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Assessment of Aboveground Net Primary Productivity and Carbon Pools, Detrital Biomass, Community Structure, and Species Composition Across a Floodplain Forest of the Congaree River

Gavin D. Blosser
Clemson University, gavinblosser@aol.com

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ASSESSMENT OF ABOVEGROUND NET PRIMARY PRODUCTIVITY AND CARBON POOLS, DETRITAL BIOMASS, COMMUNITY STRUCTURE, AND SPECIES COMPOSITION ACROSS A FLOODPLAIN FOREST OF THE CONGAREE RIVER

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by
Gavin D. Blosser
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Accepted by:
William H. Conner, Committee Chair
Alex Chow
Bo Song
William Bridges
B. Graeme Lockaby

ABSTRACT

Floodplain forests offer services to society in the form of species diversity, wood production, sequestration of carbon, and buffering capacity critical to water quality. These services are dependent upon maintenance of hydrological connections and sedimentation dynamics of these systems that determine site specific heterogeneous microsite distributions yielding specific community structure, species composition, and productivity rates. The study area was within South Carolina's Congaree National Park (CONG), and consisted of a micro-topographic gradient across the Congaree River floodplain differing in sedimentation rates and inundation periodicity and intensity. The research was designed to take advantage of this gradient to help bridge information gaps regarding how communities vary across the floodplain. Specific objectives included: (i) describing community composition and structure of both live and dead wood to define community types, (ii) quantifying net aboveground primary productivity, (iii) determining litter decomposition rates and litter nutrient dynamics, (iv) calculating sequestered carbon in aboveground wood, and (v) synthesizing these data to qualitatively assess the stability of, and possible shifts in, community composition. Utilizing 20 plots, we characterized four distinct forest community groups: younger mixed bottomland hardwoods at higher elevations; old-growth mixed bottomland hardwoods at both higher and intermediate elevations; and mature cypress backswamp at lowest elevations. The annual percentage of mass gain for tree wood was greater at higher and intermediate elevations compared to the backswamp. Additionally, the percentage of tree wood gained annually is greater at a given elevation for plots having the majority of tree biomass in younger trees. However, the actual magnitude of mass gain, and thus carbon sequestration, is greater when old growth trees are present. Litter turnover times were 64-80 weeks, thus litter decomposition and cycling of nutrient contents of the litter are comparatively rapid processes within CONG. For all pools of aboveground sequestered carbon, we found cumulative values of 14840, 18878, and 7460 (younger stands) grams C/m^2 for bottomland hardwood forest and 19076 grams C/m^2 for the bald cypress swamp. The species composition, wood mass and volume, and unit quantities between the dead and live wood fractions, in conjunction with decay class of dead wood used as a temporal proxy, suggests that there are ongoing shifts in both the canopy and understory in the bottomland hardwood forest stands while the cypress swamp appears to be stable. We conclude that topographic position, a surrogate for both hydrology and sedimentation, as well as stand age and size metrics result in differing productivity rates and thus carbon sequestration within forested floodplains of the southeast.

DEDICATION

This work is dedicated to the loving and honorable memory of Steven “Hutch” Hutchinson; one of the most outstanding and intelligent human beings I have ever had the pleasure to know and work with.

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CHAPTER ONE

INTRODUCTION

Of the original four million hectares of bottomland hardwood forests in the southern US, approximately one million hectares remain. Due to species and size specific harvesting practices and the drastic increase in floodplain sedimentation rates related to agriculture and development, species composition and canopy structure of the remaining forest is often altered (Lockaby 2009). Forested floodplains and their associated wetlands function to both preserve water quality and buffer the effects of global warming via net sequestration of atmospheric carbon, but these functions may be degraded when hydrologic connections are severed or manipulated (Naiman et al. 2005, Noe and Hupp 2005). Paramount to these functions is sediment type and deposition rates which strongly influence the composition, succession, and structure of the floristic community of bottomland hardwood forests (Hodges 1997). Deposited material tends to have heterogeneous texture, mineralogy, and origin in major stream bottomlands of the coastal plain and, as such, are generally more fertile and productive (Hodges 1997). Lower piedmont and coastal river valleys of the southeast typically have active floodplains resulting in a distinct series of fluvial landforms which often differ in species composition, reflecting changes in historical deposition patterns (Wharton et al. 1982, Hodges 1997). Successional patterns may be interrupted or reversed by construction of dams which change site hydrology and alter rates and composition of deposited materials and reduce recruitment success from the seed bank (Hodges 1997, Walls et al. 2005, Jensen et al. 2008).

Sedimentation rates in floodplain forests are variable, depending upon the nature of the upstream geology and watershed, intensity and periodicity of flooding, and anthropogenic activities. Materials trapped by these forests can contribute to maintenance of water quality and include sediment, nutrients, pollutants, and organic matter (Noe and Hupp 2005). The amount of materials trapped annually can be large. Hupp et al. (2008) estimated amounts at over 40 mm/yr in the Atchafalaya Basin in Louisiana with a mass of 6.7 Mg overall and 0.8 million Mg of the total organic matter. In the southeastern US, sediment deposition rates are highest in the coastal plain, and in systems with relatively high sediment loads, rates may range between 5-10 mm annually (Hupp 2000).

STUDY AREA

The Congaree River begins at the confluence of the Broad and Saluda rivers near Columbia, South Carolina and ends at its confluence with the Wateree River to form the Santee River after flowing 85 river km. For most of its length, the Congaree River occupies a broad floodplain bounded on the north by a fluvial landscape and to the south by a steep bluff cut into upper coastal plain deposits known as the Orangeburg scarp (Shelley and Cohen 2010). The Congaree National Park (CONG) protects a vast, old growth floodplain forest in the lower Congaree River Valley representing the last remaining major tract of mature bottomland hardwood forest in the southeastern United States (Gaddy et al. 1975, Shelley and Cohen 2010). Within the floodplain are spatially complex changes in elevation (generally < 75 cm) yielding areas that experience distinct flooding regimes, sedimentation processes and soil drainage characteristics. This results in a complex spatial array of forest types having distinct community structure and composition (Conner et al. 2002).

The study area is located on the major alluvial floodplain associated with the Congaree River located within CONG and is predominantly forested except following major natural disturbances or anthropogenic activities (Messina and Conner 1998). The spatially complex topographic areas, despite low relief, experience differential hydroperiods via overbank and backwater flooding (Sharitz and Mitsch 1993, Kellison et al. 1998). Backwater flooding can occur via channels known locally as “guts” which connect levee breeches to backwater swamps, thus allowing flooding of these swamps at flow levels below bank full (Shelley and Cohen 2010). The backwater swamp areas within the study area may be inundated for a majority of the year or may be free of standing water for much of the year, depending on annual fluctuations in rainfall amounts and timing (Sharitz and Mitsch 1993, Conner and Buford 1998).

Floodwater characteristics (duration, intensity, frequency, timing) and groundwater levels determine the hydroperiod (or hydrologic regime) of a given area (Hupp 2000). The hydrologic regime of the Congaree River watershed remained mostly unaltered by humans until 1929 with the exception of scattered low head dams associated with mills (Conrads et al. 2008). Regulated streamflow of the Saluda River, which joins the Broad River to form the Congaree River, began in 1929 with operation of the Saluda Dam at Lake Murray (Patterson et al. 1985). Studies have indicated operation of the dam has affected the hydrologic regime within the Congaree Swamp; however parsing out to what extent dam operation is responsible for hydrologic and ecologic changes directly from the contributory effects of shifting precipitation patterns associated with climate change remains difficult (Patterson et al. 1985, Minchin and Sharitz 2007, Conrads et al. 2008). While operation of the dam has had no discernible effect on the probability that base flood stage would be equaled or exceeded in a given year (Patterson et al. 1985), the recurrence intervals of higher flood levels has increased by 6.1% for two year peak flows and 17.6% for 100 year peak flows (Conrads et al. 2008). The analysis by Conrads et al. (2008) comparing pre and post dam hydrologic regimes indicates the following: high water levels from December to May have been reduced; low water levels between June and November have increased; high ground water elevations have decreased and low ground water elevations have increased; minimum incremental gage heights have increased up to 23.9% and maximum values have decreased up to 7.2%. Along with the decrease in frequency and magnitude of larger floods associated with dam operation, the dynamics of flood pulse are shifted as the duration of inundated conditions associated with a given event has increased. Overbank flow has also been reduced leaving mainly backwater flooding through levee breaches contributory to backswamp inundation and limiting deposition to the levee and higher elevation flats (Patterson et al. 1985).

COMMUNITIES AND ABOVEGROUND PRODUCTIVITY

A complex mosaic of microsites defined by available soil oxygen due to differences in sedimentation and inundation is a common characteristic of floodplain forests. Species have differential response and specificity to microsite type (Broadfoot 1976, Hupp 2000). As a result, alteration of microsite distribution and physical characteristics via changes in sedimentation and hydrology will lead to species specific productivity responses and a shift in species composition (Ewing 1996, Oswalt and King 2005).

It is often thought that red-water river floodplains and associated wetlands of the piedmont and upper coastal plain (like the Congaree floodplain) should be more productive compared to black-water systems of the lower coastal plain because of the greater nutrient subsidy associated with higher sediment loads and allochthonous organic matter transport, but this can be offset by the stress associated with prevalence of anaerobic conditions (Schilling and Lockaby 2005). Aboveground net primary productivity (ANNP) in southeast floodplain forests varies from 200-2000 g/m^2 per year (Conner 1994). ANPP may be affected via the stress-subsidy hypothesis from one growing season to the next or even within the same growing season via the physiological and growth rate differences related to anaerobic conditions, drought stress, and nutrient inputs associated with flooding, rainfall, and anthropogenic alterations to flow and flooding regimes (Megonigal et al. 1997). Increasing sedimentation rates in floodplain forests has been shown to bolster the productivity of bald cypress and ash (Galicki et al. 2002, DuFour and Piegay 2008, respectively) while other studies have found species specific declines in productivity either experimentally or in situ (Clewell and McAninch 1977, Ewing 1996, Walls et al. 2005).

Although seed banks in wetlands can be species rich with relatively high seed densities, potential recruitment from the seed bank is limited in areas of annual deposition as burial with only 2 cm of sediment precludes or greatly depresses germination of most seeds (Leck 1989, Petru and Menges 2004). Seed abundance and richness has been found to be greater in sediments under deeper water while recruitment is inversely related to water depth within the same wetland, with turbidity likely a key factor suppressing recruitment (Barry et al. 2004).

Succession in these systems may be punctuated and rapid following disturbances such as logging, fire, hurricanes, etc., but are generally slow as the mosaic of habitats change spatially and temporally as the river continually reworks the floodplain (Conner and Buford 1998). Without major disturbances, stands can persist for centuries before canopy trees begin to decline and die (Hodges 1997). Evidence suggests fluvial forested wetlands will be more productive and support greater species diversity when punctuated and interactive disturbances augment the habitat heterogeneity created by long term fluvial processes (Frost 1987, Conner et al. 1989, Myers and Van Lear 1998, Gagnon 2009). Successional patterns may be interrupted or reversed by construction of dams which change site hydrology and alter rates and composition of deposited materials and reduce recruitment success from the seed bank (Hodges 1997, Walls et al. 2005, Jensen et al. 2008). Flood control levees and dam operations deprive the floodplain of flood born sediments and nutrients resulting in decreased productivity and subsidence rates exceeding sedimentation rates. Water depth may then become too deep in certain stands for tree survival and in others the selective pressure of flooding is diminished allowing generalists and exotic species to invade the system (Conner and Buford 1998, Penland and Ramsey 1990, Ernst and Brooks 2003, Catford et al. 2011). Although changes in hydrology may not be exceedingly detrimental to the present community,

Biological integrity and productivity of an ecosystem like that within CONG can be affected by both natural and anthropogenic forces. Naturally occurring agents of change influencing the ecology of CONG over the past 250 years include floods, drought, fire, and powerful storms such as hurricanes and tornados (Conner et al. 1989). These selective forces, along with the dynamics of the river itself, have acted singly and in concert over many centuries and generations to produce a mosaic of community types across the floodplain. European settlement of the watershed brought into play additional agents of change with the potential to affect the biological integrity of the system, however these new anthropogenic forces, including development, climate change, agriculture, logging, invasive species, and alteration of the hydrologic regime, have only applied selective pressure on populations for limited generations compared to natural agents.

LITTER DECOMPOSITION AND NUTRIENT CYCLING

Decomposition of litter is controlled by three main factors; the physiochemical environment, litter quality, and the decomposer community (Hattenschwiler et al. 2005). Leaf production accounts for an average of 43% of the annual aboveground primary productivity in southeastern floodplain forests and the decomposition rate of this litterfall is an important component of nutrient cycling and the composition and population dynamics of the bacteria, fungi, microinvertebrates, and macroinvertebrates that constitute the decomposer community (Conner 1994). The decomposer community relies upon and processes litterfall into byproducts returning nutrients to the soil which perpetuates the productivity of the forest and helps shape the composition and structure of the floral community and the structure of the soil (Wharton et al. 1982, Hodges 1997, Messina and Conner 1998).

In general, at a broad spatial scale, litter decomposition rates are faster with increased temperature and increased precipitation, are maximized when consistent moisture and elevated temperature coincide, and exhibit variance dependent upon litter quality and forest type (Meetemeyer 1978, Vogt et al. 1986, Zhang et al. 2008). At the local scale, even within the same floodplain, litter decomposition rates differ based on the litter quality of the specific community type, timing of leaf drop for community constituents (early drop coincides with warmer temperatures), nutrient content of deposited sediment, and the hydrologic regime (Groffman et al. 1996). While high quality litter will decay faster if other factors are held constant, litter decay rates are dependent upon numerous other factors at a given location at a given time.

