

ESTABLISHMENT AND TWO-YEAR RE-SURVEY OF A TWELVE-HECTARE FOREST
DYNAMICS PLOT IN A 70-YEAR OLD PIEDMONT SECOND GROWTH FOREST

by

MARK D. ZENOBLE

(Under the Direction of Chris Peterson)

ABSTRACT

I sought to determine community characteristics including stem density and species diversity in a 12-hectare permanent forest plot to determine if the community present suggests mesophication. Additionally, aboveground biomass (AGB) and carbon (AGC) were recorded. Five hectares were surveyed in 2016, and all in 2018-2019. Stems greater than 5cm in diameter were measured, identified, tagged and mapped. Across the 12 hectares, 50 species were found, dominated by white oak (*Quercus alba* L.), red maple (*Acer rubrum* L.) and American beech (*Fagus grandifolia* Ehrh.). Density was 779.92 stems/ha and total AGB was 2,945.85Mg with a mean of 245.49Mg/ha. In 2018, the total AGC was 1,472.93Mg, mean AGC was 122.74±12.92Mg/ha. AGC in the resurveyed hectares increased by 33.24Mg (5.4%). Although oaks were the dominant species, the smaller stems present suggest a shift to a more mixed-mesic species composition in future decades.

INDEX WORDS: Forest Dynamics Plot, Forest Community Diversity, Biomass, *Quercus*, *Acer*, Mesophication, Shannon-Wiener Index, Species Richness, Simpson's Diversity Index

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DEDICATION

To my family, my friends, and all the teachers that encouraged me

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CHAPTER 1

INTRODUCTION

Long term plots are one of the best tools available to monitor changes in vegetation as well as inform predictions of coming changes (Chytrý et al., 2020). Permanent study plots have many benefits and are useful across many fields of study; allowing additional hypotheses and questions to be tested that may have not been considered at the time of inception (de Bello et al., 2020). Vegetation resurvey studies have been used to clarify the complex effect disturbance can have on diversity, as well as the cyclical nature of population dynamics, but they are most often to observe trends in response to environmental changes (Hobbs et al., 2007). They can be used to test long standing ecological theories, compare patterns across environments, and to explore which factors maintain biodiversity (de Bello et al., 2020). Long term plots inform our understanding of the resistance and resilience of the ecosystem in response to stressors like shifts in climate, extreme weather events, or introduction of novel non-native plants, pests, and pathogens. Among the common ecosystem responses to these stressors have been shifts in demographics that could remain unobserved without decades of records (de Bello et al., 2020). Funding, timing, and logistics may prevent shorter studies from detecting such shifts. Long term community level data enables research on species aggregation, segregation, displacement or facilitation, as well as distinguishing deterministic components of community dynamics from demographic stochasticity, assisting in parameterizing models of communities. Better understanding

of these factors will help predict and model changes in biodiversity during the Anthropocene.

Before European settlement profoundly altered fire regimes, the eastern United States were covered by a diversity of pyrophytic plant communities. In western Maryland, for example, fires occurred every 8 years on average from 1615-1900, but no major fires occurred after 1900, and none at all after 1960 (Abrams, 2005). Fires in the Georgia Piedmont were considered to be frequent but of low or mixed severity (Nowacki & Abrams, 2008). Policies implemented in the 1920's focused on suppression of natural fire regimes and have converted open, fire-maintained ecosystems to closed forests, creating a positive feedback loop known as mesophication (Nowacki & Abrams, 2008, 2015). Closed canopy forests produced an increase in relative humidity and decrease in radiation, a process that increasingly excludes shade-intolerant, pyrophytic species in favor of mesophytic, fire sensitive species. Mesophication is another long-term process impacting forests of the eastern United States. Mesophication may cause changes not only in fire frequency, but also severity: currently, fires in the Georgia piedmont are infrequent but generally kill 75% of the living overstory trees, in stark contrast to the pre-European frequent yet low intensity fire regime (Abrams, 2003). If the positive feedback loop of mesophication continues, the resource investment required to revive a natural disturbance regime will only increase.

However, it has been shown that the impact of deer browsing rather than fire may be the most important process regulating eastern forest dynamics (Nuttle et al., 2013). High levels of deer browsing reduce the understory diversity found and severely

impact the tree seedling layer in a forest. Disturbances that may otherwise promote diversity may fail to have their expected influence if browsers are overabundant.

Another major anthropogenic impact on forests is the introduction of numerous insects and diseases novel to North America, an ongoing process (Mack et al., 2000). Over time these novel pests have an enormous impact on the species they plague and eventually significantly effect community assemblages. An example is the former oak-chestnut forests that became oak-hickory or mixed-oak forest due to the loss of American chestnut (*Castanea dentata* (Marshall)) caused by chestnut blight (Abrams, 1996). Invasive species, plant, pathogen, insect, or otherwise follow a lag and log phase of proliferation and spread; consequently it can take years, decades, or longer to study the effects on ecosystems (Mack & Occhipinti, 1999). Invasive species alter community assemblages by competing with natives in diverse ways, primarily for light and water.

Much of the forest area of the Piedmont region of the southeastern United States is second-growth, temperate deciduous forest. However, due to agriculture and forestry practices in the early-mid 20th century, nearly all of the arable land in the piedmont was harvested at some time for cultivation. Poor management led to land degradation and subsequent abandonment for use as cropland, leaving much area as pasture or woodland (Golden, 1979). These areas were often left to reforest through old-field succession.

Containing approximately 14% of global forest carbon and constituting nearly 30% of the forest carbon sink capacity, temperate forests play a significant role in the global carbon cycle (Pan et al., 2011); from 1990 to 2007 they saw a net increase in both total carbon stock and density in total live biomass (Pan et al., 2013). However,

natural forests must be better accounted for in models of terrestrial carbon dynamics, improved models can refine predictions of biomass and carbon changes in forest stands (Carey et al., 2001; Pan et al., 2013). It is unknown if the relationship between aboveground woody biomass productivity, represented by change in biomass per year, has any relationship with species diversity (Wang et al., 2016). Data collected at permanent vegetative plots are critical to assessing long term forest dynamics and may have significant implications considering forests ability to continually accumulate carbon and serve as critical long-term carbon sinks (Lowney et al., 2016).

The University of Georgia Forest Dynamics Plot (UGA FDP) at the State Botanical Gardens of Georgia was established in 2015 (Figure 1.1). The State Botanical Gardens forest has been growing since approximately 1938 (80 years), an age coinciding very nearly with the median age (70 years) of forests in the USDA Forest Service Eastern Region in 2011 (Gough et al., 2016). Four primary questions were addressed: a) What was the state of this UGA FDP in terms of species diversity and composition? b) Was the species composition indicative of a forest experiencing a mesophication positive feedback loop? c) Did the present community of small stems (regeneration) suggest further mesophication for the future of this forest? d) How much carbon was sequestered in aboveground living biomass at this UGA FDP? An overarching goal set for this project was to set up a long-term vegetation study site to monitor the effects of anthropogenic impacts on the forest under novel environmental conditions.

Literature Cited

- Abrams, M. D. (1996). Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. In *Annales des Sciences Forestieres* (Vol. 53, Issues 2–3). <https://doi.org/10.1051/forest:19960230>
- Abrams, Marc D. (2005). Prescribing fire in eastern oak forests: Is time running out? In *Northern Journal of Applied Forestry* (Vol. 22, Issue 3). <https://doi.org/10.1093/njaf/22.3.190>
- Abrams, Marc D. (2003). Where Has All the White Oak Gone? *BioScience*, 53(10), 927–939. [https://doi.org/10.1641/0006-3568\(2003\)053\[0927:WHATWO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0927:WHATWO]2.0.CO;2)
- Carey, E. V., Sala, A., Keane, R., & Callaway, R. M. (2001). Are old forests underestimated as global carbon sinks? *Global Change Biology*, 7(4), 339–344. <https://doi.org/10.1046/j.1365-2486.2001.00418.x>
- Chytrý, M., Chiarucci, A., Pärtel, M., & Pillar, V. D. (2020). Thirty years of the Journal of Vegetation Science. In *Journal of Vegetation Science* (Vol. 31, Issue 1, pp. 1–2). Wiley-Blackwell. <https://doi.org/10.1111/jvs.12836>
- de Bello, F., Valencia, E., Ward, D., & Hallett, L. (2020). Why we still need permanent plots for vegetation science. *Journal of Vegetation Science*, 31(5), 679–685. <https://doi.org/10.1111/jvs.12928>
- Golden, M. S. (1979). Forest Vegetation of the Lower Alabama Piedmont. *Ecology*, 60(4), 770–782. <https://doi.org/10.2307/1936614>

- Gough, C. M., Curtis, P. S., Hardiman, B. S., Scheuermann, C. M., & Bond-Lamberty, B. (2016). Disturbance, complexity, and succession of net ecosystem production in North America's temperate deciduous forests. *Ecosphere*, 7(6), e01375.
<https://doi.org/10.1002/ecs2.1375>
- Hobbs, R. J., Yates, S., & Mooney, H. A. (2007). Long-term data reveal complex dynamics in grassland in relation to climate and disturbance. *Ecological Monographs*, 77(4), 545–568. <https://doi.org/10.1890/06-1530.1>
- Lowney, C. A., Graham, B. D., Spetich, M. A., Shifley, S. R., Saunders, M. R., & Jenkins, M. A. (2016). Two decades of compositional and structural change in deciduous old-growth forests of Indiana, usa. *Journal of Plant Ecology*, 9, 256–271.
<https://doi.org/10.1093/jpe/rtv050>
- Mack, R. N., & Occhipinti, A. (1999). Biotic invasion: A global perspective and ecology of invasion: Patterns and perspectives. In *Perspectives in ecology* (pp. 67–74).
- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., & Bazzaz, F. A. (2000). Issues in Ecology BIOTIC INVASIONS: CAUSES, EPIDEMIOLOGY, GLOBAL CONSEQUENCES, AND CONTROL. In *Ecological Applications* (Vol. 10, Issue 3).
- Nowacki, G. J., & Abrams, M. D. (2008). The demise of fire and “mesophication” of forests in the eastern United States. In *BioScience* (Vol. 58, Issue 2).
<https://doi.org/10.1641/B580207>
- Nowacki, G. J., & Abrams, M. D. (2015). Is climate an important driver of post-European vegetation change in the Eastern United States? *Global Change Biology*, 21(1), 314–334. <https://doi.org/10.1111/gcb.12663>

- Nuttle, T., Royo, A. A., Adams, M. B., & Carson, W. P. (2013). Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecological Monographs*, 83(1), 3–17. <https://doi.org/10.1890/11-2263.1>
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333(6045), 988–993. <https://doi.org/10.1126/science.1201609>
- Pan, Y., Birdsey, R. A., Phillips, O. L., & Jackson, R. B. (2013). *The Structure, Distribution, and Biomass of the World's Forests*. <https://doi.org/10.1146/annurev-ecolsys-110512-135914>
- Wang, J., Cheng, Y., Zhang, C., Zhao, Y., Zhao, X., & Von Gadow, K. (2016). Relationships between tree biomass productivity and local species diversity. *Ecosphere*, 7(11), e01562. <https://doi.org/10.1002/ecs2.1562>

CHAPTER 2

CURRENT STATUS AND TWO-YEAR CHANGE OF COMMUNITY CHARACTERISTICS IN A SECOND GROWTH PIEDMONT FOREST

Introduction

Across eastern North America, forests dominated by oaks have persisted in a relatively stable state for the last 8,000 years (Signell et al., 2005). These oak dominated forests were perpetuated by naturally occurring fires which suppressed competition. Historical tree surveys show that *Quercus alba* was the most abundant species and that pines, hickories, and chestnuts were infrequently co-dominant (Hanberry & Nowacki, 2016; Signell et al., 2005). Oaks had a major influence on the ecological community, as well as on abiotic conditions, and as a dominant and defining community genus, they were a quintessential example of a foundation genus prior to European settlement (Hanberry & Nowacki, 2016).

These fire-maintained forests were logged on a massive scale in the early 1900's, and subsequent decades of fire suppression have allowed more fire-sensitive, oak competitors to grow to sizes which resist moderate surface fires (Nowacki & Abrams, 2015; Signell et al., 2005). This has led to the fire adapted species being outcompeted by more competitive species, a process known as mesophication (Nowacki & Abrams, 2008). However, this shifting community structure was not a result of fire suppression in isolation - oak forests are reacting to multiple interconnected factors (McEwan et al., 2011). Increased shade by fire-resistant competitors results in

the loss of oak seedlings as acorn energy reserves are often over-expended fueling initial taproot growth. Shade-tolerant, mesophytic species were previously more restricted to lower topographic areas, but the replacement of pre-settlement, fire-maintained ecosystems dominated by oaks by mixed mesophytic species is an ongoing process in many eastern US forests. Oak replacing species include *Fagus grandifolia* Ehrh., *Acer rubrum* L., *Acer saccharum* Marsh., *Prunus serotina* Ehrh., *Liriodendron tulipifera* L., *Nyssa sylvatica* Marsh. and others (Abrams & Downs, 1990; Abrams, 1996; Signell et al., 2005). Red maple (*A. rubrum*) is considered the most aggressive oak replacing species in eastern forests, partly due to resprouting more than oaks, a trait shared by many oak replacing species (Signell et al., 2005). Additionally, fire suppression and changes in climatic conditions may allow non-native species to cross previous thresholds to become novel aspects of communities (Walther et al., 2002).

It is important to note that disturbances, like fire, that may otherwise promote diversity, may fail to do so if browsers are overabundant (Nuttall et al., 2013). High levels of deer browsing reduce the understory diversity found and severely impact the tree seedling layer in a forest, however *Fagus* has been found to dominate sites with uncontrolled deer browsing. Additionally, deer populations in the eastern United States have been increasing for the past several decades, another novel condition eastern forests are subject to that can be better informed with long-term data (Hanberry & Hanberry, 2020).

Novel invasive pathogens can significantly impact species assemblages, classically demonstrated by the destruction of almost all American chestnuts in its

native range by Asian chestnut blight within just a few decades (Mack et al., 2000). American chestnuts gradually shifted from composing approximately 41% of basal area in 1934 to <1% in 1953. This change was so slow that the crowns of older trees grew as opposed to allowing for re-establishment by seedlings (Nelson, 1955). Contradictorily, this same study reported that under these conditions, areas previously dominated by chestnut were also found to have been invaded by multiple species not present when chestnut was a major component. It took less than 20 years for chestnut stem density to drop from 188 stems/ha to 17 stems/ha at the Coweeta Hydrologic Laboratory in North Carolina (Mack et al., 2000). However, the main species that greatly increased in stem density and/or basal area were *Carya* spp. and *Liriodendron tulipifera* L., while others saw little change (*A. rubrum* L. and *Quercus alba* L.), and some declined (*Quercus rubra*) (Nelson, 1955). Since the community reshuffling that occurs after the loss of a dominant species can be unpredictable, more research on this phenomenon is needed.

