Forest structure, species composition, and carbon storage of remnant late-successional forests in the Mid-Atlantic region

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Abstract

Following 400 years of land use, and approximately 100 years of forest re-growth, the age structure of eastern U.S. forests has shifted from the late-successional dominance of pre-settlement, to a landscape of young secondary forests ranging in age from 50 – 100 years. Scattered within this matrix of young forests are a few productive, remnant old growth stands, preserved from harvest due to historical significance or inaccessibility. These mature and old growth remnant forests are a window through which we can understand and predict the future structure, species composition and carbon (C) storage of surrounding secondary forests. However, due to their rarity, surveys of this forest type are rare, particularly in the Mid-Atlantic. Here I begin to fill in this knowledge gap by surveying the majority of remaining mature and old growth forests of the Mid-Atlantic region. In Chapter 2, I describe the forest structure and species composition of this unique ecosystem. In Chapter 3, I discuss C storage in terms of structure and species composition in live aboveground woody material (AGC), dead wood, soil organic horizon (SOC), and leaf litter pools within this forest type. I used the U.S. Forest Service regional inventory to contextualize the structural and C storage characteristics of the matrix forests in comparison to the remnant old growth stands. While I had hypothesized that stand age was the primary driver of species composition and structure among mature and old growth forests, I found environmental conditions were most highly correlated with species composition, and species composition in turn determined structure. The one exception to this trend was dead wood volume, which increased monotonically with stand age. Old growth had lower small stem and snag densities than the younger forests, and large stems and snags contributed more to overall basal area. Species-specific effects were evident in the AGC pool. Dead wood C increased with stand age, reaching levels previously unreported in eastern U.S. hardwood forests. My results suggest that as secondary forest age increased, dead wood volume will be a major contribution to overall C stores.

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Chapter 1: General introduction

1. Background

Beginning in the 1600s, settlement and agriculture in the eastern U.S. led to deforestation of the majority of eastern forests (Whitney 1996). By the mid-nineteenth century, expansion of agriculture into the Midwest, along with an increasingly urban economy, resulted in widespread farm abandonment and, in turn, 150 years of natural reforestation. Presently, ~75% of the Mid-Atlantic region is forested (Brown et al. 2005), of which 70% is 50 to 100 years old (Drummond and Loveland 2010, Pan et al. 2011b), and the relative abundance of native species has shifted dramatically from the pre-settlement period (Thompson et al. 2013). What remains of the productive late-successional forests that once dominated the landscape during pre-settlement is now a modest one-percent of all eastern forests (Davis 1996), restricted to remnant stands preserved by chance, historical significance (e.g., James Madison's Montpelier estate), or inaccessibility. Because of their rarity, little is known about this late seral stage in the eastern U.S., and in particular, the Mid-Atlantic region. Examining the forest structure, species composition, and C storage of remnant old growth forests is among the most effective mode of predicting future forest characteristics for the greater landscape.

The unique forest structure associated to old growth forest is important, because it is of direct consequence of long-term forest development, and it is a primary indicator of habitat needed to promote biodiversity (Franklin and Spies 1991). Structural traits associated with live trees in old growth forests relative to younger stands include multi-storied canopies, elevated total basal area, elevated mean tree diameter, elevated diversity in tree diameters and heights, elevated large tree stem density, and reduced overall stem density (Franklin and Spies 1991, Spies and Franklin 1991, Tyrrell and Crow 1994). Large trees predictably generate large dead wood that has an important ecological role. Because of its size, and total dead wood volume and large snag density are expected to increase with stand age (Spies and Franklin 1991, Goodburn and Lorimer 1998, Hale et al. 1999, McGee et al. 1999, Franklin et al. 2002). A landscape dominated by late-successional forests has important implications for biodiversity. Known contiguous stretches of old growth forests provide critical habitat for threatened cavity-nesting species that rely on large, dead and dying trees (Thomas et al. 1988). Old growth also tend to have higher diversity in various plant, fungal, and animal species than their younger counterparts due to the abundance of dead wood (Franklin 1988, Halpern and Spies 1995).

Temperate forests currently are the most rapidly growing C sinks (Pan et al. 2011), and the re-growth of secondary forests in the eastern U.S. over the past century is considered one of the major drivers. Eastern temperate forests take up an estimated 12-19% of the C produced annually by fossil fuel emissions (Ryan et al. 2010). Early models of aboveground C (AGC) dynamics for temperate deciduous forests in the northeast U.S. suggest that at approximately 150 years, forests reach a ‘C neutral’ stage, in which C storage reaches a maximum and holds constant with time. The rate of C accumulation in AGC slows due to declining growth rates of dominant large trees and a subsequent release of C as large trees die and decay. Regeneration of stems in canopy gaps balance C loss through dead wood decomposition (Bormann and Likens 1979). In recent decades, old growth temperate forests have been identified as potential significant terrestrial carbon (C) sinks in the global C cycle (Luyssaert et al. 2008). Evidence of continued accumulation of aboveground live biomass with age well into late succession in the form of high densities of large trees was observed for hardwood forests in the northeastern U.S. (e.g., Brown et al. 1997, Ziegler 2000, Keeton et al. 2011), suggesting that C storage might continue to increase in old growth forest. Excluding any “legacy” dead wood remaining from a major site disturbance, additional evidence suggests an increase in the size of the dead wood C pool with stand age due to the input of large dead wood in old growth stands paired with slow decay rates (Harcombe et al. 1990, Dahir and Lorimer 1996, D’Amato et al. 2008, Harmon 2009).

2. Approach

Remnant old growth stands in the Mid-Atlantic region offer a unique opportunity to explore trends in forest structure and C storage. In the region, rarity of old growth and the general small size of the remaining patches, paired with a diverse climate and geologic history, allow for comprehensive characterization of old growth for the region. I surveyed twenty-five productive mature and old growth remnant stands in the Mid-Atlantic region to describe species composition, forest structure, stand age, and C storage.

In Chapter 2, I define the variability in species composition, structure, and stand age among the twenty-five stands. I ask the questions, (1) What are the characteristics of these sites in terms of the live and dead wood structure? (2) How similar are these old forests in terms of tree composition? (3) Is tree composition related to stand age, structural characteristics, or to environmental variables? (4) How do structural characteristics relate to stand age? Finally, I use the U.S. Forest Service regional inventory database to contextualize the characteristics of these stands in comparison to the younger, secondary forests that dominate the Mid-Atlantic.

In Chapter 3, I apply the compositional and structural data for these stands to estimate C storage in the AGC and dead wood C pools. I also collected leaf litter and soil organic C (SOC) of the O-horizon to describe C storage in these two pools. Specifically, I ask how much C is stored in Mid-Atlantic old growth forests, and how is it allocated? Once again, I use the U.S. Forest Service regional inventory database to discuss the C storage in terms of the regional landscape.

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Chapter 2: Variability in forest structure, species composition, and stand age among remnant late successional stands in the Mid-Atlantic region.

1. Abstract

Once the dominant landscape condition, old growth forests in the eastern U.S. are currently restricted to remnant stands, preserved during the agricultural expansion that began in the early and mid-1600s due to chance, historic importance, or inaccessibility. Old growth forests in their live and, in particular, dead wood structure offer rare habitat important for biodiversity. Dead wood volume, medium (>50 cm DBH) and large (>70 cm DBH) tree stem density, and basal area are all expected to increase with stand age as the dominant forested landscape transitions from early and mid-succession to late succession. However, increased exploration of remnant old growth forests suggest not just age, but land-use histories, tree community composition, and site-specific environmental conditions all have an important role in driving old growth forest structure. Through detailed measurement of twenty-five old growth stands, I developed a detailed understanding of the variability in species composition and structural characteristics of old growth for the Mid-Atlantic region, where the rarity of old growth, paired with a diverse climate and geologic history, led to high compositional and structural variability across stands. Stand age significantly predicted dead wood volume (volume = 1.329[age] + 35.67; $r^2 = 0.313$, $P = 0.002$), but was ineffective at describing all other structural characteristics measured. Species composition instead acted as an effective predictor of forest structure, and environmental variables drove species composition. I used the U.S. Forest Service regional inventory database to discuss the characteristics of these stands in comparison to the younger, secondary forests that

dominate the Mid-Atlantic landscape. In this comparison, live and snag (dead tree) basal area were higher in the old growth forests, suggesting stand age does drive certain structural characteristics across succession.

2. Introduction

Prior to European settlement mature and old growth forests were the dominant landscape conditions in eastern North America. Today they are restricted to remnant stands, composing less than one percent of all forests in the region (Davis 1996). Beginning in the early to mid-1600s, primary forests of the eastern U.S. were extensively logged and cleared to be converted to agriculture (Whitney 1996). By the mid-nineteenth century, expansion of agriculture into the Midwest, along with an increasingly urban economy resulted in widespread farm abandonment and, in turn, 150 years of natural reforestation. Presently, ~75% of the Mid-Atlantic region is forested (Brown et al. 2005), of which 70% is 50 to 100 years old (Drummond and Loveland 2010, Pan et al. 2011b), and the relative abundance of most native species has shifted dramatically from pre-settlement (Thompson et al. 2013). Productive primary forests currently exist in the Mid-Atlantic as small fragments within the matrix of secondary forests. These sites have been preserved due to historical importance (e.g., James Madison’s Montpelier estate) or to inaccessibility that prevented harvest. Because of their rarity, little is known about the structure and species composition of this late seral stage, and how these characteristics compare to younger secondary forests of the region. By examining the compositional and structural characteristics of the remaining stands of mature and old growth forest we can better understand the trajectory of the vast matrix of secondary forest poised to reach the mature or old growth stage within the next fifty years.

The ecological implications of a landscape dominated by late versus early and mid-successional forests are profound. Late seral forests provide distinctive habitat features. For example, contiguous stretches of temperate old growth forest in the Pacific Northwest, upper Midwest and the Adirondack region of New York provide critical habitat for threatened cavity-nesting species that rely on large, dead and dying trees (Thomas et al. 1988), including birds (Fischer and McClelland 1983, Harmon et al. 1986, Schreiber and deCalesta 1992, Lanham and Guynn 1996, Lohr et al. 2002), amphibians (Welsh 1990), and mammals (Harmon et al. 1986, Gilbert and Allwine 1991a). Old forests also foster higher species abundance and diversity relative to managed secondary forests (Franklin 1988, Halpern and Spies 1995) in mammals (Carey and Johnson 1995), lichen and bryophyte communities (Lesica et al. 1991, Cooper-Ellis 1994), amphibians (Gilbert and Allwine 1991b, Dupuis et al. 1995, Ford et al. 2002), arthropods (Chandler and Peck 1992, Douglas et al. 2013), and vascular plants (Halpern and Spies 1995, D'Amato et al. 2009). The higher species abundance and diversity found in old growth forests are largely due to the structural heterogeneity and abundance of dead wood including roots, stumps, branches, and standing stems (i.e., snags) (Harmon 2009), and the prevalence of large old trees that act as habitat for species. In temperate broadleaf forests in Sweden, an estimated 30 to75 percent of all fungal diversity, and 28% of invertebrates are dependent on dead wood (Berg et al. 1994, Nordén et al. 2004). Similarly, in the Blue Mountains of Oregon and Washington, roughly 57% of vertebrate species use dead wood as habitat (Thomas and Parker 1979), and in the southeastern U.S., nearly 98% of land snails are associated with log habitats (Caldwell 1996). Large dead wood in riparian old growth stands accumulates in streams, providing unique habitat for fish and invertebrates by creating structural complexity in the form of pools, riffles, and log jams (Hassan et al. 2005, Keeton et al. 2007). The long residence time of large dead wood also promotes the formation of debris dams that may act as important points for nitrogen (N), carbon (C) and phosphorous cycling in stream channels (Creed et al., 2004; Ganjegunte et al., 2004; Kueppers et al., 2004) for organic matter retention (Bilby and Likens 1980, Díez et al. 2000, Warren et al. 2007) and fish habitat.

All studies of old growth must contend with the question: what constitutes old growth? Generalized attributes—such as large old trees, down logs, and complex vertical structure—are typically used to identify the late successional stage (Dunwiddie et al. 1996), and in turn, the presence of these traits are indicative of the ecological benefits provided by old growth forests. Spies (2004) highlights that at the most fundamental level, old growth is represented by the processes and structural trends that result in the conglomeration of maturing and senescing trees, and as such, the characteristics of old trees are inherent to any definition of old growth. Definitions of old growth combine elements of age, absence of historical human disturbance, and forest structure (Wirth et al. 2009, Hoover et al. 2012). The unique forest structure associated with old growth, in particular, is important because it is a direct consequence of long-term forest development, and it is a primary indicator of habitat needed to promote biodiversity (Franklin and Spies 1991). Structural traits associated with live trees in old growth forests relative to younger stands include elevated total basal area (BA; area occupied by stems at their base), elevated mean tree diameter, elevated diversity in tree diameters and heights, elevated large tree stem density, and reduced overall stem density (Franklin and Spies 1991, Spies and Franklin 1991, Tyrrell and Crow 1994). The abundance of large old trees with bole and canopy decay, cavities, large-diameter branches, and distinct bark features provide unique habitat (Franklin et al. 2002). Large trees predictably generate large dead wood that has an important ecological role because of its size, and total dead wood volume and large snag density are expected to increase with stand age (Spies and Franklin 1991, Goodburn and Lorimer 1998, Hale et al. 1999 p. 199, McGee et al. 1999, Franklin et al. 2002). In a comparison of northern hardwood forests under different management techniques, McGee et al. (1999) found that large snags (> 70 cm DBH; diameter-at-breast-height; 1.37 m) accounted for 32% of the total snag density in old growth, relative to one and zero percent in mature and young managed forests.

In response to the discovery of more and more remnant old growth stands in the eastern U.S., Orwig et al. (2001) note how the structure and composition of these stands seem to deviate further from the idealized definition of old growth. Specifically, the compositional and structural components used to characterize remnant mature and old growth forests can be highly varied across stands due to differences in natural disturbance regimes, stand age, and environmental variables, such as site condition, and topographic and climatic gradients (Harmon et al. 1986, Foster et al. 1996, Zenner 2004). Identifying the variability in species composition and structural characteristics of old growth may be possible, particularly for the Mid-Atlantic region, where the rarity of old growth and the general small size of the remaining patches, paired with a diverse climate and geologic history, may lead to high compositional and structural variability across stands. In recognition of their rarity and ecological significance, we characterized the compositional, structural, and environmental attributes of twenty-five remnant stands of mature and old growth forest within the Mid-Atlantic region. Specifically, I addressed the following questions: (1) What are the characteristics of these sites in terms of the live and dead wood structure? (2) How similar are these old forests in terms of tree composition? (3) Is tree composition related to stand age, structural characteristics, or to environmental variables? (4) How do structural characteristics relate to stand age? Finally, I use the U.S. Forest Service regional inventory database to discuss the characteristics of these stands in comparison to the younger, secondary forests that dominate the Mid-Atlantic landscape.

3. Methods

3.1. Study Area

The U.S. Mid-Atlantic region spans the Chesapeake and Delaware Bay watersheds. I defined the Mid-Atlantic as consisting of Virginia, Delaware, and Maryland, and parts of West Virginia, Pennsylvania, and New Jersey (Figure 2.1), however other common definitions include parts of southern New York and northern North Carolina (e.g., Jenkins et al. 2001, Pan et al. 2009). The regional landscape is high in physiographic and ecological diversity, and subdivided into six distinct ecoregions that reflect variable landform and topography, geologic origin, hydrologic function, soils, and potential plant communities (Cleland et al. 1997, Rogers and McCarty 2000, Stolte et al. 2012). The region is formed by the Middle Atlantic Coastal Plain, Southeastern Plains, Piedmont, Northern Piedmont, Ridge and Valley, and the Blue Ridge Mountains ecoregions (USEPA 1999). The climate is wet and warm, with growing seasons ranging from 100 to 250 days across the six ecoregions (Stolte et al. 2012). Forest is the prevalent cover type in the Mid-Atlantic region (Jones et al. 1997), of which the oak/hickory (*Quercus* spp. and *Carya* spp.), maple/beech/birch (*Acer* spp., *Fagus grandifolia* Ehrh., and *Betula* spp.), and oak/pine (*Pinus* spp.) forest community groups dominate (Eyre 1980, McKenney-Easterling et al. 2000). Forests in the six physiographic ecoregions share similar ranges in productivity and diversity (Belote et al. 2011). Although the Mid-Atlantic is mostly forested, it also fosters rapidly growing suburban and urban areas that spread from Philadelphia to Washington D.C. and have expanded as much as 90% from 1970 to 2000 (Morrill 2006); rates of forest cover loss in the region during this period are approximately 0.15% per year (Drummond and Loveland 2010). *Quercus alba* L. (white oak), *Quercus velutina* Lam. (black oak), *Quercus prinus* L.(chestnut oak), *Quercus rubra* L.(northern red oak), *Castanea dentata* (Marsh.) Borkh.(American chestnut), *Pinus* spp., and *Carya* spp. dominated pre-settlement forests in the Mid-Atlantic (Nowacki and Abrams 1994, Abrams and McCay 1996, Abrams 2003), and with the exception of *Castanea dentata* these species still are common in the mature and old growth forests of the region (Thompson et al. 2013).

Table 2.1. Forest community groups and associated compositional species for groups most common to the Mid-Atlantic (follows McKenney-Easterling et al. 2000).

Forest Community Group	**Compositional Species**
Oak/Hickory	Hickory (*Carya* sp.), bitternut hickory (*C. cordiformis*), pignut hickory (*C. glabra*), shagbark hickory (*C. ovata*), mockernut hickory (*C. tomentosa*), white oak (*Q. alba*), scarlet oak (*Q. coccinea*), chestnut oak (*Q. prinus*), northern red oak (*Q. rubra*), post oak (*Q. stellata*), black oak (*Q. velutina*), sweetgum (*Liquidambar styraciflua*), and tulip poplar (*Liriodendron tulipifera*).
Maple/Beech/Birch	Red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghanensis*), black cherry (*Prunus serotina*), and black walnut (*Juglans nigra*).

Oak/Pine	Eastern white pine (*P. strobus*), short leaf pine (*P. echinata*), Virginia pine (*P. virginiana*) , northern red oak, loblolly pine (*P. taeda*), water oak (*Quercus nigra*), willow oak (*Q. phellos*), post oak, and scarlet oak (*Q. coccinea*).

3.2. Site Selection

For the purposes of this study, I broadly define mature and old growth as forests with dominant overstory trees having a maximum stand age of ≥ 150 years. This age is based roughly on the definition suggested by Cogbill (1996) that mean stand age be approximately half of the maximum longevity of the dominant tree species (~ 300+ years) to qualify as eastern temperate old growth. My goal was to measure all mature and old growth sites known to exist in the Mid-Atlantic that are not anomalous in terms of their edaphic or topographic setting—i.e., I sought to measure all remnant old forests on sites typical of the Mid-Atlantic landscape. To develop a list of potential sites, I reviewed all published literature on old growth remnants in the region with reported stand ages. Past publications either provided mean stand age estimates based on tree ages from increment cores or land use history, species composition, and forest structure indicating no harvest in the past ~150 years. It is important to note that different stand age sampling methods between this study and past publications led to different estimates of maximum stand age, including maximum age estimates less than 150 years for some sites. Next, I identified potential sites from the gray literature. The majority of these stands were described in Davis (1996) *Old growth in the East: A Survey*, and Kershner and Leverett (2004) *The Sierra Club Guide to the Ancient Forests of the Northeast*. I also identified sites through peer discourse by engaging state forest agencies, and conservation and land trust associations (e.g., The Nature Conservancy). A total of 35 sites was identified for field visits. The selected sites shared similar overstory composition, and typically were dominated by *Quercus* spp., with *Liriodendron tulipifera* L. (tulip poplar), *Tsuga canadensis* L. Carr (eastern hemlock), or *Carya* spp. as co-dominant or secondary canopy species. Following a walk-through survey, 25 sites were sampled from May to August 2012 (Figure 2.1; Table 2.3). Ten of the original 35 sites were deemed unusable either due to recent natural or anthropogenic disturbance (e.g., gypsy moth outbreaks, timber harvesting) which caused large-scale mortality in the dominant overstory trees, or because the site was inaccessible or not representative of the greater Mid-Atlantic region. In total, the study area approximated 87,383 km^2.

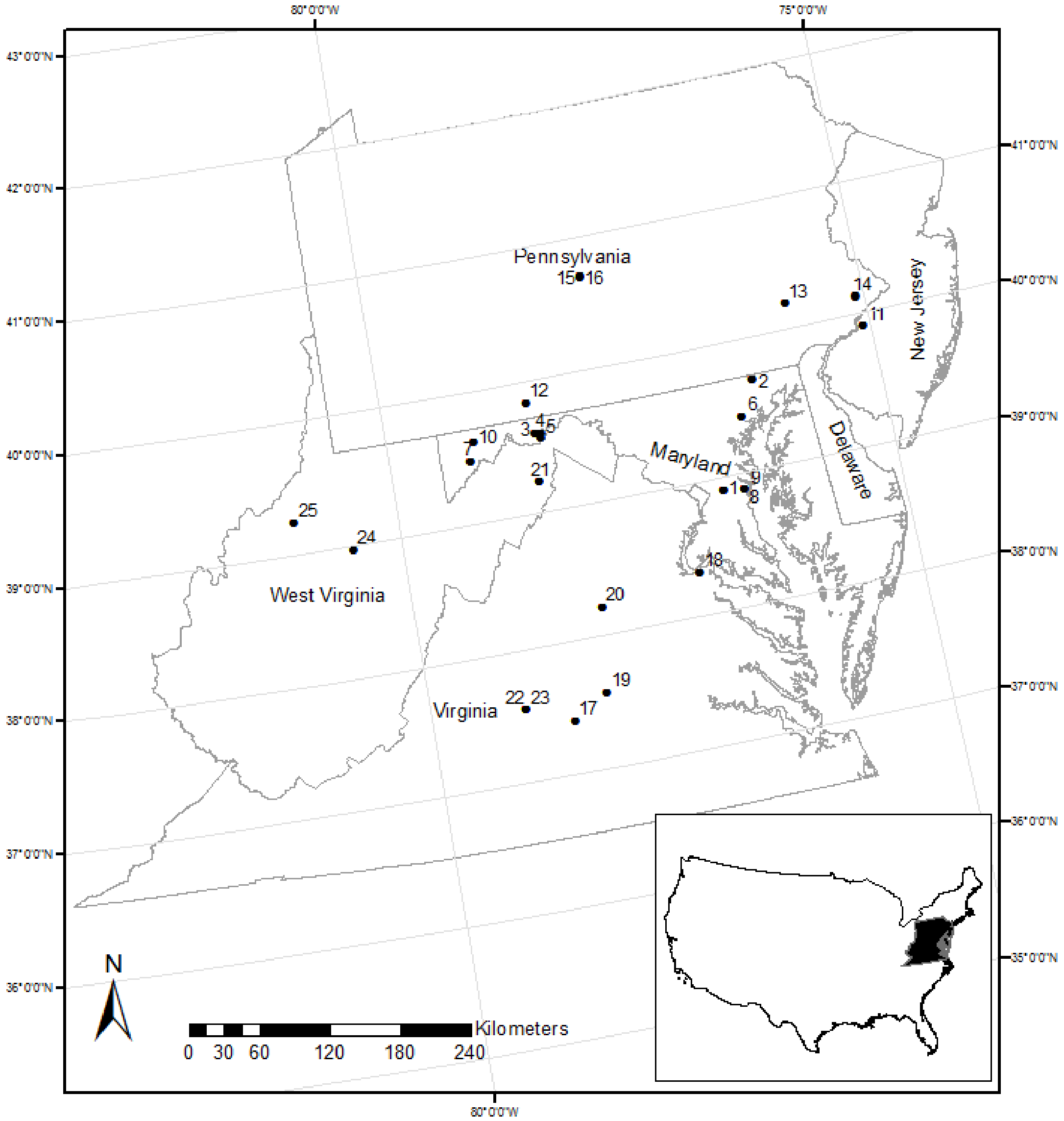

Figure 2.1. Location of the twenty-five mature and old growth forests sampled within the Mid-Atlantic study area. See Table 2.2 for key to site codes.

3.3. Structure and composition field sampling

I delineated stand boundaries using the Wirth et al. (2009) definition of old growth: (1) the abundance of large, old stems, supplemented with Pederson's (2010) external description of old trees, (2) abundance of standing and fallen dead wood at various stages of decay, (3) relatively few signs of anthropogenic disturbance, (4) a multi-layered canopy, and (5) canopy gaps. Emphasis was placed on the first three characteristics, because they are easily recognized within an older stand, and contrast strongly with conditions of younger forests. Additionally, the stand needed to be of sufficient area to fit three 0.07 ha sampling plots. In practice, defining the stand edge was a difficult process. I was conservative in my classification and therefore erred towards identifying forest as secondary as opposed to old growth. As such, it is possible that the periphery of some old growth stands were not included within the delineated stand boundary. I am confident, however, that the interior of the stand consistently was included in the delineation.