Rates of litter decomposition and litter nutrient dynamics can vary significantly among and within forested wetlands subjected to differential flooding regimes. The length of inundation and the degree of flow versus stagnation can differ substantially, even at small spatial scales, resulting in unique balances of available nutrients, moisture and oxygen to drive the decomposition process (Conner and Day 1991). While decomposition rates may be inversely related to the number and duration of flood events in one wetland, rates may be positively correlated in another indicating a complex interaction between hydrology and decomposition rate; long duration inundation may slow decomposition due to anaerobic conditions while frequent, short duration inundation may increase the decomposition rate by ameliorating moisture limitations (Megonigal and Day 1988, Groffman et al. 1996, Baker et al. 2001). The communities of bacteria, fungi, microinvertebrates, and macroinvertebrates contribute to litter decomposition and nutrient flux processes and their activities peak with warmer conditions and consistent moisture while their efficacy is related to a sites hydrologic regime (Messina and Conner 1998). Macrophages can be particularly important due to the fragmentation of litter which increases surface area of litter increasing leaching and the efficiency of bacteria, fungi, and microinvertebrates; additionally macrophage fecal material diversifies food resources for the decomposer community and increases microbial richness (Conner and Day 1991, Hattenschwiler et al. 2005).

Litter quality is most often defined by ratios of nutrients and recalcitrant compounds such as C:N, C:P, N:P, and lignin:N, as well the thickness of the cuticle layer and the toughness/thickness of the leaf structure (Meetemeyer 1978, Baker et al. 2001, Hattenschwiler et al. 2005, Prescott 2005). Litter with higher concentrations of nutrients and lower concentrations of recalcitrant components such as lignin, polyphenols, and inhibitory secondary metabolites tend to decompose more rapidly (Vogt et al. 1986). Although litter quality is considered the most important determinant factor controlling litter decay rates (Zhang et al. 2008), diversity of litter is also exceedingly important. In a review comparing litter decay rates for single species decay rates versus mixed species decay rates, Hattenschwiler et al. (2005) reported synergistic effects occurred in 50% of cases with mixed litter decaying up to 65% faster compared to the mean decay rate of component species, no effect was evident in 30% of the cases, and antagonistic effects occurred in 20% of cases with decay rates declining up to 22%. Litter diversity creates a more structurally complex litter layer which yields a diverse array of microclimatic and microhabitat niches supporting a more diverse decomposer community (Hattenschwiler et al. 2005).

Productivity and decomposition rates may be constrained in forested wetlands by N limitation, P limitation, or both with wide N:P ratios often indicating primary N limitation and secondary P limitation (Lockaby and Conner 1999). Phosphorous is imported via the sediment suspended in flood water and is readily adsorbed by soil particles (particularly clay and organic matter) while water soluble N can be transported downward via percolation. Fine clay particles carry far more P via adsorption and only settle out of impounded or extremely slow moving water, thus deposition is non-uniform across the floodplain. Increases in N are often reported early in litter decomposition studies and is attributed to deposition via precipitation and flood waters, fixation of atmospheric N by microbial community, and the N content in the decomposer community colonizing the litter (Swift et al. 1979). Increases in the density of N fixing plant species has been shown to increase with increasing sedimentation rates (Jolley et al. 2010). When the C:N ratio is greater than 20 the decomposer community tends to immobilize N for growth (i.e., protein synthesis) while the substrate C content is released as carbon dioxide as a by-product of respiration; as the ratio drops below 20, N reaches a luxury level for the decomposer community and N is lost to the soil via mineralization (Bowden 1987). A C:N ratio of approximately 16 and a C:P ratio near 200 are considered necessary by Brinson (1977) for complete decomposition of litter. A N:P ratio of 12 is considered optimum for the decomposer community to achieve efficient decomposition of litter in southeastern forested wetlands (Lockaby and Walbridge 1998). As values depart in either direction, a nutrient limitation is placed on the decomposer community. Larger ratios are often associated with a prolonged hydroperiod and low P import while smaller ratios are indicative of shorter hydroperiods but greater P load in the flood water (Lockaby and Conner 1999).

WOODY DETRITUS AND ABOVEGROUND CARBON POOLS

Forested wetland and floodplain communities are among the most effective ecosystems at sequestering atmospheric carbon (C) in addition to numerous other benefits such as improved water quality, protection from storm surge and high tides, and flood mitigation (Mitsch et al. 2013). Globally, forests contain approximately 45% of terrestrial sequestered C within four main pools: living plant material; woody detritus; forest floor – litter, senesced herbaceous vegetation, duff, and soil O horizon; and soil organic C stored in mineral horizons (Bradford et al. 2009). Tree mortality introduces important structural and functional components into these forested ecosystems in the form of both standing and fallen dead wood yielding important microclimates and spatial complexity (Jenkins et al. 2004). Dead woody material provides critical habitat elements for a myriad of plant, animal, and microbial species such as refugia, foraging, recruitment, den/nest sites, and protection (Woodall and Nagel 2006).

Although the bulk of aboveground sequestered C in these systems is found in living trees and the litter layer, woody detritus in the form of snags, stumps, fine woody debris, and coarse woody debris account for, on average, 16% of the aboveground C pool in U.S. forests (Turner et al. 1995) and consideration of detrital biomass as a C pool is often absent from many studies and inventories (Bradford et al. 2009). Components within this pool may represent long-term sequestration as in large snags and coarse woody debris that may persist for over a century or short-term sequestration in fine woody debris that persists for only 1 to 10 years depending on the decay rate of the site (Jenkins et al. 2004, Fasth et al. 2011, Sain et al. 2012, Sutfin et al. 2016). Although fine woody debris accounts for on average ≤ 4% of aboveground C, due to more rapid decay rate compared to coarse woody debris, it may contribute up to three times the percentage of heterotrophic respiration (Fasth et al. 2011).

Accurately estimating aboveground sequestered C in forested ecosystems involves not only estimating living biomass, but detrital biomass as well (Sutfin et al. 2016). Aboveground detrital biomass includes duff, litter, and dead woody material consisting of materials usually classed as fine woody debris (FWD, < 7.5 cm diameter), coarse woody debris (CWD, > 7.5 cm in diameter), and standing dead wood (SDW, snags and stumps). It has been shown that dead woody material can account for 14 to 17% of aboveground C (Fahey et al. 2005, Woodall and Liknes 2008, Bradford et al. 2009). It has also been shown that old growth sites generally have a higher dead tree/live tree ratio and the unit volume of dead wood increases with productivity of the site (Spetich et al. 1999).

As southern bottomland forests are, in general, highly productive and the Congaree National Park (CONG) floodplain forest contains old growth areas or mature secondary growth, detrital biomass is likely a major contributor to aboveground sequestered C in this system. This in turn has carbon budget implications related to climate change. While FWD remains more balanced when using latitude as a proxy for increasing temperature, the decay rate of CWD increases substantially with decreasing latitude suggesting the liberation of C from CWD will accelerate with global warming and may potentially shift this biomass pool to a net CO_2 emitter (Woodall and Liknes 2008).

Comparing the volume, quantity, and species composition of standing and down dead wood to that of living trees may be used to analyze forest stand dynamics such as successional trends or species shifts due to environmental changes driven by disease and pathogens, climate change, pollution, hurricanes, floods, and urbanization (Woodall and Nagel 2006). Distribution, unit density, and mass of dead wood by species within decay class categories may provide additional insight into the temporal and spatial extent of mortality rate changes and community shifts (Sain et al. 2012). Of particular concern in forested wetlands such as that of the CONG floodplain are shifts in community composition via differential mortality and recruitment due to changes in water quality, sedimentation rates and flood regimes associated with land use and water level manipulation in rapidly developing watersheds (Jolley et al. 2010, Jones et al. 1994, Walls et al. 2005, Zimmerman et al. 2008).

RESEARCH OBJECTIVES

While human activities worldwide continue to stress water quality, interrupt watershed connectivity, and alter sediment loads and depositional characteristics, we lack sufficient knowledge to determine the impact of such disturbances on the growth, buffering capacity, and carbon budget of floodplain forests. It is probable many floodplain systems may be exceeding sedimentation thresholds which are impacting productivity and carbon balance and over time will lead to shifts in community structure and composition (Clewell and McAninch 1977, Galicki et al. 2002, Dufour and Piegay 2008). Bridgham et al. (2006) have suggested that the largest uncertainty regarding the role of North American wetlands in global carbon cycles involves sequestration by freshwater systems on mineral soils, a category that includes the ecosystem protected within CONG.

Our research objectives included: (i) describing community composition and structure of both live and dead wood to define community types across the floodplain elevation gradient, (ii) quantifying net aboveground primary productivity, (iii) determining litter decomposition rates and litter nutrient dynamics, (iv) calculating sequestered carbon in aboveground wood, and (v) synthesizing these data to qualitatively assess the stability of and possible shifts in community composition. Each objective was examined utilizing topographic position along the floodplain elevation gradient as a surrogate for both hydrology and sedimentation. Additionally, collected metrics were related to the size/age distribution of defined communities.

Execution of the objectives helps bridge the information gaps which preclude our understanding of how anthropogenic induced changes in hydrology and sedimentation may affect floodplain forests in general and within the CONG in particular. The scope of work completed contributes to our ability to discern past and anticipate future changes in forested floodplain resources related to the pressures on these systems created by the demands of ever expanding human populations.

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CHAPTER TWO

COMMUNITY STRUCTURE AND SPECIES COMPOSITION ACROSS AN ELEVATIONAL GRADIENT WITHIN A FLOODPLAIN FOREST OF THE CONGAREE RIVER, SOUTH CAROLINA, USA

Abstract. Floodplain forests offer services to society in the form of species diversity, wood production, and sequestration of carbon to offset rising atmospheric carbon dioxide, and buffering capacity critical to water quality. These services are dependent upon maintenance of hydrological connections and sedimentation dynamics of these systems which determine site specific heterogeneous microsite distributions leading to specific community structure and species composition. While human activities worldwide continue to stress water quality, interrupt watershed connectivity, and alter sediment loads and depositional characteristics, we lack sufficient knowledge to determine the impact of such disturbances on floodplain forest communities. It is probable many floodplain systems may be exceeding sedimentation thresholds which are impacting forest ecosystems, and over time, will lead to shifts in community structure and composition. Congaree National Park consists of a series of low relief fluvial landforms across the Congaree River floodplain representing gradients in sedimentation rates and inundation periodicity and depth. This study takes advantage of these gradients to help bridge information gaps which preclude our understanding of how anthropogenic induced changes in hydrology and sedimentation affect floodplain forests. Four 20x25 m plots, blocked by *a priori* perceived elevation differences, were established in 2010 along each of five roughly parallel transects with a spacing of approximately 60 m between transects and oriented perpendicular to the river channel. Trees (stems ≥ 10 cm DBH) were inventoried by species, measured, tagged, and mapped within each plot. Saplings (stems ≥ 1m in height with a DBH or BD < 10 cm) were inventoried by species, measured, tagged, and mapped within a 5x25 m subplot within each plot. The point intercept method was used to obtain woody species composition, percent cover, and community structure within 2 m of ground surface. Herbaceous species composition, percent cover, and frequency, along with the number of seedlings, were recorded within five 1-m square sampling quadrats along a 1x25 m belt transect. Densiometer data was collected at five points within each plot to determine canopy cover. PC-ORD: multivariate analysis of ecological communities was used for the majority of statistical tests and graphs.

Key words: non-metric multidimensional scaling; old-growth; bottomland hardwood forest; bald cypress swamp; Congaree National Park

INTRODUCTION

Of the original four million hectares of bottomland hardwood forests in the southern United States, approximately one million hectares remain. Due to species and size specific harvesting practices and the drastic increase in floodplain sedimentation rates related to agriculture and development, species composition and canopy structure of the remaining forest is often altered (Lockaby 2009). Forested floodplains and their associated wetlands function to both preserve water quality and buffer the effects of global warming via net sequestration of atmospheric carbon, but these functions may be degraded when hydrologic connections are severed or manipulated (Naiman et al. 2005, Noe and Hupp 2005). Paramount to these functions is sediment type and deposition rates which strongly influence the composition, succession, and structure of the floristic community of bottomland hardwood forests (Hodges 1997). Deposited material tends to have heterogeneous texture, mineralogy, and origin in major stream bottomlands of the coastal plain and, as such, are generally more fertile and productive (Hodges 1997). Lower piedmont and coastal river valleys of the southeast typically have active floodplains resulting in a distinct series of fluvial landforms which often differ in species composition, reflecting changes in historical deposition patterns (Wharton et al. 1982; Hodges 1997). Successional patterns may be interrupted or reversed by construction of dams which change site hydrology and alter rates and composition of deposited materials and reduce recruitment success from the seed bank (Hodges, 1997; Walls et al., 2005; Jensen et al., 2008).

Sedimentation rates in floodplain forests are variable, depending upon the nature of the upstream geology and watershed, intensity and periodicity of flooding, and anthropogenic activities. Material trapped by these forests can contribute to maintenance of water quality and include sediment, nutrients, pollutants, and organic matter (Noe and Hupp 2005). The amount of material trapped annually can be large. Hupp et al. (2008) estimated amounts at over 40 mm/yr in the Atchafalaya Basin in Louisiana with a mass of 6.7 Mg overall and 0.8 million Mg of the total organic matter. In the southeastern US, sediment deposition rates are highest in the coastal plain, and in systems with relatively high sediment loads, rates may range between 5-10 mm annually (Hupp 2000).

A complex mosaic of microsites defined by available soil oxygen due to differences in sedimentation and inundation is a common characteristic of floodplain forests. Species have differential response and specificity to microsite type (Broadfoot 1976, Hupp 2000). As a result, alteration of microsite distribution and physical characteristics via changes in sedimentation and hydrology will lead to species specific productivity responses and a shift in species composition (Ewing 1996, Oswalt and King 2005).

