliaceae
Mahonia bealii	Woody	Shrub		Berberidaceae
Maianthemum racemosum	Herb	Forb		Asparagaceae
Malaxis unifolia	Herb	Forb		Orchidaceae
Matelea carolinensis	Herb	Forb		Apocynaceae
[Matelea + Gonolobus]	Herb	Forb		Apocynaceae
Medeola virginiana	Herb	Forb		Liliaceae
Melanthium virginicum	Herb	Forb		Melanthiaceae
Melica mutica	Herb	Graminoid		Poaceae
Menispermum canadense	Herb	Forb		Menispermaceae
Microstegium vimineum	Herb	Graminoid		Poaceae
Mirabilis sp;	Herb	Forb		Nyctaginaceae
Mitchella repens	Herb	Subshrub		Rubiaceae
Monarda fistulosa	Herb	Forb		Lamiaceae
Hypopitys montropa	Herb	Forb		Monotropaceae
Monotropa uniflora	Herb	Forb		Monotropaceae
Morella cerifera	Woody	Shrub		Myricaceae
Morus rubra	Woody	Tree	Understory	Moraceae
Muhlenbergia schreberi	Herb	Graminoid		Poaceae
Nandina domestica	Woody	Shrub		Berberidaceae
Nyssa sylvatica	Woody	Tree	Canopy	Cornaceae
Oenothera sp.	Herb	Forb		Onagraceae

Onoclea sensibilis	Herb	Fern		Dryopteridaceae
Ophioglossum sp.	Herb	Fern		Ophioglossaceae
Orchidaceae sp.	Herb	Forb		Orchidaceae
Ostrya virginiana	Woody	Tree	Understory	Betulaceae
Oxalis sp.	Herb	Forb		Oxalidaceae
Oxydendrum arboreum	Woody	Tree	Understory	Ericaceae
Packera anonyma	Herb	Forb		Asteraceae
Panicum anceps	Herb	Graminoid		Poaceae
Parthenium integrifolium	Herb	Forb		Asteraceae
Parthenocissus quinquefolia	Woody	Vine		Vitaceae
Paspalum sp.	Herb	Graminoid		Poaceae
Passiflora incarnata	Herb	Forb		Passifloraceae
Passiflora lutea	Herb	Forb		Passifloraceae
Paulownia tomentosa	Woody	Tree	Subcanopy	Scrophulariaceae
Penstemon australis	Herb	Forb		Scrophulariaceae
Penstemon laevigatis	Herb	Forb		Scrophulariaceae
Persicaria virginiana	Herb	Forb		Polygonaceae
Phlox sp.	Herb	Forb		Polemoniaceae
Aronia arbutifolia	Woody	Shrub		Rosaceae
Phryma leptostachya	Herb	Forb		Phrymaceae
Physalis sp.#1	Herb	Forb		Solonaceae
Physalis virginiana	Herb	Forb		Solonaceae
Phytolacca americana	Herb	Forb		Phytolaccaceae
Pinus echinata	Woody	Tree	Canopy	Pinaceae
Pinus sp.	Woody	Tree	Canopy	Pinaceae
-------------------------------	-------	-----------	------------	-----------------
Pinus taeda	Woody	Tree	Canopy	Pinaceae
Pinus virginiana	Woody	Tree	Canopy	Pinaceae
Piptochaetium avenecum	Herb	Graminoid		Poaceae
Platanus occidentalis	Woody	Tree	Canopy	Platanaceae
Pleopeltis polylepis	Herb	Fern		Polypodiaceae
Pluchea camphorata	Herb	Forb		Asteraceae
Poaeceae sp.	Herb	Graminoid		Poaceae
Poa compressa	Herb	Graminoid		Poaceae
Podophyllum peltatum	Herb	Forb		Berberidaceae
Polystichum acrostichoides	Herb	Fern		Dryopteridaceae
Polygonatum biflorum	Herb	Forb		Asparagaceae
Porteranthus trifoliatus	Herb	Forb		Rosaceae
Potentilla canadensis	Herb	Forb		Ranunculaceae
Potentilla indica	Herb	Forb		Ranunculaceae
Prenanthes altissima	Herb	Forb		Asteraceae
Prenanthes serprentaria	Herb	Forb		Asteraceae
Prenanthes sp.	Herb	Forb		Asteraceae
Prunus americana	Woody	Tree	Understory	Rosaceae
Prunus angustifolia	Woody	Tree	Understory	Rosaceae
Prunus serotina	Woody	Tree	Canopy	Rosaceae
Prunella vulgara	Herb	Forb		Lamiaceae
Pseudoghaphalium	Herb	Forb		Asteraceae