The University of Georgia Forest Dynamics Plot (UGA FDP) was established in 2015. The forest on this site has been recovering from agricultural use since approximately 1938. This project focused on recording the present state of demographics to inform long term ecosystem function and health. Three primary questions were addressed in this chapter: a) What was the state of this UGA FDP in terms of density, species diversity and size distribution? b) Was the species composition indicative of a forest experiencing a mesophication positive feedback loop? c) Did the present community of small stems (regeneration) suggest further mesophication for the future of this forest?

Methods

Site background

The University of Georgia Forest Dynamics Plot (UGA FDP) at the State Botanical Garden of Georgia (33.9015N, 83.3789W) is a second growth forest in the Georgia Southern Outer Piedmont ecoregion. It is located at the 126.7-hectare State Botanical Garden of Georgia (SBG) in Clarke County, Georgia. Approximately 87% of the SBG is natural forest in various stages of maturity, the dominant growth form in this UGA FDP is deciduous broadleaf trees.

The University System of Georgia purchased the property where the State Botanical Gardens of Georgia is located in July 1936. However, aside from black and white aerial photography acquired by the USDA, there is little information concerning the land use pre-1968, and almost no information about the landscape pre-1936. Initially, the land was used by the Agronomy Department for “research and development”. Later, the site was used by the school of Forestry and Horticulture Department for research and practice areas. There were piled rocks and remains of barbed wire, suggesting past use as agriculture and pastureland. The aerial photography taken in 1938 indicated that this UGA FDP was roughly half agriculture, pasture, or very early successional forest and half more clearly developed forest. From 1951 onward, aerial photography shows what appears to be a more closed canopy forest. Based on these images it can be inferred that the successional age of the majority of this UGA FDP was 80+ years with some areas at an age of 70-80 years. There was no record of any burn, prescribed or otherwise, taking place at this site.

The soil composition within the plot was approximately 53.8% Madison sandy loam, 22.2% Louisburg loamy sand, 15.1% Pacolet sandy clay loam, and 7.9% Pacolet sandy loam (Figure 2.1; Natural Resources Conservation Service, 2020). These soils are fine, kaolinitic, thermic Typic Kanhapludults (Pacolet sandy clay, Pacolet sandy loam, Madison sandy loam) and coarse-loamy, mixed, semi-active, thermic Typic Hapludults (Louisburg sandy loam). The elevation at this site ranges from 173m to 208m above sea level and it was located in the lower Middle Oconee River watershed basin. The majority of the site has a slope ranging from 6%-15%.

Note that there were three general topographic areas at the UGA FDP. The three northern hectares, ha1, ha2, and ha3, were a bottomland; they had a stream running through them and were generally topographically lower than much of the rest of the plot. A steep slope on the south side of the stream rose to a gentle plateau that made up much of ha4, ha5 and ha6. The six remaining hectares, 7-12, had a less steep, southern facing slope.

The climate on this site is characterized by warm, humid summers and wet, cool winters. The site has historically been classified into the USDA hardiness zone 7B, however currently the site is in zone 8A. Last frost typically occurs between March 30th and April 5th and first frost typically falls between October 30th and November 5th. Temperatures range from an average of 1.6C in the winter to 32.2C in the summer with an annual average of 17C (NOAA 1981-2010 averages). Snow and ice storms are infrequent, but trace amounts of snow are not uncommon. From 1981-2010, average precipitation ranged from 269mm in the spring to 312mm in the winter with a mean annual total of 117.7cm.

Plot establishment

A 12 hectare, rectangular, 400x300m permanent plot was established in 2015 (Figure 1.1). A Topcon CTS-2 total station was used to locate the position of grid corners every 10m. Given the precision of the total station, corner stake locations are believed to be accurate within 10cm. Slope was corrected for in determining corner stake locations so that stake locations were on a true 10x10m grid, independent of slope. The corners were marked with a PVC stake resulting in a total of 1,200 individual 10x10m cells.

For sampling, every 10m x 10m cell had its own field data sheet, each of which had a blank map section. Each woody stem 5cm in diameter at breast height (DBH) was manually placed on the map within the appropriate 10m x 10m cell, tagged with a permanent aluminum tag, and characterized by species (or genus if a definitive characterization could not be made). Diameter at breast height was measured to the nearest 0.1cm using a DBH tape and a standardized height pole (1.3m) to ensure consistent documentation. Five of the 12 hectares were surveyed in 2016, and the entire plot surveyed in 2018-2019.

Stems that were tagged but died before the first survey in 2016 were documented, measured, made note of if standing or fallen, and mapped, but were not included in this study. Stems that died between surveys were recorded as such, measured, and noted if standing or fallen; these stems were accounted for in the mortality results. Analogously, recruitment occurred when stems entered the >5cm DBH size range, these stems were accounted for in the regeneration results.

Data analysis

Final determination of tree coordinates was via visual inspection of the stem location drawn on field data sheets, which was then entered into a spreadsheet as the within-cell x, y coordinates. These coordinates were then converted to plot-scale x, y coordinates based on the location of the lower left (southwest) corner of the cell.

Standard forest descriptors (e.g. density, species richness, mean \pm standard deviation of DBH) were calculated by species, by hectare and for the entire plot from the data collected in five hectares in 2016, the original five hectares again in 2018, as well as for the full twelve hectares in 2018. If an individual plant had a stem or stems with a DBH of 5cm-10cm, the individual was considered to be in the regeneration category, and summary statistics were presented separately. Species importance values can range from 0 to 300 and was calculated based on relative basal area, (species total basal area / total basal area), relative density (species stem count / total stem count), and relative frequency (number of cells species present / total number of cells with any stem present) for the 2018 survey only. Skewness of diameter distribution histograms will be used to characterize stand structure and make assessments on trends in species populations.

Species diversity across the whole plot as well as for each individual hectare was found using the Shannon-Wiener index, Simpson's Index, Pielou's evenness index and species richness. Species richness (S) was the count of unique species present. Simpson's diversity Index (D) was a measure of the probability that two individuals taken at random from a dataset will be the same species. This index gives more weight

to abundant species. Simpson's reciprocal index was used in this study, meaning this value will range from 1 up to the number of species found in the area surveyed.

$$D = 1 / \sum p_i^2$$

where p_i was the proportion of individuals belonging to a given species.

The Shannon-Wiener index of diversity (H') was a measure of uncertainty in predicting the species of a random individual from the dataset. If an area has a low species richness, was dominated by an individual species, or otherwise has an unequal abundance of species, H will be lower, reflecting the lower diversity.

$$H' = -\sum (p_i \times \ln[p_i])$$

Pielou's evenness index (E) was a measure of the relative abundance of the different species in a community and reflects how similar the abundances of different species are. This value will have a range between 0 and 1. A higher value means that the members of the community surveyed are present in similar quantities

$$E = H' / \ln(S)$$

Results

Full plot survey (2018)

a) All stems >5cm DBH

Out of the 1,200, 10x10m cells in this UGA FDP, 1,198 cells had at least one stem present. A total of 9,359 stems were documented in the 2018 survey. The density of stems across the 12 hectares was 779.92 stems/ha. The hectare with the greatest stem density was ha12 at 1,205 stems/ha and ha1 had the fewest stems at 519 stems/ha (Figure 2.2). The five most common species in order of abundance were

Ulmus alata (1,028 individuals), *Acer rubrum* (994 individuals), *Quercus alba* (986 individuals), *Fagus grandifolia* (935 individuals), and *Liquidambar styraciflua* (888 individuals). There were 16 species represented by less than 10 individuals and 8 species represented by a single individual (Table 4).

The total basal area (BA) across the 12 hectares in 2018 was 400.23m² with a mean of 33.35m² per ha. The hectare with the greatest BA was ha10 at 37.81m² and the hectare with the lowest total BA was ha1 at 29.65m² (Figure 2.2). The five species with the greatest total BA across the 12 hectares in 2018 were *Q. alba*, *Q. falcata*, *L. tulipifera*, *P. taeda*, and *Q. rubra*. There were 21 species that each had a total BA of less than 0.5m² (Table 4).

The mean DBH across the 12 hectares in 2018 was 18.14±14.96cm. The hectare with the greatest mean DBH was ha5 at 20.99±16.11cm and the hectare with the lowest mean DBH was ha12 at 14.44±10.67cm (Figure 2.2). The five species with the greatest mean DBH across the 12 hectares in 2018 were *Catalpa bignonioides*, *Q. velutina*, *Platanus occidentalis*, *Q. rubra*, and *Pinus echinata* (Figure 2.5). It should be noted that *Q. rubra* was the only one of these five species with more than 20 individuals and that *C. bignonioides* and *P. occidentalis* were represented by a single individual. There were 15 species that had a mean DBH of less than 10cm (Table 4).

The species richness across the 12 hectares in 2018 was 50, Simpson's Diversity index was 13.72, Pielou's evenness index was 0.74, and the Shannon-Wiener index was 2.89. The species richness ranged from 33 in ha4 to 24 in ha1, Simpson's Diversity index ranged from 11.85 in ha12 to 5.56 in ha1 (Figure 2.2), Pielou's evenness

index ranged from 0.81 in ha6 to 0.71 in ha1, and Shannon-Wiener index ranges from 2.74 in ha6 to 2.26 in ha1.

Species importance values range from 82.74 in *Q. alba* to 0.09 in *Campsis radicans*, *Sassafras albidum*, and *Crataegus sp.* After *Q. alba*, the next most important species were *Acer rubrum* (62.53), *Fagus grandifolia* (59.82), *Ulmus alata* (57.37), and *Liquidambar styraciflua* (50.61). It should be noted that this importance value is based on relative count, frequency, and basal area totals of all stems for each individual species.

Diameter distribution histograms for all hectares and the plot as a whole were found to have a positive skew. The diameter distribution skewness of all 12 hectares was found to be 1.95, individual hectares ranged in diameter distribution skewness from 1.5 in ha2 to 2.31 in ha7. All species were found to have a positively skewed diameter distribution except for *C. ovalis*, *Q. nigra*, *J. virginiana* and *I. opaca*. The greatest skewness of diameter distributions in the top ten most important species was found in *Ostrya virginiana* (3.18), *Ulmus alata* (2.86), and *Fagus grandifolia* (2.38); the least skewed diameter distributions were found in *Quercus rubra* (0.85), *Quercus alba* (0.48), and *Liriodendron tulipifera* (0.11) (Figure 2.3).

b) Regeneration (stems 5–10cm DBH)

Almost 45% of trees in this UGA FDP fell into the regeneration category for a total count of 4,178 individuals, density of regeneration was 348.17 stems/ha. The five species with the greatest number of individuals in the regeneration category were *Ulmus alata* (744 individuals), *Ostrya virginiana* (731 individuals), *Acer rubrum* (582 individuals), *Fagus grandifolia* (536 individuals), and *Liquidambar styraciflua* (371

individuals). There were 27 species with fewer than 10 stems in the regeneration category and 8 species with no stems in the regeneration category. The species richness of individuals with stems in the regeneration category was 42 species, the regeneration Simpson's Diversity index was 8.73, regeneration Pielou's evenness index was 0.67, and the regeneration Shannon-Wiener index was 2.52. The hectare with the greatest regeneration species richness was ha12 at 28 species, ha5 had the least at 14 species. Simpson's index for individuals with stems in the regeneration category was highest in ha6 at 8.61, the lowest D value was found in ha1 at 5.56. Shannon-Wiener index for individuals with stems in the regeneration category was highest in ha12 at 2.5, the lowest value was found in ha10 at 1.72. Pielou's evenness index for individuals with stems in the regeneration category was highest in ha5 at 0.79 and lowest in ha10 at 0.6 (Table 1).

Five Hectare Change (2016-2018)

a) All stems >5cm DBH

Standard forest descriptors (e.g. density, species richness, and mean DBH \pm standard deviation) were calculated by species, by hectare, for the entire five hectares and compared between the 2016 and 2018 surveys (Table 2, Figure 2.4).

The total number of stems found in hectares 1-5 decreased from 3,241 in 2016 to 3,198 in 2018. The density of stems in hectares 1-5 decreased from 648.2 stems/ha to 639.6 stems/ha across the five hectares. Three out of the five hectares saw a net decrease in number of stems; the greatest change was in ha1 with a loss of 24 individuals, the greatest gain was in ha3 with a gain of 10 individuals. The species with the highest mortality was *A. rubrum* with a loss of 29 individuals, however considering

new individuals, the net change in count was a loss of 23 (still greatest loss). There was a total of 17 out of the 39 species that saw zero mortality from 2016 to 2018. Only four species saw a net increase in population from 2016 to 2018: *Fagus grandifolia* (25 individuals), *Ostrya virginiana* (14 individuals), *Acer floridanum* (8 individuals), and *Carpinus caroliniana* (2 individuals).

Total BA increased by 6.22m² in hectares 1-5, from 159.18m² to 165.40m². All hectares increased in total BA, the greatest change in BA was in ha3 with a gain of 1.51m² from 32.53m² to 34.04m². The hectare with the least change in BA was ha4 with a gain of 1.07m² from 32.52m² to 33.59m². Out of the 39 species, 28 increased in total BA. *L. tulipifera* was the species that saw the greatest change in BA with an increase of 2.43m² (8.50%) from 28.60m² to 31.03m². The species with the greatest loss of BA was *C. glabra* with a loss of 0.43m² (2.87%) from 15.08m² to 14.64m².

Mean DBH increased by 0.45cm, from 19.59±15.86cm to 20.04±16.37cm. Trees in all hectares increased in mean DBH with the greatest change in mean DBH was in ha1 with a gain of 0.9cm, from 20.01±16.80cm to 20.91±17.66cm. The hectare with the least change in mean DBH was ha2 with a gain of 0.16cm from 19.8±15.76cm to 19.96±16.23cm (Table 2). All species increased in mean DBH, 9 species increased by 1cm or greater and 5 species saw an increase of less than 0.1cm. The species that saw the greatest change was *P. virginiana* with an increase of 2.94cm from 35.40±11.09cm to 38.34±9.69cm.

The total number of species recorded in hectares 1-5 was 39, this did not change between 2016 and 2018. The Simpson's Diversity index decreased from 11 to 10.7 across hectares 1-5 between 2016 and 2018. Pielou's evenness index equaled 0.74

and did not change between surveys. The Shannon-Wiener index decreased from 2.71 in 2016 to 2.69 in 2018. Simpson's Diversity index changed most in ha1 and ha2, decreasing by 0.46 in both cases, from 6.03 to 5.56 and 7.75 to 7.28 respectively. Pielou's evenness index changed by 0.02 or less in all hectares between measurements. The Shannon-Wiener index changed the most in ha1 from 2.32 in 2016 to 2.26 in 2018.