Much less information is available regarding sedimentation effects on forests as opposed to individual species. In south central Georgia, sedimentation rates as low as 0.03 cm/yr over a 25-year period have been associated with major alterations in structure of riparian forests along intermittent streams (Cavalcanti and Lockaby 2005, 2006, Lockaby et al. 2005, Jolley et al. 2010). These levels of accretion were linked to significant increases in overstory mortality.

While human activities worldwide continue to stress water quality, interrupt watershed connectivity, and alter sediment loads and depositional characteristics, we lack sufficient knowledge to determine the impact of such disturbances on the growth, buffering capacity, and carbon budget of floodplain forests. It is probable many floodplain systems may be exceeding sedimentation thresholds which are impacting productivity and carbon balance and over time will lead to shifts in community structure and composition (Clewell and McAninch 1977, Galicki et al. 2002, Dufour and Piegay 2008). Bridgham et al. (2006) have suggested that the largest uncertainty regarding the role of North American wetlands in global carbon cycles involves sequestration by freshwater systems on mineral soils, a category that includes the Congaree Swamp.

MATERIALS AND METHODS

The Congaree River begins at the confluence of the Broad and Saluda rivers near Columbia, South Carolina and ends at its confluence with the Wateree River to form the Santee River after flowing 85 river km. For most of its length, the Congaree River occupies a broad floodplain bounded on the north by a fluvial landscape and to the south by a steep bluff cut into upper coastal plain deposits (Shelley and Cohen 2010). The Congaree National Park (CONG) protects a vast, old growth floodplain forest in the lower Congaree River Valley (Figure 2.1) representing the last remaining major tract of mature bottomland hardwood forest in the southeastern United States (Gaddy et al. 1975, Shelley and Cohen

2010). Within the floodplain are spatially complex changes in elevation (generally < 75 cm) yielding areas which experience distinct flooding regimes, sedimentation processes and soil drainage characteristics. This results in a complex spatial array of forest types having distinct community structure and composition (Conner et al. 2002).

Communities within the CONG can generally be categorized as backswamps, transition flats, and natural levees based on a range of flood duration from temporary to semi-permanent (AIS 1998). In the proposed study area, the natural levee community is dominated by a canopy of sugarberry (*Celtis laevigata* Willd.), sweetgum (*Liquidambar styraciflua* L.), box elder (*Acer negundo* L.), and American elm (*Ulmus americana* L.) with pawpaw (*Asimina triloba* [L.] Dunal) and Chinese privet (*Ligustrum sinense* Lour.) common in the understory. The backswamp canopy is almost exclusively composed of baldcypress (*Taxodium distichum* [L.] Richard) with swamp cottonwood (*Populous heterophylla* L.) as a minor canopy element and water elm (*Planera aquatic* alter ex JF Gmelin) dominant in a sparse understory. The transitional flats contain elements of both the levee and backswamp communities with the addition of green ash (*Fraxinus pennsylvanica* Marshall), sycamore (*Platanus occidentalis* L.), red maple (*Acer rubrum* L.), overcup oak (*Quercus lyrata* Walter), and laurel oak (*Quercus laurifolia* Michaux) as canopy components with pawpaw and possumhaw (*Ilex decidua* Walter) most common in the understory (Allen et al., 2005).

The proposed study area consists of a mosaic of low relief fluvial landforms across the floodplain which experience differential periods of inundation and sedimentation. Adjacent to the river channel and scattered farther from the river are the highest elevation areas which include the active natural levee and relict levees. Scattered across the floodplain are intermediate flats of slightly lower elevation abutting the levee areas which experience intermediate inundation. The lowest areas experience seasonal to semi-permanent flooding and the study area is represented by a cypress backswamp which is part of a complex known locally as Butterfly Pond. A total of 20 data collection plots, blocked by *a priori* perceived elevation differences, were established in 2010 along five roughly parallel transects with a spacing of approximately 60 m between transects and oriented perpendicular to the river channel. Four 20x25 m plots (0.05 hectare) were established along each transect with the transect azimuth bisecting the short sides of the rectangular plot; one plot in each of four perceived *a priori* elevation zones. Subplots and transects were established within each plot to facilitate collection of various data discussed below (Figure 2). The plant nomenclature of Radford et al. (1968) was followed for all vegetation data collected in this study. Four letter codes (first two letters of genus and first two letters of specific epithet) were assigned to each species encountered in this study; a species list table is provided in Appendix 1.

Trees and saplings

Trees were defined as all stems ≥ 10 cm diameter at breast height (DBH) and were inventoried by species, measured, tagged, and mapped on a grid within each 20x25 m plot (each stem of multi-trunked individuals was inventoried as a separated stem for both trees and saplings (Megonigal et al. 1997)). Saplings (stems ≥ 1m in height with a DBH or basal diameter (BD) < 10 cm) were inventoried by species, measured, tagged, and mapped within a 5x25 m subplot within each plot. Stamped numerical aluminum tags were attached with an aluminum nail for stems > 5 cm DBH; diameter was measured just below the bottom of the tag. When trees had noticeable buttresses, the tag was placed 0.5 m above buttress taper (Zhao et al. 2006). Stems smaller than 5 cm DBH had the tag attached with a nylon cable tie to avoid splitting and, as a backup, a pin flag bearing the tag number was placed at the base of the stem. A dot of tree paint was placed on the smaller stems where the initial diameter measurement is taken so additional measurements are taken at the same place. During collection of initial diameter data, the following was noted: tag number; species; conditions such as broken top, dead top, hollow, etc.; tool used - caliper or tape; DBH or BD measured; and a description to insure measurements are repeatable (*e.g.*, fixed end of caliper placed under tag). These steps were taken to ensure consistency of repeated measurements of DBH.

Plant community composition and structure

A variety of techniques were employed to quantify and describe the species composition, species distribution, and plant community structure across the floodplain gradient of the study area. Using DBH data, basal area and stem density were calculated for all species of saplings and trees within each sample plot. Basal area was converted to m^2 per hectare. These data represented the canopy (tree) layer and sub-canopy (sapling) layer.

The point intercept method was used to obtain woody species composition, percent cover, and community structure within 2 m of the ground surface. This layer would traditionally be interpreted as the shrub layer; however, in the study area, there were very few species which are considered shrubs (exceptions include buttonbush (*Cephalanthus* *occidentalis* L.), parsley hawthorn (*Crataegus marshallii* Eggl.), spicebush (*Lindera benzoin* [L.] Blume), and Chinese privet; only Chinese privet was common; see Appendix 1 for a list of all species). Many of the species recorded were young saplings and woody vines. River cane (*Arundinaria gigantea* [Walter] Muhl.) was included with woody plants due to the plant's height and persistence of culms throughout the year. In each plot, one 25 m transect was established (Figure 2). A 2-m rod delineated by alternating colors into 4 height zones (0-0.5 m; 0.5-1.0 m; 1.0-1.5 m; 1.5-2.0 m) was dropped every 0.2 m for a total of 125 data collection points. Within each zone, plants touching the rod were identified and recorded. Percent cover for each plant in each height zone was calculated by number of hits/125*100. This data was collected in June 2010 after leaves were fully expanded, but before leaf loss due to drought stress or autumnal abscission.

Quadrat sampling was used to assess herbaceous species composition, percent cover, and frequency; the number of seedlings was also counted within the quadrats. A 1-m square sampling quadrat divided into twenty-five 400-cm² sub-grids was constructed and used to collect data at five stations per plot within the 1x25 m belt transect. Within the belt transect, quadrat stations were selected using random numbers from the 25 possible stations until five stations were established. Small sections of PVC pipe were driven into the ground at the corners to permanently mark quadrat stations. For each species, a count was made of how many sub-grids contain an individual of that species which is rooted within a sub-grid (this count was divided by 25 to produce a frequency). Using the sub-grids as a guide, percent cover was estimated for each herbaceous species occupying aerial space to a height of 2 m above the quadrat. Plants not rooted within the quadrat were also included in estimate of percent cover. Since southeastern forests tend to have both spring ephemerals and late emerging fall blooming plants, herbaceous quadrat data was collected three times (April, June, and September of 2011).

Canopy cover

Available light under a mature deciduous forest is important for the structure and composition of the understory and is related to recruitment of tree species able to take advantage of gaps created by overstory mortality. Percent canopy cover in each plot was determined using a spherical densiometer (Lemmon 1958, Korhonen et al. 2006). The densiometer was mounted on the top of a 1-m rod to maintain consistency of readings. Data was collected at five points along the four cardinal azimuths (plot center and the four corners, Figure 2.2) and averaged to obtain a mean value by plot. Data was collected four times: early spring during leaf expansion (March 2011), mid-summer after full leaf expansion (June 2011), mid-fall during the abscission period (October 2011), and during the winter after leaf fall (January 2012). Percent canopy cover was collected for analysis in relation to sapling density, herbaceous layer percent cover (< 0.5 m), and woody understory percent cover (0.0 – 2.0 m).

Data analysis

PC-ORD: multivariate analysis of ecological data (version 6.0, MjM Software Design, Gleneden Beach, Oregon; McCune and Mefford 2011) and JMP® Pro (Version 12.2.0, SAS Institute Inc., Cary, NC, 2015-2017) were used for statistical tests and graphs. Non-parametric multivariate techniques were employed to define community groups as they are well suited to data such as plant cover which often fails normality tests, contains many zero values, and exhibits discontinuous scales (McCune and Grace 2002). To test the hypothesis of no difference in variable means among community groups, one-way ANOVA was employed; multiple comparisons used the Tukey test (corrects for multiple comparisons). In cases where normality (Shapiro-Wilk W test) or equal variance (Brown-Forsythe test) assumptions on the residuals were not met at the $P = 0.05$ level, the data were subjected to the Kruskal Wallis test (rank sums); multiple comparisons following Kruskal Wallis test used Dunn's method for joint ranking (corrects for multiple comparisons). The ≤ sign is used in the results section when several pairwise comparisons are significant and only the largest P value is reported.

All plant species data was reduced to means by sample plot and then placed into several matrices. A master matrix contained all the data while additional matrices contained either a single value such as tree basal area or a combination of values such as tree basal area and sapling basal area. These served as main matrices for further analysis outlined below. PC-ORD produced values for species evenness, richness, and diversity indices from the raw data as outputs using the matrix row and column data summarization function. The row and column coefficients of variation (CV) and skew were examined for each matrix. Data adjustments were used to reduce CV and skew to levels that would have a small effect on the outcome of further analysis (McCune and Grace 2002). Outlier analysis was used first to find and remove, if necessary, plant species which are strong outliers (having a standard deviation > 2). Relativizations or transformations, which maintain the original zero values, were applied as needed following removal of outliers to reduce CV and skew.

Secondary matrices were constructed containing the categorical variables transect, perceived *a priori* elevation zones, and *post-hoc* cluster analysis group to test the hypothesis of no difference between categorical groups via the nonparametric tests multi-response permutation procedure when group sizes are unbalanced (MRPP; Mielke 1984) and permutation based multiple analysis of variance when group sizes are balanced (perMANOVA; Anderson 2001). Since the PC-ORD output for MRPP and perMANOVA does not correct for multiple comparisons, a sequential Bonferroni procedure correction (Rice 1989) was applied to multiple comparisons to maintain the experiment-wise error rate. These matrices also included both measured and calculated quantitative variables including: species richness, species evenness, Shannon-Wiener diversity index, and Simpson diversity index for infinite population; percent canopy cover; basal area of trees and saplings; percent cover for herbs and woody vegetation below 2 meters; plot elevation. Once all matrices were constructed, the Mantel test and partial Mantel test were used to test the hypothesis of no relationship between pairs of matrices and no contribution of a third matrix to the relationship between the other two matrices.

In order to define sample plots as ecologically significant groups (*i.e.,* not necessarily the *a priori* blocking by perceived elevation zone), hierarchical cluster analysis was used on each main matrix with flexible beta at a value of -0.250 as the linkage method. The pruning point to select the most ecologically significant grouping of sample plots for each dendrogram involved calculating the mean indicator species analysis P value across all species in each matrix and the proportion of the species having a significant indicator species value of $P > 0.10$ for all likely pruning points and choosing the point at which these values are optimal (Dufrene and Legendre 1997, McCune and Grace 2002). Indicator species analysis is a non-parametric technique to determine how each species characterizes a group of sample units based on relative species abundance, cover, or frequency.

To extract the most important relational variables from a large number of possibilities contributing to plant species composition and community structure, ordination using the non-metric multidimensional scaling (NMS) technique (Kruskal 1964, Mather 1976) was employed to distribute the 20 sample plots in plant species space. The program PC-ORD was used, employing the slow and thorough autopilot mode to yield the ordination(s) with the lowest stress which meet an instability criterion of 0.0001 and analysis of scree plot(s) to choose the number of dimensions. A Monte Carlo test of significance was used to determine the probability that a similar final stress could have been obtained by chance. Quantitative variables will be overlain as joint plots on the NMS ordination to examine correlation with the ordination axes. The percent of variation in the data represented by the ordination axes is calculated as 100*Pearson's r^2 correlating the distances between sample plots in the ordination with the distances in the original data (Peterson and McCune 2001). Correlation between the ordination and quantitative variables is calculated by PC-ORD as both Pearson's (r^2) and Kendall's (τ) correlation coefficients. The entire process was repeated many times for each possible main matrix to produce the most informative and stable solution.

During preliminary screening of the data set, it was discovered that there were substantial effects on statistical analyses due to covariation. The main source of this covariation could be attributed to the uneven inclusion of very large trees in some plots. It was desired that this covariation be built into the main matrix via column addition, thus allowing examination of real means and not adjusted means. A main matrix was constructed consisting of basal area within plot for each tree and sapling species and four additional columns which gave the percent of tree biomass within four DBH classes: > 25, 25-50, 50-75, and > 75 cm for each plot. This matrix produced the most stable solution and yielded an ordination maximizing the representation of variation within the data.