I established sampling points at 15 m intervals along a transect oriented to be the greatest possible length spanning the greatest possible area of each stand (Figure 2.2). Transect length varied among sites depending on the size and shape of the stand. To define structural variability for each stand, I estimated total basal BA (m^2 ha^{-1}) of all stems within a variable radius of all sampling points within each stand using a 10-factor prism. I then took detailed plot measurements within 15m radius circular plots centered at the three sampling points that represented the 10th, 50th, and 90th quantiles in terms of prism-estimated BA. This technique was intended to capture the range of structural variability present within the stand. Interestingly, subsequent data analysis showed that total BA estimations based on the variable radius (prism) plot and the fixed area methods were not correlated, and so I dropped stratification by BA prism estimates across plots and based all subsequent analysis on site averages. At the center of each plot, I collected topographic measurements including transformed aspect, slope, and geographic coordinates.

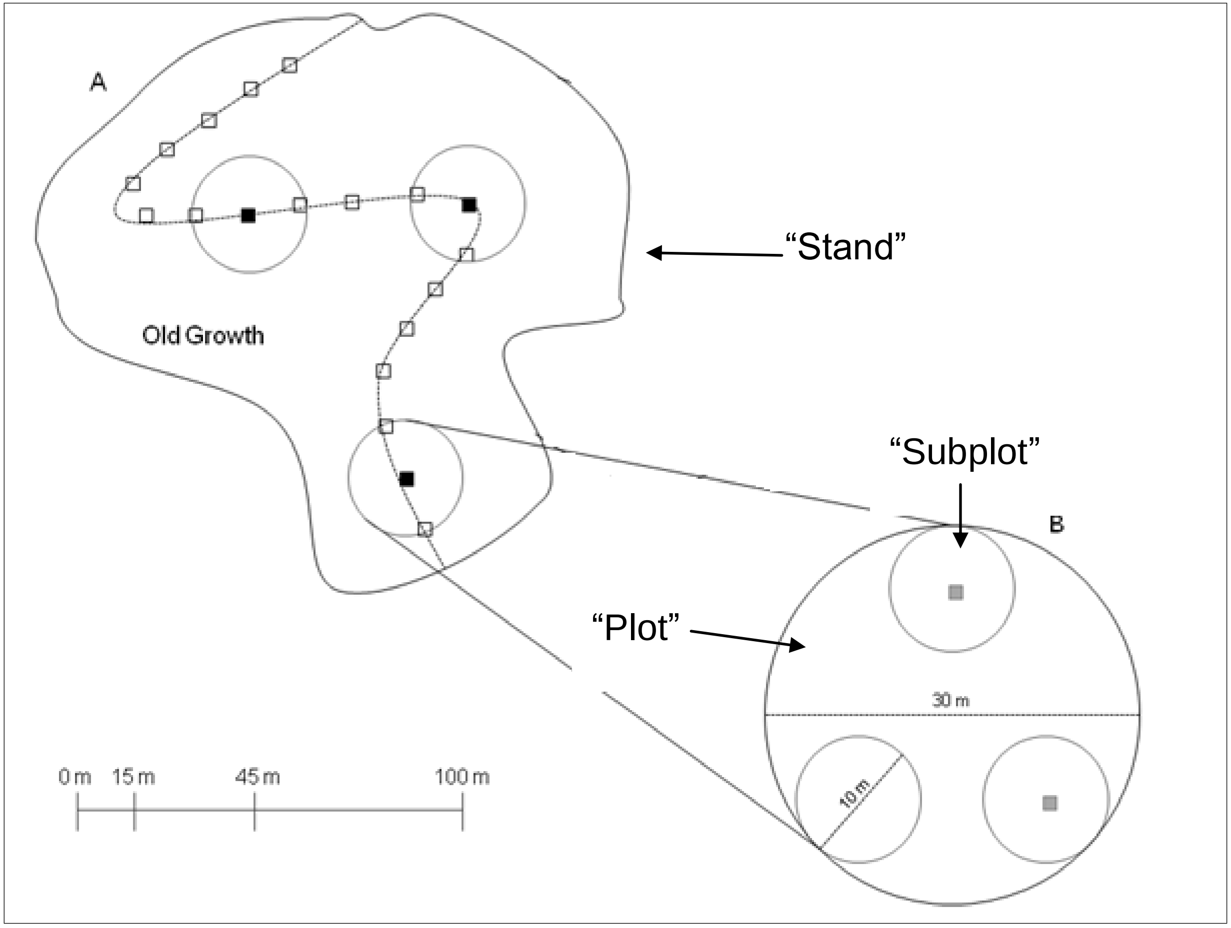

Figure 2.2. An example of transect and plot layout for old growth field sampling. (A) Within each stand, a transect (dashed line) was oriented to cover the maximum possible area within the stand boundary (solid line). BA was estimated at sampling points (empty squares) placed 15-m apart along the transect. From these BA estimates, three to four 30-m diameter plots (circles) were placed at sampling points. The number of plots depended on size of the stand. (B) Within each plot, all large dead wood and live stems greater than 5 cm DBH were recorded, and slope and aspect were measured at the center of the plot. Additionally within each plot, three 10-m diameter subplots (small circles) were surveyed for medium dead wood and live stems 1-4.9 cm DBH. Soil O-horizon and leaf litter samples were collected from 0.9 m^2 quadrats (squares) at the center of two randomly selected subplots.

Within each plot, I recorded the species and canopy height of all live woody stems ≥ 5 cm DBH. Heights were measured with an Impulse 200 Laser Rangefinder (Laser Technology, Inc., Norristown, PA). I recorded all stems 1-5 cm DBH for species and DBH within three non-overlapping 5 m radius subplots nested within the larger plot. I measured dead wood volume using field protocols developed by Harmon and Sexton

(1996) within the plots. The minimum diameter for identifying dead wood was 10 cm. I classified all dead wood as a log, snag, or stump. For logs (≤ 45° relative to the ground), I measured the diameters at both ends and the midpoint, and the length of the piece of wood; for snags (> 45° relative to the ground and > 1.37 m height), the DBH and height; for stumps (> 45° relative to the ground and < 1.37 m height), the length, and top and base diameters. Following McGee et al. (1999), all large dead wood (≥ 25 cm diameter) was inventoried in the 15 m radius plots and medium dead wood (10-25 cm diameter) in the 5 m radius subplots.

To estimate maximum age of the plots, I collected two to three cores of the dominant canopy stems from each plot for a total of ten tree cores per site, taken at 1.37 m along the mid-slope of the tree. At four sites, heart rot in large canopy stems prevented the collection of complete cores for the largest trees in the plots. The number of medium to large stems (> 50 cm DBH) with signs of rot ranged from 6 to 29 percent of all stems in this size class measured at these four sites. When heart rot prevented the collection of a complete core, I took a sample from the next-largest tree in the plot. I used a 40.6 cm borer and was unable to reach the center of some of the larger trees. I did not attempt to estimate the number of rings missing if the pith was missing. Due to ecological or historical significance, landowners denied me permission to collect cores at nine sites. However, reliable stand age data were available for all but one of these sites (see Table 2.3 for sources). I dried, mounted, and sanded all samples, then estimated maximum plot age by counting tree-rings under a Wild M8 stereozoom microscope, and cross-dated counts by comparing shared narrow rings across cores (Yamaguchi 1991). I selected the oldest tree cored at each site as an estimate of maximum site age – hereafter referred to as "stand age."

At the center of two randomly chosen subplots within each plot, I collected samples of the O-horizon within a 0.1 m^2 frame at 23 of the 25 stands. One of the two sites was not sampled because sampling equipment was unavailable at the time of collection, and for the other site, a suitable secondary stand could not be found. The frame method (Burton and Pregitzer 2008) worked best for the generally rocky soils or shallow O-horizons at the majority of field sites in order to collect a large enough volume of soil for homogenization. Because I collected a specific horizon versus a uniform depth, I took five soil cores using a 2.5 cm diameter corer to determine the mean depth of the O-horizon at each sampling point. I brought all soil samples back to the laboratory for processing, passed the samples through a 2-mm sieve to remove roots and other large organic matter, dried them at 105°C for 24 hours, and finely ground them using a ball mill. I obtained estimates for percent C and N from each sample using a CE elemental analyzer (CE Elantech, Inc., Lakewood, NJ), and calculated a C:N ratio from the percentages.

3.4. Other measurements

In addition to field measurements of stand structure, I compiled elevation, topographic wetness index (TWI), latitude, longitude, and spatial climate variables, including average annual temperature and precipitation for between 1981 and 2010, and heating degree days with a base temperature of 10°C for the same time period. I assigned climatic variables to each site based on a complete data set provided from the geographically nearest weather station (See Appendix B for weather station information).

I estimated TWI and elevation through GIS analyses of digital elevation models (DEM) performed in ArcGIS 10.1 (ESRI 2013). The DEM resolution varied between 10 and 30 m across the study region due to limited availability of the highest resolution data. TWI is a function of the natural logarithm of the ratio of local upslope contributing area and slope, and can represent relative soil moisture availability (Moore et al. 1993). A value of seven or less indicates the most xeric conditions and a score of 10 indicates the most mesic conditions (Moore et al. 1993).

3.5. Data processing and analysis

I used different equations for volumetric estimates of dead wood based on type-specific classification and measurements (Harmon and Sexton 1996). For logs, I used the Newton formula which requires three diameter measurements:

$$V = L\ (A_b + 4A_m + A_t)/6 \qquad [1]$$

Where L is length, A_b, A_m, and A_t are area at the bottom, middle, and top, respectively. For stumps, I used the formula for a frustrum of a cone:

$$V = L(A_b + (A_b A_t)^{0.5} + A_t) \qquad [2]$$

For snags, I used a modified Huber formula (Wenger 1984) for a cylinder:

$$V = L * BA \qquad [3]$$

Of the three volume equations, the Huber formula is the most simplified and potentially more prone to error in estimating true volume. Dead wood pieces are generally irregular in shape, and error in volume estimates increases with fewer diameter measurements collected. However, this formula has been shown to provide unbiased estimates (Van

Wagner 1968, Brown 1971), and so I used the Huber formula to approximate true snag volume.

I examined patterns in overstory (stems ≥ 5 cm DBH) community structure and vegetation-environment relationships using non-metric multidimensional scaling ordination (NMS; McCune and Grace 2002) through the *metaMDS()* function of the vegan package (Oksanen et al. 2011) within the R statistical language (R Development Core Team 2010). I applied 30 random starts, used Bray-Curtis distance, and rotated to principle components for the NMS ordination. The ordination provided an effective means of visually describing community composition and identifying patterns across species and environmental and structural gradients (Bray and Curtis 1957). The NMS approach is considered the most robust unconstrained ordination methodology for community ecology, because it does not assume a multivariate normal distribution and is robust to a large number of zero values (Minchin 1987, Peterson and McCune 2001, McCune and Grace 2002). I plotted the ordinations based on spatial relationships between sites. Using relative BA ($\text{RBA} = \text{individual species BA}/\sum \text{BA}$ of all species), I summarized species composition and abundance. To reduce noise in the dataset, I removed both individual species with a relative BA lower than 0.05 and unidentified species. The original dissimilarities between sites were preserved well in a two-dimensional solution (stress = 0.16; number of axes selected by visual inspection of a scree plot of stress values).

I explored the relationships among environmental, structural, and diversity variables and species composition by fitting bi-plots onto the ordination, in which the direction of the vector indicates directionality of influence, and the magnitude of the vector indicates the correlation coefficient (r^2) of the variable, i.e., its explanatory power. Structural variables were the same as those used in the univariate analyses, and diversity variables include mean species richness, Shannon-Weaver's species diversity index (Shannon and Weaver 1963), and Pielou's species evenness index (Pielou 1966). I included variables with an r^2 of 0.25 or greater on the bi-plot. The bi-plot axes were rotated to place the environmental variable with the greatest explanatory power parallel to the x-axis to improve graphical interpretation (McCune and Mefford 2006) using the *MDSrotate()* function in the vegan package (Oksanen et al. 2011).

To objectively describe the similarity among forests in terms of tree composition and reinforce species centroids defined by the NMS ordination, I used a two-way hierarchical agglomerative cluster analysis using the *vegdist()* function in the vegan package (Oksanen et al. 2011). Using the same qualifiers as the NMS ordination, I defined species composition by RBA. Old growth sites were grouped based on compositional dissimilarity and measured using Sørensen distance. I used Ward's as the agglomerative method. By examining the resulting dendrogram and the percentage of information remaining after the formation of each cluster I settled on four groups. I mapped clusters polygons on the NMS ordination bi-plot to simplify subsequent analysis of the relationship between species composition and structure, stand age, and environmental variables.

I explored univariate relationships between site age and structural variables including mean stand BA (m^2 ha^{-1}), mean stand stem density (trees ha^{-1}), mean large (>70 cm DBH) and medium (> 50 cm DBH) stem density, mean sapling (<5 cm DBH) density (saplings ha^{-1}), maximum tree height of canopy stems (> 50 cm DBH), mean snag volume (m^3 ha^{-1}), mean large snag (> 50 cm DBH) density (m^2 ha^{-1}), and mean dead wood volume (m^3 ha^{-1}) using linear regressions. I selected these variables as definitive structural characteristics of old growth forests, and of large trees in the case of maximum tree height. For live tree variables, I further explored significant relationships to determine if there were cluster group-specific confounding effects. Species identification of dead wood was too infrequent for similar analyses.

2.5. Comparison of old growth structural characteristics to secondary forests

To understand how the mature and old growth stands compare to the matrix of younger forests in the Mid-Atlantic, I plotted stem density, snag density, live BA, and dead BA against regional averages obtained from the U.S.D.A. Forest Service Forest Inventory Assessment (FIA) program. The FIA program has divided the U.S. into a network of permanent 2,400-ha plot hexagons, with one forest inventory plot randomly placed within each hexagon. Within each plot, there are four 17.3-m radius subplots, from which the diameter and species identification of all trees >12.7 cm DBH are collected (for details on the FIA field protocol, see www.fia.fs.fed.us). I used the "The Southern On-Line Estimator (SOLE)" to query statistical tables on user selected variables (Spinney et al. 2004). I queried all states in the Mid-Atlantic study region to calculate mean and standard deviation values of stem density (stems ha^{-1}) and BA (m^2 ha^{-1}) for live stems greater than 2.5 cm diameter and dead snags greater than 13 cm diameter for plots inventoried in 2011 (n = 1855). No other structural variables of interest were available for query in the study region. Stem density and BA were broken down by diameter class, and bin ranges reflect diameters originally measured in inches and converted to centimeters. SOLE automatically selects against non-forest cover plots, but otherwise, no additional queries were made for site selection. I then compared the mean values and standard deviations of the FIA plots with the mature and old growth sites. As part of this exploratory analysis, I applied locally weighted regression splines (loess models) to illustrate smoothed diameter distributions of the selected structural variables. The loess models were fitted as informal tools to better visualize differences between the FIA plots and the mature and old growth sites, and not as a formal statistical test; differences in study area, plot design, and sampling methods prevented a more rigorous statistical comparison between my dataset and the FIA plots.

4. Results

4.1. Stand age and composition

The mean stand age of remnant old forests in the study region was 208 years. Site-specific stand ages ranged from 72 to 361 years (Table 2.3). Across all sites, average BA was 47.0 m^2 ha^{-1} and ranged from 30.1 to 84.9 m^2 ha^{-1}. *Liriodendron tulipifera* was the most abundant overstory species by BA (13.9 m^2 ha^{-1}) followed by *Quercus alba* (8.8 m^2 ha^{-1}) then *Q. prinus* (7.1 m^2 ha^{-1}) (Figure 2.3A). The sites clustered into four groups based on their tree species composition (Figure 2.3). Of the four groups, Group One included the largest number of sites (n = 12), followed by Group Two (n = 7), Group Three (n = 4), and Group Four (n = 2). The ten most dominant species in cluster Group One occurred across similar ranges in BA, with *Q. alba* occurring at a slightly higher mean value than the other species. Groups Two and Three appear to be defined by the predominance of one or two species. In Group Two, *L. tulipifera* contributed a mean of 36.9 m^2 ha^{-1} to total BA of the sites, a value three-fold greater than the next most abundant species. In Group Three, *Q. prinus* and *Tsuga canadensis* contributed a mean of

26.3 m^2 ha^{-1} and 20.7 m^2 ha^{-1} to the overall BA of these sites, respectively. *Acer saccharum* Marshall (sugar maple) and *Q. rubra* were similarly prevalent in the two sites that comprise Group Four, with mean BAs of 19.2 m^2 ha^{-1} and 17.7 m^2 ha^{-1}, respectively. There are other species within Group Four that have high mean BA values, but appear only in one of the two sites, and so do not characterize the group as a whole.

4.2. Ordination

Not surprisingly, the compositional grouping identified by the cluster analysis was reinforced within the two-dimensional NMS ordination diagram. The centroid for *Q. alba* fell within Group One and *L. tulipifera* within Group Two (Figure 2.4). The abundances of these two species within their respective cluster groups and centralities in the ordination led me to identify the two groups as the *Q. alba* dominant forest type and the *L. tulipifera* dominant forest type. As expected, the centroid for *Q. prinus* shared ordinational space with Group Three and *A. saccharum* with Group Four, and *T. canadensis* and *Q. rubra* fell near the two respective cluster polygons.

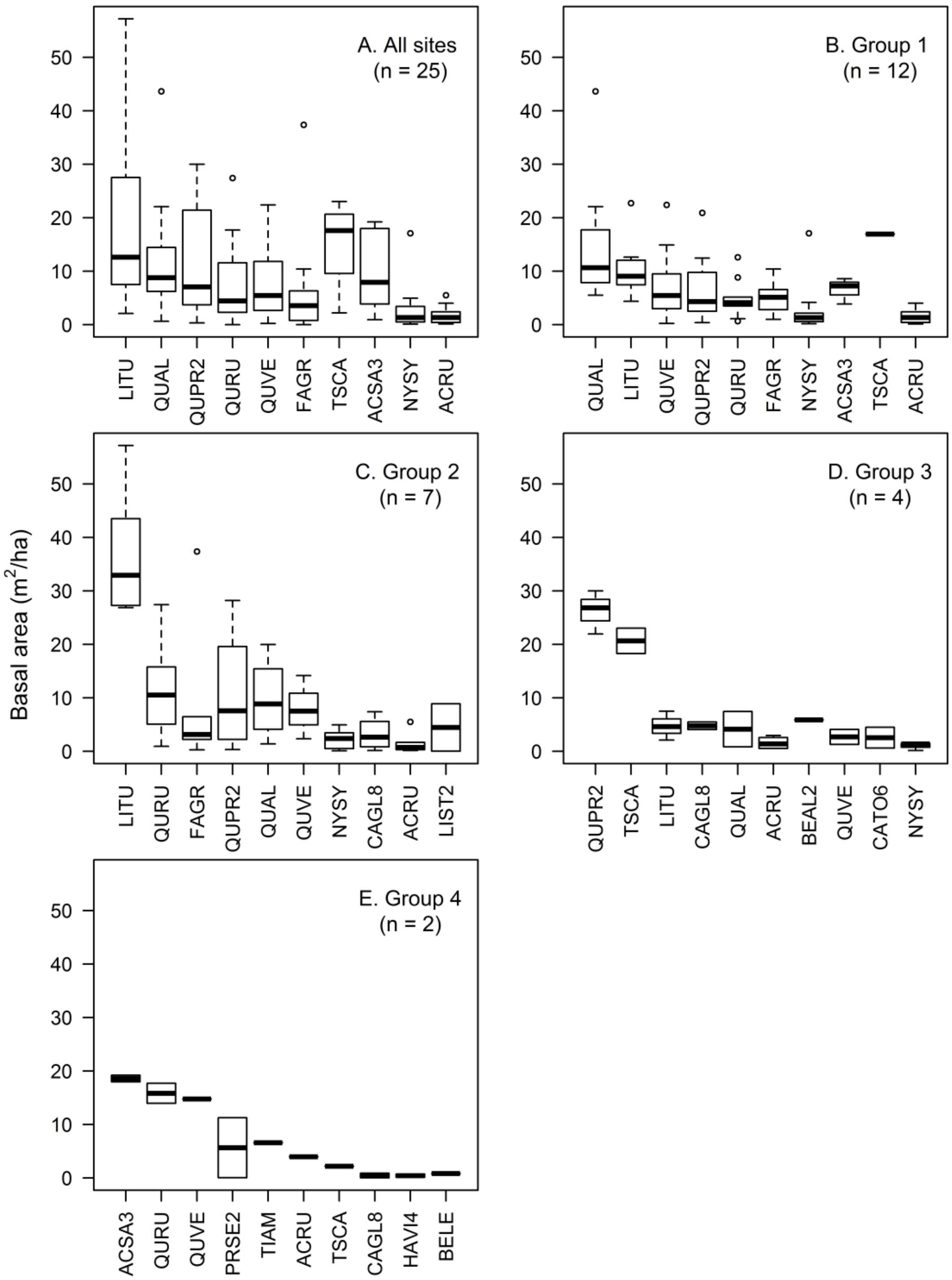

Figure 2.3. Box plots of basal area (m^2 ha^{-1}) of the ten most dominant species across sites and characterizing the four cluster groups derived from the two-way cluster analysis. See Appendix A for species codes

The overlay of the cluster polygons further defined distinctions in species composition among the old growth sites. For example, Group Three had the lowest Axis 2 values and Group Four had the highest Axis 1 values, whereas the *L. tulipifera* and *Q. Alba* dominant sites plotted centrally in the ordination.

Of the twenty-five environmental and structural variables fit to the NMS ordination of sites, six variables had correlation coefficients greater than 0.25 and were included in the ordination bi-plot (Table 2.2; Figure 2.4). These variables included annual mean temperature, elevation, TWI, percent N in the O-horizon, longitude, and maximum tree height. Of these variables, elevation had the highest r^2 value. Mean stem density, species evenness, slope, annual maximum temperature, and heating degree days were also important in explaining differences in species composition ($r^2 > 0.20$), but were not included in the bi-plot. The factor that most strongly correlated with Axis 1 was elevation ($r^2 = 0.64$), and the factor that most strongly correlated with Axis 2 was TWI ($r^2 = 0.50$; Figure 2.4). Stand age often relates to species composition in late successional stands (Gilliam and Platt 1999), but contrary to predictions, had little explanatory power in the ordination ($r^2 = 0.14$).

Bi-plots indicate the four groups were best explained by different sets of environmental variables (Figure 2.4). Sites dominated by *Q. alba* (Group One) placed centrally across Axis 1 and high on Axis 2, consistent with high TWI, low percent N in the O-horizon, and high annual average temperatures. The *L. tulipifera* dominated sites (Group Two) placed low on Axis 1, which was associated with low elevation, the tallest trees, and easterly locations (more positive longitudinal values). Group Three associated with low TWI and the two sites in Group Four associated with high elevation, high percent N, and westerly locations (more negative longitudinal values).