obtusifolium				
Pteridium aquilinum	Herb	Fern		Dennsteadiaceae
Ptilinium capillaceum	Herb	Forb		Apiaceae
Pycanthemum incanum	Herb	Forb		Lamiaceae
Pyrola americana	Herb	Forb		Pyrolaceae
Pyrus communis	Woody	Tree	Understory	Rosaceae
Quercus alba	Woody	Tree	Canopy	Fagaceae
Quercus coccinea	Woody	Tree	Canopy	Fagaceae
Quercus falcata	Woody	Tree	Canopy	Fagaceae
Quercus marilandica	Woody	Tree	Canopy	Fagaceae
Quercus michauxii	Woody	Tree	Canopy	Fagaceae
Quercus montana	Woody	Tree	Canopy	Fagaceae
Quercus nigra	Woody	Tree	Canopy	Fagaceae
Quercus phellos	Woody	Tree	Canopy	Fagaceae
Quercus rubra	Woody	Tree	Canopy	Fagaceae
Quercus stellata	Woody	Tree	Canopy	Fagaceae
Quercus velutina	Woody	Tree	Canopy	Fagaceae
Ranunculus sp.	Herb	Forb		Ranunculaceae
Rhododendron periclymenoides	Woody	Shrub		Ericaceae
Rhus copallinum	Woody	Shrub		Anacardiaceae
Rhus glabra	Woody	Shrub		Anacardiaceae
Robinia pseudoacacia	Woody	Tree	Canopy	Fabaceae
Rosa carolina	Woody	Shrub		Rosaceae
Rubus spp.	Woody	Shrub		Rosaceae
Rudbeckia laciniata	Herb	Forb		Asteraceae
Ruellia caroliniensis	Herb	Forb		Acanthaceae

Rumex verticillatus	Herb	Forb		Polygonaceae
Saccharum alopecuroides	Herb	Graminoid		Poaceae
Salix humilis	Woody	Shrub		Saliaceae
Salvia lyrata	Herb	Forb		Lamiaceae
Sambucus nigra	Woody	Shrub		Caprifoliaceae
Sanguinaria canadensis	Herb	Forb		Papaveraceae
Sanicula spp.	Herb	Forb		Apiaceae
Sassafras albidum	Woody	Tree	Understory	Lauraceae
Sceptridium biternatum	Herb	Fern		Ophioglossaceae
Scirpus cyperinus	Herb	Graminoid		Cyperaceae
Scirpus georgianus	Herb	Graminoid		Cyperaceae
Scleria oligantha	Herb	Graminoid		Cyperaceae
Scrophularia sp.	Herb	Forb		Scrophulariaceae
Scutellaria elliptica	Herb	Forb		Lamiaceae
Scutellaria integrifolia	Herb	Forb		Lamiaceae
Scutellaria lateriflora	Herb	Forb		Lamiaceae
Scutellaria serrata	Herb	Forb		Lamiaceae
Scutellaria sp.	Herb	Forb		Lamiaceae
Sedum ternatum	Herb	Forb		Crassulaceae
Selaginella sp.	Herb	Fern		Sellaginalaceae
Seriocarpus asteroides	Herb	Forb		Asteraceae
Seriocarpus liniflolius	Herb	Forb		Asteraceae
Seriocarpus sp.	Herb	Forb		Asteraceae
Silene virginica	Herb	Forb		Caryophyllaceae
Silphium astericus	Herb	Forb		Asteraceae