RESULTS

Classification of sample plots

The main matrix used to classify plots within community groups consisted of 20 rows (sample plots) and 29 columns (basal area of 16 tree species, 9 sapling species, and % tree dry mass within four DBH classes). After construction, all columns in the main matrix which had nonzero values for only one plot were deleted. The coefficient of variation (CV) for both row and columns were examined. The raw data in the main matrix exhibited a CV of 168% while the row value was 33%. Use of the distance measure Relative Sørensen applies relativization based on column total prior to analyses; therefore, no data transformations or relativizations were necessary as use of this distance measure reduces column CV to zero (McCune and Grace 2002). Outlier analysis showed that plot 10 was a very slight outlier at ~ 2.052 the standard deviation, but since the conventional cutoff is 2.0, the plot was retained. The resulting main matrix contained 20 rows and 29 columns; a good size to define plot groups. The relative Sørensen distance measure was used for all matrices in the following analyses unless otherwise indicated.

The cluster analysis dendrogram yielding the most ecologically significant grouping of sample plots based on plant species composition and DBH class is presented in Figure 2.3. The mean indicator species P value was minimized at 0.334 and the number of significant species indicator values (IV) was maximized at 14 (Table 2.1) when the tree was pruned at 45% information remaining to yield the four community groups shown in Figure 2.3. Community group names are based on species representing $\geq 12\%$ of tree basal area within the group.

Confirmation of differences in the four community groups derived from the cluster analysis was analyzed with perMANOVA and confirmed at a Bonferroni corrected level of $P < 0.0083$ (Table 2.2; $F = 11.8$; $P = 0.0002$; all pairwise comparisons significantly different ($P \leq 0.0064$)). Figure 2.4 illustrates a distinct difference in the *a priori* blocking by perceived elevation zone and the community groups defined via *post-hoc* cluster analysis. The *post-hoc* grouping of plots produced a much more stable solution indicating that small elevation differences are difficult to perceive and occur in a mosaic pattern with anastomosing boundaries rather than along clear gradients that can be neatly segregated along a group of roughly parallel transects.

Tree and sapling basal area data and DBH size classes were arranged along synthetic axes of sample plots in plant species space using NMS with relative Sørensen as the distance measure. The best solution was chosen by examining a scree plot of stress versus dimensionality and a plot of stress versus iteration number (Figure 2.5). There was little reduction in stress when increasing dimensionality past three axes and stress becomes flat at iteration 35 and remains stable with additional iterations. The result was a three-dimensional ordination representing 94.2% of the total variation with a final stress of 6.09, final instability < 10^{-5}, and a Monte Carlo probability of $p = 0.004$ that a similar final stress could have been obtained by chance (Figure 2.6). The Monte Carlo test of significance was executed with a random start, 250 runs of real data and 250 runs of randomized data, and the final solution was truncated at 61 iterations by the program PC-ORD using the slow and thorough autopilot mode. McCune and Grace (2002) state that one should strive for instability < 10^{-4} and that the final stress of the best solution for most ecological community data sets will fall between 10 and 20 with values less than 15 being quite satisfactory.

Figure 2.6 shows clear separation of the four community groups with each group occupying a distinct area within the ordination space defined by separation along one or more axes of the three-dimensional solution. Group 1 separates from group 2 along axis 3; from group 3 along axis 2; and from group 4 along axis 1. The space occupied by group 2 is separated from group 3 along axis 2 with minor separation along axis 3 while separation from group 4 is mostly along axis 1 with minor separation along both axes 2 and 3. Group 3 occupies a space differentiated from that of Group 4 along axes 1 and 2. Groups 2 and 3 are at the same elevation (means N = 5; 134.43 and 134.46 meters, respectfully) and are primarily separated by DBH size class differences rather than species composition.

The original, unmodified main matrix of species data was parsed out to create two separate matrices; one matrix contained only percent of total basal area occupied by each tree species by plots (20 plots by 18 species) and the second contained only percent basal area occupied by each sapling species by plot (20 plots by 16 species). The purpose of this was to use the Mantel Test to test the hypothesis of no relationship between the two matrices. The null hypothesis specifically is there is no relationship between tree and sapling species; a hypothesis important to succession. Raw data was used without modifications and Euclidean distance was used to calculate both matrices; the Monte Carlo randomization method was chosen to execute the Mantel Test. The result indicates there is no relationship between the tree and sapling layer (standardized Mantel statistic r = 0.075; P = 0.310).

Community group composition and structure

A second matrix containing the same data as the main matrix (basal area of 16 tree species, 9 sapling species, and % tree dry mass within four DBH classes) and mean plot elevation in meters was created and NMS was rerun so these values could be translated to correlation vectors and displayed as a joint plot (Figure 2.6; joint plot cutoff $r^2 \geq 0.250$). Correlation between the ordination axes and matrix components are calculated by PC-ORD as Pearson's (r^2) correlation coefficients and these values are used to elucidate which components contribute the most to ordination axes (Peterson and McCune 2001, Peck 2010). Mean elevation shows a very strong positive correlation with axis 1 (r^2 = 0.636). Percentage of tree mass within DBH size classes exhibits correlation values suggesting that all classes contribute to ordination axes. DBH classes >25 cm, 50-75 cm, and >75 cm all had significant indicator values ($P \leq 0.0141$; Table 2.1). Percentage in trees < 25 cm is negatively correlated with axis 2 (r^2 = 0.477); 25-50 cm class is also negatively correlated with axis 2 (r^2 = 0.762); 50-75 cm class is positively correlated with axes 1 and 3 (r^2 = 0.273; r^2 = 0.384; respectively); and percentage in trees > 75 cm is positively correlated with axis 2 (r^2 = 0.326).

Box elder tree basal area is negatively correlated with axis 2 (r^2 = 0.309) and sugarberry tree basal area is positively correlated with axis 1(r^2 = 0.310); both species most common in community group 3. Green ash and green haw (*Crataegus marshallii* Eggl.) trees are negatively correlated with axis 3 (r^2 = 0.310; r^2 = 0.625; respectively); green haw tree occurs only within group 1 and green ash tree is most common within community group 1. Possumhaw tree only occurs in community groups 1 and 3 and is negatively correlated with axis 2 (r^2 = 0.342). Sweetgum tree is positively correlated with both axis 1 and 2 (r^2 = 0.268; r^2 = 0.424; respectively) and is present in all community groups, but most common in groups 1 and 2. Water elm tree is negatively correlated with axis one (r^2 = 0.550) and is present in community groups 1 and 4. Swamp cottonwood tree is only present within community group 4 and is negatively correlated with axis 1 (r^2 = 0.250). Baldcypress tree shows a very strong negative correlation with axis 1 (r^2 = 0.820) and is prevalent in community group 4 and a minor component in group 1. Saplings of green ash only occur in community group 4 and is negatively correlated with axis 1 (r^2 = 0.304).

Community group 1 occurs at an intermediate mean elevation compared to other groups and tree biomass is dominated by large trees having a DBH between 25-50 cm and greater than 75 cm (21.5% and 50.7% of biomass; respectfully; Table 2.3). Significant indicator species within the tree layer (Tables 2.1 and 2.3) include green ash and green haw (*P* = 0.0081 and 0.037; respectively). Sugarberry is the only significant indicator species in the sapling layer (*P* = 0.0949; Tables 2.1 and 2.3). There were no significant indicator species in either the woody understory or herbaceous strata (Table 2.3; Appendices 2 and 3). The tree layer of community group 1 is comprised of fifteen species; more than the other three groups. Based on the percent of total tree basal area, the canopy is dominated by green ash, sweetgum, and sugarberry (59.5% collectively) with subordinate species overcup oak and bald cypress accounting for 16.9% of the total tree basal area (Table 2.3; Appendix 4). The sapling layer is moderate and consists of six species. Based on the percent of total sapling basal area, the sub-canopy is dominated by pawpaw and possumhaw (75.4% collectively) with subordinate species water elm and sweetgum representing 6.8% of total sapling basal area (Table 2.3; Appendix 4). The woody understory layer is relatively sparse with 17 species contacted during point intercept readings. The highest percentage of point intercept hits occurred in the 0-0.5 meter increment (20.3%) and the cumulative point intercept value across all increments was 35.4% (Table 2.3; Appendix 5). Based on cumulative percent of positive point intercept intersections the woody understory is dominated by pawpaw, roundleaf greenbriar (*Smilax rotundifolia* L.), cane (*Arundinaria gigantea* [Walter] Muhl.), cross vine (*Anisostichus capreolata* [L.] Bureau), and American elm (collectively 56.1%) with the less common species poison ivy (*Toxicodendron radicans* L.), possumhaw, box elder, and green ash accounting for 24.3% of positive point intercept intersections (Table 2.3; Appendix 5). The herbaceous layer is of moderate density with a total of 24 species recorded within the sampling quadrats over three sampling periods and the maximum herbaceous cover value of 13.5% was recorded September 2011 (Tables 2.3 and 2.4; Appendix 6). Species dominant in the herbaceous layer based on maximum percent cover by species included Gray's sedge (*Carex grayi* Carey), richwoods sedge (*Carex oligocarpa* Schkuhr), and wood rush (*Luzula multiflora* Retzius [Lej]) (64.6% collectively) with the subordinate taxa squarrose sedge (*Carex squarrosa* L.), yellow fumewort (*Corydalis flavula* [Raf.] DC), and false nettle (*Boehmeria cylindrical* Swartz) contributing an additional 16.4% of maximum percent cover (Tables 2.3 and 2.4; Appendix 6).

Community group 2 occurs at the high end of elevation compared to groups 1 and 4 and tree biomass is dominated by trees having a DBH between greater than 50 cm (Table 2.3). Sweetgum is the sole significant indicator species within the tree layer and pawpaw is the only significant indicator species in the sapling layer (Tables 2.1 and 2.3; $P = 0.0004$ and 0.0757; respectively). There were no significant indicator species in the woody understory stratum (Table 2.3; Appendix 2). Yellow fumewort (*Corydalis flavula* [Raf.] DC.), bedstraw (*Galium aparine* L.), and green dragon (*Arisaema dracontium* [L.] Schott) were significant indicator species in the herbaceous layer (Table 2.3; Appendix 3; $P =$ 0.0671, 0.0327, and 0.0615; respectively). The tree layer of community group 2 is comprised of ten species. Based on the percent of total tree basal area, the canopy is dominated by sweetgum (71.2%) with subordinate species American elm, sugarberry, box elder, and sycamore accounting for 22.2% of the total tree basal area (Table 2.3; Appendix 4). The sapling layer is rather dense and consists of nine species; more than the other three groups. Based on the percent of total sapling basal area, the sub-canopy is dominated by pawpaw (67.5%) with subordinate species laurel oak, American holly (*Ilex opaca* Aiton), sugarberry, and box elder representing 24.5% of total sapling basal area (Table 2.3; Appendix 4). The woody understory layer is dense with 17 species contacted during point intercept readings. The highest percentage of point intercept hits occurred in the 0-0.5 m increment (63.0%) and the cumulative point intercept value across all increments was

122.64% (Table 2.3; Appendix 5). Based on cumulative percent of positive point intercept intersections the woody understory is dominated by cane, pawpaw, and cross vine (collectively 71.1%) with the less common species poison ivy, Chinese privet, sweetgum, and box elder accounting for 18.8% of positive point intercept intersections (Table 2.3; Appendix 5). The herbaceous layer is of moderate density with a total of 17 species recorded within the sampling quadrats over three sampling periods and the maximum herbaceous cover value of 13.0% was recorded April 2011 (Tables 2.3 and 2.4; Appendix 6). Species dominant in the herbaceous layer based on maximum percent cover by species included Gray's sedge, richwoods sedge, yellow fumewort, and wood rush (77.0% collectively) with the subordinate taxa wild chervil (*Chaerophyllum procumbens* L. [Crantz]), bedstraw, baby blue eyes (*Nemophila microcalyx* [Nuttall] F & M), and green dragon contributing an additional 16.3% of maximum percent cover (Tables 2.3 and 2.4; Appendix 6).

Community group 3 occurs at the high end of elevation compared to groups 1 and 4 and tree biomass is dominated by trees having a DBH between 25-75 cm (Table 2.3). Sugarberry is the sole significant indicator species within the tree layer and sweetgum is the only significant indicator species in the sapling layer (Tables 2.1 and 2.3; $P = 0.0998$ and 0.0007; respectively). Within the woody understory stratum, the exotic species Chinese privet was the sole significant indicator species (Table 2.3; Appendix 2; $P = 0.0344$). Butterweed (*Senecio glabellus* Poiret) was the only significant indicator species in the herbaceous layer (Table 2.3; Appendix 3; $P = 0.0998$). The tree layer of community group 3 is comprised of ten species. Based on the percent of total tree basal area, the canopy is dominated by Sugarberry, box elder, and sweetgum (66.6% collectively) with subordinate species American elm, laurel oak, and green ash accounting for 20.7% of the total tree basal area (Table 2.3; Appendix 4). The sapling layer is dense and consists of five species. Based on the percent of total sapling basal area, the sub-canopy is dominated by pawpaw, the exotic shrub Chinese privet, and possumhaw (95.9% collectively) with minor species American elm and sycamore representing the remaining 4.1% of total sapling basal area (Table 2.3; Appendix 4). The woody understory layer is dense with 13 species contacted during point intercept readings. The highest percentage of point intercept hits occurred within the 0-0.5 m increment (38.7%) and the cumulative point intercept value across all increments was 100.3% (Table 2.3; Appendix 5). Based on cumulative percent of positive point intercept intersections the woody understory is dominated by cane, pawpaw, Chinese privet, and cross vine (collectively 81.3%) with the less common species muscadine grape (*Vitis rotundifolia* Michaux), Virginia creeper (*Parthenocissus quinquefolia* L. [Planchon]), and box elder accounting for 12.1% of positive point intercept intersections (Table 2.3; Appendix 5). The herbaceous layer is of moderate density with a total of 21 species recorded within the sampling quadrats over three sampling periods and the maximum herbaceous cover value of 15.9% was recorded April 2011 (Tables 2.3 and 2.4; Appendix 6). Species dominant in the herbaceous layer based on maximum percent cover by species included the exotic species Japanese stilt-grass (*Microstegium vimineum* [Trinius] A. Camus.) (exotic), richwoods sedge, Gray's sedge, and wood rush (72.8% collectively) with the subordinate taxa autumn bluegrass (*Poa autumnalis* Muhl ex. Ell.), yellow fumewort, and butterweed contributing an additional 17.2% of maximum percent cover (Tables 2.3 and 2.4; Appendix 6).