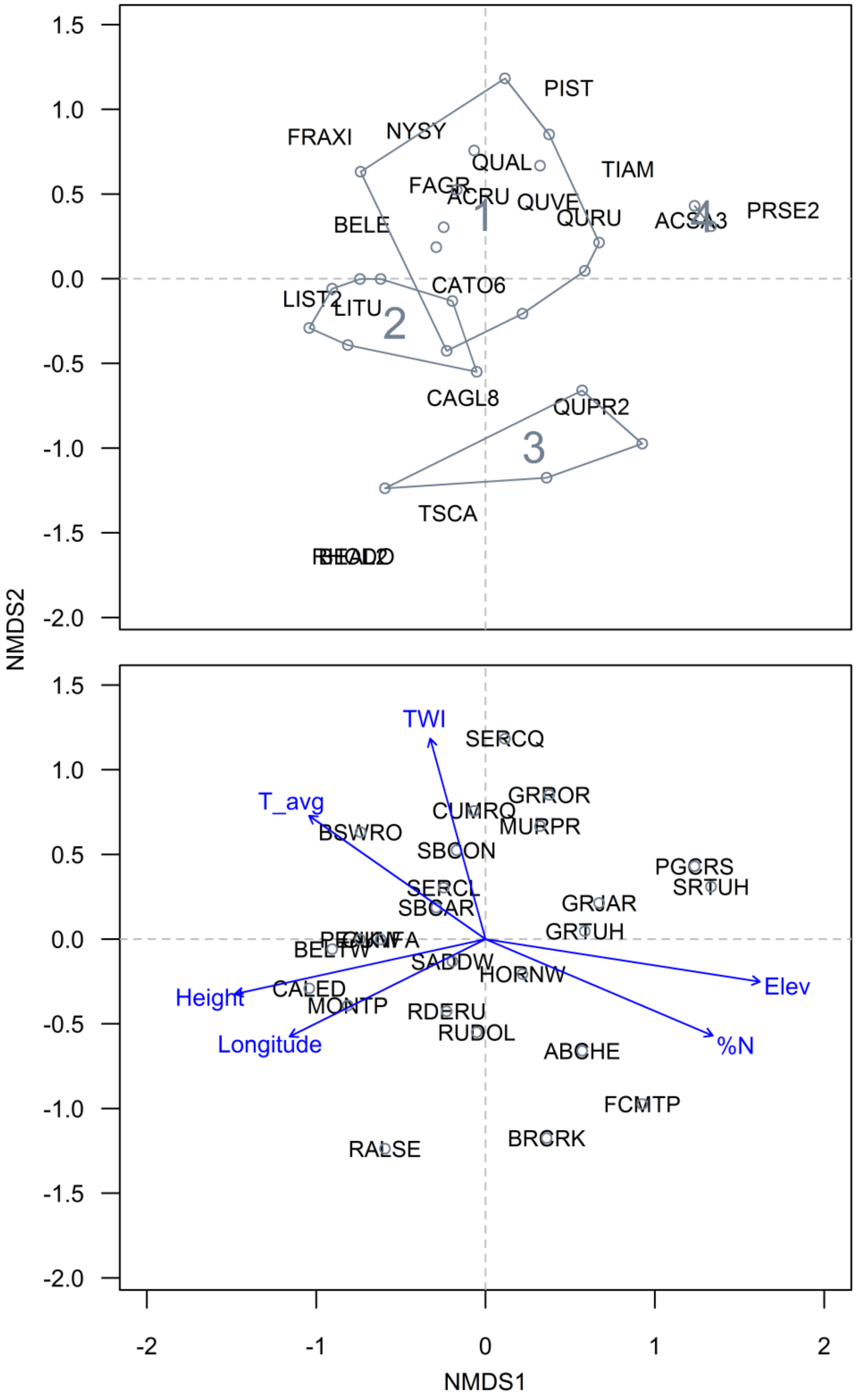

Figure 2.4. NMS ordination of the twenty five mature and old growth sites in tree species composition space defined by relative BA. Small points indicate site locations in ordination space. The ordination is rigidly rotated to parallel the elevation vector against axis 1. Vectors indicate the strength and direction of the correlation coefficients between sites and environmental variables. Bi-plot vectors with an r^2 of 0.25 or greater were plotted. The overlay (above) indicates the four cluster groups derived from the two-way cluster analysis. See Table 1.3 for site abbreviations, Table 1.2 for environmental variable codes, and Appendix A for species codes.

Table 1.2. The correlation coefficients (r^2) for environmental variables used in the NMS ordination. The P-value (P) refers to the significance of the r^2 value. Variables with an r^2 of 0.25 or greater are in bold.

Variables		r^2	*P*
Structural			
Mean stem density (trees ha^{-1})	Stem density	0.2217	0.1014
Mean basal area (m^2 ha^{-1})		0.0242	0.8019
Mean large stem density (m^2 ha^{-1})		0.1674	0.1876
Tallest tree height (m)	Height	**0.3928**	**0.0182**
Mean dead wood volume (m^3 ha^{-1})		0.1713	0.1823
Mean large snag density (m^2 ha^{-1})		0.1942	0.1445
Sapling stem density (trees ha^{-1})		0.1674	0.1922
Stand age		0.1365	0.2439
Diversity			
Species richness		0.1889	0.1539
Species diversity		0.1863	0.1639
Species evenness		0.2306	0.0961
Environmental			
Elevation (m)	Elev	**0.4530**	**0.0042**
Slope		0.2194	0.1073
Aspect		0.0093	0.9193
Topographic wetness index	TWI	**0.2590**	0.0616
Mean O-horizon depth		0.1764	0.1698
Percent N in O-horizon	% N	**0.3579**	**0.0182**
C:N ratio in O-horizon		0.1307	0.2633
Latitude		0.1021	0.3804
Longitude		**0.2862**	**0.0479**
Annual precipitation normals (cm)		0.1136	0.3360
Annual temperature average normals (°C)	T_avg	**0.2729**	0.0550
Annual temperature maximum normals (°C)		0.2036	0.1272
Annual heating degree day normals		0.2305	0.0951

4.3. Living tree structure and maximum estimated stand age

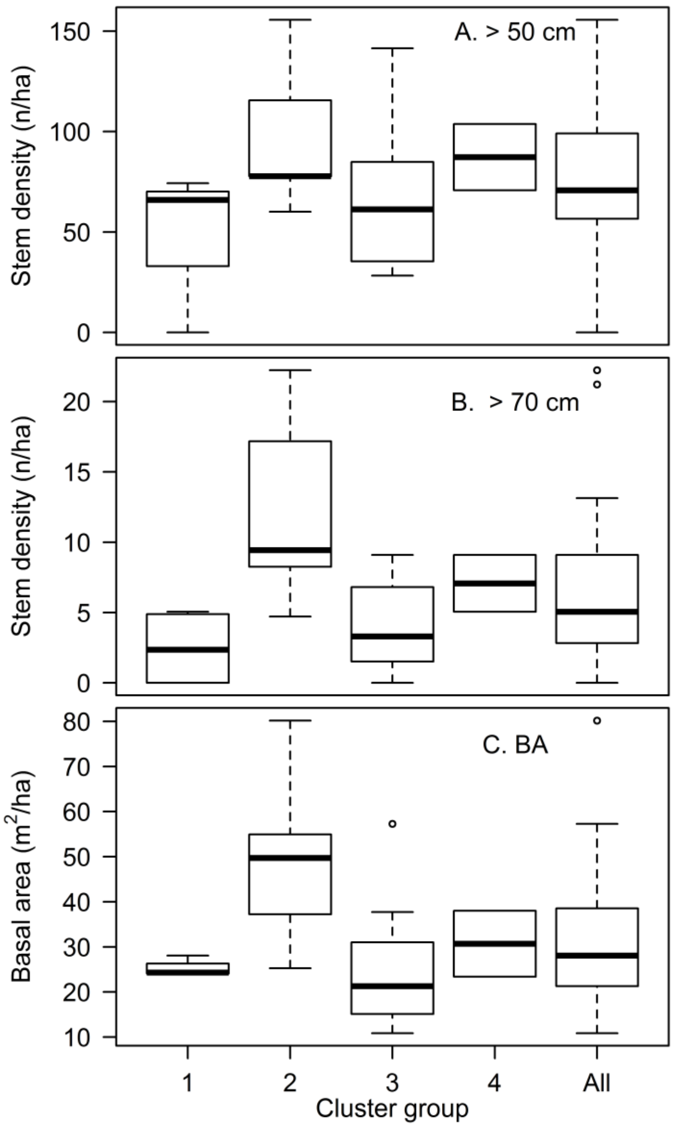

Figure 2.5. Boxplot of (A) medium tree stem density, (B) large tree stem density, and (C) total BA by cluster groups and all sites.

Overall stem densities varied widely, with a mean stem density (> 5 cm DBH) of 599 stems ha^{-1} (*sd* = 514 stems ha^{-1}), ranging from 217 to 938 stems ha^{-1} (Table 2.3). There was no significant relationship ($P < 0.05$) between total stem density and stand age ($r^2 = 0.04$, $P = 0.837$, $n = 24$). Mean medium (>50 cm DBH) and large (>70 cm DBH) stem densities were 73.8 and 6.4 stems ha^{-1}. There were significant correlations between stand age and medium and large tree densities, in which stem density linearly decreased with age (medium [Density = 24.305 – 0.033(age); $r^2 = 0.18$, $P = 0.024$], large [Density = 10.008 – 0.016(age); $r^2 = 0.17$, $P = 0.038$]. Prevalence of medium and large diameter *L. tulipifera* in five stands, aged 140 to 170, drove the observed decline; the negative trend disappeared when *L. tulipifera* was removed from all sites. Furthermore, the median density of large trees in the *L. tulipifera* forest type (Group 2) was greater than the other three groups and the study median (Figure 2.5B).

There was a significant negative linear trend observed between total live BA and site age (BA = 64.304 – 0.079(Age); $r^2 = 0.12$, $P = 0.049$). Again the prevalence of large *L. tulipifera* at five of the younger stands drove the trend. When *L. tulipifera* stems were removed from all sites, the trend no longer was negative or significant. Also, median BA of the *L. tulipifera* dominant sites was higher than those of the other three groups and study median (Figure 2.5C).

The structure of the understory varied across stands, ranging from 14 to 1401 stems ha^{-1} in sapling (< 5 cm DBH) density with a mean of 374 saplings ha^{-1} (*sd* = 340 saplings ha^{-1}; Table 2.3). The 100-fold difference between the minimum and maximum sapling densities was due to the abundance of prolific single shrub species at the highest density sites. *Lindera benzoin* (L.) Blume (spice bush) composed an estimated 99.5% and 84.1% of the understory in the two highest density sites, respectively, and *Rhododendron*

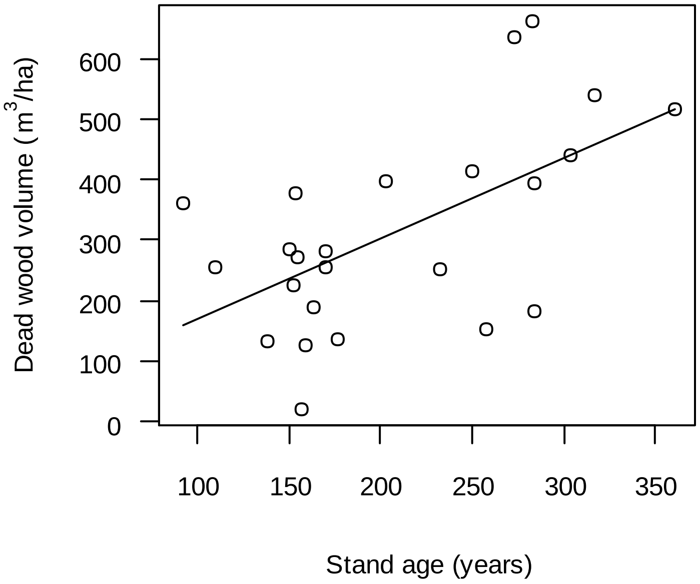

Figure 2.6. Relationship between stand age and dead wood volume for the twenty-five old growth sites.

sp. L. (rhododendron) accounted for 88.2% of all saplings in the third highest density stand. There was no significant linear relationship between sapling density and site age ($r^2 = 0.03$, $P = 0.613$).

4.4. Dead wood structure

Mean dead wood volume (m^3 ha^{-1}) across sites was 311.7 m^3 ha^{-1} ($sd = 161.8$ m^3 ha^{-1}) and ranged from 21.2 m^3 ha^{-1} to notably high values of 661.5 m^3 ha^{-1} (Table 2.4). Large snag densities ranged from zero to 18 snags ha^{-1} with a mean of 6 snags ha^{-1}. Of the dead wood characteristics measured, mean dead wood volume alone increased significantly with age (volume = 1.329[age] + 35.67; $r^2 = 0.313$, $P = 0.002$; Figure 2.6).

4.5. Comparison with forest inventory data

In comparing the old growth stands to the average landscape conditions, I found the greatest differences occurred in the diameter class extremes. In the largest diameter class (stems > 53 cm DBH), old growth contributed on average 30 m^2 ha^{-1} to live BA, a value nearly six-fold higher than that of the FIA sites (Figure 2.7A). Similarly, snag BA in the largest size class was over twice as great in the old growth stands as the younger forests (Figure 2.7C). This trend was observed to a lesser extent in live and dead snag densities. The comparisons of stem densities instead highlighted differences in the smallest size classes. Density of live stems in the smallest size class (3 – 13 cm DBH) for FIA plots was 1248 stems ha^{-1}, four times larger than the old growth sites. Small diameter snag density (13 – 28 cm DBH) also was greater in the FIA plots than the old growth sites (Figure 2.7D). The differences in the smallest and largest size classes led to greater total stem and snag densities in younger forests (stem density [FIA = 1477 stems ha^{-1}, old = 1186 stems ha^{-1}], snag density [FIA = 42 snags ha^{-1}, old = 22 snags ha^{-1}]), and greater total live and snag BA in old growth forests (live BA [FIA = 25.9 m^2 ha^{-1}, old = 53.8 m^2 ha^{-1}], dead BA [FIA = 1.6 m^2 ha^{-1}, old = 21.9 m^2 ha^{-1}]).

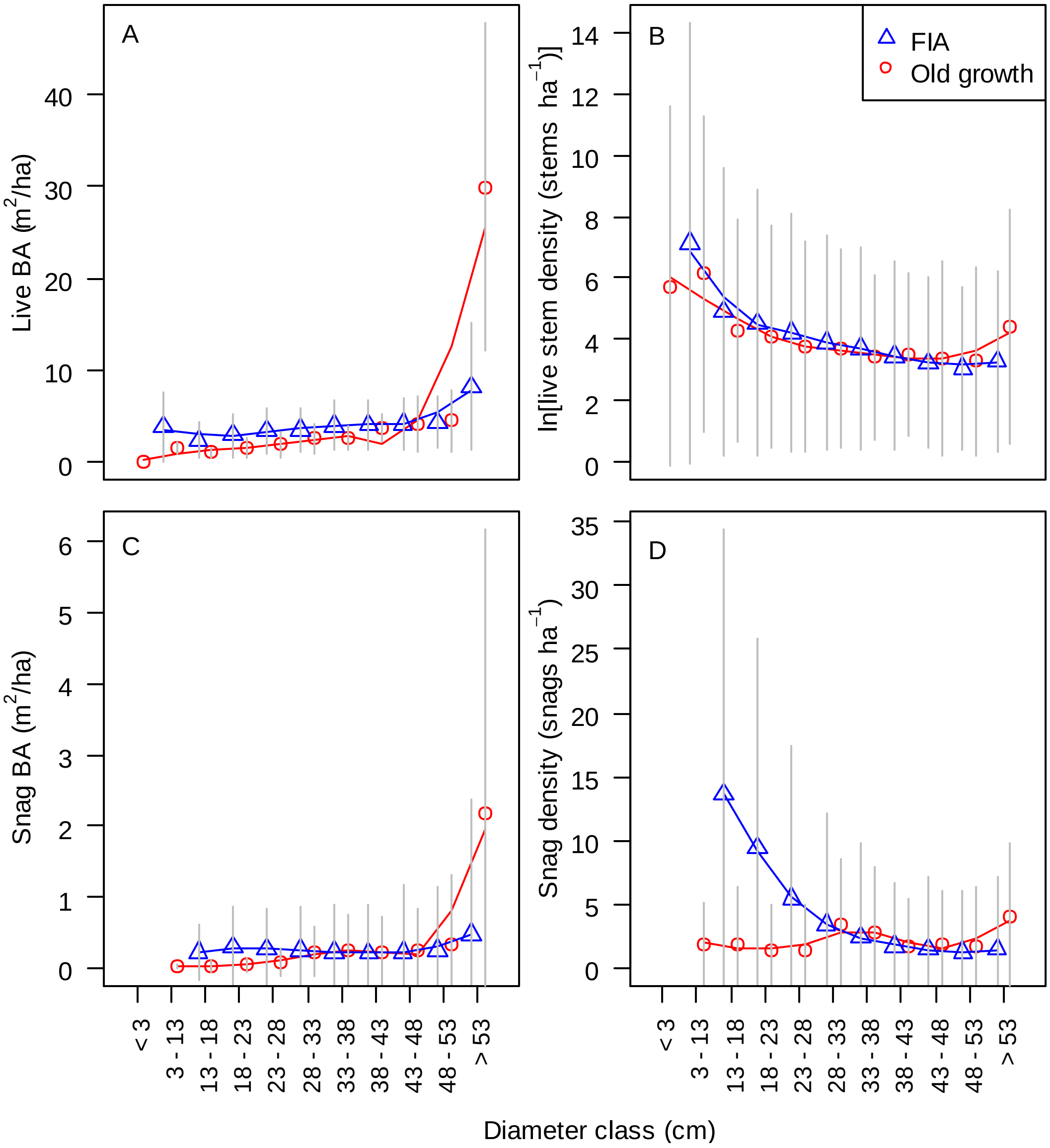

Figure 2.7. (A) Mean aboveground live BA (m^2 ha^{-1}), (B) natural log of mean live stem density (stems ha^{-1}), (C) mean snag BA (m^2 ha^{-1}), and (D) mean snag stem density (snags ha^{-1}) of the mature and old growth and FIA forest sites by diameter size class. Bars indicate one SD.

Table 2.3. Summary information for aboveground live structural characteristics of the twenty-five mature and old growth stands. All values presented, with the exception of site age, are site means.

Site name	Code (Fig 1. map key)	State	Cluster	No. plots	Max site age (years)	Basal area (m^2 ha^{-1}) ‡	Stem density (stem ha^{-1})			Source for Age estimate*
							All‡	Sapling ‡	Large tree‡	
Belt Woods	BELTW (1)	MD	2	4	250	47.9	375	1050	35	Rucker 2004
Broad Creek Memorial Reserve	BRCRK (2)	MD	3	4	283	47.1	743	95	18	
Green Ridge State Forest, Jacob's Road	GRJAR (3)	MD	1	3	110	44.1	481	453	5	
Green Ridge S.F., Roby Ridge 1	GRROR (4)	MD	1	3	232	35.8	726	236	0	
Green Ridge S.F., Tunnel Hill	GRTUH (5)	MD	1	3	163	40.5	712	118	0	
Gunpowder Falls State Park	GUNFA (6)	MD	2	4	170	50	502	410	35	
Potomac-Garrett S.F., Crabtree Woods	PGCRS (7)	MD	4	3	150	49.7	542	330	42	
Smithsonian Ecological Research Center (SERC), Frog Canyon	SERCL (8)	MD	1	3	138	49.3	486	52	42	J. Parker, personal comm.
SERC, Hog Island	SERCQ (9)	MD	1	2	258	71.9	891	170	64	
Savage River S.F., Turkey Lodge	SRTUH (10)	MD	4	3	92	46.2	599	448	24	
Saddler Woods	SADDW (11)	NJ	2	3	159	60.7	308	203	74	
Buchanan S.F., Sweet Root Natural Area	BSWRO (12)	PA	1	3	–	26.9	401	302	9	
French Creek State Park, Mount Pleasure	FCMTP (13)	PA	3	3	157	30.1	872	250	0	
Peak Woods	PEAKW (14)	PA	2	3	152	84.9	217	1401	104	
Rothrock S.F., Allan Seeger Natural Area	RALSE (15)	PA	3	3	273	31.8	580	1000	24	Nowacki and Abrams 1994
Rothrock S.F., Detweiler Run Natural Area	RDERU (16)	PA	1	3	203	39.9	745	637	14	Ruffner and Abrams 1998
Appomattox Buckingham S.F., Chestnut Ridge Natural Area	ABCHE (17)	VA	3	3	176	54.1	938	476	0	
Caledon State Park	CALED (18)	VA	2	3	154	67.1	531	74	46	
Cumberland S.F., Rock Quarry	CUMRQ (19)	VA	1	3	155	52.3	858	594	28	
Montpelier	MONTP (20)	VA	2	4	304	39.6	470	290	18	Dierauf 2011

Site name	Code (Fig 1. map key)	State	Cluster	No. plots	Max site age (years)	Basal area (m^2 ha^{-1}) ‡	Stem density (stem ha^{-1}) All‡	Sapling ‡	Large tree‡	Source for Age estimate*
Rudolph Family Farm	RUDOL (21)	VA	2	4	170	65.6	545	19	25	
Sweetbriar College, Carry Sanctuary	SBCAR (22)	VA	1	4	284	29.4	594	187	18	Druckenbrod et al. 2005
Sweetbriar College, Constitution Oaks	SBCON (23)	VA	1	4	284	35	576	159	28	Druckenbrod et al. 2005
Horner Woods Game Refuge	HORNW (24)	WV	1	3	317	44.5	717	226	19	Rentch et al. 2003
Murphy Preserve	MURPR (25)	WV	1	3	361	30.9	571	160	14	Rentch et al. 2003
Mean (SD)					208 (72.8)	47 (14.5)	599 (184)	374 (340)	27 (25)	

‡ All refers to all stems greater than five cm DBH, saplings refer to all stems between one and five cm DBH, large trees to all stems greater than 70 cm DBH, and canopy tree refers to all stems greater than 50 cm DBH. BA refers to all stems greater than five cm DBH.

* Sources are provided for sites where permission was not given to collect tree cores, but reliable age estimates were available.

Table 2.4. Summary information for aboveground dead structural characteristics of the twenty-five mature and old growth stands. All values presented, with the exception of site age, are site means. See Table 2.3 for stand age sources.

Site	State	Cluster	Max stand age	Dead wood volume (m^3 ha^{-1})	Large snag density (n ha^{-1}) ‡	Large snag volume (m^3 ha^{-1}) ‡
BELTW	MD	2	250	413.7	9	105.2
BRCRK	MD	3	283	661.5	18	120.3
GRJAR	MD	1	110	255.9	0	0
GRROR	MD	1	232	251.6	0	0
GRTUH	MD	1	163	187.5	0	0
GUNFA	MD	2	170	280.4	0	0
PGCRS	MD	4	150	283.4	9	38.7
SERCL	MD	1	138	133.1	0	0
SERCQ	MD	1	258	151.6	0	0
SRTUH	MD	4	92	360.6	7	59.3
SADDW	NJ	2	159	127.1	0	0
BSWRO	PA	1	–	296.3	0	0
FCMTP	PA	3	157	21.2	0	0
PEAKW	PA	2	152	226.8	0	0
RALSE	PA	3	273	636.1	14	135.1
RDERU	PA	1	203	395.1	7	81.2
ABCHE	VA	3	176	136.0	0	0
CALED	VA	2	154	378.3	14	43.0
CUMRQ	VA	1	155	271.0	0	0
MONTP	VA	2	304	439.8	7	155.5
RUDOL	VA	2	170	254.6	5	12.0
SBCAR	VA	1	284	181.4	0	0
SBCON	VA	1	284	394.2	14	156.1
HORNW	WV	1	317	539.4	0	0
MURPR	WV	1	361	515.1	5	41.4
Mean (SD)			208 (72.8)	311.7 (161.8)	6 (4)	37.9 (54.7)

‡ Large refers to snags greater or equal to 50 cm DBH.

5. Discussion

Remnant old growth forests constitute one percent of all eastern forests (Davis 1996), and even this estimate seems high for the Mid-Atlantic. I surveyed the structure and composition of the relic stands within the region to determine whether these forests share common characteristics resulting from their age, distinguishing them from the expanse of younger forests that surround them. Stand age was not a singular predictor of structure and composition among old growth sites – on the contrary, stand age in general was a poor indicator of structure and composition, with the exception of dead wood volume. Rather, there was no singular characteristic that determined both composition and structure of these sites. Composition was driven by site-specific environmental variables, and on the other hand, structure was influenced more by species. My sites are not a random sample, nor do they represent a scope of inference any larger than themselves. Instead, they represent virtually all that is left of the productive primary forests that once blanketed this landscape. The information gleaned from these stands illustrates the idiosyncratic traits of an invaluable dataset.