Diameter distribution skewness became more positive in five species, *F. americana*, *Q. rubra*, *N. sylvatica*, *A. floridanum*, and *C. florida*. Skewness decreased in 19 species and only became more negative in one already negatively skewed species, *C. ovalis*. All other negatively skewed species, along with a total of 15 species, showed no change in diameter distribution skewness between surveys.

b) Regeneration (stems 5–10cm DBH)

The total number of stems in the regeneration category decreased by 28 individuals from 1,313 individuals to 1,285 individuals and the density of individuals with stems in the regeneration category decreased by 5.6 from 262.6 individuals/ha to 257 individuals/ha (Table 3). All but one hectare saw a loss in regeneration density, ha3 increased by 7 stems from 314 and ha4 lost the greatest number of stems with a loss of 18 stems. All diversity metrics declined across ha1-5 in the regeneration layer. The species richness declined by 1 from 29 and Pielou's evenness index decreased slightly from 0.7 to 0.69. The Simpson index decreased by 0.48 from 7.59 to 7.04 and the Shannon diversity index decreased by 0.06 from 2.37 to 2.31. Three hectares declined in Simpson's index, the greatest of which was ha1 and ha2 with a loss of 0.46. The Simpson's index in ha5 had the greatest increase of 0.18, from 10.67 to 10.85. All five

hectares showed a decline in Shannon-Wiener index for individuals with stems in the regeneration category, except for ha4 which showed no change in H. ha1 had the greatest change with a decline of 0.06 from 2.32 to 2.26. Pielou's evenness decreased in two hectares (most in ha1 by 0.02), increased in one (ha5 by 0.01) and showed no change in ha3 and ha4.

Discussion

Patterns in community structure were observed apparently in association with topographic variation between the bottomland, plateau and southern slope areas of the UGA FDP. Many large *Fagus* were found in the bottomland area of the UGA FDP while *Q. alba* and *A. rubrum* were found in lower abundance. The majority of *Pinus taeda* and a very high density of small *Ulmus* were found in the southern slope area of the UGA FDP. There were two species exclusively observed in an area of the plateau with higher evidence of past human impact; *Catalpa bignonioides* and *Platanus occidentalis*. Additionally, *Acer negundo*, a species that is typically associated with growing in floodplains and other lower topographic elevations, was found primarily in this area of the plateau.

Ha1 was least diverse by every index and also had the total lowest stem density. Evenness did not seem to be an effective indicator for this site as it varied very little between hectares or years. Hectares with a greater density were found to have a higher Simpson's index (D) ($R^2 = 0.63$). Areas with a Simpson's index above 10 in 2016 saw an increase between surveys in D where hectares with less, declined in D. Herbaceous understory communities in Appalachian forests appear to take greater than 90 years to

recover from clearcutting, suggesting a long-term loss of diversity that is still recovering (Duffy & Meier, 1992). Of greater concern is the loss of secondary succession following current logging due to increasingly unfavorable environmental shifts (Duffy & Meier, 1992). Diversity metrics across the hectares followed similar patterns when comparing overall values and regeneration values, but the regeneration values were usually lower than the overall values. Hectares with a higher species richness overall were found to have a slightly higher regeneration Simpson's index. This relationship was weaker when applied to regeneration species richness.

According to the diameter distribution charts, the majority of *A. rubrum*, *F. grandifolia* and *U. alata* were mostly smaller stems whereas most oak (*Q. alba*, *Q. rubra*, *Q. falcata*) stems were 30-60cm DBH and showed a distinct lack in replacement stems in the 5-10cm DBH category range (Figure 2.3). There were two significant outliers in the size of individuals, one *F. grandifolia* with a total DBH between two stems of 137cm (81cm+56cm), the next largest was 67cm. The largest individual stem was a *Q. falcata* at 131cm, the next largest was 82cm. Note that *Ostrya* and *Ulmus* were generally composed of very small stems (Figure 2.3). Reverse J-shaped diameter distribution histograms have traditionally been thought to be characteristic of old-growth forests in an equilibrium state (Leak, 2002; Westphal et al., 2006). This is explained by near equal mortality rates between stems of all diameter sizes (Mcgee et al., 1999). Without a regeneration of oak to maintain the current community structure, oaks will lose dominance over time to species regenerating in greater quantities.

Using the definition provided by Hanberry (2016) that co-dominance is the ratio of count of the most important species to other species <2 , *U. alata*, *A. rubrum*, *F.*

grandifolia, *L. styraciflua*, and *O. virginiana* were the species co-dominant with *Q. alba*. This matches closely with the species that ranked highest in importance value. When considering the genus as opposed to individual species, *Acer* was the only genus that was co-dominant with *Quercus*. Four of the five co-dominant species, *U. alata*, *O. virginiana*, *A. rubrum*, and *F. grandifolia*, were also the top species by regeneration stem count. Two of which (*Acer* and *Fagus*) have been considered to be major, mesophytic, oak replacing species (Abrams & Downs, 1990; Abrams, 1996). When looking only at stems in the regeneration category, *Q. alba* was the tenth most abundant species. Co-dominance among regeneration stems revealed 15 species co-dominant with *Q. alba* and 11 genera co-dominant with the *Quercus* genus. When considering only stems 10cm DBH or greater, *L. styraciflua* was the only species co-dominant with *Q. alba*.

An old growth forest in southwestern Pennsylvania was found to have 62% of importance value total represented by *Fagus grandifolia* Ehrh., *Acer rubrum* L., and *Liriodendron tulipifera* L. and all oaks were represented by only 18% of the total importance value. This forest was considered to be a primary example of a forest that has undergone the mesophication cycle (Abrams & Downs, 1990). Across the full UGA FDP, *Fagus grandifolia* Ehrh., *Acer rubrum* L., and *Liriodendron tulipifera* L. importance values were 24.05% of the total where all oaks were found to comprise 24.78% of total importance value. By importance value, the forest that was considered to be a primary example of a mesified forest was dominated by mesic species whereas oaks as a genus comprise less than 20% of importance value. It was found this UGA FDP has not yet reached that level, but the oaks and mesic species were close in overall importance.

Because mesophication is an ongoing process occurring following a period of large-scale logging of eastern forests and organized fire suppression, affected forests will remain in an unnatural state of recovery for the foreseeable future (Nowacki & Abrams, 2015).

The same hectare had the lowest mean DBH, second to lowest total basal area, yet had the highest count and stem density, as has been found in other studies (Luyssaert et al., 2008). Frequent burning has been found to maintain generally lower tree density and higher proportion of oak species, and significantly higher density of oak saplings were found in burned sites (Signell et al., 2005). A study near Harrisburg, PA, found *Acer rubrum* to be far more abundant in unburned stands, with zero red maple saplings found in three out of four burned areas (Signell et al., 2005). Oak saplings were far more abundant under a less dense overstory; oak regeneration was found to be nearly absent when overstory or understory tree density exceeded 400 or 200 trees/ha, respectively. Under favorable conditions discussed above, oak seedlings experience little competition and continued oak dominance appears likely. It has been found that periodic burning reduces stand density and does work to foster the regeneration of more shade intolerant species like oak, however even with periodic burning, high canopy density still suppresses oaks (Signell et al., 2005).

In this UGA FDP, by both importance value and count, *Acer rubrum*, the most aggressive oak replacement species in eastern forests (Signell et al., 2005), was ranked second only to *Q. alba* and *U. alata*, respectively. Under a regime of fire suppression, highly competitive, opportunistic, mesophytic trees including red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), birch

(*Betula*), cherry (*Prunus*), tulip poplar (*Liriodendron tulipifera* L.), and blackgum (*Nyssa sylvatica* Marsh.) outcompete fire tolerant species (Nowacki & Abrams, 2008). Although the species with the highest importance value was *Q. alba*, without maintenance by fire, the site will become dominated by pyrophobic species like *O. virginiana*, *F. grandifolia*, *U. alata*, *A. rubrum*, *L. tulipifera* and *L. styraciflua* (Nowacki & Abrams, 2015). Based on the species found and those suggested to be indicative of mesophication, this UGA FDP did seem to be under the mesophication cycle.

However, the impact of deer herbivory has been shown to be the most important regulating process of eastern forests (Nuttall et al., 2013). Overabundance of deer has been found to reduce understory diversity, *Fagus* was found to dominate sites with uncontrolled deer browsing. Because *Fagus* is highly tolerant to over browsing, casts deep shade, and is highly shade tolerant, dense patches that severely depress other species are often formed, a phenomenon that may have been observed at the UGA FDP in individuals below the minimum size used in this study. Although not directly measured, the low overall amount of understory and shrub foliage observed suggest high amounts of deer herbivory. Unless deer abundance is reduced, areas where deer are overabundant will eventually have forest canopies where a few highly shade and browsing tolerant species dominate.

Invasive plants have been considered to be the largest threat posed by invasive organisms (Mack et al., 2000). Prior studies found the invasive shrubs *Lonicera maackii* and *Lonicera sinense* had greater impacts on below-ground soil characteristics than the aboveground plant community present (Kuebbing et al., 2013). However, this UGA FDP had a low number of invasive plants greater than five centimeters in diameter and

representing just a small number of species. Of the 50 species found across the 12 hectares, 2 were non-native (*Ligustrum* and *Elaeagnus*). There were only 8 of these stems and all were under 10cm DBH.

As a dominant species declines, species dominance distributions and abundances will shift in response to large availabilities in habitat. Over 60 years ago, the question of which species were replacing the blight killed chestnuts was considered to be “one of the most important problems facing regional ecologies” (Nelson, 1955). During any loss of a major species, this data will inform shifts in community assemblage at the UGA FDP.

Oaks were the most important species on this site, but based on the current maintenance regime, lack of burning, and younger stems present, a shift from oak to a more mixed-mesic dominated site can be expected. Improved parameterization of models using growth and mortality rates can be used to predict biomass and carbon changes in forest stands. Models such as these can be used to scale up characteristics observed in individual trees to population, community and ecosystem levels (Pan et al., 2013).

Literature Cited

- Abrams, M. D. (1996). Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. *Annales Des Sciences Forestieres*, 53(2–3), 487–512. <https://doi.org/10.1051/forest:19960230>
- Abrams, M. D., & Downs, J. A. (1990). Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. *Canadian Journal of Forest Research*, 20(12), 1864–1870. <https://doi.org/10.1139/x90-250>
- Duffy, D. C., & Meier, A. J. (1992). Do Appalachian Herbaceous Understories Ever Recover from Clearcutting? In *Conservation Biology* (Vol. 6, Issue 2).
- Hanberry, B. B., & Hanberry, P. (2020). Regaining the History of Deer Populations and Densities in the Southeastern United States. *Wildlife Society Bulletin*, 44(3), 512–518. <https://doi.org/10.1002/wsb.1118>
- Hanberry, B. B., & Nowacki, G. J. (2016). *Oaks were the historical foundation genus of the east-central United States*. Quaternary Science Reviews. <https://doi.org/10.1016/j.quascirev.2016.05.037>
- Kuebbing, S. E., ee Classen, A. T., & Simberloff, D. (2013). *Two co-occurring invasive woody shrubs alter soil properties and promote subdominant invasive species*. <https://doi.org/10.1111/1365-2664.12161>
- Leak, W. B. (2002). Origin of sigmoid diameter distributions. *USDA Forest Service, Res. Pap.*, 10. <http://www.fs.fed.us/ne>
- Luyssaert, S., Schulze, E. D., Börner, A., Knohl, A., Hessenmöller, D., Law, B. E., Ciais, P., & Grace, J. (2008). Old-growth forests as global carbon sinks. *Nature*, 455(7210), 213–215. <https://doi.org/10.1038/nature07276>

- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., & Bazzaz, F. A. (2000). Issues in Ecology BIOTIC INVASIONS: CAUSES, EPIDEMIOLOGY, GLOBAL CONSEQUENCES, AND CONTROL. In *Ecological Applications* (Vol. 10, Issue 3).
- McEwan, R. W., Dyer, J. M., & Pederson, N. (2011). Multiple interacting ecosystem drivers: Toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography*, 34(2), 244–256. <https://doi.org/10.1111/j.1600-0587.2010.06390.x>
- Mcgee, G. G., Leopold, D. J., & Nyland, R. D. (1999). STRUCTURAL CHARACTERISTICS OF OLD-GROWTH, MATURING, AND PARTIALLY CUT NORTHERN HARDWOOD FORESTS. In *Ecological Applications* (Vol. 9, Issue 4). [https://doi.org/10.1890/1051-0761\(1999\)009](https://doi.org/10.1890/1051-0761(1999)009)
- Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online at the following link: <http://websoilsurvey.sc.egov.usda.gov/>. Accessed [1/20/2021].
- Nelson, T. C. (1955). Chestnut Replacement in the Southern Highlands. *Ecology*, 36(2), 352–353. <https://doi.org/10.2307/1933248>
- Nowacki, G. J., & Abrams, M. D. (2008). The demise of fire and “mesophication” of forests in the eastern United States. In *BioScience* (Vol. 58, Issue 2). <https://doi.org/10.1641/B580207>
- Nowacki, G. J., & Abrams, M. D. (2015). Is climate an important driver of post-European vegetation change in the Eastern United States? *Global Change Biology*, 21(1), 314–334. <https://doi.org/10.1111/gcb.12663>

- Nuttle, T., Royo, A. A., Adams, M. B., & Carson, W. P. (2013). Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecological Monographs*, 83(1), 3–17. <https://doi.org/10.1890/11-2263.1>
- Pan, Y., Birdsey, R. A., Phillips, O. L., & Jackson, R. B. (2013). *The Structure, Distribution, and Biomass of the World's Forests*. <https://doi.org/10.1146/annurev-ecolsys-110512-135914>
- Signell, S. A., Abrams, M. D., Hovis, J. C., & Henry, S. W. (2005). Impact of multiple fires on stand structure and tree regeneration in central Appalachian oak forests. *Forest Ecology and Management*, 218(1–3), 146–158. <https://doi.org/10.1016/j.foreco.2005.07.006>
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. In *Nature* (Vol. 416, Issue 6879, pp. 389–395). Nature Publishing Group. <https://doi.org/10.1038/416389a>
- Westphal, C., Tremer, N., Oheimb, G. Von, Hansen, J., Gadow, K. Von, & Härdtle, W. (2006). Is the reverse J-shaped diameter distribution universally applicable in European virgin beech forests? *Forest Ecology and Management*, 223(1–3), 75–83. <https://doi.org/10.1016/j.foreco.2005.10.057>

CHAPTER 3

ABOVEGROUND BIOMASS AND CARBON ACCUMULATION OF TREES IN A PIEDMONT FOREST OVER TWO YEARS

Introduction

Worldwide, temperate forests play a large role in the carbon cycle. Globally they contain approximately 14% of global forest carbon and constitute nearly 30% of the forest carbon sink capacity (Pan et al., 2011). Temperate forests the world over saw a net increase in both total carbon stock and density in total live biomass from 1990 to 2007 (Pan et al., 2013). Current international efforts to limit greenhouse gasses necessitate a thorough understanding of the current and future state of forest carbon dynamics (Pan et al., 2011). In 2007, predictions of net carbon uptake by terrestrial ecosystems have ranged from less than 1.0 to as much as 2.6 PgC/yr for the 1990s (Pan et al., 2011), a wide range that illustrates the necessity in improving understanding of terrestrial carbon dynamics. The data collected at permanent vegetative plots are critical to assessing long term forest dynamics and may have significant implications considering forests ability to continually accumulate carbon and serve as critical long-term carbon sinks (Lowney et al., 2016).