Community group 4 occurs at the lowest mean elevation compared to other groups and tree biomass is dominated by trees having a DBH between 25-75 cm (Table 2.3). Significant indicator species within the tree layer (Tables 2.1 and 2.3) include bald cypress, water elm, and swamp cottonwood ($P = 0.0003$, 0.0005, and 0.0338; respectively). Water elm is the only significant indicator species in the sapling layer ($P = 0.1008$; Tables 2.1 and 2.3). Within the woody understory stratum, the species, green ash, water elm, and swamp cottonwood were significant indicator species (Table 2.3; Appendix 2; $P \leq 0.0220$). Rice cutgrass (*Leersia oryzoides* [L.] Swartz), Savannah panic grass (*Panicum gymnocarpon* Ell.), false nettle (*Boehmeria cylindrical* Swartz), bottlebrush sedge (*Carex comosa* Boott), Frank's sedge (*Carex frankii* Kunth), swamp wood reed (*Cinna arundinacea* L.), and water willow (*Justicia ovata* [Walter] Lindau) were significant indicator species in the herbaceous layer (Table 2.3; Appendix 3; $P \leq 0.0658$). The tree layer of community group 4 is comprised of nine species. Based on the percent of total tree basal area, the canopy is dominated by bald cypress (91.7%) with subordinate species water elm, swamp cottonwood, sweetgum, and red maple accounting for 7.6% of the total tree basal area (Table 2.3; Appendix 4). The sapling layer is sparse and consists of seven species. Based on the percent of total sapling basal area, the sub-canopy is dominated by water elm and possumhaw (77.0% collectively) with minor species bald cypress, buttonbush, and laurel oak representing the remaining 21.1% of total sapling basal area (Table 2.3; Appendix 4). The woody understory layer is sparse with 14 species contacted during point intercept readings. The highest percentage of point intercept hits occurred within the 0-0.5 meter increment (16.5%) and the cumulative point intercept value across all increments was 25.8% (Table 2.3; Appendix 5). Based on cumulative percent of positive point intercept intersections the woody understory is dominated by green ash, water elm, and red maple (collectively 67.7%) with the less common species swamp cottonwood, trumpet vine (*Campsis radicans* [L.] Seemann), and possumhaw accounting for 19.9% of positive point intercept intersections (Table 2.3; Appendix 5). The herbaceous layer is of moderate density with a total of 23 species recorded within the sampling quadrats over three sampling periods and the maximum herbaceous cover value of 19.1% was recorded September 2011 (Tables 2.3 and 2.4; Appendix 6). Species dominant in the herbaceous layer based on maximum percent cover by species included rice cutgrass, Savannah panic grass, false nettle, bottlebrush sedge, and Frank's sedge (72.5% collectively) with the subordinate taxa Gray's sedge (*Carex grayi* Carey), swamp wood reed, lizard's tail (*Saururus cernuus* L.), and water willow contributing an additional 18.2% of maximum percent cover (Tables 2.3 and 2.4; Appendix 6).

Analyses of quantitative variables among community groups

Quantitative variables, both measured and calculated, as factors were subjected to analysis of variance (ANOVA or Kruskal-Wallis test) among levels of community group (Tables 2.4 and 2.5). Herbaceous percent cover, neither temporal readings nor annual means, differed significantly among community groups due to excessive variation among plots within community groups (Table 2.4). Seedling density expressed as the number of seedlings counted per square meter in community group 4 (36.6 seedlings/m^2) was significantly greater compared to all other groups ($F_{3, 16} = 7.94$, $P \leq 0.007$; Table 2.4). Significant differences in point intercept data were present for the woody understory from 0-2.0 m. Cumulative percent point intercept positive intersections across all increments were significantly greater in community groups 2 and 3 (122.72 and 100.32% respectively; maximum possible 400%) compared to groups 1 and 4 (35.36 and 25.73% respectively; $F_{3, 16} = 8.08$, $P \leq 0.047$; Table 2.4). Community group 2 had significantly greater percent positive intersections within the increments 0-0.5 and 0.5-1.0 meters compared to groups 1 and 4 ($F_{3, 16} \geq 10.84$, $P \leq 0.003$ and $H_{0.05, 3} = 10.84$; $P \leq 0.049$, respectively; Table 2.4). Community group 2 was also significantly greater in the 1.0-1.5 m increment compared to group 4 ($F_{3, 16} = 3.69$, $P \leq 0.049$; Table 2.4). Positive intersections within the 1.5-2.0 m increment was greatest in community group 3 and significantly greater than the intersections recorded in groups 1 and 4 ($F_{3, 16} = 3.69$, $P \leq 0.049$; Table 2.4). The number of saplings per hectare was significantly greater in community groups 2 and 3 (2800 and 2480, respectively) compared to a value of 368 in group 4 ($F_{3, 16} = 6.18$, $P \leq 0.024$; Table 2.4). Sapling basal area was significantly greater in community group 3 at 3.77 m²/ha compared to groups 1 and 4 (1.67 and 0.44 m²/ha, respectively) and group 2 (2.94) was significantly greater than group 4 ($F_{3, 16} = 7.67$, $P \leq 0.048$; Table 2.4).

Tree density expressed as number of trees per hectare was greatest in community group 4 (504) which was significantly greater than the density in groups 2 and 3 (328 and 320, respectively; $F_{3, 16} = 4.56$, $P \leq 0.030$; Table 2.4). Tree basal area was significantly greater in community group 4 at 63.70 m²/hectare compared to groups 1 and 3 (36.37 and 20.61 m²/hectare, respectively; $F_{3, 16} = 7.20$, $P \leq 0.047$; Table 2.4). The percentage of trees within the < 25 cm DBH size class for each community group was 60.6%, 58.0%, 58.2%, and 37.3%, respectively (Appendix 4). The percent of total tree biomass within this DBH class was significantly greater for community group 3 compared to all other groups ($F_{3,16} = 4.10$, $P \leq 0.049$; Table 2.4). The percentage of trees within the 25-50 cm DBH size class for each community group was 26.6%, 17.3%, 34.2%, and 34.9%, respectively (Appendix 4). Community group 3 has a significantly greater percent of total tree biomass within this DBH size class compared to groups 1 and 2 and group 4 was significantly greater than group 2 ($F_{3,16} = 10.39$, $P \leq 0.048$; Table 2.4). The percentage of trees within the 50-75 cm DBH size class for each community group was 6.4%, 17.3%, 7.6%, and 26.2%, respectively (Appendix 4). Community groups 4 and 2 have percent total tree biomass values within this DBH size class significantly greater than group 1 and values considerably greater, but not significant, compared to that of group 3 ($F_{3,16} = 7.20$, $P \leq 0.048$; Table 2.4). The percentage of trees within the > 75 cm DBH size class for each community group was 6.4%, 7.4%, 0.0%, and 1.6%, respectively (Appendix 4). The percent of total tree biomass within this DBH class was significantly greater for community group 1 compared to groups 4 and 3 ($F_{3,16} = 6.42$, $P \leq 0.018$; Table 2.4).

Sample plot elevation in meters above sea level based on the mean values of plots within each group showed significant differences (elevation data provided by Hupp, 2013). Mean elevations for each community group were 133.77, 134.43, 134.46, and 132.94 m, respectively (Table 2.4). Elevations of community groups 3 and 4 were significantly greater compared to groups 1 and 4 and group 1 was significantly greater than group 4 ($F_{3,16} = 30.33$, $P \leq 0.012$; Table 2.4). The values of mean percent canopy opening throughout a year for each community group were 10.77%, 11.63%, 12.38%, and 8.81%, respectively; values for community groups 3 and 2 were significantly greater than group 4 ($H_{0.05,\,3}$ = 10.55, $P \leq 0.045$; Table 2.4). Spring percent canopy opening was greatest for community group 2 which was significantly greater than group 4 ($H_{0.05,\,3}$ = 11.08, $P \leq 0.011$; Table 2.4). Percent canopy opening for the summer and fall readings did not differ significantly among community groups (Table 2.4). Winter percent canopy opening values for community groups 3 and 2 were significantly greater than group 4 ($H_{0.05,\,3}$ = 9.96, $P \leq$ 0.045; Table 2.4).

Analyses of calculated variables among community groups

Herbaceous layer species richness and species evenness did not differ significantly among community groups, but diversity indices did differ significantly (Table 2.5). Community group 4 had a significantly higher Shannon-Wiener Index compared to group 2 ($F_{3,\,16}$ = 3.94, $P \leq 0.029$; Table 2.5) and the Simpson Diversity Index was significantly greater for community group 4 compared to groups 1 and 2 ($H_{0.05,\,3}$ = 8.70, $P \leq 0.039$; Table 2.5). The woody understory layer species evenness and diversity indices did not differ significantly among community groups (Table 2.5). Species richness in the woody understory stratum was significantly greater for community group 2 compared to groups 1 and 4 ($F_{3,\,16}$ = 5.18, $P \leq 0.028$; Table 2.5). Community groups did not differ significantly for species richness, species evenness, or diversity indices in the sapling layer (Table 2.5). Tree species richness was highest in community group 1 but did not differ significantly from the other groups (Table 2.5). Tree species evenness was significantly greater in community groups 1 and 3 compared to group 4 ($F_{3,\,16}$ = 10.17, $P \leq 0.0012$; Table 2.5).

Tree diversity as defined by the Shannon-Wiener Index was significantly greater for community group 1 compared to groups 2 and 4 and community groups 2 and 3 were significantly greater than group 4 ($F_{3,\,16} = 13.64$, $P \leq 0.048$; Table 2.5). Tree diversity as defined by the Simpson Diversity Index was significantly greater for community groups 1 and 3 compared to group 4; group 1 was significantly greater than groups 2 and 4; and group 2 was significantly greater than group 4 ($F_{3,\,16} = 17.16$, $P \leq 0.017$; Table 2.5).

Herbaceous percent cover was partitioned into percentages of the total based on categories of life form/structure (fern, forb, grass, sedges/rushes) and life history/duration (annual and perennial; one species that is listed as either annual or biennial, CAPE - *Cardamine pensylvanica*, was included within the annual category). All community groups showed a higher percent cover by perennials compared to annuals with the higher elevation groups 2 and 3 (64.6%, 62.4%, respectively) having a lower percent cover by perennials compared to intermediate elevation group 1 and lowest elevation group 4 (86.8%, 83.1%, respectively; Table 2.6). Ferns were a minor component of herbaceous cover across the study area and no ferns were recorded in community group 1. Ferns made a minimal contribution of 0.16% within community group 3 and represented a slightly greater contribution to herbaceous cover in groups 2 and 4 (1.69% and 1.59%, respectively; Table 2.6).

The percentage of herbaceous cover represented by forbs was greatest in community group 2 at 38.8% with fairly similar lower values in groups 1, 2 and 3 (19.7%, 15.8%, and 24.2%, respectively; Table 2.6). There was high variability in the percentage of herbaceous cover represented by grasses with no grass species recorded in community group 2 and a minor contribution by grasses of 7.6% in group 1. Grasses were the highest percent cover category in community group 4 at 38.1% and were a major component of herbaceous cover in group 3 at 34.9% (Table 2.6). Sedges/rushes were the highest category of herbaceous percent cover in community group 1 (72.6%), community group 2 (59.5%), and community group 3 (49.2%). Sedges/rushes were a major component of herbaceous coverage in community group 4 as well (36.1%); only slightly less than the percent cover of grasses (Table 2.6).

Two invasive plant species were recorded in this study. Japanese stilt-grass accounted for 31% of the herbaceous cover in community group 3 while accounting for only 0.2% cover in group 1 and no cover in groups 2 and 4. Likewise, Chinese privet followed the same gradient, accounting for 31% of the sapling basal area within community group 3 while being absent from groups 1 and 4 and accounting for only 1.6% of sapling basal area in group 2. Percent positive point intercept data for Chinese privet was also greatest in community group 3 at 18.3%, while recorded values were 5.0% in group 2, 0.9% in group 1, and zero in group 4.

DBH was recorded for four years in this study; concurrently with measurement of DBH, notes were taken on major tree damage (broken top, major limb loss, bent top, blow downs, broken bole, etc.). Over the study period major damage was recorded for 32.9% of the trees in community group 3, 18.8% of trees in group 2, 13.7% of trees in group 1, and only 3.2% in group 4. Approximately half the damage occurred to trees prior to initiation of this study and approximately 40% occurred during a winter ice storm occurring between the 2013 and 2014 DBH measurements.

DISCUSSION

The study area was located on a major alluvial floodplain (often called bottomland forests) associated with the Congaree River located at the interface of the lower piedmont and coastal plain and is predominantly forested except following major natural disturbances or anthropogenic activities (Messina and Conner 1998). The area is characterized by a wide floodplain with diverse topographic areas, which despite low relief, experience differential hydroperiods via overbank and backwater flooding (Sharitz and Mitsch 1993, Kellison et al. 1998). Backwater flooding can occur via channels known locally as "guts" which connect levee breeches to backwater swamps, thus allowing flooding of these swamps at flow levels below bank full (Shelley and Cohen 2010). The backwater swamp areas within the study area may be inundated for a majority of the year or may be free of standing water for much of the year, depending on annual fluctuations in rainfall amounts and timing (Sharitz and Mitsch 1993, Conner and Buford 1998).