5.1. Stand age as a predictor of old growth

Within the mature and old growth sites surveyed, stand age was an imperfect predictor of old growth structure and composition. I selected these sites to survey because they were identified as old growth based on age, and frequently had developed site histories indicating minimal anthropogenic disturbances. However, I measured a wide range of maximum ages (72 – 361 years) across stands. The youngest stands were less than half the original reported age used to select the sites (150 years), and more closely approximated the age of the younger secondary forest matrix for the region than that of mature and old growth forests (Drummond and Loveland 2010). Additionally, some of these forests still exhibited direct and indirect evidence of past land use. At Belt Woods, one of the best historically verified old growth forests in this study, barbed-wire fencing was found running through the interior of the stand (Figure 2.8). Less obvious evidence was the prevalence of early seral *L. tulipifera* across all sites, and particularly within the identified *L. tulipifera* dominant cluster group. *L. tulipifera* is classically described as an early to mid-succession species in many eastern temperate forests, frequently dominating the canopy during this period (Della-Bianca 1983, Beck 1990). Dominance of *L. tulipifera* into late succession is unique because it cannot regenerate under a closed canopy. The opportunity for *L. tulipifera* to flourish may relate to the suppression of oak regeneration in old growth of the eastern U.S. in the 1900s (McCarthy et al. 1987, 2001, Abrams and Downs 1990). Chronological surveys of old growth stands in southwestern Pennsylvania and northeastern Virginia identified a proliferation of *Fagus grandifolia*, *Acer rubrum*, and *L. tulipifera* around 1900 (Abrams and Downs 1990, Abrams and Copenheaver 1999). The recruitment of mixed-mesophytic species in old growth oak forests in the eastern U.S. is thought to be due to anthropogenic disturbances, such as logging, land clearing, fire suppression, and selective deer browsing (Abrams et al. 1998). The common denominator for all twenty-five sites was therefore not old age or minimal anthropogenic disturbance, but rather the abundance of large diameter trees. On average, medium and large diameter stem density is 62.5 stems ha^{-1} for eastern old growth (Burrascano et al. 2013). Mean medium and large stem density for my sites was 73.8 stems ha^{-1}, higher than the average for other old growth in the eastern U.S. High densities of large trees was an important criterion for my stand delineation method, thus the significance is expected.

Dead wood volume was the structural attribute most related to stand age (Figure 2.6). Chronosequences of mature and old growth forests in upland deciduous forests in the Midwest (Spetich et al. 1999) and northern hardwoods (Keeton et al. 2011) have also demonstrated an increase in dead wood volume through late succession. Dead wood recruitment is a slow process that is affected by anthropogenic disturbance, which may explain why dead wood volume was the best predictor of stand age. High volumes of dead wood are due to the mortality of large canopy stems in late succession and the resulting tree-fall damage to surrounding stems directly, and indirectly by increasing vulnerability to disturbances such as wind-throw or pest outbreaks (Harcombe et al. 1990, Dahir and Lorimer 1996, D’Amato et al. 2008, Harmon 2009). Forests affected by anthropogenic disturbances, ranging from large-scale modifications such as settlement, to small-scale disturbances like selective logging, tend to contain less dead wood than undisturbed primary forests (Webster and Jenkins 2005). More than all other structural attributes, dead wood volume is most important for habitat (Thomas et al. 1988). Thus the increase in dead wood volume into late succession has important implications for promoting and preserving biodiversity within Mid-Atlantic old growth forests.

5.2. Species composition as a predictor of forest structure

The decline in medium and large stem density and BA with increasing stand age goes against a fundamental understanding of previously observed gradients in structural variation associated with stand age (Spies and Franklin 1991, Tyrrell and Crow 1994, Poage and Tappeiner II 2005, Keeton et al. 2011, Burrascano et al. 2013). Rather than age-related processes, differences in tree community composition drove the observed relationship between stand age and these structural variables. Indeed, composition was the best predictor of forest structure because the different communities identified by the cluster analysis had such different structural characteristics.

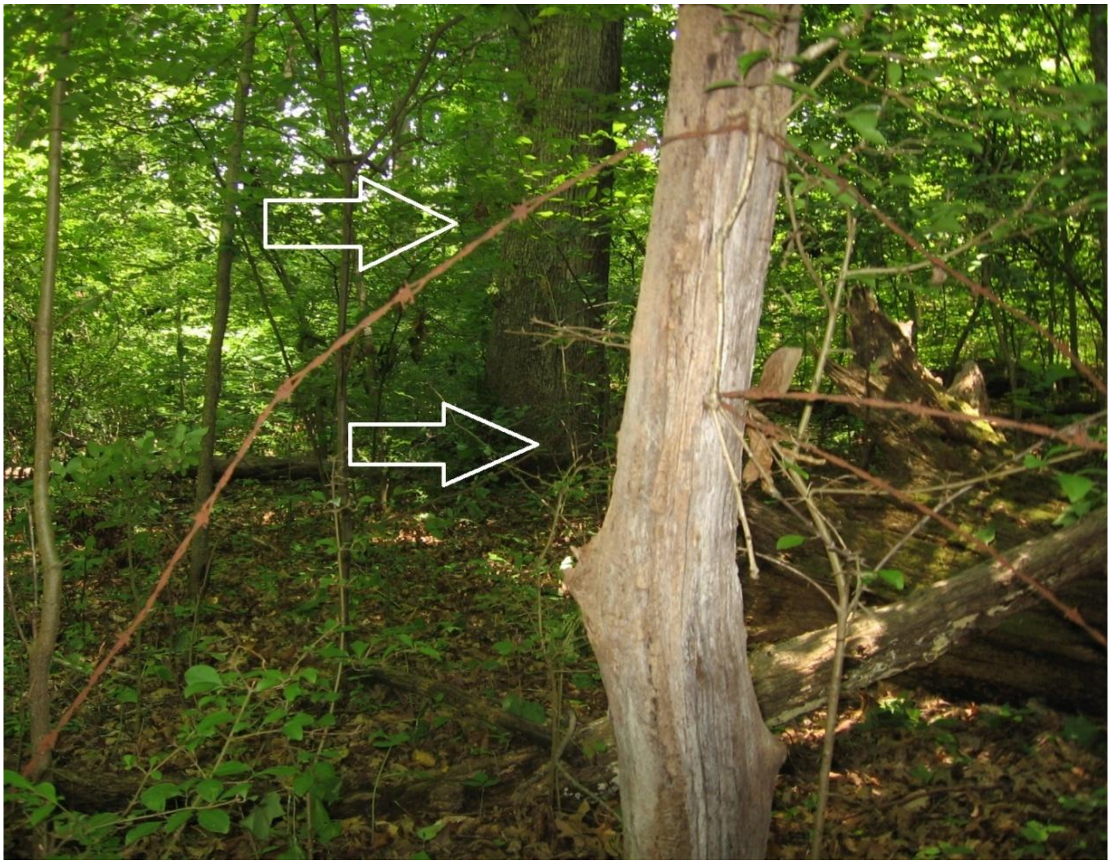

Figure 2.8. In the foreground, barbed wire is strung across an old fence post (arrows) in the interior of Belt Woods, MD. In the background, a large diameter tree and a large volume log are visible, both classic indicators of undisturbed old growth forests. Photo: J.C. McGarvey.

The sites that most closely resembled characteristic old growth structure were within the *L. tulipifera* dominant forest type (Group Two). Specifically, large stem density and BA were the highest in this forest type relative to the three other compositional groups (Figure 2.5). Ironically, they were also among the youngest sites sampled. For example, Peak Woods in Pennsylvania had the highest large stem density (*mean* = 104 stems ha^{-1})

and BA (*mean* = 84.9 m^2 ha^{-1}) of all twenty-five sites, but narrowly qualified as old growth at 152 years. As previously discussed, *L. tulipifera* is an early seral species, and typically anomalous within old growth forests. Preservation of *L. tulipifera* into late succession has been observed in old growth southern Appalachian cove forests. In this forest type, *L. tulipifera* occurs at high densities in stands older than its maximum life span of approximately 300 years (Buckner and McCracken 1978, Busing 1995). Busing (1995) suggests that *L. tulipifera* can dominate for 50-150 years following stand initiation, and another 150-250 years is required for this species to decline from dominance. For *L. tulipifera* to regenerate into late succession at 100-200 year intervals, mortality must create large enough gaps (0.1 ha) to allow for re-establishment. Gaps of this size are dependent on *L. tulipifera* being among the tallest of eastern broadleaf trees (Burns and Honkala 1990), and they must reach the maximum diameters observed in the *L. tulipifera* dominant forest type. In their dependence on large gaps to regenerate, *L. tulipifera* proliferation in Mid-Atlantic old growth is analogous to *Pinus strobus* (white pine) in the northeastern U.S. and *Pseudotsuga menziesii* (douglas fir) in the Pacific Northwest. Regeneration and perpetuation of these early seral, shade-intolerant species in late succession are dependent on reoccurring disturbances, such as fire or catastrophic wind events, to form large gaps (Franklin and Dyrness 1973, Hemstrom and Franklin 1982, Frelich and Reich 1995, Abrams et al. 1995, Spies 1997). *L. tulipifera* differs from these two species in decay rates. Specifically, *L. tulipifera* has a relatively high decay rate in comparison to many soft- and hardwood species (Harmon et al. 1986). As a result, *L. tulipifera* does not produce enduring dead wood.

Oaks, particularly *Q. alba*, remain the dominant tree in the majority of remaining old growth in the Mid-Atlantic region (Figure 2.4C). Based on previous descriptions of hardwood old growth in the eastern United States, the sites within the *Q. alba* dominant forest type are typical of the mixed mesophytic forests that once covered the region (Braun 1950, Muller 1982, Abrams and Downs 1990, McCarthy et al. 2001). The major dominants of this forest type are *Q. alba*, *Fagus grandifolia*, *Acer saccharum*, and *L. tulipifera*, but there is also an important mixture of *Q. rubra*, *Q. velutina*, *Nyssa sylvatica*, *A. rubrum*, and minor contributions by *Carya* spp., *Fraxinus americana*, and *Ulmus rubra* (slippery elm; Braun 1950). BA estimates of mixed mesophytic old growth forests outside of the study sites for stems greater than 10 cm DBH range from 26 to 68 m^2 ha^{-1} (Muller 1982, Greenberg et al. 1997). The median BA for the *Q. alba* dominant forest type falls well within that range (Figure 2.5C). The *Q. alba* dominant forest is a generalist type in the Mid-Atlantic in that no environmental variables associate strongly with it, evident by how the cluster concentrates at the center of the NMS ordination (Figure 2.4). McEwan et al. (2005) also identified overstory *Q. alba* at the center of an ordination for old growth mixed mesophytic forests in eastern Kentucky. The generalist qualities of this forest type make it the best allegory for potential late successional forest structure for much of the regional forest mosaic of the Mid-Atlantic.

However, no blanket statements about the old growth of the Mid-Atlantic are likely to encapsulate the diversity of conditions that once existed. Even within this limited sample of sites, two smaller cluster groups emerged, unique in both composition and environmental drivers (Figure 2.4). For example, Group Three represented four sites in which *Quercus prinus* and *Tsuga canadensis* were similarly dominant. *Tsuga canadensis* is a late successional, shade tolerant foundation species in northeastern forests; its southern extent is absent in eastern Virginia and Maryland, and it is not a common species in the dominant forest community types of the Mid-Atlantic (Table 2.1; Burns and Honkala 1990). As such, I emphasize that the scope of inference for this study is limited to the remaining late successional forests for the Mid-Atlantic region, and is not intended to define all potential old growth conditions for the younger secondary forest matrix.

5.3. Implications and context of structural variation within the greater matrix of young, secondary forests

Implicit to the discussion of stand age and structural attributes in old growth is the assumption that old growth structure is inherently different from that of younger, secondary forests. So although old growth forest structure, with the exception of dead wood volume, was driven by species composition, the critical question for future management of secondary and old growth forests alike is whether forest structure is different between these two age classes. Several studies have used FIA plots as a reliable, unbiased sample of the existing population of forests in the Mid-Atlantic region (Jenkins et al. 2001, Pan et al. 2009). I found the largest differences between the FIA plots and the old growth sites occurred in the smallest and largest size classes, where old growth had higher total snag and live BA, and the FIA plots had greater total snag and live stem density (Figure 2.7). My findings confirm former studies that found significant structural differences between young, secondary forests and old growth (Hale et al. 1999, McGee et al. 1999). The differences between the two age classes are not surprising, considering large stem and snag BA were important qualifiers in identifying the old growth stand from the surrounding secondary forest.

6. Conclusion

By characterizing the structure and species composition of remnant mature and old growth forests of the Mid-Atlantic, I have learned much about a unique forest condition, previously understudied in this geographic region. The most prevalent characteristic of these stands is high BA, regardless of species composition or environmental conditions. In contrast, the one assumed shared trait of all these stands, maturity, was indeed not shared, and was an ineffective predictor of structural characteristics. Species composition instead was the most important driver of structural differences among stands, where some of the youngest and possibly anthropogenically disturbed stands best approximated classic old growth structure – i.e., high BA and large tree stem density. This study is not intended as a benchmark for defining potential old growth structure and composition in the Mid-Atlantic, but rather to continue developing current understanding of variability within this rare forest condition.

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Appendix A. Definitions of USDA-NRCS species codes.

USDA-NRCS Code	Species	Common Name
ACRU	*Acer rubrum*	red maple
ACSA3	*Acer saccharum*	sugar maple
BEAL2	*Betula alleghanensis*	yellow birch
BELE	*Betula lenta*	sweet birch
CAGL8	*Carya glabra*	pignut hickory
CATO6	*Carya tomentosa*	mockernut hickory
FAGR	*Fagus grandifolia*	American beech
FRAXI	*Fraxinus* sp.	ash
LITU	*Liriodendron tulipifera*	tulip poplar
HAVI4	*Hamamelis virginiana*	witch hazel
NYSY	*Nyssa sylvatica*	blackgum
PIST	*Pinus strobus*	white pine
PRSE2	*Prunus serotina*	black cherry
QUAL	*Quercus alba*	white oak
QUPR2	*Quercus prinus*	chestnut oak
QURU	*Quercus rubra*	red oak
QUERC	*Quercus* sp.	Oak
QUVE	*Quercus velutina*	black oak
TIAM	*Tilia Americana*	American basswood
TSCA	*Tsuga Canadensis*	eastern hemlock

Appendix B. Weather station locations and associated study sites. All weather data were acquired from NOAA NCDC Climate Data Online (see www.ncdc.noaa.gov/cdo-web for data).

Site code	Weather station	State	Latitude	Longitude
BELTW	UPPER MARLBORO 3 NNW	MD	38.86528	-76.77667
BRCRK	CONOWINGO DAM	MD	39.65583	-76.17556
CALED	QUANTICO MCAS	MD	38.5	-77.3
GRJAR/GRROR/GRTUH	CUMBERLAND 2	MD	39.6419	-78.7561
GUNFA	ABERDEEN PHILLIPS FIELD	MD	39.47167	-76.16972
PGCRS/SRTUH	SAVAGE RIVER DAM	MD	39.51028	-79.14
SERCL/SERCQ	UPPER MARLBORO 3 NNW	MD	38.86528	-76.77667
BSWRO	EVERETT	PA	40.01361	-78.36528
FCMTP	POTTSTOWN LIMERICK AIRPORT	PA	40.23833	-75.55722
PEAKW	PHILADELPHIA NE PHILADELPHIA AIRPORT	PA	40.08194	-75.01111
RALSE/RDERU	STATE COLLEGE	PA	40.79333	-77.86722
SADDW	PHILADELPHIA FRANKLIN INST	PA	39.9576	-75.1727
ABCHE	APPOMATTOX	VA	37.3558	-78.8313
CUMRQ	BREMO BLUFF	VA	37.7091	-78.2885
MONTP	PIEDMONT RESEARCH STATION	VA	38.23222	-78.12028
RUDOL	WINCHESTER	VA	39.1881	-78.1514
SBCAR/SBCON	TYE RIVER 1 SE	VA	37.6383	-78.9344
HORNW	STONEWALL JACKSON DAM	WV	39.0044	-80.4744
MURPR	HARRISVILLE	WV	39.21889	-81.04861

Chapter 2: Stand age and carbon storage of remnant late-successional stands in the Mid-Atlantic region.

1. Abstract

Forests are the world's largest terrestrial C sinks and store an estimated ~45% of all terrestrial C. Additionally, of the three major forest types, including tropical and boreal, temperate forests are the only growing C sink. Temperate forests in the eastern United States are considered to be major C sinks in northern temperate ecosystems, taking up an estimated 12-19% of the C produced annually by fossil fuel emissions. Exactly how long they will provide this service is unknown. The rate of C sequesteration for eastern temperate forests (0.11 to 0.15 Pg C year^{-1}) is largely a function of forest recovery following agricultural clearing. Conventional wisdom suggests that net ecosystem production will approach zero when these forest reach late-succession. However, recent surveys of old growth forest, now restricted on the landscape to remnant stands, suggest C may continue to accrue well into late-succession. I surveyed twenty-five of the remaining mature and old growth forests in the Mid-Atlantic region to measure C storage in this late seral stage, and to determine how C is stored in live aboveground (AGC), dead wood, soil organic horizon (SOC), and leaf litter pools. I used the U.S. Forest Service regional inventory database to discuss the C storage of these stands in comparison to the younger, secondary forests that dominate the Mid-Atlantic landscape. Overall, the majority of C is stored in AGC (69.7%), followed by dead wood (20.7%), SOC (7.4%), and leaf litter (1.1%) in the old growth sites; However, C storage increased significantly with stand age alone only in the dead wood C pool (dead wood C = 0.25[age] – 5.695; $r^2 = 0.34$, $P = 0.002$). AGC, in contrast, decreased with stand age and elevation (AGC =

237.86 – 0.138 [elevation] – 0.243 [age]; $r^2 = 0.31$, $F(2,20) = 5.91$, $P = 0.009$). The negative relationship between AGC and stand age highlights the dominance of large-diameter *Liriodendron tulipifera* (tulip poplar) among the younger stands, suggesting a species-specific relationship with AGC in old growth. As a result, I predict AGC potential storage for young, secondary forests will approximate that of *Quercus* (oak) spp. dominant old growth stands (~155 Mg C ha^{-1}). Dead wood, in contrast, suggests C storage will continue to grow well beyond the age of our oldest stand (361 years), and a possible ten-fold increase is expected from current C storage in secondary forests.

2. Introduction

Forests are central to the global carbon (C) cycle, second only to oceans in overall magnitude of net C fluxes and C storage (Falkowski et al. 2000). C enters forests primarily as the gross primary production (GPP) of biomass by the vegetative community, and is lost through autotrophic and heterotrophic respiration, natural disturbance, land-use change, and run-off in the form of dissolved organic and inorganic C (Schimel 1995). The net C uptake by vegetation is the difference between GPP and plant respiration, defined as net primary productivity (NPP). The net C uptake by an ecosystem is the net ecosystem productivity (NEP), which represents the balance between NPP and heterotrophic respiration (R_h). Decomposition of organic matter by mycorrhizal and microbial organisms is the primary source of R_h. Positive NEP signifies a C sink, and negative NEP indicates a C loss. Because trees are long-lived and can accrue biomass over time, C gains by forests are typically slightly greater than C losses by respiration, and so forests become C sinks. Forests contribute approximately 50% to total terrestrial NEP annually (Sabine et al. 2004, Bonan 2008), and global C uptake by forests in the past decade was estimated at 2.3 ± 0.5 Pg C year^{-1} (Pan et al. 2011a). Forests also store an estimated 45% of all terrestrial C (Sabine et al. 2004, Bonan 2008). Calculating the amount of C stored in a system allows for predictions of how much potential C may transition from terrestrial stores into the atmosphere (Luo 2007).

Increased attention has been given to forest C dynamics and storage as part of a growing effort to mitigate the global rise in CO_2 emissions from anthropogenic sources. Since the Industrial Revolution, atmospheric CO_2 concentrations have increased from an estimated 278 parts per million (ppm) to 390.5 ppm, largely due to land use and combustion of fossil fuels (IPCC 2013). Land and ocean reservoirs act as vital buffers in reducing atmospheric CO_2. Over the past 50 years, approximately 55% of anthropogenic CO_2 emissions have accumulated in land and ocean reservoirs (Ballantyne et al. 2012), of which forest re-growth recovered approximately 3 Pg C y^{-1}, representing the majority of the terrestrial C sink (Dixon et al. 1994, Le Quere et al. 2009, McKinley et al. 2011). Afforestation and the protection of existing forests are virtually universal components of greenhouse gas mitigation strategies.

NEP and subsequent C storage are both functions of disturbance and forest age during secondary succession. Secondary succession is the resulting change in plant community and vegetation structure following a disturbance that alters the previous physical and biotic state, without removing all of the original soil. In a review of forest C dynamics, McKinley et al. (2011) cite large-scale disturbances, such as fire, pest outbreak, fungal infestation, timber harvest, or weather damage, as having substantial effects on forest C. Disturbance alters vegetation development and decomposition dynamics by removing biomass from the system, leading to an immediate loss of C and a decrease in NEP, followed by a subsequent recovery period as the forest transitions back to a C sink (Odum 1969, Bormann and Likens 1979, Peet 1981, Birdsey et al. 1993, Caspersen et al. 2000, Hurtt et al. 2002, Amiro et al. 2010). During the recovery period, age-related successional patterns drive changes in NEP (Chapin et al. 2002). At the beginning of secondary succession, NEP is negative because of high decomposition rates and limited NPP (Figure 3.1A). In early to mid-succession, NEP becomes positive as NPP from accumulating biomass exceeds C loss through heterotrophic respiration, and then peaks. By late-succession, NEP approaches zero as R_h matches NPP.

Total C storage is similarly dependent on the rates of C uptake, decomposition, and time since disturbance. However, the pattern in C storage over time differs from that of NEP (Figure 3.1B). Simplistically, C storage reflects the cumulative difference between the mass gain of C and the mass loss of C (Keeling and Phillips 2007). Plant C and, to a lesser extent, soil C, both decline substantially as the result of disturbance. In the absence of further disturbance, theory predicts that C accrues until a ‘steady state’ is reached in late-succession, where the total C storage is balanced by the loss through tree mortality and subsequent decomposition and the gain from photosynthesis. The rate and asymptote of biomass recovery might vary among forest types; however, these general patterns in C storage and NEP apply (Johnson et al. 2000, Clark et al. 2004).

For temperate forest ecosystems, the long-standing view that NEP approaches zero and C storage is held constant in late forest succession (i.e., old growth stage) is largely based on a model of aboveground C (AGC) dynamics for a northern hardwood forest developed by Bormann and Likens (1979) at Hubbard Brook Experimental Forest in New Hampshire. Within this model of forest dynamics, ‘stand break-up’ is the mechanism leading to the stabilization of AGC and decline in NPP when a stand reaches the old growth stage (Bormann and Likens 1979). Throughout succession, as trees compete for resources and experience self-thinning (Yoda 1963), the stand transitions from many small stems to a small number of typically large stems (Luyssaert et al. 2008). The ‘stand break-up’ hypothesis states that canopy break-up will occur with a synchronized mortality of the large canopy stems, and tree-fall will damage surrounding stems directly or indirectly, by increasing vulnerability to disturbances such as wind-throw or pest outbreaks (Bormann and Likens 1979, Oliver and Larson 1996). Bormann and Likens (1979) estimated that, at Hubbard Brook, the size of the C pool reaches a maximum at approximately 170 years, decreases between 200-350 years, and reaches a ‘steady state’ at approximately 350 years.