Forests remove carbon from the atmosphere, however, rates vary with climate and environmental conditions (Luyssaert et al., 2008). Warmer temperatures and decreasing water availability may act to shift ecosystem function such that forests that previously acted as a carbon sink, become net carbon sources due to increased tree

mortality (Walther, 2010). Shifting climatic conditions may lead to trade-offs in tree growth patterns as more stressful conditions reduce overall tree size or restrict rates of cell division (Pan et al., 2013). The exact quantity of forest carbon sink capabilities has not been precisely defined, it is essential that multi-aged, multi-species natural forests are accounted for in future models of terrestrial carbon dynamics (Carey et al., 2001). The environmental shift from more frequent, severe, multi-year droughts in the southeastern United States to more infrequent droughts and greater moisture availability has bolstered mesophication and impacted oak regeneration (McEwan et al., 2011).

The shift from xeric and pyrophytic to shade tolerant, mesophytic species may affect long term sustainability of eastern forests ecosystems and cause a loss of ecosystem services such as carbon sequestration (Knott et al., 2019). This self-reinforcing feedback loop excludes fire-resistant, shade-intolerant species like oak in favor of mesophytic species (Nowacki & Abrams, 2008). The ecological availability provided with the loss of chestnut gave red maples an opportunity to regenerate unsuppressed by fire (McEwan et al., 2011). Forest carbon dynamics will change over time as large trees die and the forest transitions from oak dominated to mix-mesic dominated (Schedlbauer & Polohovich, 2020). While temperate forests have a large carbon sink capacity, the long-term stability of these abilities are uncertain in the face of large changes.

When the maple species began to regenerate in greater numbers than oaks and the mesophication cycle were just beginning to develop, a significant canopy species, the American chestnut, was lost on a massive scale (McEwan et al., 2011; Nelson,

1955). The suppression of fire in combination with the loss of a dominant overstory species led to regeneration of maples unhindered by fire, suppressing the naturally dominant oak community (McEwan et al., 2011). Additionally, anthropogenic disturbance regimes underwent a dramatic shift from low density Native American populations to increasingly dense European settlement with more intense land utilization practices like logging and cropland (McEwan et al., 2011).

In addition to fire and drought, US forests have shown significantly increased stem mortality in recent decades due in large part to insect outbreaks, (Pan et al., 2011). Impacts such as these can affect millions of trees over vast areas, resulting in extreme impacts to ecosystem dynamics caused by wide scale mortality and stunted growth (Kurz et al., 2008). In modeling carbon forest dynamics, it is critical to account for the significant impact large outbreaks of forest pests and pathogens have on the ability of forests to uptake and store carbon. Invasive species are known to have significant impacts on invaded forest ecosystems but the exact effect on carbon dynamics over time are not well known (Bradford et al., 2012; Kurz et al., 2008; Litton et al., 2006). Clearly changes to distribution of carbon in the ecosystem can have significant impacts on ecosystem carbon dynamics (Litton et al., 2006).

The long-term plot will allow researchers to focus on monitoring carbon sequestration rates to inform the continued carbon sink effectiveness of the eastern forest ecosystem as they shift in response to anthropogenic impacts. This chapter focuses on biomass accumulation and carbon sequestration rate of the site as well as interspecific variation. The primary questions were: how much biomass and carbon was stored in living aboveground stems in this second growth temperate hardwood

ecosystem? What was the variation in the quantity of biomass and carbon stored across the species present? How much biomass and carbon was accumulated in living aboveground stems between the 2016 and 2018 survey? What was the variation in rate of species biomass and carbon accumulation?

Methods

Site background

The University of Georgia Forest Dynamics Plot (UGA FDP) at the State Botanical Garden of Georgia (33.9015N, 83.3789W) is a second growth forest in the Georgia Southern Outer Piedmont ecoregion. It is located at the 126.7-hectare State Botanical Garden of Georgia (SBG) in Clarke County, Georgia. Approximately 87% of the SBG is natural forested cover in various stages of maturity, the dominant growth form in this UGA FDP is deciduous broadleaf trees.

The University System of Georgia purchased the property where the State Botanical Gardens of Georgia is located in July 1936. However, aside from black and white aerial photography acquired by the USDA, there is little information concerning the land use pre-1968, and almost no information about the landscape pre-1936. Initially, the land was used by the Agronomy Department for “research and development”. Later, the site was used by the school of Forestry and Horticulture Department for research and practice areas. There were piled rocks and remains of barbed wire, suggesting past use as agriculture and pastureland. The aerial photography taken in 1938 indicated that this UGA FDP was roughly half agriculture, pasture, or very early successional forest and half more clearly developed forest. From

1951 onward, aerial photography shows what appears to be a more closed canopy forest. Based on these images it can be inferred that the successional age of the majority of this UGA FDP was 80+ years with some areas at an age of 70-80 years. There was no record of any burn, prescribed or otherwise, taking place at this site.

The soil composition within the plot is approximately 53.8% Madison sandy loam, 22.2% Louisburg loamy sand, 15.1% Pacolet sandy clay loam, and 7.9% Pacolet sandy loam (Figure 2.1; Natural Resources Conservation Service, 2020). These soils are fine, kaolinitic, thermic Typic Kanhapludults (Pacolet sandy clay, Pacolet sandy loam, Madison sandy loam) and coarse-loamy, mixed, semi-active, thermic Typic Hapludults (Louisburg sandy loam). The elevation at this site ranges from 173m to 208m above sea level and it is located in the lower Middle Oconee River watershed basin. The majority of the site has a slope ranging from 6%-15%.

The climate on this site is characterized by warm, humid summers and wet, cool winters. The site has historically been classified into the USDA hardiness zone 7B, however currently the site is in zone 8A. Last frost typically occurs between March 30th and April 5th and first frost typically falls between October 30th and November 5th. Temperatures range from an average of 1.6C in the winter to 32.2C in the summer with an annual average of 17C (NOAA 1981-2010 averages). Snow and ice storms are infrequent, but trace amounts of snow are not uncommon. From 1981-2010, average precipitation ranged from 26.9cm in the spring to 31.2cm in the winter with a mean annual total of 117.7cm.

Plot establishment

A 12 hectare, rectangular, 400x300m permanent plot was established in 2015 (Figure 1.1). A Topcon CTS-2 total station was used to locate the position of grid corners every 10m. Given the precision of the total station, it is likely that the corner stake locations to be accurate within 10cm. Slope was corrected for in determining corner stake locations so that stake locations were on a true 10x10m grid, independent of slope. The corners were marked with a PVC stake resulting in a total of 1,200 individual 10x10m cells.

Every 10m x 10m cell had its own field data sheet, each of which had a blank map section. Each woody stem 5cm in diameter at breast height was manually placed on the map within the appropriate 10m x 10m cell, tagged with a permanent aluminum tag, and characterized by species (or genus if a definitive characterization could not be made). Diameter at breast height was measured to the nearest 0.1cm using a DBH tape and a standardized height pole (1.3m) to ensure consistent documentation. Five of the 12 hectares were surveyed in 2016, and the entire plot surveyed in 2018-2019.

Stems that were tagged but died before the first survey in 2016 were documented, measured, made note of if standing or fallen, and mapped, but were not included in this study. Stems that died between surveys were recorded as such, measured, and noted if standing or fallen; these stems were accounted for in the mortality results.

Data analysis

Final determination of tree locations was via visual inspection of the drawn stem location from the map on field data sheets, which was then entered into a spreadsheet

as the within-cell x, y coordinates. These coordinates were then converted to plot-scale x, y coordinates based on the location of the lower left (southwest) corner of the cell.

Aboveground biomass (AGB) and carbon stored in living stems was calculated by species, by hectare and for the entire plot from the data collected in five hectares in 2016, the five resampled hectares in 2018, as well as for the full 12 hectares in 2018. Biomass for each measured stem was calculated using allometric equations (Jenkins et al., 2003):

$AGB = \text{Exp} (\beta_0 + \beta_1 \ln DBH)$ where

AGB = total aboveground biomass (kg) for trees $\geq 2.5\text{cm}$ DBH

β_0 and β_1 = species-specific parameters for estimating biomass.

Each stem was placed in a species group from Jenkins et al (2003) and the β_0 and β_1 parameters appropriate to that species group were used in the calculations. Only aboveground biomass was included, belowground biomass includes coarse and fine roots, and although consuming a large portion of the net primary productivity of a forest, fine roots constitute a small portion of total carbon of a forest (Keyser, 2011).

Results

The total aboveground biomass (AGB) recorded across the 12 hectares in 2018 was 2,945.85Mg. The hectare with the greatest AGB was ha5 at 279.62Mg and the hectare with the least AGB was ha12 at 191.24Mg (Figure 3.1). The five species with the greatest total AGB in the plot were *Quercus alba*, *Quercus falcata*, *Quercus rubra*, *Liriodendron tulipifera* and *Pinus taeda*. *Q. alba* alone constitutes 25% of the aboveground biomass in the plot at 738.75Mg. There were ten species in the plot with a

total AGB of less than 100kg. Biomass increased by a total of 66.48Mg in hectares 1-5, from 1229Mg to 1295.49Mg. All hectares gained in biomass between surveys; the greatest change in AGB was in ha1 with a gain of 15.75Mg from 229.60Mg to 245.35Mg and the hectare with the least change in AGB was ha2 with a gain of 10.7Mg from 228.96Mg to 239.66Mg.

Across all 12 hectares in 2018, the total amount of above ground carbon (AGC) in living stems greater than 5cm DBH was 1,472.93Mg. The mean amount of AGC across the 12 hectares was 122.74 ± 12.92 Mg. The hectare with the greatest quantity of AGC was ha5 with 139.81MgC, the lowest quantity recorded was found in ha12 with 95.62MgC (Figure 3.2). Across all 12ha in 2018, the species with the greatest total carbon was *Q. alba* with 369.38MgC. There were five species with total carbon values of over 100MgC in 2018: *Q. alba*, *Q. falcata*, *Q. rubra*, *L. tulipifera*, and *P. taeda*. There were 37 out of the 50 species that each constituted less than 1% of the total aboveground carbon found in this UGA FDP and 18 species that each had less than 1MgC total.

From 2016 to 2018, the species with the greatest change in biomass was *Q. alba* with a gain of 25.80Mg (7.89%) from 327.13Mg to 352.93Mg. Along with *Q. alba*, there were five additional species that gained 1Mg or more: *Liriodendron tulipifera* (22.88Mg), *Fagus grandifolia* (8.18Mg), *Quercus rubra* (7.23Mg), *Liquidambar styraciflua* (2.15Mg), and *Quercus falcata* (1.45Mg) (Figure 3.3). There were 7 species that saw a loss in total biomass; *Juniperus virginiana*, *Nyssa sylvatica*, *Prunus serotina*, *Cornus florida*, *Acer rubrum*, and *Pinus echinata*. The species with the greatest loss in total biomass was *C. glabra* with a loss of 3.17Mg (2.39%) from 132.44Mg to 129.273Mg.

The total aboveground carbon in ha1-5 increased by 33.24MgC (5.4%) from 614.5MgC to 647.74MgC. All hectares increased in total carbon from 2016 to 2018 (Figure 3.4). The hectare with the greatest gain in aboveground carbon was ha1 with an increase of 7.87MgC (6.86%), the least overall gain in carbon was seen in ha2 with an increase of 5.35MgC (4.67%), and the mean gain in carbon per hectare was 6.65 ± 1.12 MgC (5.43%). Interestingly, hectares with a greater initial starting biomass did not gain more carbon than hectares with lower initial biomass. Additionally, denser hectares, plots with greater number of stems/ha, did not result in more total carbon sequestered between surveys. In 2016, the species with the greatest total carbon was *Q. alba* at 163.56MgC, *Q. alba* was also the species that gained the most total carbon between surveys at 12.90MgC for an increase of 7.89%. 31 out of the 39 species found in ha1-5 increased in carbon, 8 species saw a loss in total carbon. The species with the greatest decrease in carbon was *C. glabra* with a decrease of 1.58MgC (2.39%).

Discussion

In a review of 519 forest dynamic plot studies covering boreal and temperate sites, forests 200 years of age or greater sequester on average 2.18 ± 0.73 MgC/ha/yr (Luyssaert et al., 2008); this UGA FDP was found to sequester 3.32 ± 0.56 MgC/ha/yr. A recent summary of carbon storage capacity in remaining old growth forests of the mid-Atlantic provides an approximate upper limit on aboveground carbon storage for living tree biomass in old growth forests of 154 ± 47 Mg/ha, in contrast to the surrounding younger forest at 120Mg/ha. (Mcgarvey et al., 2015). Total starting biomass and stem density of a hectare were not found to impact amount of carbon gained between

surveys. Unlike a metric like species diversity which was relatively consistent between surveys, every hectare increased in biomass between surveys, suggesting the significance of frequent repeated surveys if the objective of a study is higher resolution data on community carbon dynamics. Depending on study objectives, mortality rates could also be beneficial to resurvey frequently.

There has been some interest in whether the relationship between aboveground woody biomass productivity, represented by change in AGB per year, has any relationship with species diversity (Wang et al., 2016). Data collected at this UGA FDP showed a non-significant, moderate negative relationship between change in AGB per year and all diversity indices.

Interestingly, all 6 of the highest count species, except for *Q. alba*, were found to have atypically low total biomass values, compared to other species present at this UGA FDP. Those five species were found to have less biomass than other species that had half of the number of stems. Oaks (*Q. alba*, *Q. rubra*, *Q. falcata*) were 3 of the species that gained the most biomass and carbon between surveys. Red maple (*A. rubrum*) was one of the species that lost the most biomass. In other studies, fire tolerant oak species store larger reserves of carbon in belowground tissue than maples (Abrams, 1992; McEwan et al., 2011). The fact that these pyrophytic species sequester more carbon per unit of time gives more reason to try to combat mesophication with more rigorous prescribed burn regimes. Although *A. rubrum* does respond to heightened atmospheric carbon dioxide with elevated photosynthetic rate and biomass production, this response may not be greater than other species present (Abrams, 1998), more research at a site like this UGA FDP is needed.