In this study community groups were established *post hoc* based on numerous recorded community metrics and variables using ordination and Indicator Species Analyses to take all these parameters into consideration and define the most meaningful ecological groupings. Differences in elevation and the associated differences in the frequency, duration, and intensity of flooding in conjunction with tree species composition were the defining gradients separating communities with additional refinement of communities defined by tree size classes. Community groups 2 and 3 were mixed bottomland hardwood forests located at higher elevations on the active natural levee and on remnant levees separated from the active levee by intervening intermediate elevation flats. Flooding occurs during overbank flooding, is of relatively short duration, and of limited depth. Canopy species composition in these two communities consists of facultative species and is very similar with differences in the proportion of the canopy represented by a given species. These groups are separated in the analyses by the size class of trees with group 2 having 24.7% of trees > 50 cm DBH and group 3 with only 7.6% of trees this large. Community group 4 is a backwater swamp located in two adjoining sloughs representing abandoned channel meanders with a canopy of obligate species dominated by bald cypress at 91.7% of the tree layer. Flooding occurs via overbank and backwater flooding via "gut" channels with seasonal interaction with ground water. Duration of inundation is variable depending on amount and seasonality of rainfall, may experience several periods of inundation and dry down in a single year, and has an extended inundation maximum depth of 0.6 to 0.9 m. However, water marks on tree trunks indicate pulse inundation depths of 1.8 to 2.4 m did occur. The herbaceous layer in this community is more diverse and species rich compared to the other groups containing mostly obligate species capable of enduring an extended period of inundation. Community group 1 occupies an intermediate elevation as intervening flats located between the active levee and relict levees. Species composition is a mix of facultative, facultative wet, and obligate species with a greater preponderance of facultative wet tree species compared to community groups 2 and 3. Due to the mix of species and a position intermediate in hydrologic regime, this community exhibits higher tree richness, evenness, and diversity compared to the other community groups. Flooding in this community is intermediate in frequency and duration experiencing overbank flooding with occasional interaction with groundwater and receipt of water via backwater flooding. Extended inundation periods have a maximum depth of a 0.05 to 0.3 m; however, water marks on tree trunks indicate pulse inundation depths of 0.9 to 1.5 m do occur.

The reason for the significant differences in tree size classes among community groups defined in this study cannot be answered with confidence. Stochastic variability exists in systems both disturbed, and undisturbed. Chance alone may be responsible, a portion of the reason, or in combination with an inadequate number of sample plots. Other contributing factors may be historical patterns created by natural disturbances such as Hurricane Hugo or by historic and/or continuing patterns induced by anthropogenic disturbances such as water level controls, shifts in the fire regime, or selective logging.

Putz and Sharitz (1991) surveyed canopy tree damage in the Congaree Swamp following Hurricane Hugo. Hurricanes, tornados, ice storms, and thunderstorm downdrafts can result in wind throw to shallow rooted wetland trees or cause other damage such as bole breakage or loss of major limbs. They found that bald cypress in the backswamp were not nearly as damaged by the hurricane as species occurring in other portions of the floodplain. Our observations are in agreement with those of Putz and Sharitz (1991) as to the resistance of bald cypress to weather related damage. Our observations also indicate that the percentage of trees damaged was inversely related to the percent of trees within the community having a DBH ≥ 50 cm suggesting that a more even aged stand may be more resilient than a mixed aged stand to wind and ice damage.

It is well known that invasive species can alter community composition and structure as well as the fire regime. Invasions can alter ecosystem processes on a large scale changing the functions and degrading values to humans (Ellis 2011). The introduced animal species nutria (*Myocastor coypus*) and feral pigs (*Sus scrofa*) change regeneration dynamics by causing significant seedling mortality through direct predation. Pigs also cause mortality and disrupt microsite recruitment refuges indirectly while rooting (Conner and Buford 1998, Mayer et al. 2000). Feral pigs are common in the study area, were often sighted during field work, and excessive soil disturbance causing very high seedling mortality was observed related to rooting associated with foraging. We recorded the percent of the soil disturbed by feral pigs on three occasions using the herbaceous cover/seedling count quadrats (July, 2012, October, 2012, June, 2013). The mean percent feral pig disturbance was 60.3% in community group 4, 9.3% in group 1, 5.7% in group 2, and 3.5% in group 3; suggesting the pigs had a strong foraging preference along a hydroperiod gradient and their activity is likely to affect succession patterns over time, particularly in the backswamp.

Although spread of exotic plant species is often thought of in terms of displacing native species, many exotic species can alter the fire regime; something rarely thought of on floodplains. The shift in fire regime can alter species interactions, composition, structure, and resource availability (D’Antonio and Vitousek 1992, Dwire and Kauffman 2003). Catford et al. (2011) demonstrated that invasive species cover increased in fluvial wetlands with reduction in peak flow. The work suggests periodic management of release volumes to amplify seasonal high flows could be an important tool to control invasive species.

Two rapidly expanding invasive species in alluvial floodplains are Japanese stilt-grass and Chinese privet. Both species were recorded in the study area and are capable of invading both disturbed and intact floodplains and seem more prevalent where sedimentation rates have decreased due to changes in the hydrologic regime (Kellison et al. 1998). Chinese privet is shade tolerant, exhibits rapid growth, and resprouts vigorously after fire. Areas infested by Chinese privet usually shift the fire regime from low severity to mixed severity due to patchy distribution and role as a ladder fuel, especially in habitats such as fluvial forested wetlands where the shrub stratum is normally very sparse (Munger 2003, Sutter et al. 2011, this study). Restoration of the hydrologic regime is likely to both eliminate an infestation and prevent subsequent establishment (Munger 2003). Japanese stilt-grass can form dense monospecific stands in forested wetlands where natural herbaceous cover is low to moderate (Barden 1987, D'Antonio and Vitousek 1992). The annual grass produces abundant litter which decays slowly, is capable of producing a second annual cohort from seed after fire, and alters pre-invasion fire regimes, especially during extended drought in mesic systems (Barden 1987, Fryer 2011). Although the species has a high silica content, ignition and fire spread can occur under a wider range of conditions compared to litter and fine woody debris because stilt-grass surface/volume ratio promotes rapid drying and the packing characteristics of dead grass improves oxygen availability (Fryer 2011). Both species are associated most strongly with community group 3 in this study suggesting a preference for both higher elevation locations on the floodplain and areas where the majority of the trees are less than 50 cm DBH (mixed age stand and higher end of percent canopy opening). Reduced flooding events due to flow manipulation on the Congaree River have likely opened a window for establishment and spread of these exotic species.

Succession in these systems may be punctuated and rapid following disturbances such as logging, fire, hurricanes, etc., but are generally slow as the mosaic of habitats change spatially and temporally as the river continually reworks the floodplain (Conner and Buford 1998). Without major disturbances, stands can persist for centuries before canopy trees begin to decline and die (Hodges 1997). Evidence suggests fluvial forested wetlands will be more productive and support greater species diversity when punctuated and interactive disturbances augment the habitat heterogeneity created by long term fluvial processes (Frost 1987, Conner et al. 1989, Myers and Van Lear 1998, Gagnon 2009). Construction of levees, channelization/dredging, and ditching to drain wetlands within the floodplain are practiced to confine water to the channel and expedite its movement downstream or to facilitate agriculture/forestry. Changes in community composition and structure result, however it may be decades or centuries before the transition from wetland obligates such as water tupelo and bald cypress to facultative species such red maple becomes apparent.

Successional patterns may be interrupted or reversed by construction of dams which change site hydrology and alter rates and composition of deposited materials and reduce recruitment success from the seed bank (Hodges 1997, Walls et al., 2005, Jensen et al. 2008). Flood control levees and dam operations deprive the floodplain of flood born sediments and nutrients resulting in decreased productivity and subsidence rates exceeding sedimentation rates. Water depth may then become too deep in certain stands for tree survival and in others the selective pressure of flooding is diminished allowing generalists and exotic species to invade the system (Conner and Buford 1998, Penland and Ramsey 1990, Ernst and Brooks 2003, Catford et al. 2011). Although changes in hydrology may not be exceedingly detrimental to the present community, those changes will shift the pool of potential recruits when succession is reset by disturbance. While much research relates regeneration to fire, comparatively little work addresses the importance of hydrology to regeneration.

The present extent of flow control has reduced or nearly eliminated both frequency and duration of flooding to higher elevation flats which were once inundated via overland flow. Overland flow is often cut off from backswamps, leaving only backwater flooding contributing to inundation. The extent of modification to the hydrology of major alluvial floodplains is immense. For example, 47 dams existed in the Santee River watershed by 1955 (Kellison et al. 1998). Dam release is often managed so as to keep impoundment levels as consistent as possible, leaving the downstream floodplain drier when precipitation is low and wetter when precipitation is high. The normal cycle of inundation and dry down is thus altered, leading to increased seedling and sapling mortality, decreased recruitment, decline in the overstory, and a shift in community composition and structure (Kellison et al. 1998). Results of this study showed little relation between tree and sapling layer matrices raising questions about successional patterns in this system and suggesting manipulations to hydrology and sedimentation may be responsible for an influx of exotic species and may have changed successional patterns (Oswalt and King 2005, Lockaby 2009).

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Table 2.1. Indicator Species Analysis results for main matrix of tree, sapling, and DBH size class data.

Species Code/stratum	Cluster Group with max IV	Observed Indicator Value (IV)	IV from randomized groups		p *
			Mean	SD	
ACNE/tree	3	44.8	31.2	11.14	0.131
ACRU/tree	2	18.3	29.3	10.85	0.889
ASTR/tree	2	18.4	23.8	11.03	0.762
CAAQ/tree	3	26.4	20.7	11.75	0.387
CELA/tree	3	43.1	32.5	7.91	***0.099***
CRVI/tree	1	60.0	20.0	12.17	***0.037***
FRPE/tree	1	67.6	29.1	11.93	***0.008***
ILDE/tree	3	28.1	24.9	12.27	0.349
LIST/tree	2	74.2	35.8	10.01	***0.0004***
PLAQ/tree	4	92.6	26.0	11.68	***0.0005***
PLOC/tree	1	12.0	21.4	12.55	1.000
POHE/tree	4	60.0	20.7	12.45	***0.034***
QULA/tree	3	19.3	29.6	13.00	0.885
QULY/tree	3	19.6	28.1	11.24	1.000
TADI/tree	4	95.4	26.6	11.31	***0.0003***
ULAM/tree	2	27.2	30.7	10.66	0.522
ASTR/sapling	2	47.4	33.0	9.18	***0.076***
CELA/sapling	1	38.5	25.9	11.90	***0.095***
FRPE/sapling	4	40.0	19.7	10.57	0.213
ILDE/sapling	3	33.2	32.5	13.53	0.467
LISI/sapling	3	96.3	34.0	14.91	***0.001***
LIST/sapling	1	18.3	22.9	8.89	1.000
PLAQ/sapling	4	45.8	27.0	13.54	***0.100***
QULA/sapling	2	39.2	27.9	11.26	0.383
ULAM/sapling	3	10.2	16.5	12.18	1.000
%mass DBH <25cm	3	41.8	32.9	3.60	***0.014***
%mass DBH 25-50cm	3	43.4	32.6	3.49	***0.004***
%mass DBH 50-75cm	4	33.7	31.1	3.67	0.254
%mass DBH <75cm	1	58.7	28.9	9.30	***0.008***
Column Averages	N/A	43.2	27.43	10.62	0.334

Notes: Monte Carlo test of significance of observed maximum indicator value for basal area (m^2) by tree and sapling species (species occurring in only one plot removed prior to analysis). For complete species information and translation of species codes used consult Appendix 1. *Proportion of randomized trials with indicator value (IV) equal to or exceeding the observed IV. Significant IV bold and in italics at $p \leq 0.10$. $p = (1 + \text{number of runs} \geq \text{observed})/(1 + \text{number of randomized runs})$. Randomization test for sum of IV_{max} - 1253.5 = observed sum of IV_{max} across all columns; 0 = number of randomization runs with sum of $\text{IV}_{max} \geq$ observed value; 15000 = number of randomization runs; p = 0.00007.

Table 2.2. PerMANOVA results for relative Sørensen distances among sample plots by community groups.

Source	df	*SS*	*MS*	*F*	*P*	*P* < 0.05
Community Group	3	3.028	1.009	11.8	0.0002	yes
Residual	16	1.375	0.086			
Total	19	4.403				
Community Group		*t*	*P*	*Bonferroni corrected P value*	*P < Bonferroni value*	
1 versus 2		2.281	0.0064	0.0083	yes	
1 versus 3		2.253	0.0070	0.0100	yes	
3 versus 4		5.683	0.0076	0.1250	yes	
2 versus 3		2.907	0.0080	0.0167	yes	
2 versus 4		4.244	0.0082	0.0250	yes	
1 versus 4		4.124	0.0084	0.0500	yes	

Notes: Non-parametric perMANOVA on relative Sørensen distances from a one factor balanced design based on basal area for 25 tree and sapling species and the percent of total biomass within four DBH size classes (N =29). Source is from 20 sample plots. A Bonferroni correction was applied to pairwise comparisons among community groups to maintain the experiment-wise error rate as *P*-values are not corrected for multiple comparisons in the PC-ORD output for perMANOVA.

Table 2.3. Summary of species composition and Indicator Species Analyses by stratum within community groups.