Silphium compositum	Herb	Forb	Asteraceae
Sisyrinchium albidum	Herb	Forb	Iridaceae
Sisyrinchium angustifolium	Herb	Forb	Iridaceae
Smallanthus uvedalius	Herb	Forb	Asteraceae
Smilax bona-nox	Woody	Vine	Smilacaceae
Smilax glauca	Woody	Vine	Smilacaceae
Smilax herbacea	Woody	Vine	Smilacaceae
Smilax rotundifolia	Woody	Vine	Smilacaceae
Solanum carolinense	Herb	Forb	Solonaceae
Solanum sp.	Herb	Forb	Solonaceae
Solidago sppo.	Herb	Forb	Asteraceae
Sorghastrum nutans	Herb	Graminoid	Poaceae
Staphylea trifolia	Woody	Shrub	Staphyleaceae
Stellaria media	Herb	Forb	Caryophyllaceae
Stellaria pubera	Herb	Forb	Caryophyllaceae
Stylosanthes biflora	Herb	Forb	Fabaceae
Styrax grandifolia	Woody	Shrub	Styracaceae
Symphotrichum dumosum	Herb	Forb	Asteraceae
Symphotrichum patens	Herb	Forb	Asteraceae
Symphotrichum sp.	Herb	Forb	Asteraceae
Symphotrichum undulatum	Herb	Forb	Asteraceae
Tephrosia virginiana	Herb	Forb	Fabaceae

Thalictrum revolutum	Herb	Forb		Ranunculaceae
Thaspium barbinode	Herb	Forb		Apiaceae
Thaspium sp.	Herb	Forb		Apiaceae
Thasptium trifoliatum	Herb	Forb		Apiaceae
Tiarella wherryi	Herb	Forb		Saxifragaceae
Tipularia discolor	Herb	Forb		Orchidaceae
Toxicodendron radicans	Woody	Vine		Anacardiaceae
Tradescantia virginiana	Herb	Forb		Commelidaceae
Tragia urticifolia	Herb	Forb		Euphorbiaceae
Triadenum walteri	Herb	Forb		Clusiaceae
Trifolium pratense	Herb	Forb		Fabaceae
Trifolum sp.	Herb	Forb		Fabaceae
Trillium catesbeai	Herb	Forb		Trilliaceae
Tripsacum dactyloides	Herb	Graminoid		Poaceae
Ulmus alata	Woody	Tree	Canopy	Ulmaceae
Ulmus americana	Woody	Tree	Canopy	Ulmaceae
Ulmus rubra	Woody	Tree	Canopy	Ulmaceae
Ulmus sp.	Woody	Tree	Canopy	Ulmaceae
Uvularia perfoliata	Herb	Forb		Colchicaceae
Uvularia puberula	Herb	Forb		Colchicaceae
Uvularia sessilifolia	Herb	Forb		Colchicaceae
Vaccinium arboreum	Woody	Tree	Understory	Ericaceae
Vaccinium fuscatum	Woody	Shrub		Ericaceae
Vaccinium pallidum	Woody	Shrub		Ericaceae

Vaccinium corymbosum + stamineum	Woody	Shrub	Ericaceae
Vaccinium tenellum	Woody	Shrub	Ericaceae
Verbesina alternifolia	Herb	Forb	Asteraceae
Verbesina occidentalis	Herb	Forb	Asteraceae
Verbesina sp.	Herb	Forb	Asteraceae
Verbascum thapsis	Herb	Forb	Asteraceae
Vernonia glauca	Herb	Forb	Asteraceae
Vernonia sp.	Herb	Forb	Asteraceae
Viburnum acerifolium	Woody	Shrub	Adoxaceae
Viburnum nudum	Woody	Shrub	Adoxaceae
Viburnum prunifolium	Woody	Shrub	Adoxaceae
Viburnum rafinesqueanum	Woody	Shrub	Adoxaceae
Viburnum rufidulum	Woody	Shrub	Adoxaceae
Viola sp.	Herb	Forb	Violaceae
Vitis aestivalis (including V. labrusca and V. vulpina)	Woody	Vine	Vitaceae
Vitis rotundifolia	Woody	Vine	Vitaceae
Vitis sp.	Woody	Vine	Vitaceae
Wisteria sinense	Woody	Vine	Fabaceae
Woodwardia areolata	Herb	Fern	Blechnanceae
Youngia japonica	Herb	Forb	Asteraceae
Zizia aurea	Herb	Forb	Apiaceae