Because the carbon released through decay is generally offset by increased photosynthesis in gap-adjacent individuals, it is widely thought that stable state old-growth forests are carbon neutral, in that net photosynthesis and respiration are roughly equal (Carey et al., 2001; Luyssaert et al., 2008). However, whether in boreal or temperate forest, data consistently indicate that carbon sequestration endures in centuries old forests, although not indefinitely (Luyssaert et al., 2008). Globally, biomass in soils, litter, and coarse woody debris is greater than living biomass (Pan et al., 2013). Although this UGA FDP was not an old growth forest, it will be important to record quantities of carbon stored in coarse woody debris and litter to better observe rates of carbon sequestration over time as ecosystem dynamics change in response to shifting environmental conditions.

Typically, older stands of trees hold relatively fewer individuals but of a larger size while an increase in density of stems has been shown to accumulate significantly less biomass per hectare (Luyssaert et al., 2008). Small scale disturbances, rather than large, stand replacing events, maintain multilayered, multi-aged stands at a density that are expected to maintain biomass accumulation for decades (Luyssaert et al., 2008). Data collected at this UGA FDP showed less dense hectares tend to store more biomass and carbon per unit area (Figure 3.5). Data collected at long term forest dynamics plots like this UGA FDP will be key in quantifying how carbon accumulation develops as the forest ages under long term fire suppression.

Sites like these should be burned frequently, every two years, to maintain less dense, more open systems that encourage larger trees and species that sequester more carbon (Nowacki & Abrams, 2008). More frequent burns create open systems with

lower stem density and fire suppression results in denser systems (Nowacki & Abrams, 2008). Landowners should be burning both to preserve and maintain diversity and high carbon sequestration ecosystems and land stewardship organizations should increasingly focus on education on the importance of burning and its impact on carbon dynamics and biodiversity.

Increased precipitation in the southeastern United States favors mixed-mesic species like maples over xeric adapted species like oak (McEwan et al., 2011). If a regime of fire suppression continues under these wetter environmental conditions, increasingly unfavorable conditions for oak regeneration can be expected (McEwan et al., 2011). However, this shifting community structure was not a result of fire suppression in isolation, oak forests have been reacting to multiple interconnected factors (McEwan et al., 2011). Under the current suppressed fire regime at this UGA FDP, it can be expected that oaks will continue to be replaced by shade adapted, fire intolerant, mixed-mesophytic species like red maple, tulip poplar and beech.

Invasive species are known to have significant impacts on invaded forest ecosystems but the exact effect on carbon dynamics over time are not well known (Bradford et al., 2012; Litton et al., 2006). The presence of an invasive grass, *Microstegium vimineum* (Trin.) A. Camus, was observed but not formally recorded at this UGA FDP (Bradford et al., 2012). Bradford et al. stated this invasive has been found to increase net carbon sequestration of invaded sites, but shifts carbon below-ground, impacting ecosystem food webs, illustrating how invasive species can affect ecosystem carbon (Bradford et al., 2012). Additionally, it has previously been found that the invasive shrubs *Lonicera maackii* and *Ligustrum sinense* had greater impacts on

below-ground soil characteristics than the aboveground plant community present (Kuebbing et al., 2014). In other studies, presence of *Ligustrum* was found to increase net carbon in the shrub layer (Burton & Samuelson, 2008). Invasive plants can have varied and dramatic effects on ecosystem carbon dynamics and the minimal number of non-native shrubs and trees currently present make this a good site to observe future impacts invading plants may have on ecosystem carbon dynamics (Vilà et al., 2011).

In modeling carbon forest dynamics, it is critical to account for the significant impact large outbreaks of forest pests and pathogens have on the ability of forests to uptake and store carbon. However, the impact of insects on carbon dynamics is currently not well documented (Kurz et al., 2008). Insect outbreaks can affect millions of trees over vast areas, resulting in extreme impacts to ecosystem dynamics caused by mortality and stunted growth to trees (Kurz et al., 2008).

The exact quantity of forest carbon sink capabilities is currently too ill defined to precisely estimate global carbon budget (Carey et al., 2001). The terrestrial carbon sink total size and location remain uncertain, quantifying forest metrics and observing shifts over time is critical to determining these parameters (Pan et al., 2011). Improved parameterization of models using growth and mortality rates can be used to predict biomass and carbon changes in forest stands. Models such as these can be used to scale up characteristics observed in individual trees to population, community and ecosystem levels (Pan et al., 2013). It is essential that multi-aged, multi-species natural forests are accounted for in future models of terrestrial carbon dynamics (Carey et al., 2001). With aid of high-resolution remote imaging such as aerial photography or LiDAR, a model can simulate carbon sequestration patterns and shifts in species demographics

at a landscape scale (Pan et al., 2013). Forest carbon dynamics will change over time as large trees die and the forest transitions from oak dominated to mix-mesic dominated (Schedlbauer & Polohovich, 2020). In order to be considered old growth, a forest must avoid stand replacing disturbance for centuries (Luyssaert et al., 2008). Yet since cumulative probability of disturbance increases along with aboveground biomass, older forests are rarer than younger, even in unmanaged landscapes (Luyssaert et al., 2008). Carefully monitoring changing ecosystem function and carbon dynamics of taxonomic groups and evaluating varying responses to shifting environmental conditions will be critical to informing management and policy decision making (Pan et al., 2011).

Literature Cited

- Abrams, M. D. (1992). Fire and the Development of Oak Forests. *BioScience*, 42(5), 346–353. <https://doi.org/10.2307/1311781>
- Abrams, M. D. (1998). The red maple paradox: What explains the widespread expansion of red maple in eastern forests? In *BioScience* (Vol. 48, Issue 5). <https://doi.org/10.2307/1313374>
- Bradford, M. A., Strickland, M. S., DeVore, J. L., & Maerz, J. C. (2012). Root carbon flow from an invasive plant to belowground foodwebs. *Plant and Soil*, 359(1–2), 233–244. <https://doi.org/10.1007/s11104-012-1210-y>
- Burton, M. L., & Samuelson, L. J. (2008). Influence of urbanization on riparian forest diversity and structure in the Georgia Piedmont, US. *Plant Ecology*, 195(1), 99–115. <https://doi.org/10.1007/s11258-007-9305-x>
- Carey, E. V., Sala, A., Keane, R., & Callaway, R. M. (2001). Are old forests underestimated as global carbon sinks? *Global Change Biology*, 7(4), 339–344. <https://doi.org/10.1046/j.1365-2486.2001.00418.x>
- Jenkins, J. C., Chojnacky, D. C., Heath, L. S., & Birdsey, R. A. (2003). National-scale biomass estimators for United States tree species. *Forest Science*, 49(1), 12–35. <https://doi.org/10.1093/forestscience/49.1.12>
- Keyser, T. L. (2011). *Carbon Dynamics Following the Creation of Early Successional Habitats in Forests of the Central Hardwood Region* (pp. 271–287). https://doi.org/10.1007/978-94-007-1620-9_15

- Knott, J. A., Desprez, J. M., Oswalt, C. M., & Fei, S. (2019). Shifts in forest composition in the eastern United States. *Forest Ecology and Management*, 433, 176–183. <https://doi.org/10.1016/j.foreco.2018.10.061>
- Kuebbing, S. E., Classen, A. T., & Simberloff, D. (2014). Two co-occurring invasive woody shrubs alter soil properties and promote subdominant invasive species. *Journal of Applied Ecology*, 51(1), 124–133. <https://doi.org/10.1111/1365-2664.12161>
- Kurz, W. A., Dymond, C. C., Stinson, G., Rampley, G. J., Neilson, E. T., Carroll, A. L., Ebata, T., & Safranyik, L. (2008). *Mountain pine beetle and forest carbon feedback to climate change*. 452. <https://doi.org/10.1038/nature06777>
- Litton, C. M., Sandquist, D. R., & Cordell, S. (2006). Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii. *Forest Ecology and Management*, 231(1–3), 105–113. <https://doi.org/10.1016/j.foreco.2006.05.008>
- Lowney, C. A., Graham, B. D., Spetich, M. A., Shifley, S. R., Saunders, M. R., & Jenkins, M. A. (2016). Two decades of compositional and structural change in deciduous old-growth forests of Indiana, usa. *Journal of Plant Ecology*, 9, 256–271. <https://doi.org/10.1093/jpe/rtv050>
- Luyssaert, S., Schulze, E. D., Börner, A., Knohl, A., Hessenmöller, D., Law, B. E., Ciais, P., & Grace, J. (2008). Old-growth forests as global carbon sinks. *Nature*, 455(7210), 213–215. <https://doi.org/10.1038/nature07276>

- McEwan, R. W., Dyer, J. M., & Pederson, N. (2011). Multiple interacting ecosystem drivers: Toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography*, 34(2), 244–256. <https://doi.org/10.1111/j.1600-0587.2010.06390.x>
- Mcgarvey, J. C., Thompson, J. R., Epstein, H. E., & Shugart, H. H. (2015). Carbon storage in old-growth forests of the Mid-Atlantic: toward better understanding the eastern forest carbon sink. In *Reports Ecology* (Vol. 96, Issue 2).
- Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online at the following link:
<http://websoilsurvey.sc.egov.usda.gov/>. Accessed [1/20/2021].
- Nelson, T. C. (1955). Chestnut Replacement in the Southern Highlands. *Ecology*, 36(2), 352–353. <https://doi.org/10.2307/1933248>
- Nowacki, G. J., & Abrams, M. D. (2008). The demise of fire and “mesophication” of forests in the eastern United States. In *BioScience* (Vol. 58, Issue 2).
<https://doi.org/10.1641/B580207>
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world’s forests. *Science*, 333(6045), 988–993.
<https://doi.org/10.1126/science.1201609>
- Pan, Y., Birdsey, R. A., Phillips, O. L., & Jackson, R. B. (2013). *The Structure, Distribution, and Biomass of the World’s Forests*. <https://doi.org/10.1146/annurev-ecolsys-110512-135914>

Schedlbauer, J. L., & Polohovich, S. (2020). Current and Future Carbon Storage Capacity in a Southeastern Pennsylvania Forest.

Https://Doi.Org/10.3375/043.040.0402, 40(4), 300–308.

<https://doi.org/10.3375/043.040.0402>

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. In *Ecology Letters* (Vol. 14, Issue 7, pp. 702–708). John Wiley & Sons, Ltd.

<https://doi.org/10.1111/j.1461-0248.2011.01628.x>

Walther, G.-R. (2010). The effects of climate change on biotic interactions and ecosystem services. *Philosophical Transactions: Biological Sciences*, 365(1549), 2019–2024. <https://doi.org/10.1098/rstb.2010.0021>

Wang, J., Cheng, Y., Zhang, C., Zhao, Y., Zhao, X., & Von Gadow, K. (2016). Relationships between tree biomass productivity and local species diversity. *Ecosphere*, 7(11), e01562. <https://doi.org/10.1002/ecs2.1562>

Table 1. Diversity Values for the entire plot per hectare in 2018.

Ha	Density (Stems /ha)	Basal Area (m ²)	Mean DBH \pm Standard Deviation	Species Richness (S)	Simpson's Index (D)	Shannon- Wiener index (H)	Evenness (E)
1	519	29.65	20.91 \pm 17.66	24	5.56	2.26	0.71
2	630	32.54	19.96 \pm 16.23	27	7.28	2.43	0.74
3	728	34.04	18.78 \pm 16.06	30	9.61	2.58	0.76
4	670	33.59	19.89 \pm 15.98	33	10.55	2.66	0.76
5	651	35.58	20.99 \pm 16.11	27	10.85	2.62	0.80
6	775	31.94	18.46 \pm 13.94	29	11.70	2.74	0.81
7	767	32.95	17.68 \pm 15.72	33	10.66	2.73	0.78
8	674	35.20	19.98 \pm 16.36	32	9.99	2.65	0.77
9	964	31.87	16.27 \pm 12.65	31	10.82	2.67	0.78
10	880	37.81	18.12 \pm 15.22	25	6.92	2.39	0.74
11	896	34.80	17.06 \pm 14.47	33	10.47	2.67	0.76
12	1205	30.25	14.44 \pm 10.67	31	11.85	2.72	0.79
Full FDP (total)	779.92 (9359)	400.23	18.14\pm14.96	50	13.72	2.89	0.74

Table 2. Data for changes from 2016 to 2018

	Plot1-5,'16	Plot1-5,'18	Plot1-5Δ	Plot1-12,'18
Species Richness	39	39	0	50
Biomass (Mg)	1229.0018	1295.4859	66.48408	2945.85136
Basal Area	159.18	165.40	6.22	400.23
Count	3241	3198	-43	9359
Number Died	x	133	x	x
Percent Died	x	4.10	x	x
DBH \pm Standard Deviation	19.59 \pm 15.86	20.04 \pm 16.37	0.45 \pm 0.51	18.14 \pm 14.96
Density	648.2	639.6	-8.6	779.92
Simpson's Index	11.00	10.70	-0.30	13.72
Shannon Weiner Index	2.71	2.69	-0.02	2.89

Table 3. Diversity data for stems in the regeneration category from 2016 to 2018.

	Hectare 1-5, 2016	Hectare 1-5, 2018	Hectare 1-5Δ	Hectare 1-12, 2018
Evenness	0.70	0.69	-0.01	0.67
Species Richness	29	28	-1	42
Count	1313	1285	-28	4178
Density	262.6	257	-5.6	348.17
Simpson's Index	7.52	7.04	-0.48	8.73
Shannon Weiner Index	2.37	2.31	-0.06	2.52

Table 4. List of all species with botanical authorities and collected data in 2018.