Stratum – data source (number of species)	Community Groups - sample plot group means based on Cluster and Indictor Species Analyses (N=5 plots per group)			
	Group 1 FRPE/LIST/CELA	Group 2 LIST	Group 3 CELA/ACNE	Group 4 TADI
	Most common species and their % of total within group and species having significant Indicator Values (IV) from Indicator Species Analyses (ISA) by stratum; species with significant IV of $P \leq 0.10$ bold font; species occurring in only one plot not included in ISA.			
Trees – based on % by species of total tree basal area (m²) within community group ($N = 18$; $N = 16$ for ISA)	LIST 23.7% **FRPE 23.2% *P* = 0.0081** CELA 12.6% QULY 9.2% TADI 7.7% **CRVI 0.62% *P* = 0.037**	**LIST 71.2% *P* = 0.0004** ULAM 8.2% CELA 7.3% ACNE 3.8% PLOC 2.9%	**CELA 30.9% *P* = 0.0998** ACNE 25.5% LIST 10.2% ULAM 7.0% QULA 6.9% FRPE 6.8%	**TADI 91.7% *P* = 0.0003** **PLAQ 3.6% *P* = 0.0005** **POHE 1.7% *P* = 0.0338** LIST 1.2% ACRU 1.1%
Saplings – based on % by species of total sapling basal area (m²) within community group ($N = 16$; $N = 9$ for ISA)	ASTR 41.7% ILDE 33.7% **CELA 17.7% *P* = 0.0949** PLAQ 4.4% LIST 2.42%	**ASTR 67.5% *P* = 0.0757** QULA 8.6% ILOP 6.7% CELA 5.6% ACNE 3.6%	ASTR 41.1% **LISI 31.0% *P* = 0.0007** ILDE 23.8% ULAM 2.3% PLOC 1.9%	**PLAQ 53.8% *P* = 0.1008** ILDE 23.2% TADI 17.1% CEOC 2.8% QULA 1.2%
Woody species 0-2 meters height range – based on % of point intercept hits by species of total point intercept hits within community group ($N = 22$; $N = 22$ for ISA)	ASTR 20.8% SMRO 13.6% ARGI 13.1% ANCA 8.6% ULAM 7.7%	ARGI 30.1% ASTR 23.3% ANCA 17.7% TORA 5.2% LISI 4.9%	ARGI 30.0% ASTR 19.3% **LISI 18.3% *P* = 0.0344** ANCA 13.7% VIRO 6.5%	**TADI 29.8% *P* = 0.0012** **FRPE 16.8% *P* = 0.0220** **PLAQ 11.2% *P* = 0.0003** ACRU 9.9% **POHE 8.1% *P* = 0.0042**
Herbaceous species – based on maximum % cover by species of total % cover within community group ($N = 40$; $N = 39$ for ISA)	CAGR 32.6% CAOL 21.8% LUMU 10.2% CASQ 6.3% COFL 5.6%	CAGR 25.3% CAOL 21.8% **COFL 16.6% *P* = 0.0671** LUMU 13.3% CHPR 7.7% **GAAP 4.3% *P* = 0.0327** **ARDR 1.2% *P* = 0.0615**	MIVI 24.8% CAOL 19.0% CAGR 16.6% LUMU 12.4% POAU 7.2% **SEGL 3.1% *P* = 0.0998**	**LEOR 17.9% *P* = 0.0327** **PAGY 16.2% *P* = 0.0002** **BOCY 15.8% *P* = 0.0658** **CACO 12.7% *P* = 0.0018** **CAFR 9.9% *P* = 0.0002** **CIAR 3.7% *P* = 0.0002** **JUOV 2.4% *P* = 0.0013**
Mean elevation (meters above sea level)	133.77	134.43	134.46	132.94
Mean % biomass within community group				
Trees < 25 cm DBH	8.9%	7.4%	15.4%	5.2%
Trees 25-50 cm DBH	21.5%	11.6%	50.3%	32.5%
Trees 50-75 cm DBH	18.9%	53.4%	34.3%	54.3%
Trees > 75 cm	50.7%	27.6%	0.0%	8.0%

Notes: For complete species information and translation of species codes used consult Appendix 1. This table is a condensation of multiple Indicator Species Analyses (ISA) and data tables specific to strata. Complete ISA information may be found in Table 2.1 and Appendices 2 and 3. Complete strata data tables may be found in Appendices 4 through 6. Analysis of elevation and DBH classes can be found in Table 2.4. Elevation data provided by Hupp (2013).

Table 2.4. Results of analysis of variance and group comparisons conducted on community group means for recorded community variables.

Community Variables	Analysis of variance test statistic and results of multiple comparisons	Sample plot groups based on cluster analysis			
		Group 1 FRPE/LIST/CELA	Group 2 LIST	Group 3 CELA/ACNE	Group 4 TADI
		mean ± SE	mean ± SE	mean ± SE	mean ± SE
Herbaceous % cover; April 2011	$F_{3, 16} = 0.59$; $P = 0.63$	13.08 ±2.63	12.96 ±3.05	15.88 ±4.03	9.44 ±3.85
Herbaceous % cover; June 2011	$F_{3, 16} = 2.18$; $P = 0.13$	9.96 ±0.76	5.68 ±1.58	11.76 ±3.82	18.48 ±5.87
Herbaceous % cover; September 2011	$F_{3, 16} = 1.46$; $P = 0.26$	13.48 ±0.95	8.20 ±2.14	15.48 ±5.11	19.08 ±4.99
Mean Herbaceous % cover	$F_{3, 16} = 0.80$; $P = 0.51$	12.17 ±1.05	8.95 ±1.83	14.38 ±4.01	15.67 ±4.79
Point Intercept % 0-0.5 meters	**2 > 1 = 4** **$F_{3, 16} = 8.84$; $P \leq 0.003$**	20.32 ±3.81	63.04 ±10.14	38.72 ±8.93	16.48 ±2.59
Point Intercept % 0.5-1.0 meters	**2 > 1 = 4** **$H_{0.05, 3} = 10.84$; $P \leq 0.049$**	5.44 ±2.21	28.96 ±5.88	22.56 ±9.75	4.80 ±1.62
Point Intercept % 1.0-1.5 meters	**2 > 4** **$F_{3, 16} = 3.69$; $P \leq 0.048$**	4.64 ± 1.76	19.04 ± 5.64	17.28 ± 6.53	2.40 ± 1.16
Point Intercept % 1.5-2.0 meters	**3 > 1 = 4** **$F_{3, 16} = 3.69$; $P \leq 0.049$**	4.96 ±1.46	11.68 ±5.61	21.76 ±6.29	2.08 ±1.12
Cumulative Point Intercept % positive 0-2.0 meters	**2 = 3 > 1 = 4** **$F_{3, 16} = 8.08$; $P \leq 0.047$**	35.36 ±8.09	122.72 ±23.69	100.32 ±22.19	25.76 ±3.44
Seedlings per m²	**4 > 1 = 2 = 3** **$F_{3, 16} = 7.94$; $P \leq 0.007$**	8.44 ±2.72	8.08 ±1.60	6.20 ±1.56	36.60 ±9.71
Number of saplings per hectare	**2 = 3 > 4** **$F_{3, 16} = 6.18$; $P \leq 0.024$**	1120 ±366	2800 ±702	2480 ±450	368 ±130
Sapling Basal Area 2010 baseline (m²/hectare)	**3 = 2 > 4; 3 > 1** **$F_{3, 16} = 7.67$; $P \leq 0.048$**	1.67 ±0.41	2.94 ±0.68	3.77 ±0.66	0.44 ±0.21
Number of trees per hectare	**4 > 2 = 3** **$F_{3, 16} = 4.56$; $P \leq 0.030$**	376 ±17	328 ±47	320 ±35	504 ±51
Tree Basal Area 2010 baseline (m²/hectare)	**4 > 1 = 3** **$F_{3, 16} = 7.20$; $P \leq 0.047$**	36.37 ±3.58	44.76 ±9.53	20.61 ±2.49	63.70 ±8.32

% of tree biomass in trees < 25 cm. DBH	**3 > 1 = 2 = 4** **$F_{3,16} = 4.10$; $P \leq 0.049$**	8.85 ±1.37	7.35 ±2.16	15.36 ±3.01	5.14 ±1.81
% of tree biomass in trees 25-50 cm. DBH	**3 > 1 = 2; 4 > 2** **$F_{3,16} = 10.39$; $P \leq 0.048$**	21.52 ±4.91	11.58 ±1.79	50.28 ±6.34	32.52 ±6.18
% of tree biomass in trees 50-75 cm. DBH	**4 = 2 > 1** **$F_{3,16} = 7.20$; $P \leq 0.048$**	18.88 ±8.80	53.44 ±10.26	34.36 ±8.65	54.30 ±3.00
% of tree biomass in trees > 75 cm. DBH	**1 > 4 = 3** **$F_{3,16} = 6.42$; $P \leq 0.018$**	50.74 ±6.89	27.63 ±15.65	0.00 ±0.0	8.04 ±5.15
Sample plot elevation (meters above sea level)	**3 = 2 > 1 > 4** **$F_{3,16} = 30.33$; $P \leq 0.012$**	133.77 ±0.23	134.43 ±0.06	134.46 ±0.07	132.94 ±0.08
Spring % canopy opening; March 2011	**2 > 4** **$H_{0.05,3} = 11.08$; $P \leq 0.011$**	17.71 ±0.22	19.79 ±0.49	17.19 ±1.08	15.57 ±0.36
Summer % canopy opening; June 2011	$F_{3,16} = 2.28$; $P = 0.119$	4.26 ±0.87	3.86 ±0.76	4.96 ±0.71	2.48 ±0.28
Fall % canopy opening; Oct. 2011	$H_{0.05,3} = 5.57$; $P \leq 0.135$	9.81 ±0.40	9.72 ±0.82	9.31 ±0.38	8.39 ±0.14
Winter % canopy opening; Jan. 2012	**3 = 2 > 4** **$H_{0.05,3} = 9.96$; $P \leq 0.045$**	21.95 ±0.61	22.75 ±0.79	24.86 ±2.03	18.68 ±0.50
Mean % canopy opening	**3 = 2 > 4** **$H_{0.05,3} = 10.55$; $P \leq 0.044$**	10.77 ±0.59	11.63 ±0.88	12.38 ±1.34	8.81 ±0.09

Notes: Groups are those defined via cluster analysis and Indicator species analysis; N = 5 sample plots for each group. F statistic with degrees of freedom from one-way ANOVA testing the hypothesis of no difference in variable means among sample plot groups; multiple comparisons used the Tukey test (corrects for multiple comparisons). In cases where normality (Shapiro-Wilk W test) or equal variance (Brown-Forsythe test) assumptions on the residuals were not met at the $P = 0.05$ level, the data were subjected to the Kruskal Wallis test (rank sums) and the H statistic with alpha level and degrees of freedom is reported; multiple comparisons following Kruskal Wallis test used Dunn's method for joint ranking (corrects for multiple comparisons). P values reported are either the highest significant value from multiple comparisons or from the analysis of variance when the groups did not differ. Elevation data provided by Hupp (2013)

Table 2.5. Results of analysis of variance and community group comparisons conducted on group means of community structure measures.

Community Variables	ANOVA test statistic and results of multiple comparisons	Sample plot groups based on cluster analysis			
		Group 1 FRPE/LIST/CELA	Group 2 LIST	Group 3 CELA/ACNE	Group 4 TADI
		mean ± SE	mean ± SE	mean ± SE	mean ± SE
Herbaceous layer species richness	$F_{3, 16} = 2.18$; $P = 0.13$	10.60 ±1.29	8.60 ±1.08	9.60 ±1.17	12.80 ±1.32
Herbaceous layer species evenness	$F_{3, 16} = 0.83$; $P = 0.49$	0.75 ±0.036	0.76 ±0.036	0.76 ±0.073	0.84 ±0.020
Herbaceous layer Shannon-Wiener Index	**4 > 2** **$F_{3, 16} = 3.94$; $P \leq 0.029$**	1.75 ±0.13	1.61 ±0.12	1.68 ±0.13	2.11 ±0.05
Herbaceous layer Simpson diversity index	**4 > 1 = 2** **$H_{0.05, 3} = 8.70$; $P \leq 0.039$**	0.763 ±0.034	0.735 ±0.036	0.740 ±0.051	0.842 ±0.012
Point Intercept 0-2 meters species richness	**2 > 1 = 4** **$F_{3, 16} = 5.18$; $P \leq 0.028$**	7.60 ±0.81	11.20 ±0.73	9.40 ±0.87	7.20 ±0.80
Point Intercept 0-2 meters species evenness	$F_{3, 16} = 2.57$; $P = 0.09$	0.821 ± 0.025	0.720 ± 0.025	0.680 ±0.061	0.783 ±0.034
Point Intercept 0-2 meters Shannon-Wiener Index	$F_{3, 16} = 0.52$; $P = 0.67$	1.64 ±0.079	1.74 ±0.095	1.53 ±0.186	1.54 ±0.149
Point Intercept 0-2 meters diversity index	$H_{0.05, 3} = 2.22$; $P \leq 0.53$	0.753 ±0.022	0.764 ±0.028	0.684 ±0.078	0.707 ±0.042
Sapling layer species richness	$F_{3, 16} = 2.02$; $P = 0.15$	2.40 ±0.40	3.20 ±0.37	3.00 ±0.45	2.00 ±0.32
Sapling layer species evenness	$F_{3, 16} = 0.38$; $P = 0.77$	0.565 ±0.169	0.465 ±0.151	0.486 ±0.148	0.325 ±0.178
Sapling layer Shannon-Wiener Index	$F_{3, 16} = 0.81$; $P = 0.51$	0.542 ±0.150	0.592 ±0.227	0.573 ±0.222	0.238 ±0.121
Sapling layer Simpson diversity index	$F_{3, 16} = 0.64$; $P = 0.60$	0.344 ±0.095	0.318 ±0.131	0.302 ±0.124	0.146 ±0.091

Tree layer species richness	$F_{3,\ 16} = 2.64$; $P = 0.08$	7.40 ±1.12	5.40 ±0.68	4.80 ±0.58	4.80 ±0.49
Tree layer species evenness	**1 = 3 > 4** **$F_{3,\ 16} = 10.17$; $P \leq 0.0012$**	0.768 ±0.053	0.564 ±0.060	0.760 ±0.090	0.285 ±0.075
Tree layer Shannon-Wiener Index	**1 > 2 > 4; 3 > 4** **$F_{3,\ 16} = 13.64$; $P \leq 0.048$**	1.49 ±0.13	0.93 ±0.08	1.13 ±0.09	0.469 ±0.15
Tree layer Simpson diversity index	**1 = 3 > 4; 1 > 2 > 4** **$F_{3,\ 16} = 17.16$; $P \leq 0.017$**	0.719 ±0.032	0.468 ±0.032	0.599 ±0.054	0.215 ±0.077

Notes: Groups are those defined via cluster analysis and Indicator Species Analysis; N = 5 sample plots for each group. F statistic with degrees of freedom from one-way ANOVA testing the hypothesis of no difference in variable means among sample plot groups; multiple comparisons used the Tukey test (corrects for multiple comparisons). In cases where normality (Shapiro-Wilk W test) or equal variance (Brown-Forsythe test) assumptions on the residuals were not met at the $P = 0.05$ level, the data were subjected to the Kruskal Wallis test (rank sums) and the H statistic with alpha level and degrees of freedom is reported; multiple comparisons following Kruskal Wallis test used Dunn's method for joint ranking (corrects for multiple comparisons). P values reported are either the highest significant value from multiple comparisons or from ANOVA when the groups did not differ.