The Bormann and Likens (1979) model implies that old growth forests are neutral in the global C cycle. However, the potential for C sequestration in old growth forests is still a subject of active research and debate. Since the 1970s, researchers have discovered more old growth stands than previously were known to exist (Foster et al. 1996). Increasing empirical evidence suggests that NPP may increase in late-succession, and an upper limit of C storage may be greater than previously predicted (Luyssaert et al. 2008). Specifically, when ‘stand break-up’ occurs in the old growth stage, there are new individuals growing in the shade of the overstory that eventually take over the canopy and maintain productivity in the stand (Luyssaert et al. 2008). Additionally, although tree mortality may be a relatively rapid event (ranging from days to years), the decomposition of dead wood and subsequent release of CO_2 occur at the decade to century time scales (Luyssaert et al. 2008). There also may be potential for increased concentrations of soil

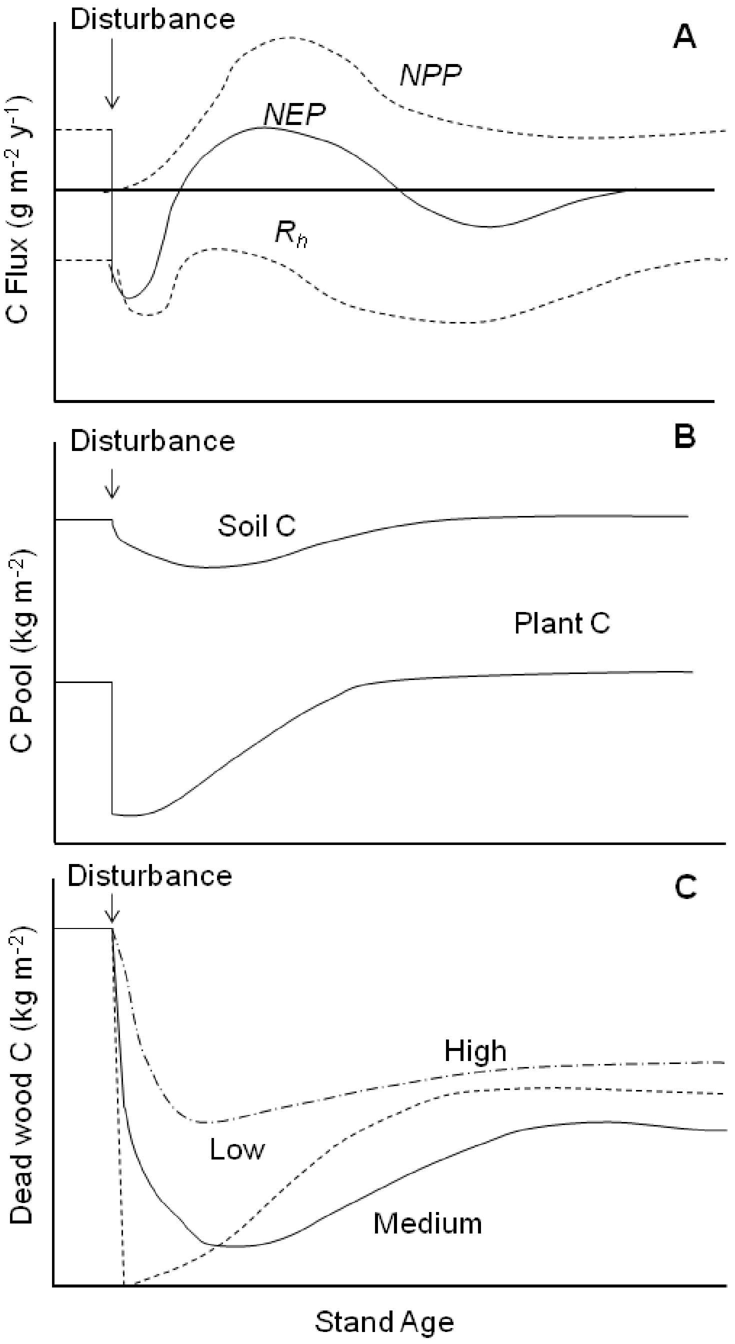

Figure 3.1. Hypothetical patterns of (A) C-flux (from Chapin et al. 2002), (B) plant and soil C pools (from Chapin et al. 2002), and (C) dead wood C pool with high, medium, and low total volume of legacy wood (adapted from Spies and Franklin 1988, Harmon 2009), in secondary succession across stand age.

organic carbon (SOC) stocks in old growth forests (Zhou et al. 2006). Therefore, old growth forests may continue to function as a net C sink. The potential of C storage in old growth forests is further confounded by possible increases in temperature, growing season length, CO_2, and nutrient fertilization associated with predictions of future climate change (McMahon et al. 2010). Greater empirical evidence of C storage in live biomass, dead wood, and soil C in old growth forests is necessary to determine if C storage is held constant in late succession.

Tropical and boreal forests currently store 41 and 18%, respectively, more C than temperate forests on a per area basis. Of these forest types, however, temperate forests are the only growing C sink (Pan et al. 2011a) and tend to have higher rates of long-term NEP than tropical forests (Huston and Wolverton 2009). In the conterminous United States, temperate forests cover approximately 251 million hectares (ha) that store nearly 41,000 Tg C (McKinley et al. 2011), with upper limits of C storage ranging between 500 and 700 tC ha^{-1} in the Pacific Northwest (Van Tuyl et al. 2005, Luyssaert et al. 2008). The majority of C, however, is stored in the eastern United States (~66%) (Woodbury et al. 2007, McKinley et al. 2011). Temperate forests in the eastern United States sequester a range of 0.11 to 0.15 Pg C $year^{-1}$ (Pacala et al. 2001) and are considered to be major C sinks in northern temperate ecosystems (Birdsey et al. 1993, Houghton et al. 1999). Eastern temperate forests take up an estimated 12-19% of the C produced annually by fossil fuel emissions (Ryan et al. 2010).

The main mechanisms forming active C sinks in the eastern United States have been forest re-growth following abandonment of agro-pastoral lands in the mid- to late- 1800s, a reduction in timber harvest, and woody plant encroachment due to fire suppression starting in the 1930s (Houghton et al. 1999, Houghton and Hackler 2000). Deforestation by European colonists from the 1600s to the late 1800s transformed an almost completely forested landscape in the eastern United States into one dominated by agricultural fields and pasturelands (Foster et al. 1998, Birdsey et al. 2006). In the late 1800s, the wide-spread human migration from rural to urban areas allowed land cover in the eastern United States to transition from agro-pastoral land to forests. Currently, 70% of all eastern forests are in the 50 to 100 year age range (Drummond and Loveland 2010, Pan et al. 2011b). Forests in the Mid-Atlantic region of the eastern United States are prime representatives of the historical land-use change experienced across the region. Having been established primarily on abandoned farmland or cut over woodlots in the 18th century, current forests in the Mid-Atlantic are recovering from additional large-scale harvest of secondary forest in the late 1930s (Pan et al. 2004). While many regions of the United States have experienced similar land-use histories as the eastern United States, none are poised to transition sooner into the late-succession phase than eastern forests (Foster et al. 1998). Currently, re-growing forests are transitioning away from the early, aggrading stage of succession (Birdsey et al. 2006). Secondary forests are predicted to remain a major driving mechanism for C accumulation for decades to come (Albani et al. 2006, Keeton et al. 2011, Thompson et al. 2011), but with an estimated 1% of old growth remaining in the eastern United States (Davis 1996), empirical estimates are limited for the long-term C storage potential, particularly for the Mid-Atlantic region.

2.1. Forest C pools and dynamics throughout succession

Total forest ecosystem C storage is a sum of aboveground and belowground pools. Aboveground pools may include live trees, shrubs, and herbaceous vegetation, dead wood in the form of stumps, logs, and standing dead stems, and leaf litter. Belowground pools include fine and coarse roots, and SOC stored in both the mineral and organic soil horizons. Forest C is stored mainly in soil (~44% to a 1-m depth) and live above- and belowground biomass (~42%), and to a lesser extent in dead wood (~8%) and litter (~5%) (Pan et al. 2011a). The longevity and stability of C varies among the different pools. SOC is considered to be the most stable C pool (Vesterdal et al. 2002, Chen et al. 2005, Laganiere et al. 2010), in comparison to live and dead wood which change more rapidly throughout succession (Davis et al. 2003, Kloeppel et al. 2007, Fahey et al. 2009). The response of each of these pools to successional dynamics differs substantially, and so each pool will be discussed separately.

2.1.1. AGC

The long-term potential for live AGC storage in eastern temperate forests is largely dependent on successional processes and the relative storage capacities of structural components of the forest stand. As previously discussed, the long-standing theory proposed by Bormann and Likens (1979) suggests that the live AGC pool will decrease rapidly as the result of a stand disturbance, and then steadily increase, eventually reaching an asymptote in late-succession (Peet 1981, Birdsey et al. 1993, Caspersen et al. 2000, Hurtt et al. 2002). During early succession, AGC accumulates quickly within tree bole volume, and trees experience low rates of mortality. In mid-succession, AGC begins to level off as the canopy fills in, competition begins to intensify, and by late-succession, stand structure transitions from many small stems to fewer, large stems. The rate of C storage also slows in late-succession as sapwood maintenance, reduced photosynthetic rates, and structural limitations on water transport begin to limit the growth of mature trees (Ryan and Waring 1992, Friend 1993, Turner et al. 2004, Woodward 2004).

Underlying the theory proposed by Bormann and Likens (1979), however, are assumptions about stand dynamics that are not universally applicable in eastern temperate forests. As an even-aged, mid-successional stand transitions to an uneven-aged, old growth forest, AGC will not necessarily stabilize. The size of the AGC pool depends on the mortality and growth rates of the surviving canopy stems, and the rate of biomass accumulation of the understory stems (Lichstein et al. 2009a). There is also uncertainty regarding the biomass estimates in the Bormann and Likens (1979) model for old growth stands. The biomass curves for the first two stages of forest development were based on empirical data collected from a large sample of secondary stands. The biomass estimates for later successional stages, however, were largely based on simulation models, due to the scarcity of old growth stands available for field sampling. The question that arises is not so much whether the general trend proposed by Bormann and Likens (1979) is inaccurate, but if the age at which a stand becomes effectively C neutral can really be constrained based on available information.

To address the uncertainties regarding live AGC dynamics during forest stand development, it is important to quantify this C pool in primary, old growth forests from empirical data (Brown et al. 1999, Keeton et al. 2011). Recent studies of AGC in the remaining old growth forests in the eastern United States indicate that AGC may still be accruing as forests transition from mid- to late succession (Lichstein et al. 2009a). For example, Brown et al. (1997) found that old growth eastern hardwood forests had greater total AGC than secondary stands, largely due to the greater percentage of biomass stored in larger trees (> 70 cm diameter). The old growth stands had an estimated AGC of 220-260 Mg ha^{-1}, with 30-50% of biomass in large stems. In contrast, the secondary stands identified through forest inventory assessments contained maximum AGC of 175-185 Mg ha^{-1}, with only 8-10% of biomass stored in large stems. In the upper Midwest, Tyrrell and Crow (1994) found that AGC in a hemlock-hardwood forest peaked at 230 to 260 years, and then declined. Ziegler (2000) showed that, across a chronosequence of stand ages in hemlock-hardwood forests, AGC continued to accrue in stands > 400 years. Similarly, Keeton et al. (2011) observed that AGC increased into later stand development (> 400 years) in northern hardwood forests, with only a slight decline when dominant trees reached 300 years of age. Given the trends recently observed, there is potential for the AGC C pool in eastern forests to continue accumulating C for another 200+ years. However, if the Bormann and Likens (1979) model is correct, secondary forests will exhaust their C storage potential within the next 70 years.

2.1.2. Dead wood

Dead wood includes roots, stumps, branches, and standing dead (i.e., snags), and logs (Harmon 2009). The size of the dead wood pool varies substantially across temperate forest ecosystem types (Woodall et al. 2008, Woodall 2010). In the United States, Woodall et al. (2008) identified the Pacific Northwest as having the greatest mass of dead wood, at 11.35 ± 0.66 Mg ha^{-1}. In their study, the Mid-Atlantic region was grouped into the Northeast and the Southeast regions. The Northeast has relatively high estimated dead wood at 4.27 ± 0.19 Mg ha^{-1}, while the Southeast has one of the lowest at 2.73 ± 0.21 Mg ha^{-1} for the U.S. (Woodall et al. 2008). Differences in the sizes of the dead wood C pool are dependent on the inputs through mortality and outputs through decomposition or disturbance (e.g., fire or harvest). The rate of decomposition of dead wood is dependent on climate, solar radiation as related to moisture content of dead wood, decomposer biota, tree species, and structure of the dead wood (Harmon et al. 1986, 2001, Harmon 2009). The size of the entire pool may change slowly (e.g., a slow rate of decay with little to no disturbance to the stand), or rapidly, by combustion or harvest (Woodall 2010).

The mortality of large, mature stems in late-succession and the associated disturbance processes described by the ‘stand break-up’ hypothesis, lead to an increase in the size of the dead wood C pool, regardless of forest type or climate (Harcombe et al. 1990, Dahir and Lorimer 1996, D’Amato et al. 2008, Harmon 2009). When a stand is dominated by large stems in late succession, this stage will result in snags and logs with a greater diameter than in a secondary stand, leading to greater dead wood volumes (D’Amato et al. 2008). In younger forests, mortality and the input into the dead wood pool is dependent on self-thinning and the mortality of early successional species, which generally produces smaller volume dead wood (McComb and Muller 1983, Gore and Patterson III 1986, Dahir and Lorimer 1996, Goodburn and Lorimer 1998, Ziegler 2000, D’Amato et al. 2008).

The distribution of the dead wood C pool across successional time depends on the amount of dead wood remaining in the system following the initial disturbance. The amount of dead wood in a stand immediately following disturbance is dependent on the intensity and type of disturbance. For example, certain disturbances, such as fire or timber harvest, will remove dead wood from the system, and so the initial pool will be small, while pest infestations or fungal infections will create a large dead wood pool, because the formerly live material is not removed (Harmon 2009). Assuming legacy wood remains after the initial stand-removing disturbance, dead wood tends to decrease through early and mid-succession as mortality rates remain low, but decomposition rates are high. As mortality rates increase in late succession, the C pool increases due to the input of dead wood (Harmon 2009). When dead wood remaining in the stand following disturbance is equal to that found in an old growth forest, the shape of the curve for dead wood mass forms a U-shape, with high values in early succession, followed by a decline in the size of the C pool in mid-succession, and then increasing to moderately high values in late-succession (Spies and Franklin 1988). When the majority of dead wood is removed by disturbance, and the size of the dead wood C pool is entirely dependent on the growth and development of live trees, a logistic function describes changes in the C pool across secondary succession (Spies and Franklin 1988).

2.1.3. Soil Organic Carbon

The dynamics of SOC during forest stand development are less well-understood than those of live and dead AGC (Suchanek et al. 2004). However, understanding this C pool is no less crucial in constraining forest C dynamics. SOC contains an estimated two-thirds of all terrestrial C (Trumbore et al. 1996, Amundson 2001). Although SOC is found throughout the soil profile, 50% of all SOC is stored in the top meter of soil in forests, with 40% stored in the top 20 cm (Jobbagy and Jackson 2000, Gleixner et al. 2009). The top 20 cm is typically dominated by both the O-horizon and the top of the A-horizon, however the relative thickness of these layers may vary substantially across landscapes, and even within the same stand (Liski 1995). The O-horizon is composed largely of soil organic matter (SOM), defined as a mixture of plant and animal parts, in addition to both live and dead soil microbiota, degraded so that the original structure of these parts are no longer recognizable (Oades 1989). The O-horizon is further divided into the O_i, O_e, and O_a horizons (Figure 2). The O_i horizon is a surface layer of poorly decomposed fibric matter, underlain by a partially degraded and fermented organic horizon (O_e). The O_e horizon, in turn, is underlain by an intermediately decomposed hemic or highly decomposed sapric layer (O_a) that overlies the mineral A-horizon. Considering the relative amount of C stored in the top 20 cm of soil, as well as the stability of these stocks, it is of critical importance to understand SOC pools in the O-horizon for C storage potential.

SOC content is controlled by the balance of C input through plant production as leaf litter, root litter, and other types of organic residues, and C loss through decomposition and oxidation of organic matter, and erosion (Jenny 1941, Schlesinger 1977, Gleixner et al. 2009). Environmental state factors that influence productivity and decomposition, such as climate, topographic position, soil texture, microbiota, time, and human activity, are therefore critical drivers of SOC dynamics (Jobbagy and Jackson 2000). Above- and belowground litter composition, temperature, water, and nutrient availability change with stand age, and influence decomposition rates and the size of the SOC pool throughout succession (Turner and Lambert 2000, Guo and Gifford 2002, Carletti et al. 2009).

Previous studies have reached conflicting conclusions regarding the size of the SOC pool in late-succession. Some studies suggest that SOC stocks may increase slowly over time, and the stability of SOC may lead to large pools of C in late-succession (Zhou et al. 2006). In a warm temperate oak forest chronosequence in China ranging from 40 to 143 years, SOC stocks were highest in the 143-year-old stand (Luan et al. 2011). Glexiner et al. (2009) found soil C stocks increased significantly with stand age in temperate deciduous forests, and continued to grow into the 100-200 year stand age range. These increases in SOC with stand age may be related to increases in leaf litter production rates, combined with deteriorating leaf litter quality (Gleixner et al. 2009). In contrast, in a Great Lakes chronosequence of SOC stocks, Tang et al. (2009) found that SOC consistently accumulated in the top 30 cm of soil, as the stand regenerated from clear-cut to mature forest, but decreased in the 0-10 cm depth as stands transitioned from the mid- to late-succession stage. Covington (1981) and Federer (1984) found the SOC pool increased by 50% in the first 20 years of re-growth, and then stabilized after 70 years. By sampling SOC in old growth forests of the Mid-Atlantic, I hope to improve predictions of C storage within the SOC pool.

In recognition of their rarity and ecological significance, we characterized the C storage of twenty-five remnant stands of mature and old growth forest within the Mid-Atlantic region. Specifically, I addressed the following questions: How much C is stored in Mid-Atlantic old growth forests, and how is it allocated? By sampling productive fragments of remaining old growth, we estimate the upper-bounds of C storage in AGC, dead wood, leaf litter, and SOC in the O-horizon for these stands. I use the U.S. Forest Service regional inventory database to discuss the C storage characteristics of these stands in comparison to the young, secondary forests that dominate the Mid-Atlantic landscape.

3. Methods

3.1. Study Area

The U.S. Mid-Atlantic region spans the Chesapeake and Delaware Bay watersheds. I defined the Mid-Atlantic as consisting of Virginia, Delaware, and Maryland, and parts of West Virginia, Pennsylvania, and New Jersey (Figure 3.2), however other common definitions include parts of southern New York and northern North Carolina (e.g., Jenkins et al. 2001, Pan et al. 2009). The regional landscape is high in physiographic and ecological diversity, and subdivided into six distinct ecoregions that reflect variable landform and topography, geologic origin, hydrologic function, soils, and potential plant communities (Cleland et al. 1997, Rogers and McCarty 2000, Stolte et al. 2012). The Mid-Atlantic region includes the Middle Atlantic Coastal Plain, Southeastern Plains, Piedmont, Northern Piedmont, Ridge and Valley, and the Blue Ridge Mountains ecoregions (USEPA 1999). The climate is wet and warm, with growing seasons ranging from 100 to 250 days across the six ecoregions (Stolte et al. 2012). Forest is the prevalent land cover type in the region (Jones et al. 1997), of which the oak/hickory (*Quercus* spp. and *Carya* spp.), maple/beech/birch (*Acer* spp., *Fagus grandifolia* Ehrh., and *Betula* spp.), and oak/pine (*Pinus* spp.) forest community groups dominate (Eyre 1980, McKenney-Easterling et al. 2000). Forests in the six physiographic ecoregions share similar ranges in productivity and diversity (Belote et al. 2011). Although the Mid-Atlantic is mostly forested, it also fosters rapidly growing suburban and urban areas that spread from Philadelphia to Washington D.C. and have expanded as much as 90% from 1970 to 2000 (Morrill 2006); rates of forest land cover loss during this period were approximately 0.15% per year (Drummond and Loveland 2010). *Quercus alba* L. (white oak), *Quercus velutina* Lam. (black oak), *Quercus prinus* L. (chestnut oak), *Quercus rubra* L. (northern red oak), *Castanea dentata* (Marsh.) Borkh. (American chestnut), *Pinus* spp., and *Carya* spp. dominated pre-settlement forests in the Mid-Atlantic (Nowacki and Abrams 1994, Abrams and McCay 1996, Abrams 2003), and with the exception of *Castanea dentata* these species still are common in the mature and old growth forests of the region (Thompson et al. 2013).

Table 3.1. Forest community groups and associated compositional species for groups most common to the Mid-Atlantic (follows McKenney-Easterling et al. 2000).

Forest Community Group	**Compositional Species**
Oak/Hickory	Hickory (*Carya* sp.), bitternut hickory (*C. cordiformis*), pignut hickory (*C. glabra*), shAGCark hickory (*C. ovata*), mockernut hickory (*C. tomentosa*), white oak (*Q. alba*), scarlet oak (*Q. coccinea*), chestnut oak (*Q. prinus*), northern red oak (*Q. rubra*), post oak (*Q. stellata*), black oak (*Q. velutina*), sweetgum (*Liquidambar styraciflua*), and tulip poplar (*Liriodendron tulipifera*).
Maple/Beech/Birch	Red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghanensis*), black cherry (*Prunus serotina*), and black walnut (*Juglans nigra*).
Oak/Pine	Eastern white pine (*P. strobus*), short leaf pine (*P. echinata*), Virginia pine (*P. virginiana*) , northern red oak, loblolly pine (*P. taeda*), water oak (*Quercus nigra*), willow oak (*Q. phellos*), post oak, and scarlet oak (*Q. coccinea*).

3.2. Site Selection

There are multiple definitions of old growth for eastern temperate forests based on stand structure and successional processes (e.g., Foster et al. 1996, Wirth et al. 2009, Hoover et al. 2012). No clear ecological thresholds regarding disturbance frequency or age exist across these definitions (Hunter Jr and White 1997), and so identification of old growth can be problematic. In effort to simplify the initial selection of sites, and to account for variability in disturbance history across sites, I broadly define mature and old growth as forests with dominant overstory trees having a maximum stand age of ≥ 150 years. This age is based roughly on the definition suggested by Cogbill (1996) that mean stand age be approximately half of the maximum longevity of the dominant tree species (~ 300+ years) to qualify as eastern temperate old growth. My goal was to measure all mature and old growth sites known to exist in the Mid-Atlantic that are not anomalous in terms of their edaphic or topographic setting—i.e. I sought to measure all remnant old forests on sites typical of the Mid-Atlantic landscape. To develop a list of potential sites, I reviewed all published literature on old growth remnants in the region with reported stand ages. Past publications either provided mean stand age estimates based on tree ages from increment cores or land use history, species composition, and forest structure indicating no harvest in the past ~150 years. It is important to note that different stand age sampling methods between this study and past publications led to different estimates of maximum stand age, including maximum age estimates less than 150 years for some sites. Next, I identified potential sites from the gray literature. The majority of these stands were described in Davis (1996) *Old growth in the East: A Survey,* and Kershner and Leverett (2004) *The Sierra Club Guide to the Ancient Forests of the Northeast*. I also identified sites through peer discourse by engaging state forest agencies, and conservation and land trust associations (e.g., The Nature Conservancy). A total of 35 sites were identified for field visits. The selected sites shared similar overstory composition, and typically were dominated by *Quercus* spp., with *Liriodendron tulipifera* L. (tulip poplar), *Tsuga canadensis* L. Carr (eastern hemlock), or *Carya* spp. as co-dominant or secondary canopy species. Following a walk-through survey, 25 sites were sampled from May to August 2012 (Figure 3.2; Table 3.2). Ten of the original 35 sites were deemed unusable either due to recent natural or anthropogenic disturbance (e.g., gypsy moth outbreaks, timber harvesting) which caused large-scale mortality in the dominant overstory trees, or because the site was inaccessible or not representative of the greater Mid-Atlantic region. In total, the study area was approximately 87,383 km^2.

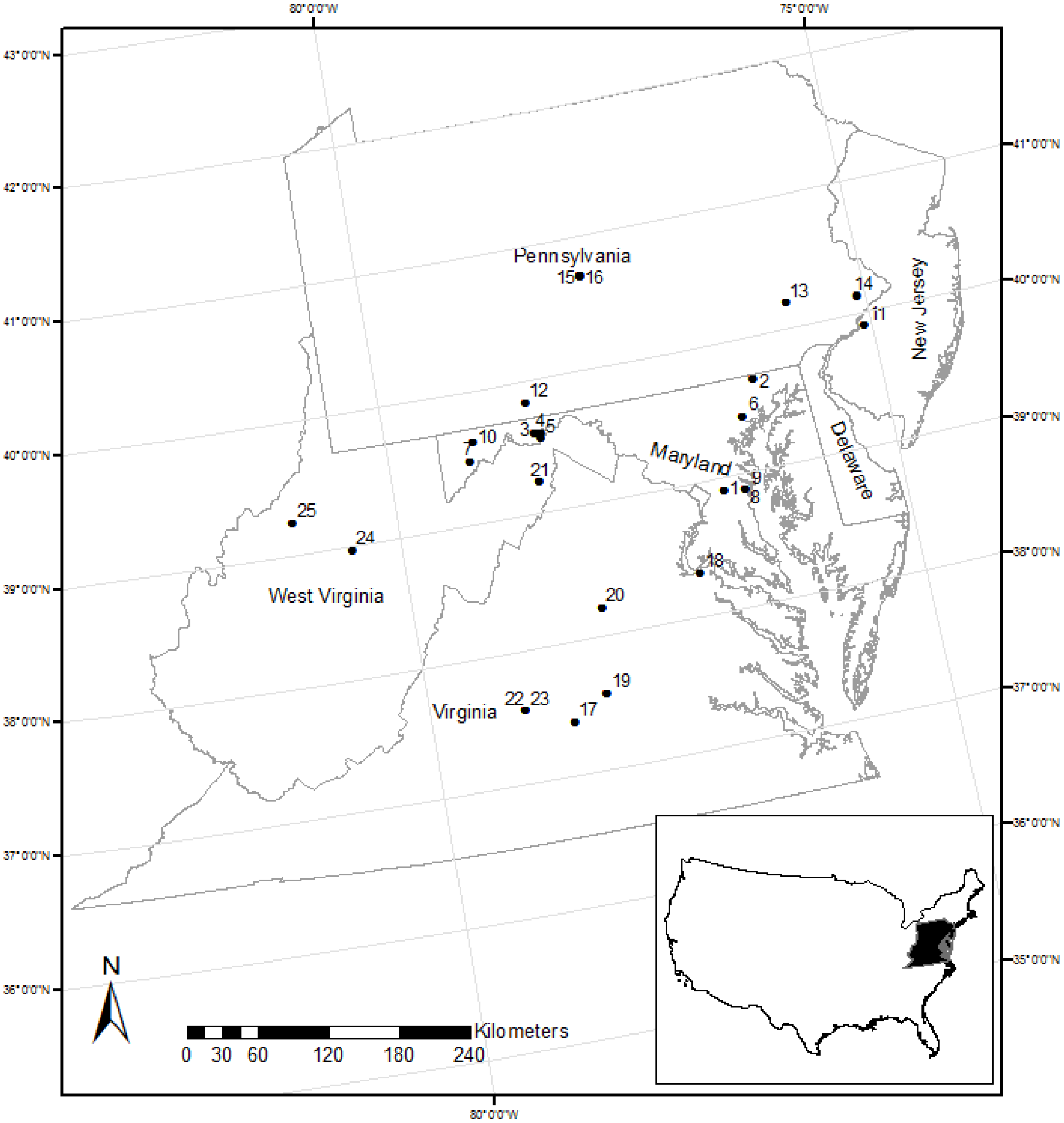

Figure 3.2. Location of the twenty-five mature and old growth forests sampled within the Mid-Atlantic study area. See Table 3.2 for key to site codes.