Species and Authority	Count	Density (count/ha)	Mean DBH	Biomass (Mg)	Basal Area (m ²)	Importance Value
<i>Acer floridanum</i> (Chapm.) Pax	282	23.50	7.78±3.48	5520.95	1.31	18.03
<i>Acer leucoderme</i> Small	27	2.25	8.32±4.19	461.04	0.12	2.24
<i>Acer negundo</i> L.	22	1.83	16.94±11.22	4547.99	0.65	1.40
<i>Acer rubrum</i> L.	994	82.83	11.29±7.07	67989.54	12.67	62.53
<i>Acer saccharinum</i> L.	13	1.08	10.08±4.9	685.80	0.13	1.26
<i>Amelanchier arborea</i> (F. Michx.) Fernald	30	2.50	8.63±2.98	647.48	0.20	2.46
<i>Campsis radicans</i> (L.) Bureau	1	0.08	6.2±0	7.78	0.00	0.09
<i>Carpinus caroliniana</i> Walter	130	10.83	8.4±4.05	2674.18	0.79	9.85
<i>Carya glabra</i> (Mill.) Sweet	214	17.83	28.02±16.9	155226.86	17.87	22.03
<i>Carya ovalis</i> (Wangenh.) Sarg.	102	8.50	29.51±16.17	77430.99	8.92	11.08
<i>Carya tomentosa</i> (Poir.) Nutt.	12	1.00	34.29±18.9	13102.37	1.42	1.40
<i>Catalpa bignonioides</i> Walter	1	0.08	69.2±0	3110.66	0.38	0.19
<i>Cercis canadensis</i> L.	8	0.67	6.71±1.58	82.71	0.03	0.76
<i>Cornus florida</i> L.	101	8.42	8.66±2.93	2195.13	0.66	9.17
<i>Crataegus</i> sp. L.	1	0.08	5.5±0	5.78	0.00	0.09
<i>Diospyros virginiana</i> L.	10	0.83	12.76±8.08	796.37	0.17	0.82
<i>Elaeagnus umbellata</i> Thunb.	2	0.17	5.2±0	10.05	0.00	0.19
<i>Fagus grandifolia</i> Ehrh.	935	77.92	13.53±11.22	161374.60	21.69	59.82
<i>Fraxinus americana</i> L.	60	5.00	16.26±11.23	10318.36	1.83	5.86
<i>Fraxinus pennsylvanica</i> Marshall	145	12.08	12.49±8.33	12691.11	2.56	12.71
<i>Gymnocladus dioica</i> (L.) K. Koch	1	0.08	10.3±0	27.44	0.01	0.10
<i>Ilex opaca</i> Aiton	6	0.50	11.97±2.05	212.35	0.06	0.58
<i>Juniperus virginiana</i> L.	9	0.75	20.91±7.41	1309.51	0.34	0.85
<i>Ligustrum sinense</i> Lour.	6	0.50	8.18±3.52	78.37	0.03	0.40
<i>Liquidambar styraciflua</i> L.	888	74.00	15.53±10.54	127319.48	23.94	50.61
<i>Liriodendron tulipifera</i> L.	429	35.75	32.11±18.74	319197.13	45.70	43.30
<i>Magnolia acuminata</i> (L.) L. or Hardin	15	1.25	20.09±12	3522.88	0.63	1.57
<i>Morus rubra</i> L.	29	2.42	11.52±8.9	2462.86	0.48	2.52
<i>Nyssa sylvatica</i> Marshall	279	23.25	10.35±7.55	17194.81	3.59	21.24
<i>Ostrya virginiana</i> (Mill.) K. Koch	841	70.08	7.86±3.53	15834.51	4.69	44.80
<i>Oxydendrum arboreum</i> (L.) DC.	292	24.33	17.57±8.8	39089.23	8.13	22.68
<i>Pinus echinata</i> Mill.	15	1.25	37.71±6.77	8622.04	1.73	2.01
<i>Pinus taeda</i> L.	422	35.17	32.83±17	240501.93	45.09	34.06
<i>Pinus virginiana</i> Mill.	17	1.42	34.64±9.81	8547.25	1.72	1.86
<i>Platanus occidentalis</i> L.	1	0.08	42.4±0	921.54	0.14	0.13
<i>Prunus serotina</i> Ehrh.	102	8.50	11.79±5.06	5316.21	1.32	7.26
<i>Quercus alba</i> L.	986	82.17	29.21±15.63	738753.02	84.86	82.74

<i>Quercus falcata</i> Michx.	424	35.33	35.63±12.34	414192.95	47.34	41.57
<i>Quercus hemisphaerica</i> W. Bartram ex Willd.	10	0.83	18.06±10.47	2349.38	0.33	1.02
<i>Quercus marilandica</i> Münchh.	1	0.08	13.6±0	76.76	0.01	0.10
<i>Quercus nigra</i> L.	130	10.83	23.15±10.58	49610.45	6.61	11.72
<i>Quercus phellos</i> L.	1	0.08	20.5±0	208.43	0.03	0.10
<i>Quercus rubra</i> L.	263	21.92	39.92±16.58	357573.76	38.30	30.49
<i>Quercus stellata</i> Wangenh.	15	1.25	27.77±18.47	11672.41	1.28	1.73
<i>Quercus velutina</i> Lam.	9	0.75	45.42±17.37	16008.97	1.65	1.18
<i>Sassafras albidum</i> (Nutt.) Nees	1	0.08	6.1±0	7.47	0.00	0.09
<i>Tilia americana</i> L.	36	3.00	17.34±11.11	6608.78	1.18	3.52
<i>Ulmus alata</i> Michx.	1028	85.67	9.4±5.55	39648.81	9.59	57.37
<i>Vaccinium arboreum</i> Marshall	6	0.50	5.75±0.93	40.28	0.02	0.57
<i>Viburnum rufidulum</i> Raf.	7	0.58	6.91±2.07	62.59	0.0	0.67

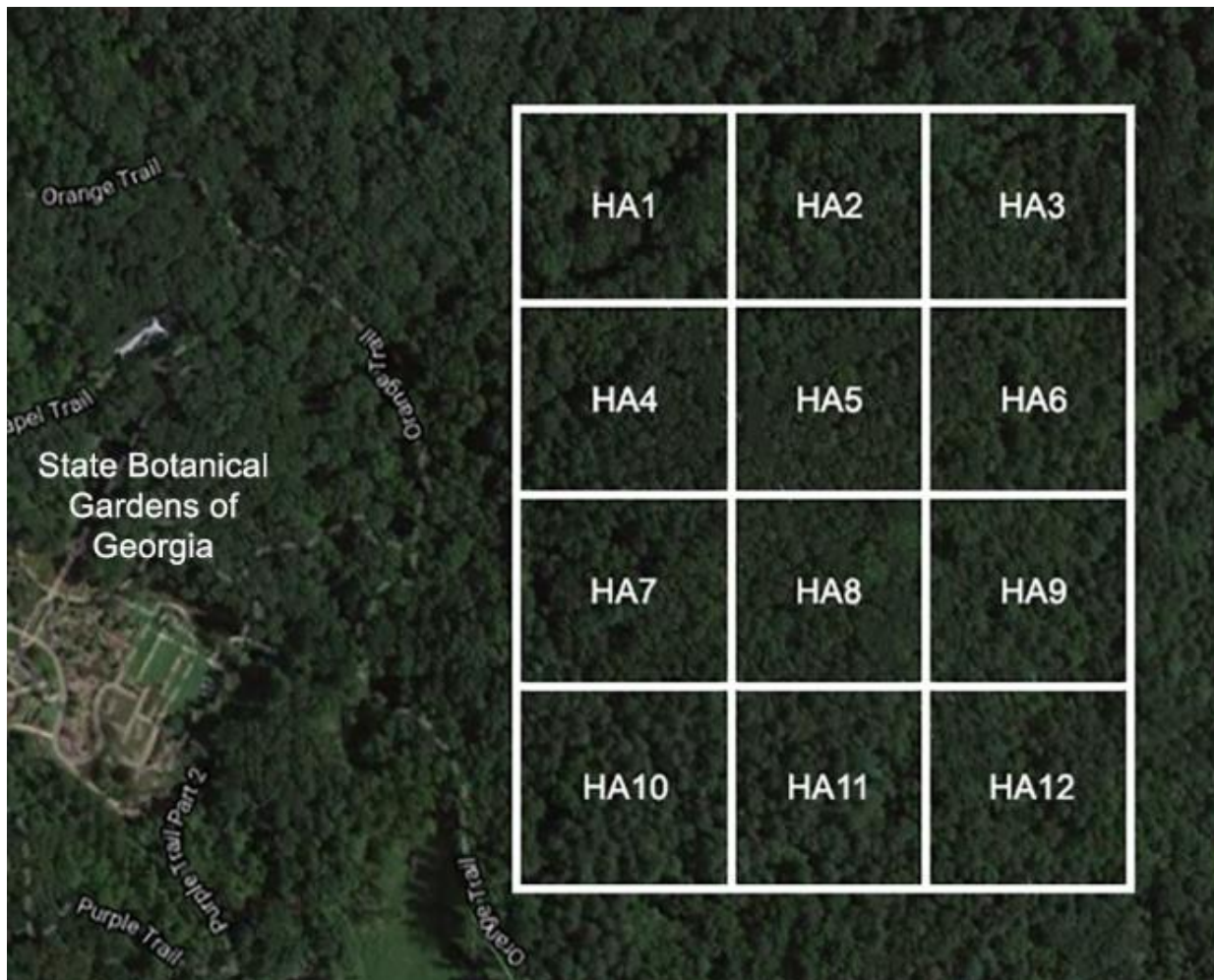


Figure 1.1. Map of the UGA FDP by hectare. The 300m x 400m plot was divided into twelve square hectares, each of which was in turn divided into 100, 10m x 10m squares. Entire plot adjacent to the managed State Botanical Gardens of GA.

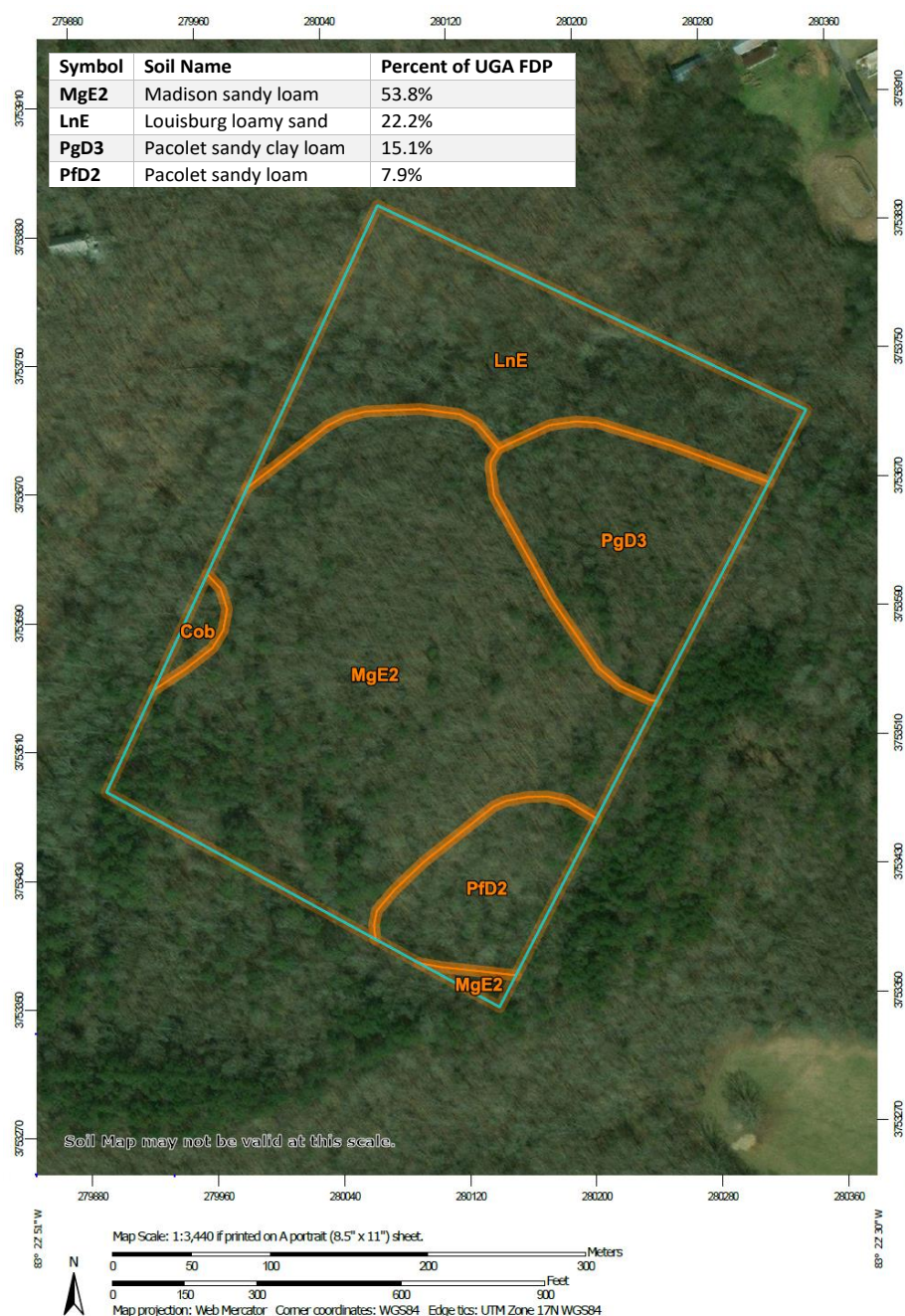


Figure 2.1. Soil Map of the UGA FDP. The UGA FDP contains a total of four different soil types. Soil types making up 1% or less of the overall plot were excluded from the study. Soil map adapted from Web Soil Survey application. Data not considered accurate below 1:15,800 scale.

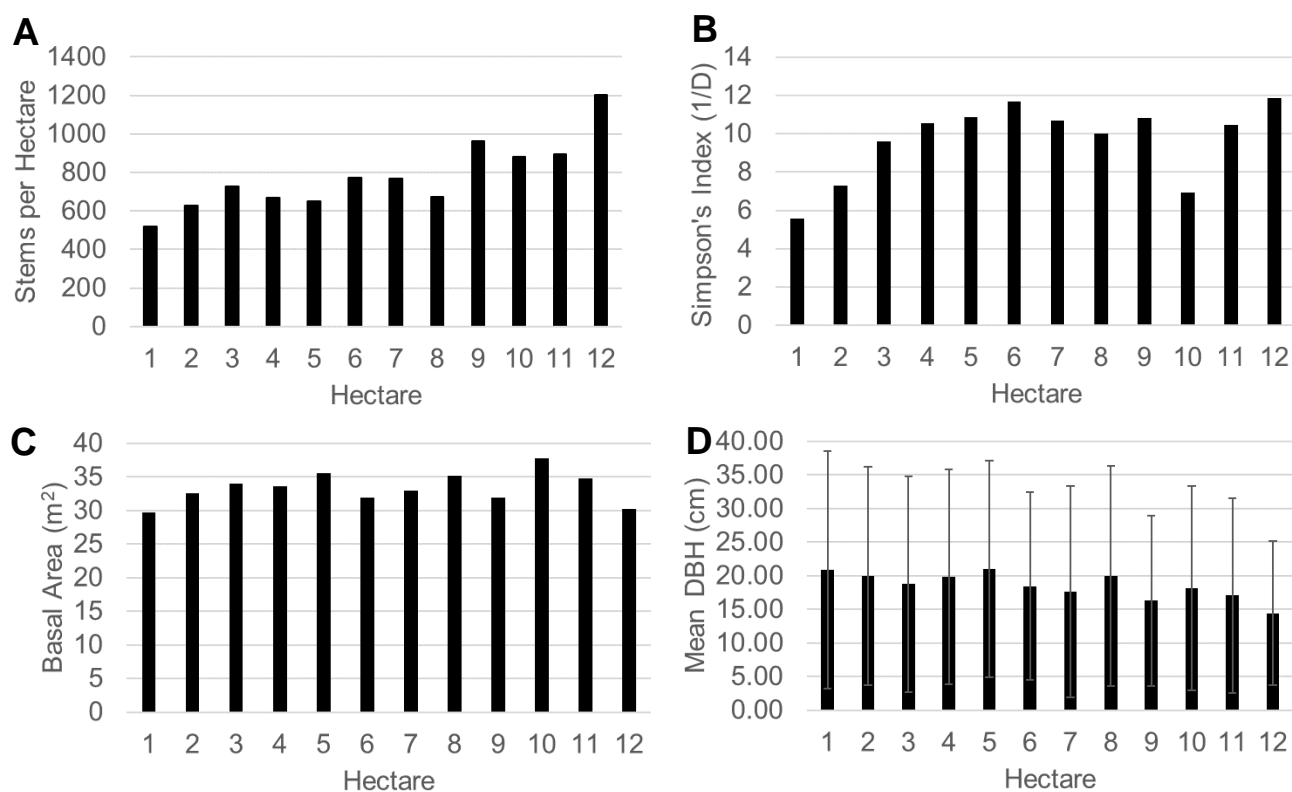


Figure 2.2. Forest metrics from the 12 hectares in 2018. **A)** Density, total stems per hectare **B)** Simpson's Index, a diversity metric **C)** Total basal area for all stems **D)** Mean diameter at breast height with standard deviation.