LITERATURE CITED

Abrams, M.D. 1998. The red maple paradox. BioScience 48: 355-364

- Abrams, M.D. and Downs, J.A. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. Canadian Journal of Forest Research 20: 1864-1870
- Cain, M.D. and Shelton, M.G. 2001. Secondary forest succession following reproductive cutting on the Upper Coastal Plain of southeastern Arkansas, USA. Forest Ecology and Management 146: 223-238
- Chorensky, E.A. and Randall, J.M. 2003. The threat of invasive alien species to biological diversity: setting a future course. Annals of the Missouri Botanical

Garden 90: 67-76

- Christensen, N.L. and Peet, R.K. 1984. Convergence during secondary forest succession. Journal of Ecology 72: 25-36.
- Clinton, B.D., Boring, L.R., and Swank, W.T. 1994. Regeneration patterns in canopy gaps of mixed-oak forests in the southern Appalachians: influences of topographic position and evergreen understory. American Midland Naturalist 132: 308-319
- Collins, B.S. and Pickett, S.T.A. 1988. Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. Journal of Ecology 76: 437-450
- Cote, S.D., Rooney, T.P, Tremblay, J., Dussault, C., and Waller, D.M. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35: 113-147
- Cowell, C. M. 1998. Historical change in vegetation and disturbance on the Georgia Piedmont. American Midland Naturalist 140: 78-89
- Faestel, M. 2012. Classification and description of alluvial plant communities of the North Carolina Coastal Plain. M.S. thesis, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA.

- Ferraro, D.O. and Oesterheld, M. 2002. Effect of defoliation on grass growth: a quantitative review. Oikos 98: 125-133
- Flory, S.L. and Clay, K. 2009. Invasive plant removal method determines native plant community responses. Journal of Applied Ecology 46: 434-442
- Gavier-Pizarro, G.I., Radeloft, V.C., Stewart, S.I., Huebner, C.D., and Keuler, N.S.
 2010. Rural housing is related to plant invasions in forests of southern Wisconsin, USA. Landscape Ecology 25: 1505-1518
- Heath, L.S. et. al. 1993. Contribution of temperate forests to the world's carbon budget. Water, Air, and Soil Pollution 70: 55-69
- Holladay, C.A., Kwit, C., and Collins, B. 2006. Woody regeneration in and around aging southern bottomland hardwood forest gaps: effects of herbivory and gap size. Forest Ecology and Management 223: 218-225
- Horsley, S.B., Stout, S.L., and DeCalesta, D.S. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13: 98-118
- Keyser, P.D., Guynn, D.C. Jr., and Hill, H.S. Jr. 2005. Population density physical condition relationships in white-tailed deer. Journal of Wildlife Management 69: 356-365
- Kirkpatrick, J.B. 2004. Vegetation change in an urban grassy woodland 1974-2000. Australian Journal of Botany 52: 597-608
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., and Bazzaz, F.A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10: 689-710
- Matthews, E.R., Peet, R.K., Weakley, A.S. 2011. Classification and description of alluvial plant communities of the Piedmont region. North Carolina, U.S.A. Applied Vegetation Science 14: 485-505.
- McCune, B. and Grace, J.B. 2002. *Analysis of Ecological Communities*. MjM Software Design, Glenden Beach, Oregon
- McDonald, R.I., Peet, R.K., and Urban, D.L. 2002. Environmental correlates of oak decline and red maple increase in the North Carolina Piedmont. Castanea 67: 84-95