3.3. Field sampling

I delineated stand boundaries using the Wirth et al. (2009) definition of old growth: (1) the abundance of large, old stems, supplemented with Pederson's (2010) external description of old trees, (2) abundance of standing and fallen dead wood at various stages of decay, (3) relatively few signs of anthropogenic disturbance, (4) a multi-layered canopy, and (5) canopy gaps. Emphasis was placed on the first three characteristics, because they are easily recognized within an older stand, and contrast strongly with conditions of younger forests. Additionally, the stand needed to be of sufficient area to fit three 0.07 ha sampling plots. In practice, defining the stand edge was difficult. I was conservative in my classification and therefore erred towards identifying forest as secondary over old growth. As such, it is possible that the periphery of some old growth stands were not included within the delineated stand boundary. I am confident, however, that the interior of the stand was consistently included in the delineation.

I established sampling points at 15 m intervals along a transect oriented to be the greatest possible length spanning the greatest possible area of each stand (Figure 3.3). Transect length varied among sites depending on the size and shape of the stand. To define structural variability for each stand, I estimated total basal area (BA; $m^2\ ha^{-1}$) of all stems within a variable radius of all sampling points within each stand using a 10-factor prism. I then took detailed plot measurements within 15m radius circular plots centered at the three sampling points that represented the 10th, 50th, and 90th quantiles in terms of prism-measured BA. This technique was intended to capture the range of structural variability present within the stand. Interestingly, subsequent data analysis showed that total BA estimations based on the variable radius (prism) plot and the fixed area methods were not correlated, and so I dropped stratification by BA prism estimates across plots and based all subsequent analysis on site averages. At the center of each plot, I collected topographic measurements including transformed aspect, slope, and geographic coordinates.

Within each plot, I recorded the species and canopy height of all live woody stems $\geq$ 5 cm DBH (diameter-at-breast-height; 1.37 m). Heights were measured with an Impulse

200 Laser Rangefinder (Laser Technology, Inc., Norristown, PA). I recorded all stems 1-5 cm DBH for species and DBH within three non-overlapping 5-m radius subplots nested within the larger plot. I measured dead wood volume using field protocols developed by Harmon and Sexton (1996)

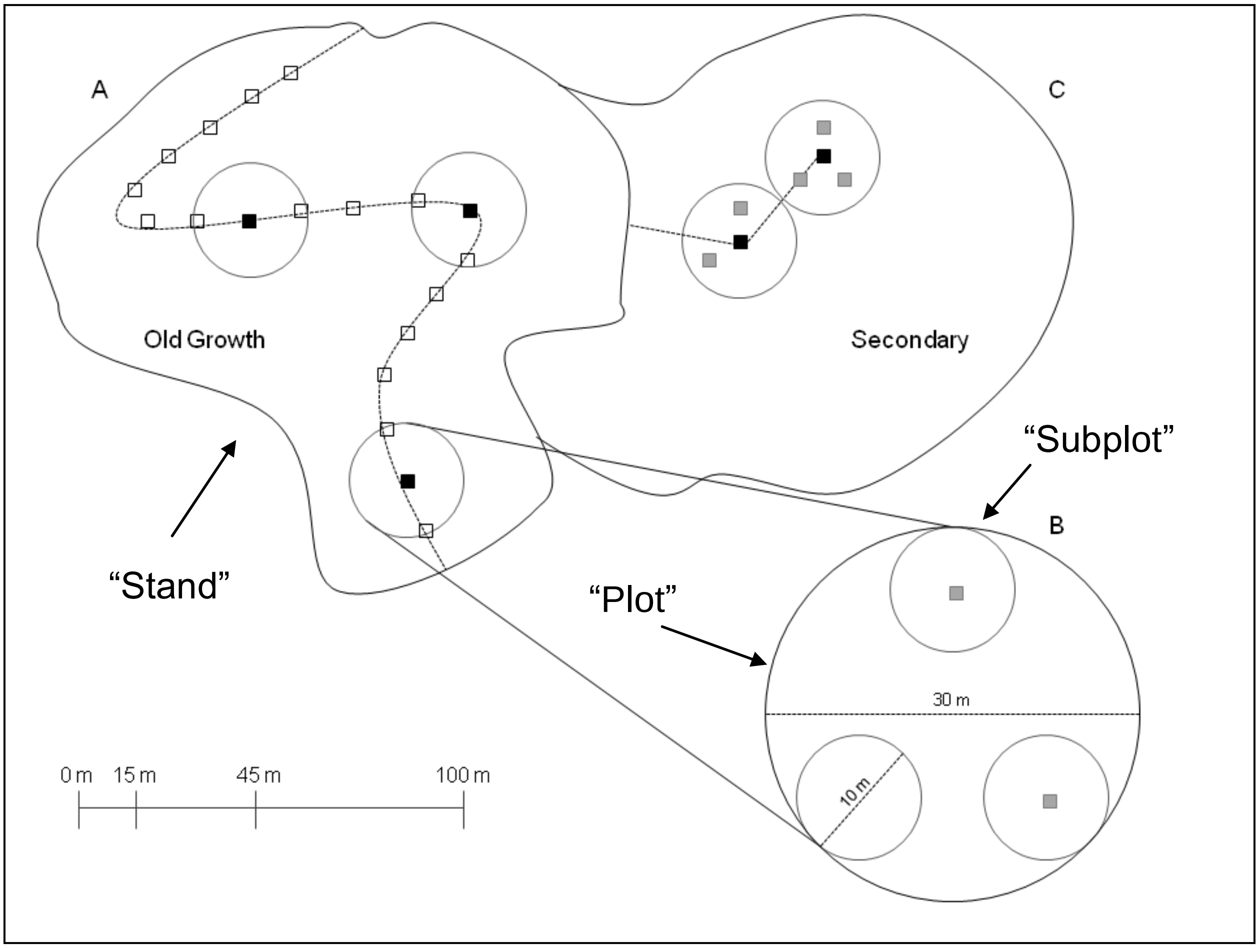

Figure 3.3. An example of transect and plot layout for old growth field sampling. (A) Within each stand, a transect (dashed line) was oriented to cover the maximum possible area within the stand boundary (solid line). BA was estimated at sampling points (empty squares) placed 15-m apart along the transect. From these BA estimates, three to four 30-m diameter plots (circles) were placed at sampling points. The number of plots depended on size of the stand. (B) Within each plot, all large dead wood and live stems greater than 5 cm DBH were recorded, and slope and aspect were measured at the center of the plot. Additionally within each plot, three 10-m diameter subplots (small circles) were surveyed for medium dead wood and live stems 1-4.9 cm DBH. At the center of two out of three subplots in each plot, soil samples (gray squares) were collected. (C) In an adjacent secondary stand, five soil samples were collected.

within the plots. The minimum diameter for identifying dead wood was 10 cm. I classified all dead wood as a log, snag, or stump. For logs (≤ 45° relative to the ground), I measured the diameters at both ends and the midpoint, and the length of the piece of wood; for snags (> 45° relative to the ground and > 1.37 m height), the DBH and height; for stumps (> 45° relative to the ground and < 1.37 m height), the length, and top and base diameters. I identified decay classes using the categories described by Waddell (2002). Following McGee et al. (1999), all large dead wood (≥ 25 cm diameter) was inventoried in the 15-m radius plots and medium dead wood (10-25 cm diameter) in the 5-m radius subplots.

To estimate maximum age of the plots, I collected two to three cores of the dominant canopy stems from each plot for a total of ten tree cores per site, taken at 1.37 m along the mid-slope of the tree. At four sites, heart rot in large canopy stems prevented the collection of complete cores for the largest trees in the plots. The number of medium to large stems (> 50 cm DBH) with signs of rot ranged from 6 to 29% of all stems in this size class measured at these four sites. When heart rot prevented the collection of a complete core, I took a sample from the next-largest tree in the plot. I used a 40.6 cm borer and was unable to reach the center of some of the larger trees. I did not attempt to estimate the number of rings missing if the pith was missing. Due to ecological or historical significance, landowners denied me permission to collect cores at nine sites. However, reliable stand age data were available for all but one of these sites (see Table 1 for sources). I dried, mounted, and sanded all samples, then estimated maximum plot age by counting tree-rings under a Wild M8 stereozoom microscope, and cross-dated counts by comparing shared narrow rings across cores (Yamaguchi 1991). I selected the oldest tree cored at each site as an estimate of maximum site age, hereafter referred to as "stand age."

At the center of two randomly chosen subplots within each plot, I collected leaf litter and SOC from the O-horizon within a 0.1 m^2 frame at 23 of the 25 stands. One of the two sites was not sampled because sampling equipment was unavailable at the time of collection, and for the other site, a suitable secondary stand could not be found. The frame method (Burton and Pregitzer 2008) worked best for the generally rocky soils or shallow O-horizons at the majority of field sites in order to collect a large enough volume of soil for homogenization. Because I collected a specific horizon versus a uniform depth, I took five soil cores using a 2.5 cm diameter corer to determine the mean depth of the O-horizon at each sampling point. For a subsample of all sites (n = 5), I collected a separate 0.01 m^2 sample at each sampling point to estimate bulk density. Bulk densities of the O-horizon were not significantly different across the five sites (one-way ANOVA; df = 4, f = 2.316, p = 0.095), and so a mean bulk density of 0.19 g cm^{-3} was assumed for all sites. I brought all soil samples back to the laboratory for processing, passed the samples through a 2-mm sieve to remove roots and other large organic matter, dried them at 105°C for 24 hours, and finely ground them using a ball mill. I obtained estimates for percentage of C from each sample using a CE elemental analyzer (CE Elantech, Inc., Lakewood, NJ).

3.4. Data processing and analysis

Estimates of AGC were based on generalized allometric equations developed by Jenkins et al. (2003) and Lambert et al. (2005). Both sets of diameter-dependent regression equations are derived from extensive data sets and designed for application at a national-scale. While widely applied, there are limitations to using these equations for estimating biomass of large and old trees. Equations developed by Jenkins et al. (2003) do not include height as an independent variable, are based on data for which the maximum DBH of hardwood stems ranges from 56 to 73 cm, and do not address how the distribution of biomass changes throughout the life cycle of a stem (Satoo and Madgwick 1982, Helmisaari et al. 2002, Peichl and Arain 2007). As identified in a review by Ahmed et al. (2013), Lambert et al. (2005) use a more statistically rigorous approach than Jenkins et al. (2003), generating species-specific best fits based on raw diameter and biomass data collected across sites in Canada. However, the Lambert et al. (2005) allometries lack species-specific equations for some important Mid-Atlantic species, most notably *Liriodendron tulipifera*. In general, the Lambert et al. (2005) equations produced slightly lower biomass estimates than Jenkins et al. (2003) for the old growth sites. As neither set of regressions stood out as superior for estimating biomass in Mid-Atlantic old growth forests, and both biomass estimates approximated each other fairly well, I used the mean biomass estimate of the two methods. For all woody biomass, I assumed C to be 50% of dry weight.

I used different equations for volumetric estimates of dead wood based on the dead wood classification and measurements for each dead wood type (Harmon and Sexton 1996). For logs, I used the Newton formula which requires three diameter measurements:

$$V = L\,(A_b + 4A_m + A_t)/6 \qquad [1]$$

Where L is length, A_b, A_m, and A_t are area at the bottom, middle, and top, respectively. For stumps, I used the formula for a frustrum of a cone:

$$V = L(A_b + (A_b A_t)^{0.5} + A_t) \qquad [2]$$

For snags, I used a modified Huber formula (Wenger 1984) for a cylinder:

$$V = L * BA \qquad [3]$$

Of the three volume equations, the Huber formula is the most simplified and potentially more prone to error in estimating true volume. Coarse dead wood pieces are generally irregular in shape, and error in volume estimates increase with fewer diameter measurements collected. However, this formula has been shown to provide unbiased estimates (Van Wagner 1968, Brown 1971), and so I used the Huber formula to approximate true snag volume. To estimate dead wood biomass, I used the equation from Waddell (2002):

$$Biomass = V \times 1\ Mg/ha \times SpG \times DCR \qquad [4]$$

Where V is volume, SpG is the specific gravity of fresh wood that varies by species, and DCR is the decay class reduction factor, which reduces the specific gravity of wood by decay class. The following four decay class reduction factors were used: II = 0.78 (softwood = 0.84) g/cm^3, III = 0.45 (0.71), and IV & V = 0.42 (0.45) g/cm^3 developed by Waddell (2002) from an assessment of dead wood biomass in FIA plots.

To calculate the mass of SOC in the O-horizon, I used the formula (Amundson 2001):

$$M_O = C_O \times BD_O \times z_O \qquad [5]$$

Where M_O is the mass of SOC, C_O is the concentration of SOC, BD_O is bulk density, and z_O is the depth of the O-horizon. I tested whether the mean SOC content in the O-horizon and mean leaf litter C significantly differed between old growth and early/mid-successional forest stands using a paired Student's t-test.

I used linear regression modeling to analyze the relationships between maximum estimated stand age and C store variables within the late-successional forest samples. Where linear trends explained significant variability around the mean or when the C pool stored at least 10% of stand level C, I further explored more defined aspects of structure to determine possible causes for the presence (or absence) of a significant relationship. I identified in Chapter 2 the importance of species composition in driving live structural characteristics in old growth, and so I also compared sites and their highest C-storing species to determine if there were species-specific effects on AGC – i.e., if certain species associated with high biomass sites. If the stand age/C relationship was insignificant, but the pool contained at least 10% of stand level C, other environmental variables were included in a multivariate model of biomass to improve the relationship. Environmental variables used included slope, aspect, elevation, and topographic wetness index (TWI). I estimated TWI and elevation through GIS analyses of digital elevation models (DEM) performed in ArcGIS 10.1 (ESRI 2013). The DEM resolution varied between 10 and 30 m across the study region due to limited availability of the highest resolution data. TWI is a function of the natural logarithm of the ratio of local upslope contributing area and slope, and can represent relative soil moisture availability (Moore et al. 1993). A value of seven or less indicates the most xeric conditions and a score of ten indicates the most mesic conditions (Moore et al. 1993). To select the minimal adequate linear model of biomass, I used a stepwise regression with backward elimination to reduce the model to a point where all remaining predictors were significant. After each predictor elimination, the current and previous models were compared using analysis-of-variance tables to test whether the model terms were significant.

To understand how the mature and old growth stands compare to the matrix of younger forests in the Mid-Atlantic, I plotted live aboveground and dead wood C against regional averages obtained from the FIA program. The FIA program has divided the U.S. into a network of permanent plot 2,400-ha hexagons, with one forest inventory plot randomly placed within each hexagon. Within each plot, there are four 17.3-m radius subplots, from which the DBH and species identification of all trees >12.7 cm DBH are collected (for details on the FIA field protocol see http://www.fia.fs.fed.us). I used the "The Southern On-Line Estimator (SOLE)" to query statistical tables on user selected variables (Spinney et al. 2004). I queried all states in the Mid-Atlantic study region to calculate mean and standard deviation values of live aboveground and dead wood biomass (Mg C ha^{-1}) for plots inventoried in 2011 (n = 1855). AGC was calculated using Jenkins et al. (2003) allometric equations, and dead wood biomass included only aboveground dead wood and no foliage. Biomass was broken down by stand age, and bins were ten years. SOLE automatically selects against non-forest cover plots, but otherwise, no additional queries were made for site selection. I then plotted the mean values and standard deviations of the FIA plots with the mature and old growth sites to qualitatively describe the relationship between biomass and stand age across secondary succession. In this way I employed an informal chronosequence approach with a space-for-time substitution to infer changes in C storage through secondary succession. Differences in plot design, study area, and sampling methods between this study and the

FIA data preclude a formal statistical design, and so the informal chronosequence is solely a qualitative way of comparing sites.

4. Results

The mean stand age of the late-successional forests was 208 years. Site-specific stand ages ranged from 72 to 361 years (Table 3.2). The sampled old growth forests contained a mean of 217.95 Mg C ha^{-1} (*sd* = 43.21 Mg C ha^{-1}) in total C, 153.94 Mg C ha^{-1} (*sd* = 47.01 Mg C ha^{-1}) in AGC and 45.94 Mg C ha^{-1} (*sd* = 29.47 Mg C ha^{-1}) in dead wood. In comparison, leaf litter and SOC in the O-horizon contributed smaller amounts of C to the stand-level storage (leaf litter [*mean* = 5.85 Mg C ha^{-1}, *sd* = 1.71 Mg C ha^{-1}], SOC [*mean* = 15.30 Mg C ha^{-1}, *sd* = 12.61 Mg C ha^{-1}]). The maximum estimates of total, AGC, and dead wood were 265.07 Mg C ha^{-1} at Peak Woods in Pennsylvania, 249.77 Mg C ha^{-1} at Saddler Woods in New Jersey, and 117.32 Mg C ha^{-1} at Alan Seeger State Natural Area in Pennsylvania, respectively. Lowest estimates for total (81.59 Mg C ha^{-1}), live aboveground (78.82 Mg C ha^{-1}), and dead wood (2.34 Mg C ha^{-1}) biomass were all at French Creek State Park in Pennsylvania. At all twenty-five sites, AGC made up over half of all C stored in the stand, averaging 69.7% (Figure 3.4). The dead wood pool in comparison stored on average 20.6% of total C. SOC and leaf litter C constituted 7.4% and 1.1%, respectively.

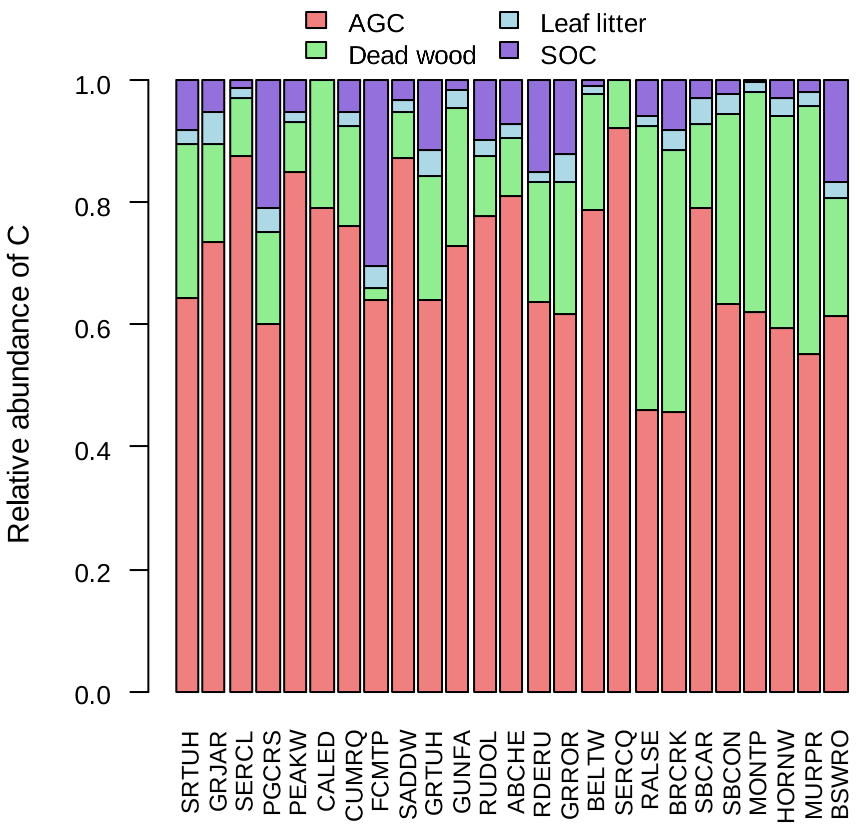

Figure 3.4. Relative proportion of mass in each C pool across mature and old growth sites. Sites are ranked from lowest to highest maximum stand age (years), with the exception of BSWRO where no stand age estimates are available. See Table 3.2 for site codes.

Stand age explained considerable variation in dead wood C ($r^2 = 0.34$, $P = 0.002$; Figure 3.5B). In contrast, stand age was uncorrelated with mean AGC, leaf litter, SOC in the O-horizon, and total C, with all linear regressions exhibiting slopes near zero (Figure 3.5). Keeton et al. (2011) applied logarithmic fits to explain variability in dead wood biomass across chronosequences of mature and old growth in northern hardwood-conifer forest, but I found the linear model to be a better fit for dead wood C in my Mid-Atlantic sites. The strong positive relationship observed indicates a C accumulation rate in the dead wood pool of 0.25 Mg C ha^{-1} year^{-1} (C mass = 0.250 [stand age] – 5.695). Additionally, relative dead wood C storage was nearly equivalent or greater than AGC among the older stands sampled. At Allen Seeger State Natural Area and Broad Creek

Boy Scout Memorial Forest, dead wood contributed 46.6% and 42.8% respectively to the total C stored, relative to 45.9% and 45.8% stored by AGC (Figure 3.4).

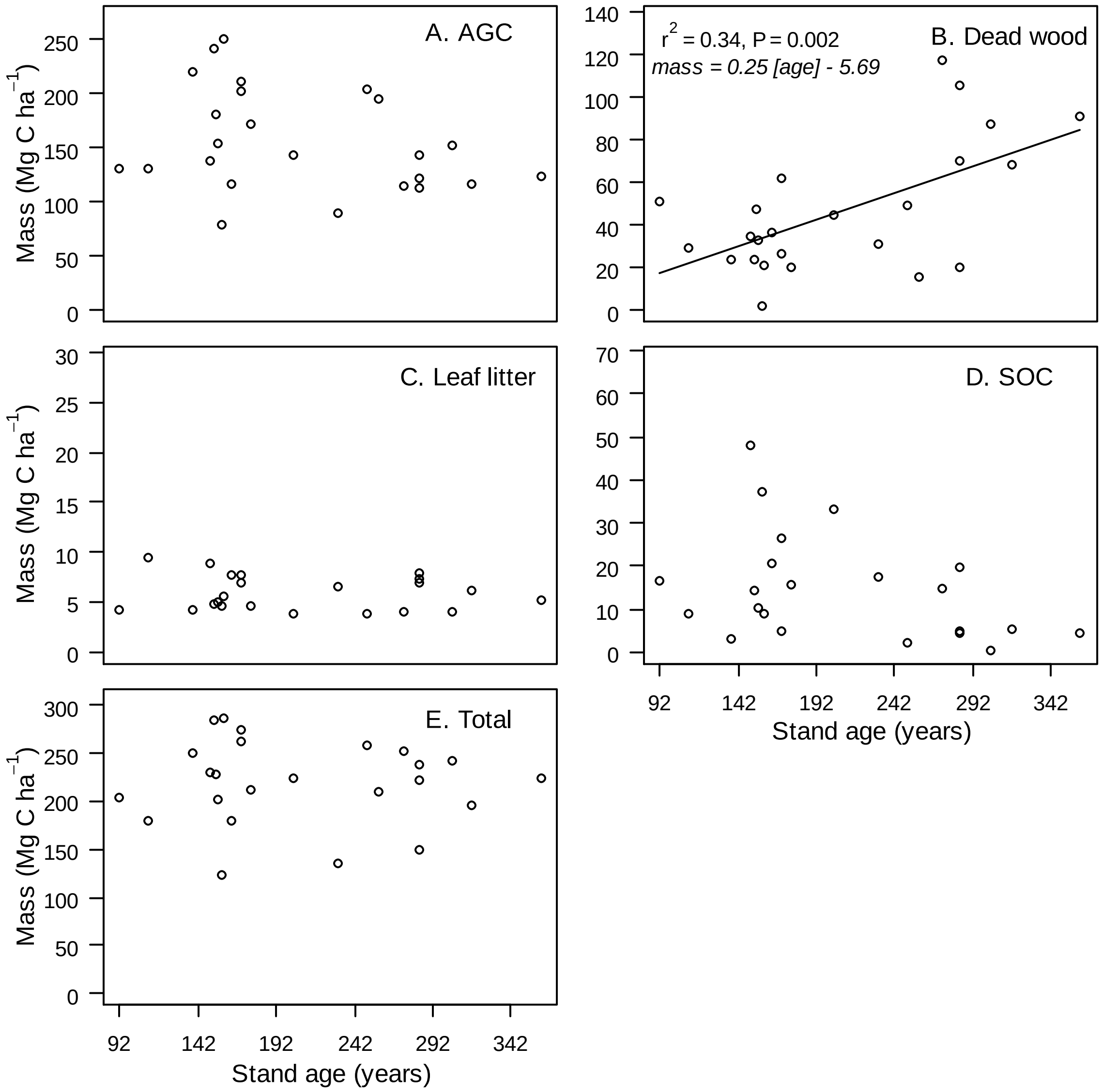

Figure 3.5. Estimated mean carbon storage (Mg C ha^{-1}) of the live and dead aboveground, leaf litter, and soil O-horizon pools as well as total C storage by maximum stand age for the twenty-five mature and old growth sites. Trend lines were included when the relationship was significant.