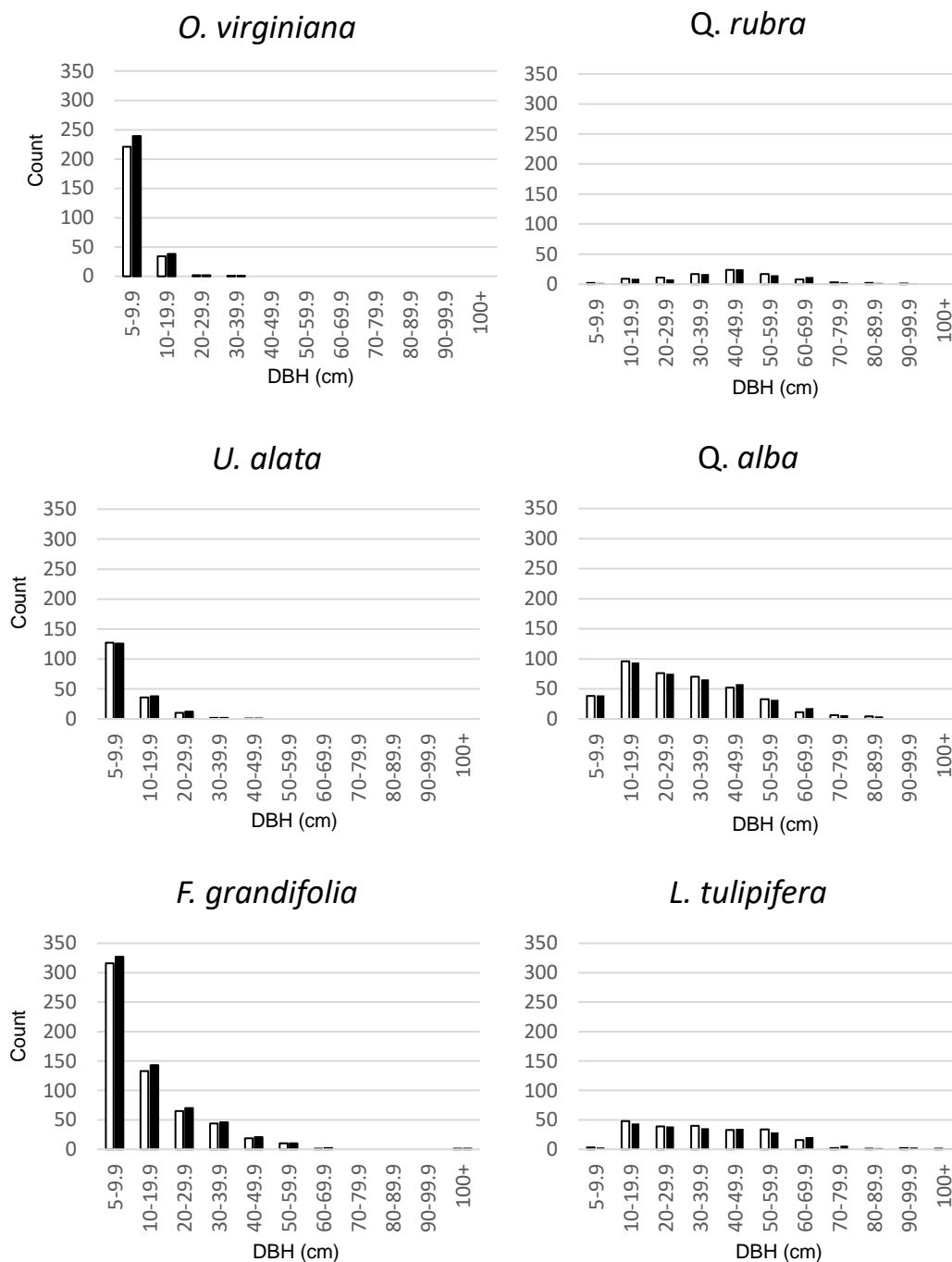


Figure 2.3. The species with most and least skewed diameter distributions among the 10 most important species.

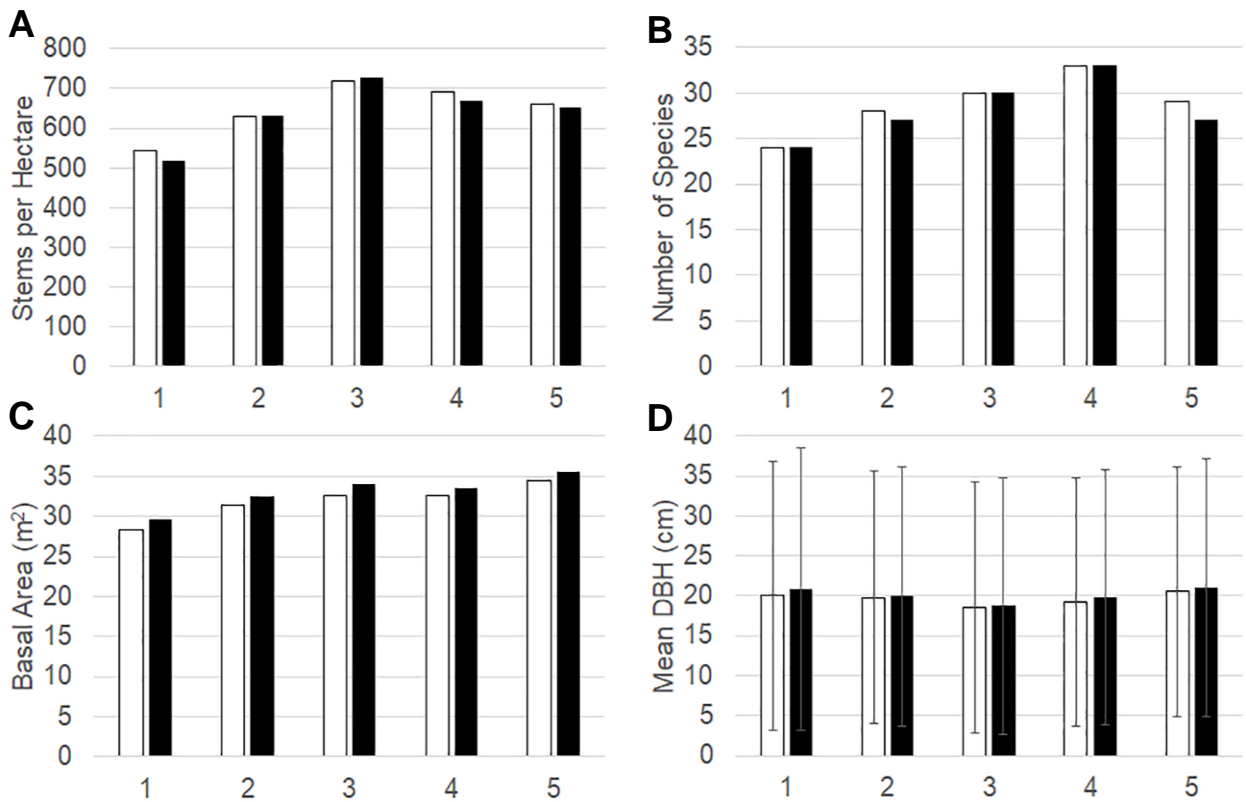


Figure 2.4. Forest metrics from hectares 1-5. White bars indicate data from 2016. Black bars indicate data from 2018. **A)** Density, total stems per hectare **B)** Species Richness, a diversity metric **C)** Total basal area, calculated using DBH **D)** Mean diameter at breast height with standard deviation.

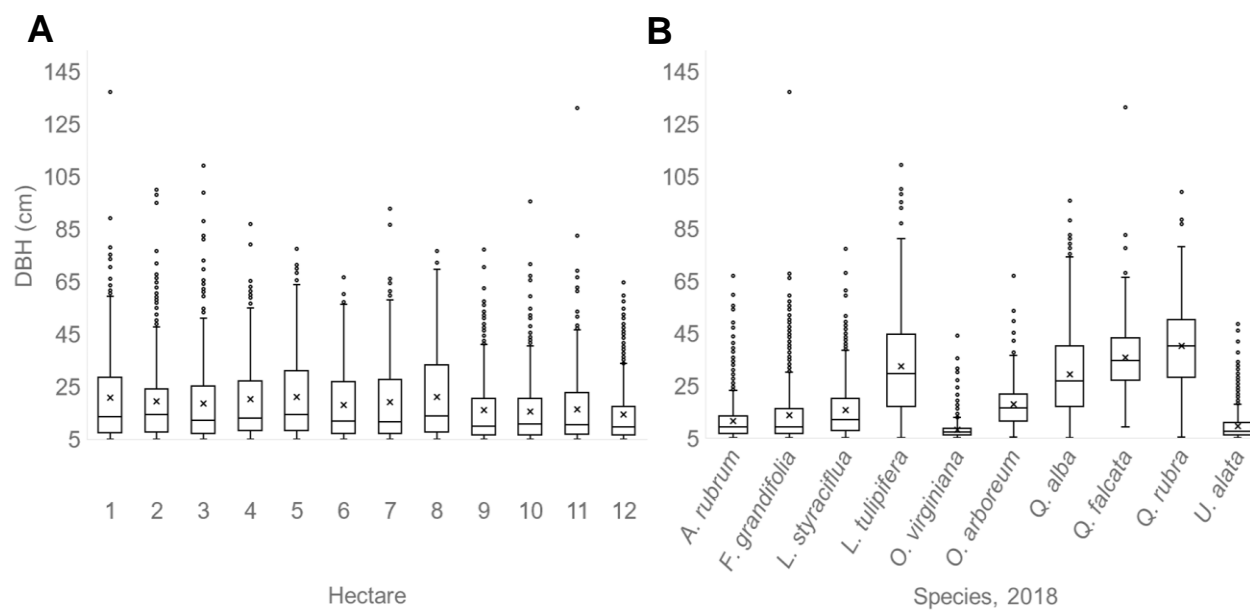


Figure 2.5. Box plot of Diameter at Breast Height for each stem **A)** by hectare and **B)** for the ten species with the top Importance Value within the UGA FDP in 2018.

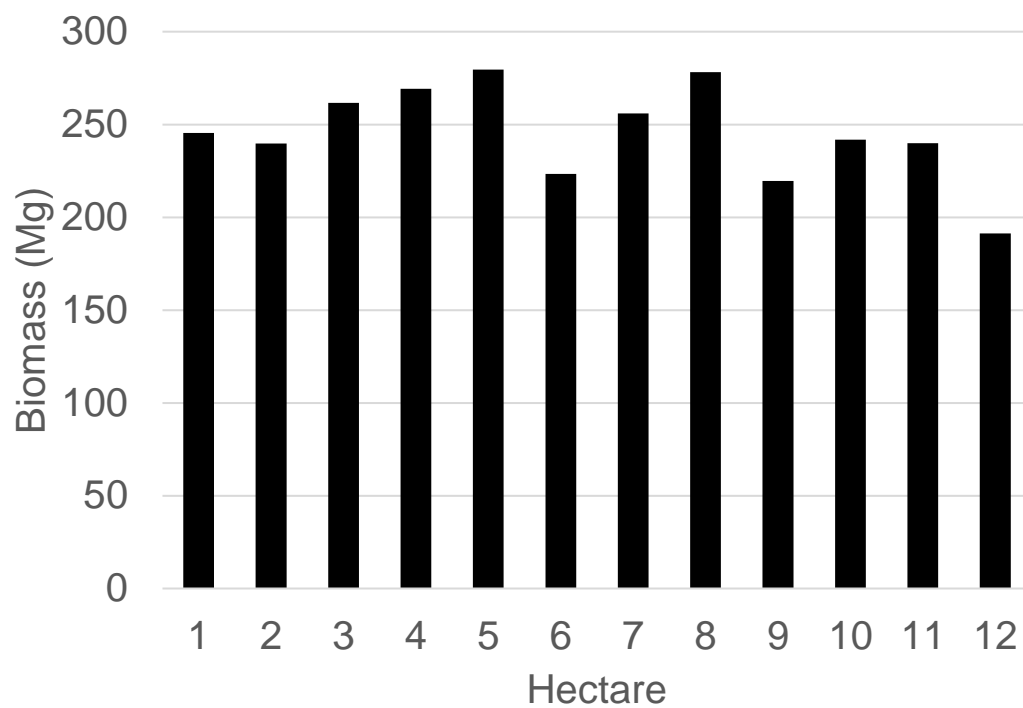


Figure 3.1. Total aboveground biomass in each hectare in 2018.