- McNab, W.H., Greenberg, C.H., and Berg, E.C. 2004. Landscape distribution and characteristics of large hurricane-related canopy gaps in a southern Appalachian watershed. Forest Ecology and Management 196: 435-447
- Nowacki, G.J. and Abrams, M.D. 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience 58: 123-138
- Oswalt, C.M., Oswalt, S.N., and Clatterbuck, W.K. 2007. Effects of Microstegium vimineum (*Trin.*) *A. Camus* on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. Forest Ecology and Management 242: 727-732
- Palmer, M.W. 1990. Vascular flora of the Duke Forest, North Carolina. Castanea 55: 229-244
- Peet, R.K. 1992. Community structure and ecosystem properties. Pages 102-151 in D.C. Glenn-Lewin, R.K. Peet and T.T. Veblen (editors). *Plant succession: theory and prediction*. Chapman and Hall, London.
- Peet, R.K. and N.L. Christensen. 1980. Hardwood forest vegetation of the North Carolina Piedmont. *Veröff. Geobot. Inst. ETH Stiftung Rübel* 69: 14-39.
- Peet, R.K. and N.L. Christensen. 1988. Changes in species diversity during secondary forest succession on the North Carolina piedmont. Pages 233-245 in H.J. During, M.J.A. Werger, and J.H. Willems (editors). *Diversity and pattern in plant communities*. SPB Academic Publishing. The Hague.
- Peet, R.K., J.D. Fridley and Joel M. Gramling. 2003. Variation in species richness and species pool size across a pH gradient in forests of the southern Blue Ridge Mountains. *Folio Geobotanica* 38:391-401.
- Peet, R.K., Wentworth, T.R., and White, P.S. 1998. A flexible, multipurpose method for recording vegetation composition and structure. Castanea 63: 262-274
- Robison, S.A. and McCarthy, B.C. 1999. Growth responses of *Carya ovata* (Juglandaceae) seedlings to experimental sun patches. American Midland Naturalist 141: 69-84
- Rooney, T.P. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecology 202: 103-111

- Schumann, M.E., White, A.S., and Withan, J.W. 2003. The effects of harvest-created gaps on plant species diversity, composition, and abundance in a Maine oak-pine forest. Forest Ecology and Management 176: 543-561.
- Schwartz, M.J., 2007. Vegetation change over decadal and century scales in the North Carolina Piedmont. Ph.D. dissertation, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA.
- Shumway, D.L., Abrams, M.D., and Ruffner, C.M. 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, U.S.A. Canadian Journal of Forest Research 31: 1437-1443
- Sotala, D.J. and Kirkpatrick, C.M. 1973. Foods of white-tailed deer, Odocoileus *virginianus*, in Martin County, Indiana. American Midland Naturalist 89: 281-286
- Stromayer, K.A.K. and Warren, R.J. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? Wildlife Society Bulletin 25: 227-234
- Taverna, K., Peet, R.K., and Phillips, L.C. 2005. Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont, USA. Journal of Ecology 93: 202-213
- Thompson, I.D. and Mallik, A.U. 1989. Moose browsing and allelopathic effects of *Kalmia angustifolia* on balsam fir regeneration in central Newfoundland. Canadian Journal of Forest Research 19:524-526
- Wakeland, B. and Swihart, R.K. 2009. Ratings of white-tailed deer preferences for woody browse in Indiana. Proceedings of the Indiana Academy of Science 118: 96-101
- Waller, D.M. and Alverson, W.S. 1997. The white-tailed deer: a keystone herbivore. Wildlife Society Bulletin 25: 217-226
- Weakley, A.S, 2011. *Flora of the Southern and Mid-Atlantic States*. UNC Herbarium, North Carolina Botanical Garden, University of North Carolina at Chapel Hill
- Wilcove, D.S, Rothstein, D., Dubow, J., and Philips, A., Losos, E. 1998. Quantifying threats to imperiled species in the United States. BioScience 48: 607-615
- Woods, K.D. 2007. Predictability, contingency, and convergence in late succession: slow systems and complex data-sets. Journal of Vegetation Science 18: 543-554

- Wright, J.P. and Fridley, J.D. 2010. Biogeographic synthesis of secondary succession rates in eastern North America. Journal of Biogeography 37: 1584-1596
- Xi, W., Peet, R.K., and Urban, D.L. 2008. Changes in forest structure, species diversity and spatial pattern following hurricane disturbance in a Piedmont North Carolina forest, USA. Journal of Plant Ecology 1: 43-57