The strong positive relationship between dead wood C and stand age reflects the linear increase in dead wood volume with stand age, previously identified as a feature of these old growth sites (Chapter 2). C stored in the form of logs increased linearly with stand age (C mass = 0.32 [stand age] – 13.3; $r^2 = 0.439$, $P < 0.001$), while C stored in the form of snags and stumps did not exhibit a significant relationship. At all sites, stumps were a minor component of dead wood C (Figure 3.6). In contrast, at certain sites, snags were major contributors to dead wood C. The majority of snag C was stored in stems 0 – 50 cm DBH (61.4%), followed by stems > 70 cm DBH (20.2%), and finally stems 50 – 70 cm DBH (17.4%). Dead wood classified as Decay Class One and Four exhibited significant linear increases in total C with stand age (Decay Class 1 [C mass = 0.2 [stand age] – 11.6; $r^2 = 0.2509$, $P = 0.017$], Decay Class 4 [C mass = 0.04 [stand age] + 1.42; $r^2 = 0.146$, $P = 0.037$]), however the greatest change in dead wood C storage with stand age occurred in Decay Class One, where the rate of C accumulation was estimated at 0.2 Mg C ha^{-1} y^{-1} (Figure 3.7). The relationship between Decay Class 5 and stand age was borderline non-significant ($P = 0.051$). I fit an exponential function to Decay Class 1 and 5 to determine if a non-linear relationship better fit these classes. In both cases, the exponential relationship was non-significant. Additionally, the linear relationships between stand age and dead wood biomass for Decay Classes 2 and 3 were non-significant.

The relationship between AGC storage and stand age was further explored using a multiple regression model. Although AGC did not vary significantly with age alone, the relationship improved significantly when elevation was incorporated into the model ($r^2 = 0.31$, $F(2,20) = 5.91$, $P = 0.009$). Slope, aspect, and TWI did not contribute to the multiple regression model either due to collinearity or because they did not individually increase explained variance. Elevation and site age had significant negative relationships with AGC (AGC = 237.86 – 0.138[Elevation] – 0.243 [Age]). The standardized, absolute regression coefficient of elevation (*ß* = 0.55) was higher than stand age (*ß* = 0.37), indicating elevation has greater influence in the model predicting AGC than stand age. Large diameter stems (> 70 cm DBH) contributed the majority of C to the AGC pool in all but four of the mature and old growth forests surveyed. On average, 58.8% of all AGC was stored in large diameter stems, followed by 33.5% in medium diameter (50 – 70 cm DBH) trees, 7.63% in stems 5 – 20 cm DBH, and < 0.1% in the sapling (< 5 cm DBH) size class. At six of the ten sites with the highest AGC stores, *Liriodendron tulipifera* was the dominant species, contributing to at least half of all AGC storage in their respective stands (Figure 3.8). *Quercus prinus*, *Q. alba*, and *Fagus grandifolia* were also important species for sites with large AGC pools.

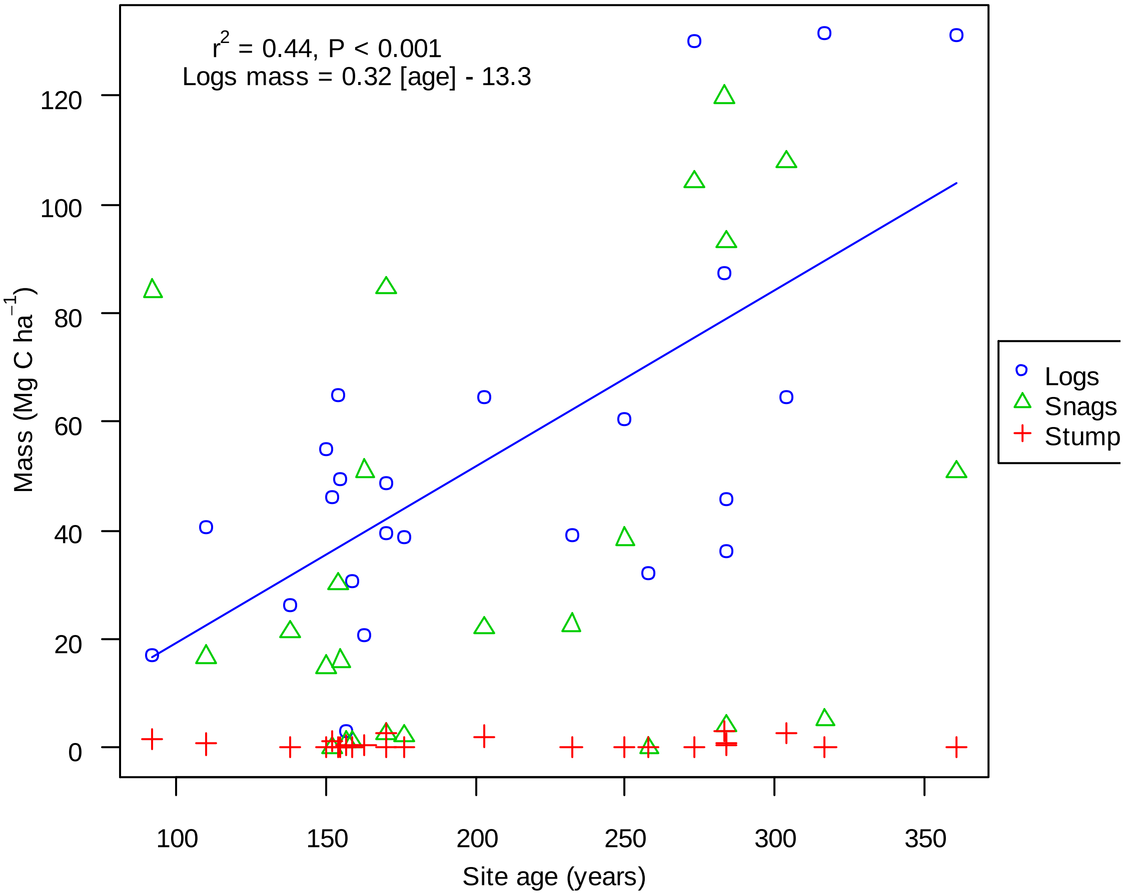

Figure 3.6. Relationship between C storage in the dead wood pool by stand age. Points are classified by dead wood type. Trend lines were included when the relationship was significant.

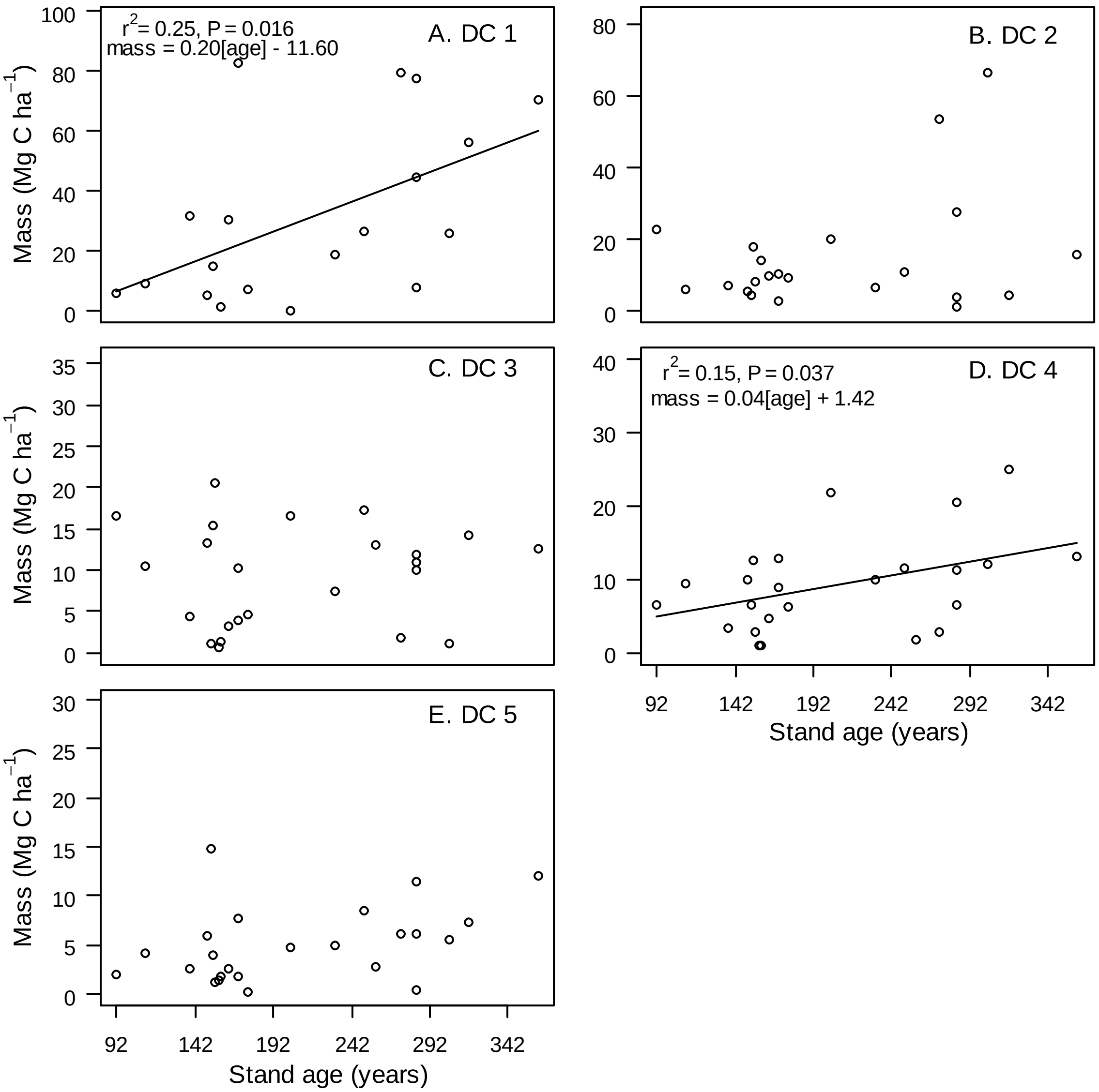

Figure 3.7. Relationship between dead wood C and stand age sorted by decay class (DC). Trend lines were included when the relationship was significant.

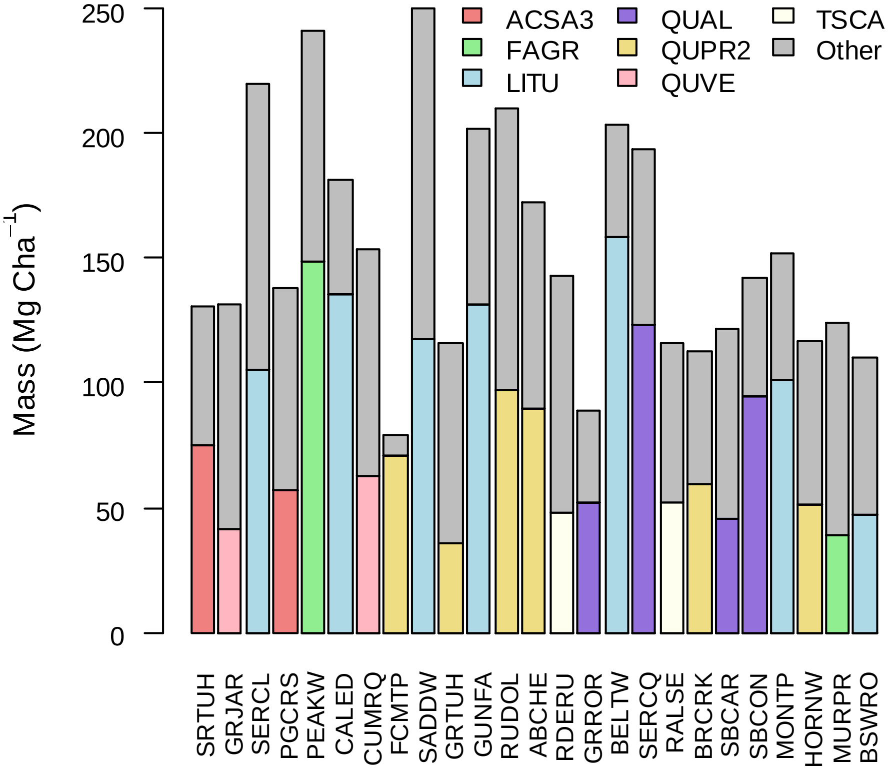

Figure 3.8. AGC storage by dominant species across mature and old growth sites. Sites are ranked from lowest to highest maximum stand age (years), with the exception of BSWRO where no stand age estimates are available. See Table 3.2 for site codes. See Appendix 1 for species codes.

FIA estimates of C storage in younger stands were in general lower than values measured in the mature and old growth stands. Among the FIA sites, AGC increased steadily until 100 years, peaked at 120.46 Mg C ha^{-1} and 110 years, with no further increase for the two oldest age classes in the sample (Figure 3.9). For eighteen of the twenty-five mature and old growth sites, estimates of AGC were higher than the maximum mean for the younger forests. For thirteen of the twenty-five sites, AGC fell above one standard deviation of the maximum mean for younger forests. Dead wood C in the FIA plots increased with age, reaching their maximum at 4.94 Mg C ha^{-1} in the 130 year age class (Figure 3.10). Unlike AGC, all but one of the older sites had a dead wood

C estimate greater than the younger stand maximum. Dead wood C storage was on average eighteen times greater in the mature and old growth sites than it was in the FIA plots with the greatest dead wood C. The old growth site with the largest dead wood C pool had thirty-six times as much C stored as the maximum estimate for the secondary forests. In the comparison of the leaf litter pool and SOC in the O-horizon to adjacent young sites, the younger sites were not significantly different from the late-successional forests (leaf litter [*t* = 1.699, *df* = 22, *p* = 0.06], SOC [*t* = -0.809, *df* = 22, *p* = 0.42]).

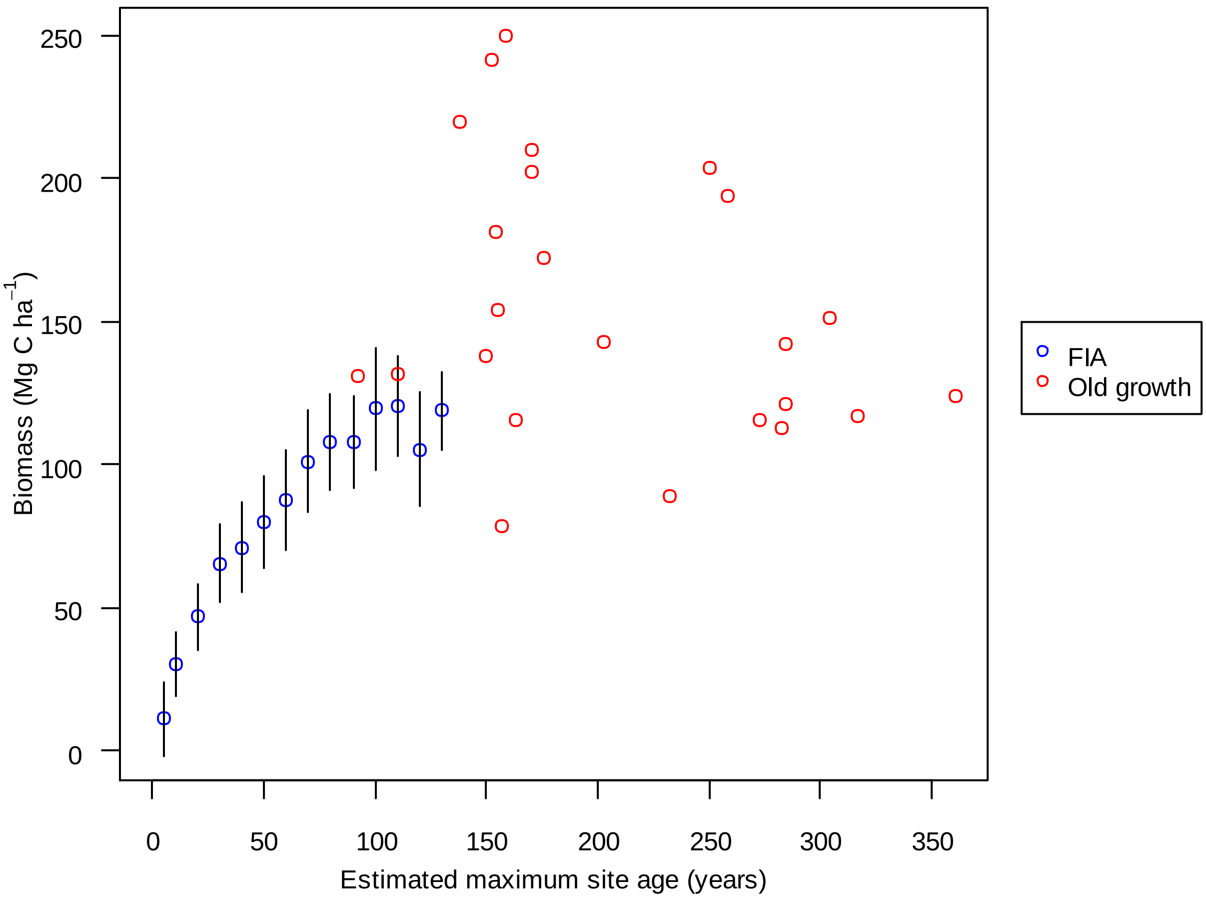

Figure 3.9. Scatter plot of AGC versus stand age for younger FIA plots and the twenty-five mature and old growth forests. Bars represent one SD.

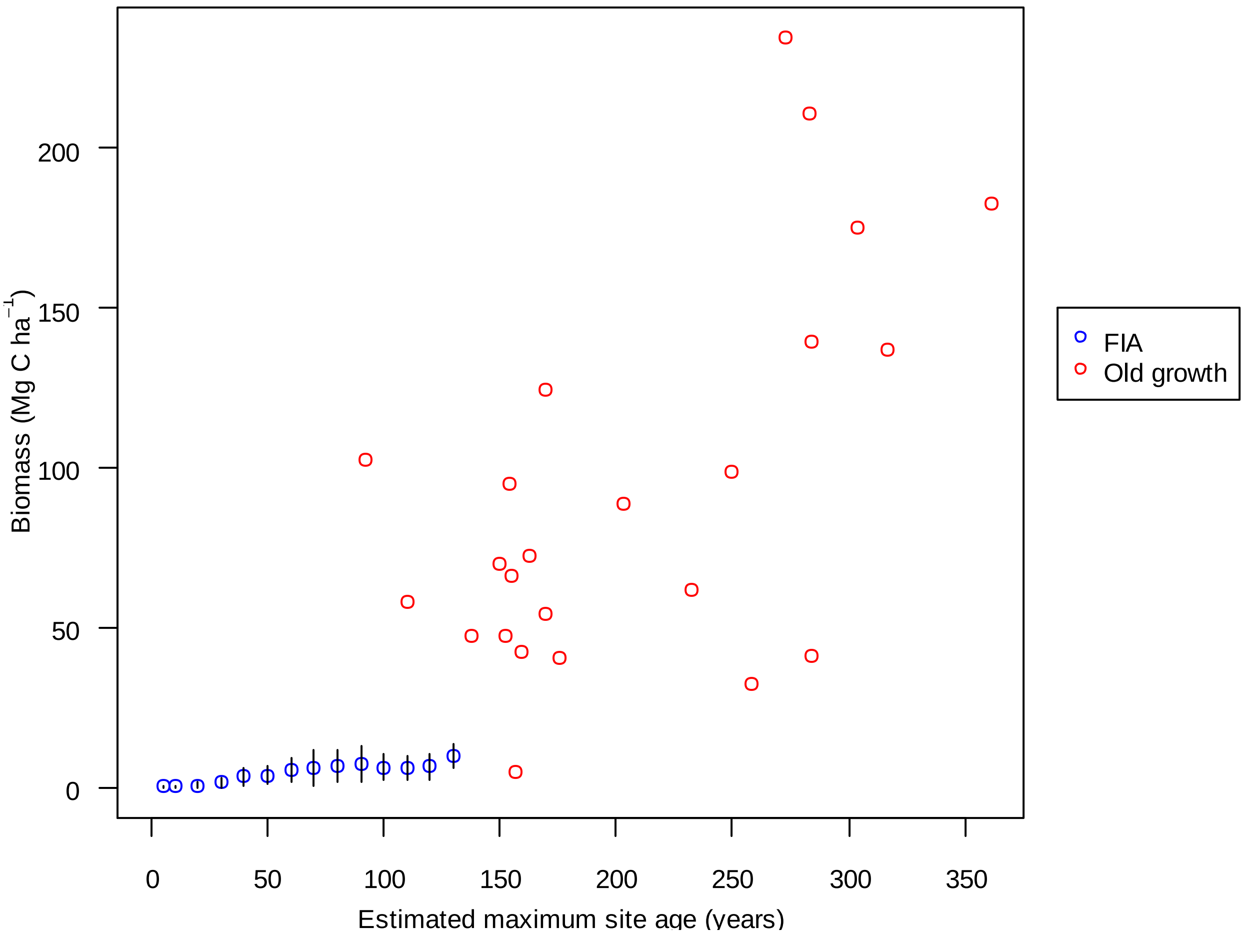

Figure 3.10. Scatter plot of dead wood biomass versus stand age for younger FIA plots and the twenty-five mature and old growth forests. Bars represent one SD.

Table 3.2. Summary information for C storage of the twenty-five mature and and old growth stands. All values represented, with the exception of site age, are site means.