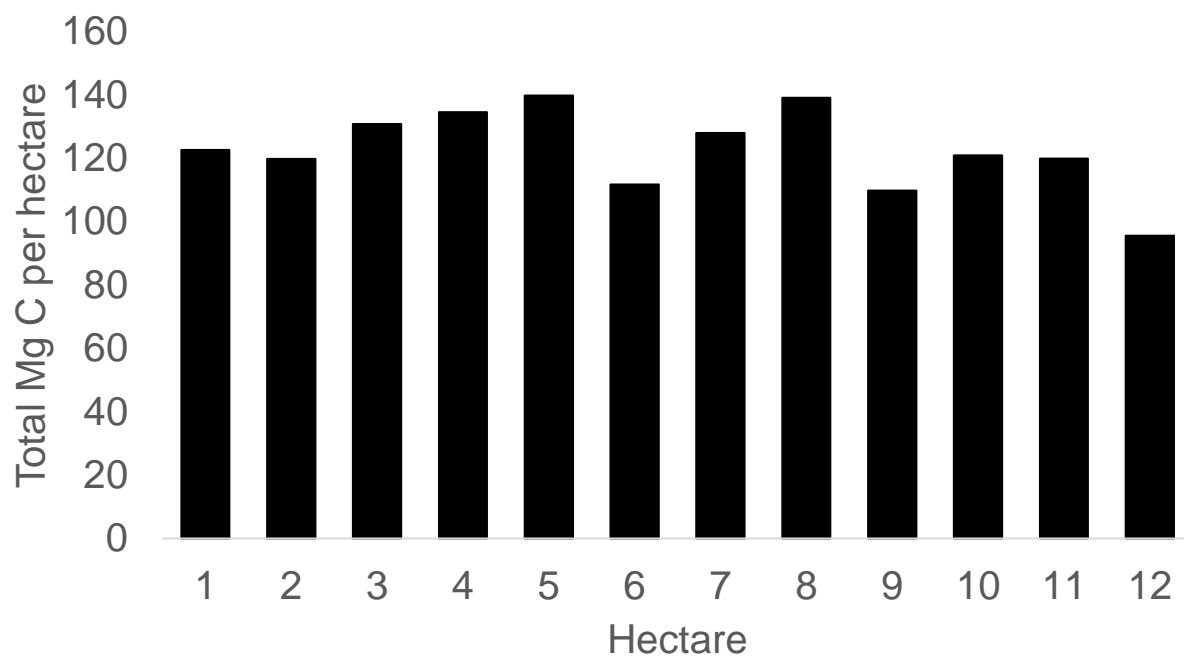


Figure 3.2. Total aboveground carbon stored in living stems 5cm DBH or greater in each hectare in 2018.

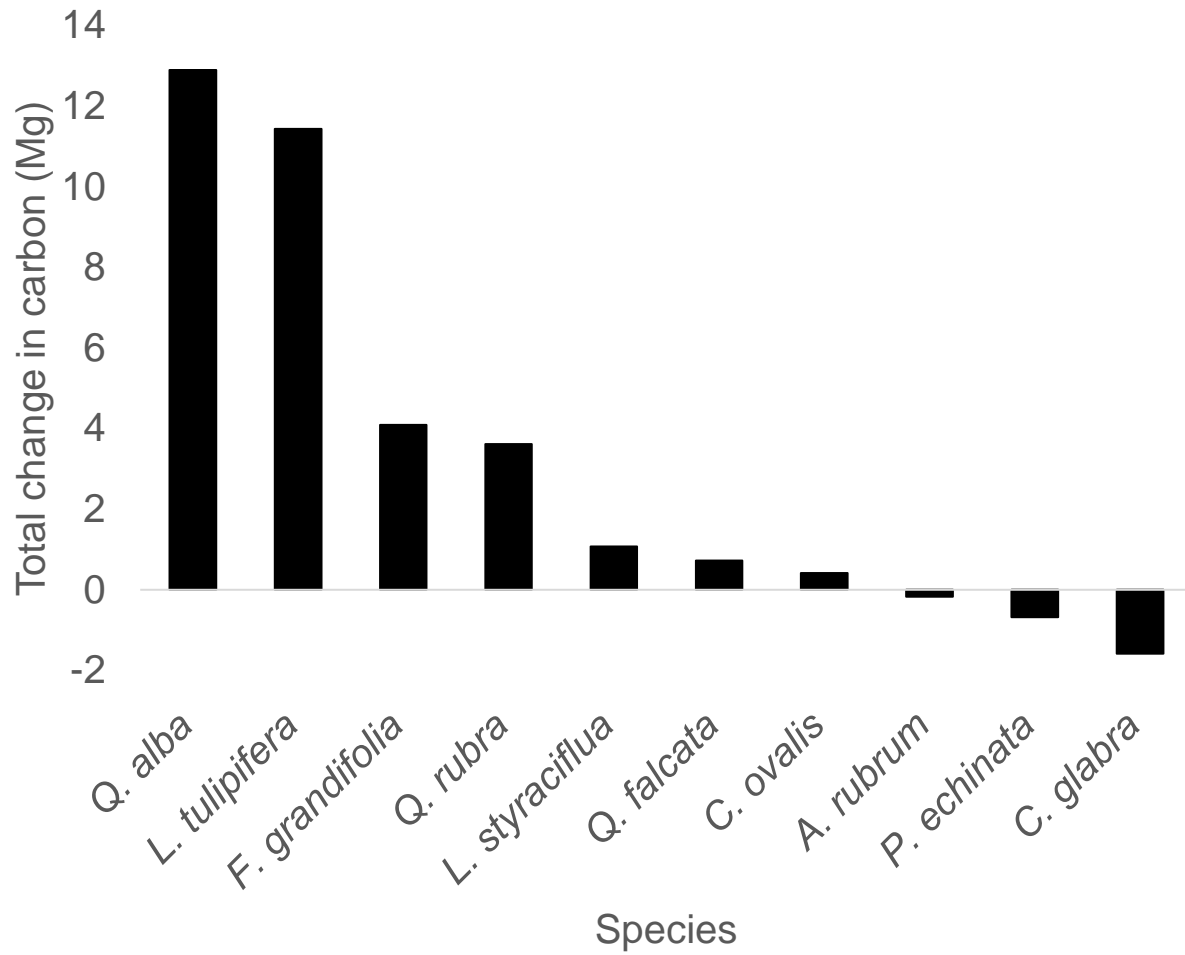


Figure 3.3. Change in total carbon stored across hectares 1-5 in the ten species that changed the greatest, all other species would be found between *C. ovalis* and *A. rubrum*.

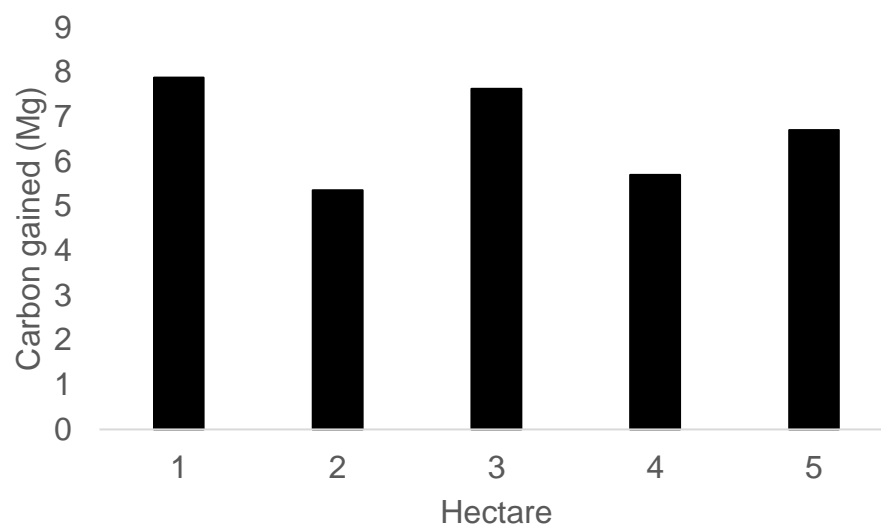


Figure 3.4. Amount of carbon gained in each hectare between 2016 and 2018.

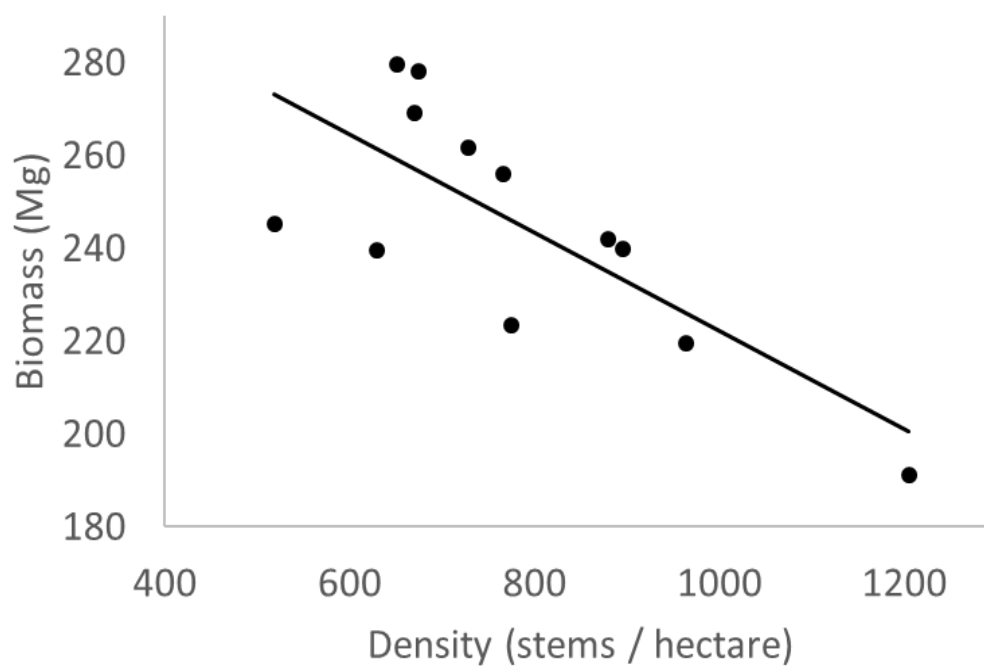


Figure 3.5. Hectares with a greater stem density tend to store less biomass in 2018.

CHAPTER 4

CONCLUSIONS

This thesis reports findings from a newly established long-term vegetation research plot in future monitoring of these threats in the southeastern Piedmont. I focused on recording the species present and monitoring carbon sequestration rates. This research will help inform the long-term carbon sink effectiveness of the eastern forest ecosystem as they shift in response to anthropogenic impacts.

During the 2018 survey of species, 50 species were found at this UGA FDP, the site had Simpson's Diversity index of 13.72, Pielou's evenness index was 0.74, and the Shannon-Wiener index was 2.89. The site was dominated by *Q. alba*, *A. rubrum*, *F. grandifolia*, *U. alata*, and *L. styraciflua* (Table 4).

I sought to determine if the species present were indicative of a forest experiencing a mesophication positive feedback loop, and did the present community of regeneration stems suggest further mesophication for the future of this forest community. Although *Q. alba* was found to be the dominant species at this UGA FDP, *U. alata*, *A. rubrum*, *F. grandifolia*, *L. styraciflua*, and *O. virginiana* were all species qualifying as co-dominant with *Q. alba*. However, when looking only at stems in the regeneration category in this UGA FDP, *Q. alba* was the tenth most abundant species with *U. alata*, *O. virginiana*, *A. rubrum*, and *F. grandifolia* the top species by regeneration stem count, two of which (*Acer* and *Fagus*) have been considered to be major, mesophytic, oak replacing species (Abrams & Downs, 1990; Abrams, 1996).

Additionally, *F. grandifolia*, *A. rubrum*, and *L. tulipifera* comprised 27.74% of regeneration stems at this UGA FDP while *Quercus* as a genus composed only 2.66% of regeneration stems. Although oaks were found to be the most important species on this site, under continued fire suppression, an ongoing shift from oak dominance to mixed-mesophytic species such as the *A. rubrum* and *Fagus* that represent much of the regeneration category can be expected. Additionally, although not directly measured, the low amount of understory and shrub foliage suggest high deer browsing. Unless deer abundance is reduced, areas where deer are overabundant will eventually have forest canopies where a few highly shade and browse tolerant species dominate (Nuttall et al., 2013). The present population of regeneration stems indicates the canopy dominance can be expected to shift towards *Acer*, *Liriodendron*, and *Liquidambar* under the current conditions. The species present appear to be characteristic of a forest undergoing the process of mesophication, but has not yet lost oak dominance. However, due to the long lifespan of oaks and the diameter distribution of the population, oak dominance will likely be maintained for another half century as the present individuals age and succumb to storms or disease.

Another objective of the study was to determine how much and at what rate carbon was sequestered in the aboveground living biomass at this UGA FDP. For forests in general the terrestrial carbon sink total size and location remain uncertain, so quantifying and observing shifts in forest metrics over time is critical to determining these parameters (Pan et al., 2011). Improved larger scale and longer-term predictions will result from better informed models (Carey et al., 2001; Kurz et al., 2008). The total

amount of above ground carbon (AGC) in this UGA FDP was 1,472.9Mg, with a mean of 122.7 ± 12.9 Mg/ha, maximum of 139.8Mg/ha and minimum of 95.6Mg/ha.

Recording variation in the carbon and biomass accumulation between species was another objective of this study. There were four species that individually comprised greater than 10% of aboveground biomass and carbon recorded, *Q. alba*, *L. tulipifera*, *F. grandifolia*, and *Q. rubra*. At 27%, *Q. alba* was the only species to make up more than 20% of total biomass. For the 39 species in the FDP, 14 showed a change in biomass of between 100kg and 1,000kg (1Mg), 17 of the species showed a change in biomass of less than 100kg. Eight species saw a change of 1Mg or greater, two of which were a loss (*C. glabra* and *P. echinata*). The 6 species that saw an increase greater than 1Mg were *Q. alba*, *L. tulipifera*, *F. grandifolia*, *Q. rubra*, *L. styraciflua*, and *Q. falcata* in order of change in biomass from greatest to least change.

An overarching goal for this project was to set up a long-term vegetative study site to monitor the effects of anthropogenic impacts on the forest under novel environmental conditions, including monitoring of recovery and reshuffling of community assemblages after loss of species. As the community is affected by anthropogenic impacts, it is important to understand how the dynamics triggered interact with other processes like deer herbivory. Because of uncertainty regarding global carbon cycle dynamics, research such as this is and will be critically important in supporting future climate action (Pan et al., 2011).

Literature Cited

- Abrams, M. D. (1996). Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. *Annales Des Sciences Forestieres*, 53(2–3), 487–512. <https://doi.org/10.1051/forest:19960230>
- Abrams, M. D., & Downs, J. A. (1990). Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. *Canadian Journal of Forest Research*, 20(12), 1864–1870. <https://doi.org/10.1139/x90-250>
- Carey, E. V., Sala, A., Keane, R., & Callaway, R. M. (2001). Are old forests underestimated as global carbon sinks? *Global Change Biology*, 7(4), 339–344. <https://doi.org/10.1046/j.1365-2486.2001.00418.x>
- Kurz, W. A., Dymond, C. C., Stinson, G., Rampley, G. J., Neilson, E. T., Carroll, A. L., Ebata, T., & Safranyik, L. (2008). Mountain pine beetle and forest carbon feedback to climate change. 452. <https://doi.org/10.1038/nature06777>
- Nuttle, T., Royo, A. A., Adams, M. B., & Carson, W. P. (2013). Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecological Monographs*, 83(1), 3–17. <https://doi.org/10.1890/11-2263.1>
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333(6045), 988–993. <https://doi.org/10.1126/science.1201609>