					C stock (Mg C ha^{-1})					
Site name	Code (Fig 1. Map key)	State	No. plots	Max site age (years)	AGC	Dead Wood	Leaf Litter	SOC	Total	Source for Age estimate*
Belt Woods	BELTW (1)	MD	4	250	203.89	49.52	3.81	1.97	257.75	Rucker 2004
Broad Creek Memorial Reserve	BRCRK (2)	MD	4	283	112.66	105.29	7.98	19.84	238.81	
Green Ridge State Forest, Jacob’s Road	GRJAR (3)	MD	3	110	131.46	29.00	9.38	8.97	178.81	
Green Ridge S.F., Roby Ridge 1	GRROR (4)	MD	3	232	89.18	30.91	6.58	17.56	136.18	
Green Ridge S.F., Tunnel Hill	GRTUH (5)	MD	3	163	115.76	36.21	7.72	20.74	180.42	
Gunpowder Falls State Park	GUNFA (6)	MD	4	170	202.14	62.20	7.77	4.68	273.68	
Potomac-Garrett S.F., Crabtree Woods	PGCRS (7)	MD	3	150	137.69	34.89	8.90	48.15	229.63	
Smithsonian Ecological Research Center (SERC), Frog Canyon	SERCL (8)	MD	3	138	219.74	23.76	4.22	3.05	250.77	J. Parker, personal comm.
SERC, Hog Island	SERCQ (9)	MD	2	258	194.04	16.15	–	–	210.19	
Savage River S.F., Turkey Lodge	SRTUH (10)	MD	3	92	130.82	51.36	4.20	16.61	202.99	
Saddler Woods	SADDW (11)	NJ	3	159	249.77	21.27	5.59	8.95	285.58	
Buchanan S.F., Sweet Root Natural Area	BSWRO (12)	PA	3	–	110.15	34.58	4.87	29.93	179.52	
French Creek State Park, Mount Pleasure	FCMTP (13)	PA	3	157	78.82	2.34	4.62	37.40	123.18	
Peak Woods	PEAKW (14)	PA	3	152	241.05	23.60	4.72	14.49	283.86	
Rothrock S.F., Allan Seeger Natural Area	RALSE (15)	PA	3	273	115.59	117.32	4.11	14.53	251.56	Nowacki and Abrams 1994
Rothrock S.F., Detweiler Run Natural Area	RDERU (16)	PA	3	203	142.52	44.40	3.92	33.38	224.23	Ruffner and Abrams 1998

Site name	Code (Fig 1. Map key)	State	No. plots	Max site age (years)	C stock (Mg C ha^{-1})					Source for Age estimate*
					AGC	Dead Wood	Leaf Litter	SOC	Total	
Appomattox Buckingham S.F., Chestnut Ridge Natural Area	ABCHE (17)	VA	3	176	172.21	20.44	4.63	15.49	212.77	Dierauf 2011
Caledon State Park	CALED (18)	VA	3	154	181.28	47.65	–	–	228.93	
Cumberland S.F., Rock Quarry	CUMRQ (19)	VA	3	155	153.77	32.97	4.99	10.34	202.08	
Montpelier	MONTP (20)	VA	4	304	151.53	87.62	4.02	0.41	242.47	
Rudolph Family Farm	RUDOL (21)	VA	4	170	210.02	27.02	6.89	26.36	261.98	
Sweetbriar College, Carry Sanctuary	SBCAR (22)	VA	4	284	121.40	20.68	6.85	4.22	150.38	Druckenbrod et al. 2005
Sweetbriar College, Constitution Oaks	SBCON (23)	VA	4	284	142.31	69.72	7.36	4.99	221.29	Druckenbrod et al. 2005
Horner Woods Game Refuge	HORNW (24)	WV	3	317	116.71	68.36	6.20	5.47	196.74	Rentch et al. 2003
Murphy Preserve	MURPR (25)	WV	3	361	124.01	91.25	5.26	4.46	224.98	Rentch et al. 2003
Mean (SD)				208 (72.8)	153.94 (47.2)	45.94 (29.47)	5.85 (1.71)	15.30 (12.61)	217.95 (43.21)	

5. Discussion

5.1. AGC

AGC notably contributed the most to the overall stand-level storage at all of the sites surveyed (Figure 3.4). Based on a review by Burrascano et al. (2013), the size of the AGC pool for late-successional temperate eastern forests is on average 138.6 Mg C ha^{-1}. The mean AGC estimate for the late-successional forests in the Mid-Atlantic was 153.94 Mg C ha^{-1}, slightly higher than the average of other old growth temperate eastern forests. Sites surveyed for the region included both the highest and among the lowest AGC estimates for old growth in the eastern U.S. The highest estimates were for Peak Woods in Pennsylvania and Saddler Woods in New Jersey, at 241.05 and 249.77 Mg C ha^{-1}, respectively. The next highest estimate for old growth outside of the study region was for a *Tsuga canadensis* (eastern hemlock), *Fagus grandifolia*, and *Acer saccharum* dominant forest in Tennessee with 220.0 Mg C ha^{-1} in the AGC pool (Busing and White 1993). Although the C estimates for these two stands are high for the eastern U.S., coastal old growth forests in the Pacific Northwest may store upwards of 800 – 1700 Mg C ha^{-1} in AGC (Waring and Franklin 1979), making estimates of C storage in the Mid-Atlantic modest relative to all temperate old growth forest types in North America. Old growth *Betula alleghanensis* (yellow birch), *Fagus grandifolia*, *Picea rubens* (red spruce), and *Tsuga canadensis* forests in the Adirondack mountains of New York are among the lowest AGC values outside of the study region at 72 – 74 Mg C ha^{-1} (Keeton et al. 2007). The mature stand on Mount Pleasant in French Creek State Park in Pennsylvania contains AGC stores only slightly higher than those in New York with 81.58 Mg C ha^{-1}.

In the study region, large stems (i.e. those > 70 cm DBH) contain most of the C in the AGC pool (58.8%). The high proportion of C in large stems falls within the range estimated in several site-specific studies for the eastern U.S. Brown et al. (1997) found large stems contributed up to 30% of total aboveground biomass for eastern hardwood old growth forests in the Midwest region, and suggested that large stems should contribute to at least 25% of total aboveground biomass for a stand to qualify as old growth. The upper range observed for our old growth sites matched those observed for Southern Appalachian cove forests of which stems > 70 cm DBH make up to 70% of AGC (Busing et al. 1993). High densities of large stems in eastern hardwood forests often are observed in late-succession and linked with stand age (e.g., Brown et al. 1997, Ziegler 2000, Keeton et al. 2011), suggesting that AGC storage might continue to increase in old growth forests. However, in my assessment of structure and species composition of late-successional forests in the Mid-Atlantic in Chapter 2, I found species composition to be a better predictor of large stem density than stand age. In particular, old growth sites dominated by the early seral species *Liriodendron tulipifera* had the highest densities of large diameter stems. *L. tulipifera* was present in sites across all stand ages, but sites dominated by this species clustered at approximately 150 years, near the younger range of the surveyed sites. Because large stems are the principle component of the AGC pool, and large stem density is driven by species composition, naturally species composition is a predictor of AGC. Indeed, *L. tulipifera* was the dominant species in the majority of the highest AGC sites (Figure 3.8).

There was no relationship observed between stand age and AGC because large stem density did not vary with stand age. However, the multivariate model shows a decline in

AGC with increasing stand age and elevation. In Chapter 2, I found *L. tulipifera* correlated strongly with low elevation. In the Mid-Atlantic, *Quercus alba* forests once prevailed in the low-elevation Piedmont and Coastal Plain ecoregions (Braun 1950, Orwig and Abrams 1994, Abrams 2003). Extensive land clearing and agriculture throughout the Mid-Atlantic removed *Quercus alba* forests, with the greatest impact on these lower elevation forests, allowing mesophytic species like *L. tulipifera* to regenerate (Abrams 2003). If *L. tulipifera* dominates the majority of low elevation sites, it is logical that the highest AGC were also at lowest elevation sites.

The relationship between age and C storage after a stand reaches 130 years appears to be dependent on tree composition. The importance of species-driven C storage was most relevant during late-succession and was less significant in the context of secondary succession as a whole. Several studies have used FIA plots as a reliable, unbiased sample of the existing population of forests in the Mid-Atlantic region (Jenkins et al. 2001, Pan et al. 2009). Within these data, stand age was a major predictor of AGC, marked by a steady increase in C storage with stand age up to 110 – 130 years (Figure 3.9). Following this trajectory, the 70% of all Mid-Atlantic forests between 50 – 100 years old (Drummond and Loveland 2010, Pan et al. 2011b) may continue to accrue C in the AGC pool for another 10 – 80 years regardless of species composition. The forest types most common in the Mid-Atlantic are Oak-Hickory and Maple-Beech-Birch (Jenkins et al. 2001; see Table 3.1 for species composition). The old growth sites dominated by *Quercus* spp., *Acer saccharum*, or *Fagus grandifolia* are thus most indicative of the C storage potential for these younger forests. As such, potential AGC should also approximate the old growth average of ~ 155 Mg C ha^{-1}. If these sites indeed well-represent the late-successional composition and structure of current secondary forests, then peak C storage potential may be reached as early as 150 years (Figure 3.9).

5.2. Dead wood

Compared to what has been reported in the literature previously, these Mid-Atlantic old growth stands have exceptionally large pools of C in dead wood. Dead wood C estimates from surveyed old growth in the eastern U.S. include 20 – 22 Mg C ha^{-1} for *Tsuga-Picea-Abies* and northern hardwood forests in Vermont and New Hampshire (Hoover et al. 2012), 27 Mg C ha^{-1} in northern hardwoods in Michigan (Fisk et al. 2002), 13.5 – 18.5 Mg C ha^{-1} in northern hardwood-conifer forests of New York and Maine (Keeton et al. 2011), and 14.9 Mg C ha^{-1} in a mixed mesophytic forest in southern Kentucky (Muller 2003). At 45.94 Mg C ha^{-1}, the mean dead wood C estimate for old forests in the Mid-Atlantic falls closer to the lower range observed in the *Pseudotsuga-Tsuga* dominated forests of the Washington and Oregon coastal range of 32 – 160 Mg C ha^{-1} (Smithwick et al. 2002, Janisch and Harmon 2002). Among *Pseudotsuga-Tsuga* forests, Janisch and Harmon (2002) observed a decline in dead wood C stores of 0.010 Mg C y^{-1} with increasing stand age. Keeton et al. (2011) estimated down dead wood C would only begin to approach an asymptote at 400 years in old growth of 22.5 Mg C ha^{-1}. Collectively the results indicate the potential for high-magnitude C storage in the Mid-Atlantic region with dead wood accrual rates of 0.25 Mg C ha^{-1} year^{-1}, unobserved in other temperate late-successional forests. Methodologically, the greatest difference between my study and other studies of temperate old growth was the use of a fixed-area plot versus line-intercept method to sample dead wood. The line-intercept method popularized by Van Wagner (1968) is the most widely used method to sample dead wood

(Woldendorp et al. 2004), and is performed by establishing a transect and recording parameters of interest for each piece of dead wood that intersects the line. However, neither the fixed area nor line-intercept methods predict significantly different per-unit area values, and so both are effective for estimating dead wood and produce comparable results (Jordan et al. 2004).

Because the dead wood dynamics of the old growth sites surveyed are so unique, it is an important exercise to discuss potential ecosystem drivers leading to the substantial increases in dead wood with stand age. I focused primarily on the following two processes: theoretical secondary succession processes of mature forests transitioning into old growth, and land use change. As discussed in the introduction, the size of the dead wood C pool relies initially on the input of legacy C following a stand replacement disturbance. During early to mid-succession, total dead wood C declines because the decomposition of legacy wood removes more C than is replaced by new dead wood inputs (Harmon 2009). As the stand transitions into late-succession, the dead wood C pool increases because of canopy mortality (Figure 3.1C). The mature and old growth sites capture the approximate 100 year age range associated with this transition from mid- to late-successional forests. The significant increase in log contribution to total dead wood C with stand age also suggests a successional-stage transition (Figure 3.6). In young stands, the contribution to the dead wood pool typically is snags due to suppression-caused mortality, while wind-related mortality is more important in old growth stands with input mainly being logs in the form of boles or large branches (Harmon et al. 1986). The sampled Mid-Atlantic forests deviate from this successional model in terms of their decay class composition. In many late-successional ecosystems, the intermediate decay class represents the largest fraction of dead wood, while the most and least decayed pieces represent the smallest fraction of the pool (Harmon et al. 1986). Although biomass stored in the second most-decayed class does increase with stand age, Decay Class 1 and 5 also increase, and Decay Class 1 contributes the most C to the oldest stands (Figure 3.7). More important, this successional process describes changes in dead wood C within a single stand, and applying it to a space-for-time chronosequence composed of unique relic sites stretches the assumptions of such a model that site conditions and histories are similar.

Given the high levels of dead wood we found across the old growth sites, it is interesting that the most C dense stands have comparatively low levels of dead wood C. This could be a product of the land use history or of the species composition. Dead wood recruitment is a slow process, affected in part by anthropogenic disturbance. In a study of dead wood C dynamics in the Southern Appalachians, Webster and Jenkins (2005) observed that primary forests contained significantly more total dead wood volume and highly decayed dead wood than areas with a documented history of settlement or small-scale disturbances such as mechanized logging. The prevalence of highly decayed dead wood in the older stands may support this hypothesis. Unfortunately, other indicators of past harvesting include significantly lower densities of large-diameter stems (Brown et al. 1997, Gronewold et al. 2010), lower densities of large-diameter snags (Gronewold et al. 2010), and lower AGC (Goodale and Aber 2001) than undisturbed forests. In my study, the sites with the highest densities of large-diameter stems were indeed among the youngest sites sampled, and were characterized by the prevalence of large-diameter *L. tulipifera* (Chapter 2). Discussed in Chapter 2, the dominance of *L. tulipifera* among the younger stands potentially resulted from selective harvest of oak species, allowing shade-intolerant *L. tulipifera* to establish (Abrams et al. 1998). These individuals may also have regenerated in tree-fall gaps of previous *L. tulipifera,* since decayed due to the relatively high decomposition rate of dead wood for this species (Harmon et al. 1986). Large dead wood at other older sites may have a longer residence time than *L. tulipifera* dominant sites, allowing more C to accumulate in the dead wood pool over time.

Rather than a single ecosystem driver leading to high dead wood C in late-succession, the dead wood C storage and stand age relationship is likely a composite of successional processes, land use history, and species composition. More important than the relationship observed within just the late-successional samples, however, is the greater quantity of dead wood C stored in even the youngest mature and old growth stands compared to the surrounding secondary forest matrix (Figure 3.10). Unlike my sampled stands, the surrounding secondary forests established after agriculture or on cut-over wood lots (Houghton et al. 1999, Houghton and Hackler 2000). Large dead wood will be one of the last C pools to develop within most of these secondary forests in the absence of legacy wood. The mean estimate of dead wood C for old growth suggests stores in young forests could increase ten-fold as they transition into late-succession. This increase has significant implications for preserving natural disturbance regimes that promote dead wood accumulation to increase C storage in secondary forests, particularly as the oldest sites begin to approach equal quantities of C stored in the AGC and dead wood pools (Figure 3.5).

5.3. Leaf litter and SOC

Relative to the AGC and dead wood pools, the leaf litter C pool and SOC pool in the O-horizon on average contributed smaller amounts of C to the overall storage of the stand (Figure 3.4). The leaf litter pool stores similar quantities of C as other eastern old growth forests. The mean C stock estimate for the leaf litter pool in the mature and old growth stands (5.85 Mg C ha^{-1}) was slightly lower than the mean value described by Hoover et al. (2012) for northern New England old growth (9 Mg C ha^{-1}). Leaf litter pools in temperate deciduous forest systems are ephemeral with annual turnover rates (Edwards and Harris 1977). There is no long-term accumulation of C within this pool, and so there should be no relationship between stand age and total C. If there were to be a relationship, it would be due to a combination of interspecies differences in leaf litter production and the rate of leaf litter decomposition (Finzi et al. 1998). Precise measurements of C concentration in the leaf litter pool, versus an assumed 50%, are needed to identify subtle differences among sites. However, because species composition was not driven by stand age in these mature and old growth forests (Chapter 2), I do not expect stand age to relate to leaf litter C if leaf litter C is driven by species composition.

SOC estimates were lower than observed in other old growth forests. On average, SOC was 63 Mg C ha^{-1} for northern New England hardwoods (Hoover et al. 2012) and 43.6 Mg C ha^{-1} in European *Fagus sylvatica* (European beech) forests (Mund 2004). These estimates are three to four-fold higher than the mean for Mid-Atlantic old growth (15.3 Mg C ha^{-1}), however these sites calculated SOC to 10 – 20 cm depths. The shallow depth of the O-horizon likely led to the differences in SOC pool. The mean depth for the humic layer (rough approximation of the organic layer) estimated by FIA plots for the

U.S. is 3.7 cm, with the majority of the Mid-Atlantic region ranging in depth of approximately 0.5 – 2 cm (Woodall et al. 2012). The mean O-horizon depth of the old forests I surveyed was 2.8 cm. Median humic layer C stocks for the same FIA plots described by Woodall et al. (2012) were ~13 Mg C ha^{-1}, more closely approximating my estimate. Although the average was low relative to other old growth forest, it is of worth noting that at certain sites, SOC levels were as high, or higher, than dead wood C (Figure 3.4).

Previous studies suggest harvest and other forms of land-use lead to a decline in O-horizon C storage regardless of species composition and soil order, by modifying the detrital C inputs, changing the microbial community, and affecting the climatic conditions governing plant and microbial processes (Covington 1981, Zak et al. 1990, Post and Kwon 2000, Nave et al. 2010). Contrary to other findings, I did not observe a difference in SOC content between the secondary and old growth forests sampled. Perhaps SOC stores have returned to pre-harvest levels in the surrounding secondary forests, which Nave et al. (2010) suggested could occur in as short as 50 -70 years. However, quantifying SOC patterns is complicated because many different factors influence its spatial variation, and small scale heterogeneity in soil conditions such as pH, temperature, and water, as well as topographic variation and canopy composition heterogeneity interact to influence SOC content (Yuan et al. 2013). A more spatially extensive and intensive sampling design would be valuable to better quantify differences among these inherently idiosyncratic stands to determine whether successional phase drives SOC storage in the O-horizon.

5.4. Limitations

This study offers valuable empirical estimates of C storage for a critical stage of forest succession that is understudied due to the rarity of old growth forests in the Mid-Atlantic region and the greater eastern U.S. It is important to be explicit about the scope of inference of this study. The study sites were not randomly selected, and so it cannot be assumed that the remaining old growth forests are necessarily representative of the late-successional stage for current early/mid-successional forests in the Mid-Atlantic. However, even with this limitation, estimates for C storage in the remaining old growth forests will allow for improved inferences regarding long-term C storage in Mid-Atlantic forests.

There are certain unavoidable limitations to the study design that may have caused potential errors in my estimation of stand C storage, specifically in missing C pools. By not including belowground biomass estimates and SOC in the mineral soil, I cannot make conclusions about overall stand C storage. Root biomass represents a substantial proportion of total stand C storage, but quantifying this pool is difficult because root biomass is hard to measure directly (Fahey et al. 2009). Similarly, current research suggests SOC stored in the mineral horizons as a potential major pool (Gleixner et al. 2009), but intensive sampling was unfeasible due to time constraints and the ecological and historical significance of many of the field sites.

There are also limitations to using a ‘space-for-time’ approach for developing a chronosequence. The implicit assumption of this approach is that state factors, such as soil conditions, microclimate, and general site history, are similar across all sites, which was not true for Mid-Atlantic old growth (Glenn-Lewin and van der Maarel 1992, Bakker et al. 1996). A more direct method of estimating biomass dynamics would be tracking biomass over time in re-measured permanent plots (e.g., Peet 1981, DeBell and Franklin 1987, Taylor and MacLean 2005), but measurements would have to be made over decades to centuries. FIA re-measurement data are not available for the entire U.S., and because old growth forests are so scarce, they are not well-represented in the FIA systematic sampling scheme; therefore I adopted this informal 'space-for-time' approach.

6. Conclusion

My findings add to the growing body of literature that suggest temperate eastern old growth forests have greater C storage and C sequestration potential than previously realized, particularly in the Mid-Atlantic region (Luyssaert et al. 2008, Lichstein et al. 2009, Keeton et al. 2011). The greatest potential for increased C storage among secondary forests will be in the development of the dead wood C pool, poised to rapidly increase as forests transition into late-succession. The dead wood C storage and C accumulation rate are unique to the Mid-Atlantic region, because they are greater than previous estimates for temperate old growth eastern forests. Also unique to these forests is the role of species driving patterns in AGC. Specifically, species-specific associations with live stand structure lead to species-specific associations with AGC. In particular, high densities of large-diameter, early seral *L. tulipifera* led representative sites, regardless of age, to have the highest AGC values. The importance of species composition in determining late-successional C storage has crucial implications for secondary forests, particularly as an extensive land-use history has shifted composition from late-successional taxa like *Quercus* spp. to early successional species such as *L. tulipifera* (Abrams 2003, Thompson et al. 2013). Future exploration of late-successional

C dynamics in the Mid-Atlantic should improve on our current understanding of how these altered disturbance regimes will affect C storage potential.

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Appendix A. Definitions of USDA-NRCS species codes.

USDA-NRCS Code	Species	Common Name
ACRU	*Acer rubrum*	red maple
ACSA3	*Acer saccharum*	sugar maple
BEAL2	*Betula alleghanensis*	yellow birch
BELE	*Betula lenta*	sweet birch
CAGL8	*Carya glabra*	pignut hickory
CATO6	*Carya tomentosa*	mockernut hickory
FAGR	*Fagus grandifolia*	American beech
FRAXI	*Fraxinus* sp.	Ash
LITU	*Liriodendron tulipifera*	tulip poplar
HAVI4	*Hamamelis virginiana*	witch hazel
NYSY	*Nyssa sylvatica*	blackgum
PIST	*Pinus strobus*	white pine
PRSE2	*Prunus serotina*	black cherry
QUAL	*Quercus alba*	white oak
QUPR2	*Quercus prinus*	chestnut oak
QURU	*Quercus rubra*	red oak
QUERC	*Quercus* sp.	Oak
QUVE	*Quercus velutina*	black oak
TIAM	*Tilia Americana*	American basswood
TSCA	*Tsuga Canadensis*	eastern hemlock

Chapter 4: Synthesis and conclusions

The research presented in this thesis investigated the majority of remaining old growth in the Mid-Atlantic region of the eastern U.S., and identified the species composition, forest structure, and C storage of this rare forest type. It is important to understand the duality of this dataset. At once, it is both invaluable and idiosyncratic. There is a great need to identify the surveyed characteristics of old growth forests as the greater forested landscape begins to transition from early and mid-succession to late-succession. However, these twenty-five mature and old growth sites do not represent a random sample, and as such, they do not warrant a formal scope of inference greater than themselves. Therefore, the findings from this research both reflect the variability among mature and old growth sites that established under different environmental conditions and disturbance histories, but also provide a baseline estimate of structure and C storage for late-successional forests compare relative to the younger surrounding forest matrix.

The unique qualities of this dataset are strongly evident in Chapter 2, where I describe structural and compositional characteristics and their relationship to stand age and environmental variables. I expected that stand age would be the main driver of structure and species composition within these stands, where the oldest sites would have elevated live BA, elevated snag densities, elevated medium (> 50 cm DBH) and large (> 70 cm DBH) stem densities, and elevated dead wood volume. In contrast, I found stand age was a weak predictor of live structural characteristics, or in the case of medium and large stem densities, and BA, indicated a relationship opposite to the expected, where these variables decreased with stand age. My findings instead suggest species composition was a better predictor of structure than stand age. In particular, the presence of large diameter

Liriodendron tulipifera (tulip poplar) at seven of the twenty-five sites associated with the highest estimates of large stem density and BA. Current understanding of the role of early seral *Liriodendron tulipifera* in old growth forests suggest their presence is due to historical loss of *Quercus* spp. from anthropogenic disturbances that allowed the shade-intolerant species to establish. The large diameter and height of *Liriodendron tulipifera* then create tree fall gaps large enough for the species to regenerate. Conventional wisdom implies that *Liriodendron tulipifera* would be present only in young stands, but I also found stand age to be a poor predictor of species composition. Instead, environmental variables drove composition.

The relationship between live structure and species composition led to a similar association between species composition and live aboveground C (AGC) in my assessment of old growth C storage in the Mid-Atlantic in Chapter 3. Large stems contributed the most to total AGC, leading to an insignificant relationship between stand age and AGC. The prevalence of *Liriodendron tulipifera* among the younger stands sampled and at lower elevation sites led to a negative relationship between AGC and stand age when elevation was incorporated into a multivariate model. Species-driven AGC values have critical implications for predicting future AGC stores among secondary forests. Here I predict that *Quercus* spp. dominant old growth best-represent the late-successional forest structure of the broader landscape.

The idiosyncratic nature of this dataset did not mask broad-scale findings regarding old growth forests in the Mid-Atlantic. In chapter 2, dead wood volume and in chapter 3, dead wood C both exhibited significant positive relationships with stand age. Dead wood C accumulated at rates previously unobserved in other old growth temperate forests, and dead wood C storage in the oldest stands approached values found only in the C-dense Pacific Northwest. The comparison between old growth and FIA sites also indicate differences in structure and C between old growth forests and the surrounding secondary forest mosaic. In terms of structure, snag density was greater in the smallest size classes in the FIA plots, while snag BA was greater in the largest size classes in the old growth sites. Similar trends were observed for live stem density and live BA. These differences fit expected trends for early and mid-successional forests and late-successional forests. The respective comparisons between AGC and dead wood in old growth and FIA plots add to the growing body of literature that indicate temperate eastern old growth forests have greater C storage and C sequestration potential than previously realized. In particular, dead wood C represents the most dynamic pool in late-succession with the greatest potential for C storage.

As the greater forested landscape in the Mid-Atlantic begins to approach late-succession, the findings of this study should be considered. It is important to recognize that this sample does not represent all potential structure and composition of old growth for the region – quite the opposite, the variability among the remnant stands highlights how structure, composition, and C storage cannot be predicted by stand age alone. Future research should consider how substantial differences in disturbance regimes, land use histories, and climate conditions under which remnant old growth versus younger secondary forests established will affect structure and C storage in secondary late-successional stands.