Table 2.6. Percentages of total herbaceous percent cover within community groups based on life form and life history.

	Community Group – % of total herb % cover			
	1 - FRPE/LIST/CELA	2 - LIST	3 - CELA/ACNE	4 - TADI
Form	Column %	Column %	Column %	Column %
fern	0.00%	1.69%	0.16%	1.59%
forb	19.74%	38.80%	15.76%	24.22%
grass	7.64%	0.00%	34.89%	38.12%
sedges/rushes	72.63%	59.52%	49.20%	36.07%
Duration				
annual	13.22%	35.42%	37.62%	16.94%
perennial	86.78%	64.58%	62.38%	83.06%

Notes: For complete species information and translation of species codes consult Appendix 1.

Figure 2.1. Forest types in the Congaree National Park and location of the study area.

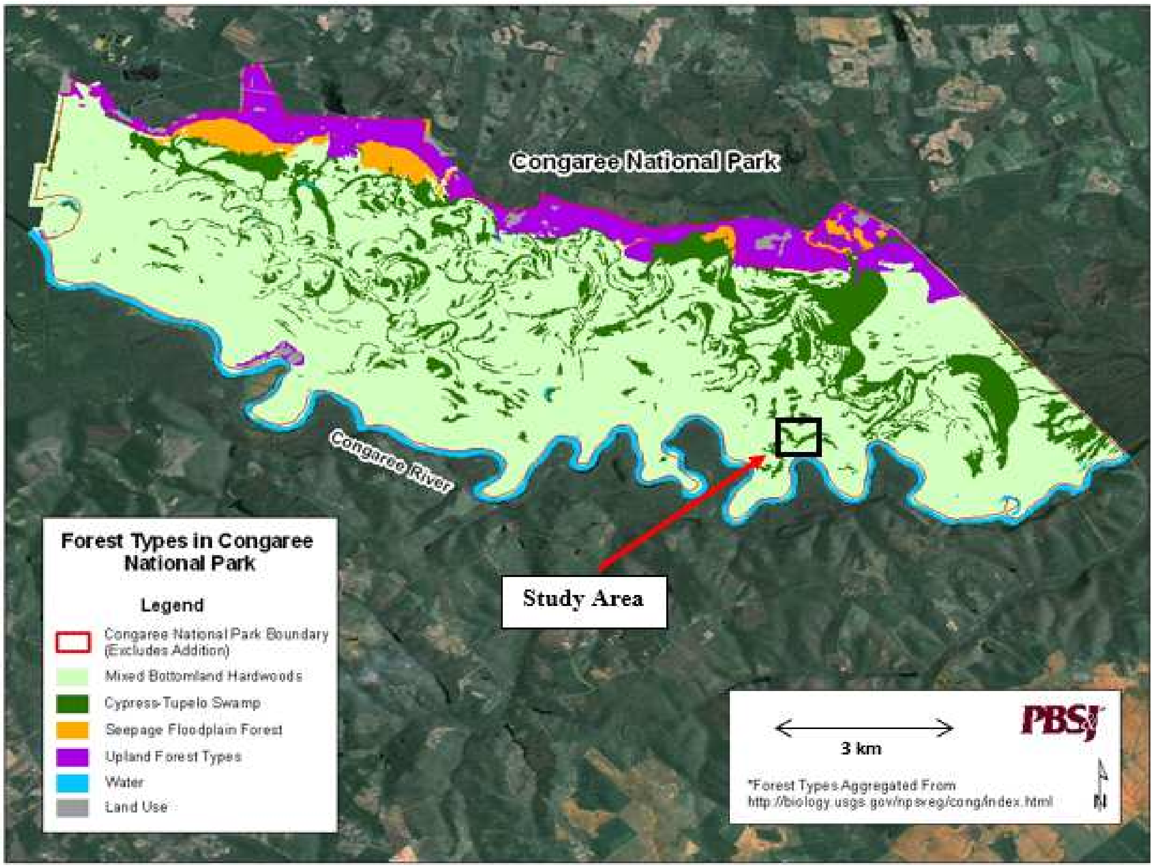


Figure 2.2. Schematic diagram of 20x25 m study plots showing locations of sub-plots, transects, and data collection points.

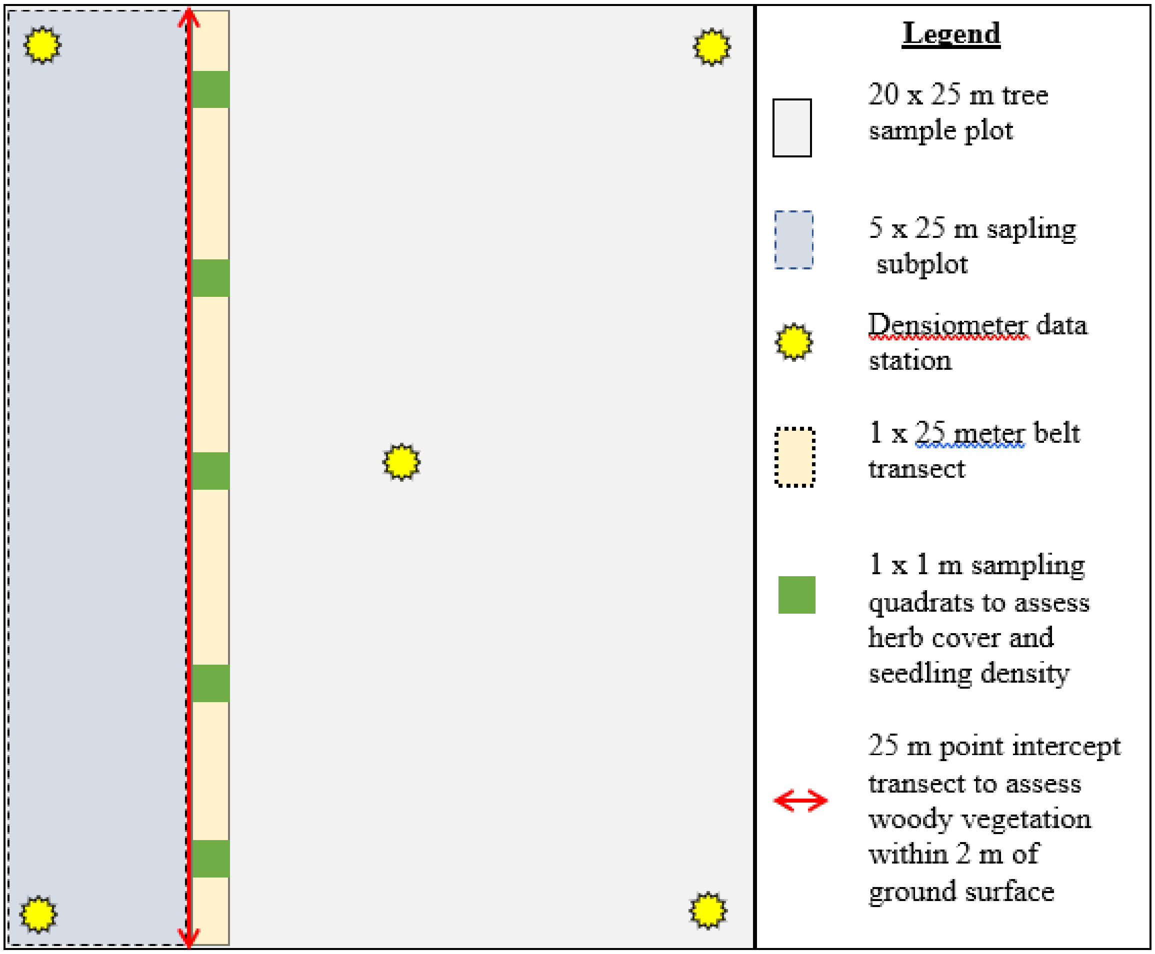
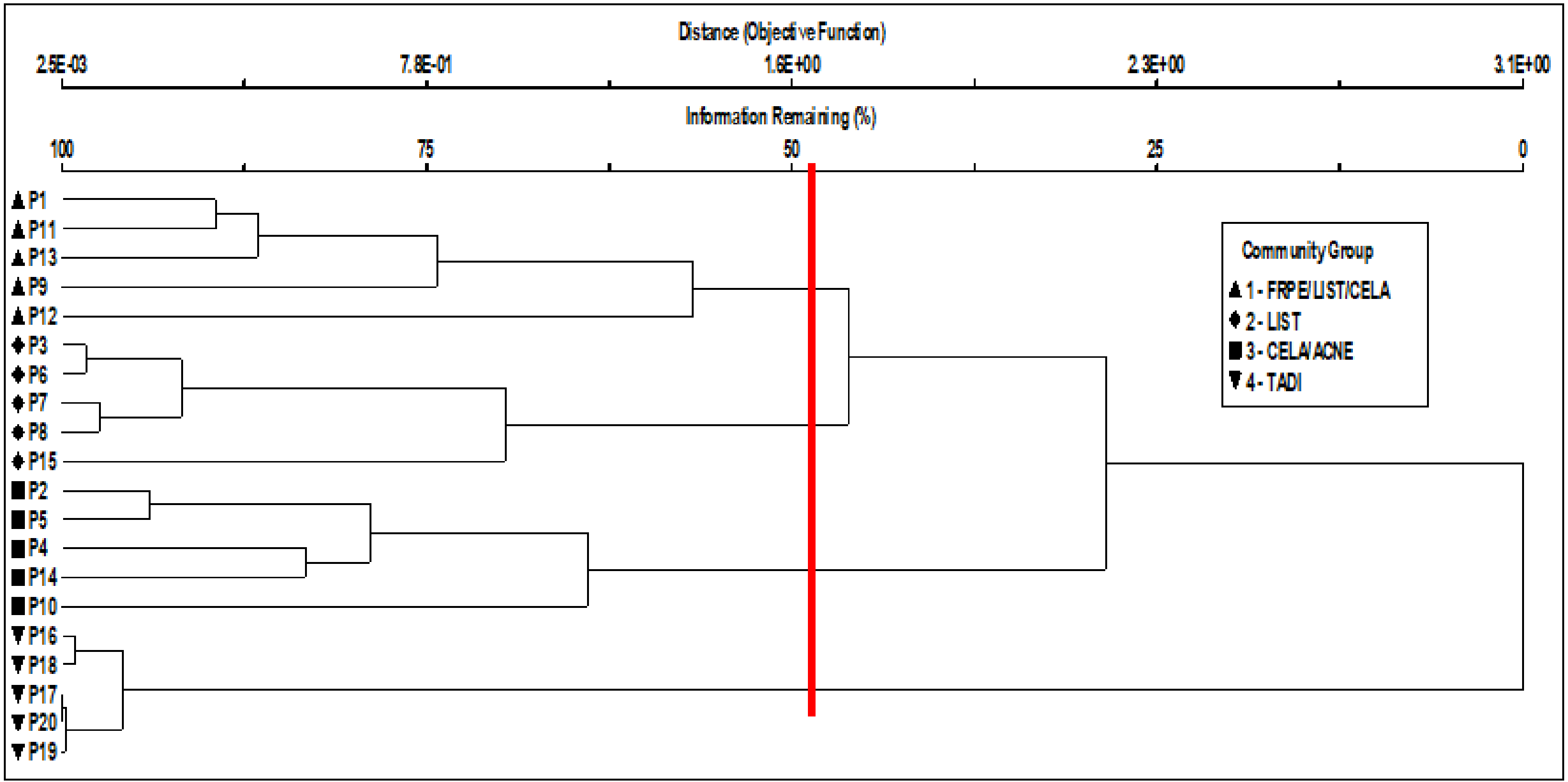


Figure 2.3. Dendrogram produced by cluster analysis to define community groups on the floodplain of the Congaree River.



Notes: Cluster analysis dendrogram based on a main matrix of 20 rows (sample plots) and 29 columns (basal area of 16 tree species, 9 sapling species, and % tree dry mass within four DBH classes. Relative Sørensen was used for the distance measure and flexible beta linkage set at -0.25 was employed as the group linkage method (% chaining = 7.44; total sums of squares = 53.80). A pruning point at 45% information remaining maximized the number of significant IV during Indicator Species Analyses (shown as red line in figure).

Figure 2.4. Sample plot distribution on floodplain illustrating the difference in *a priori* blocking versus *post-hoc* cluster analysis community groups.

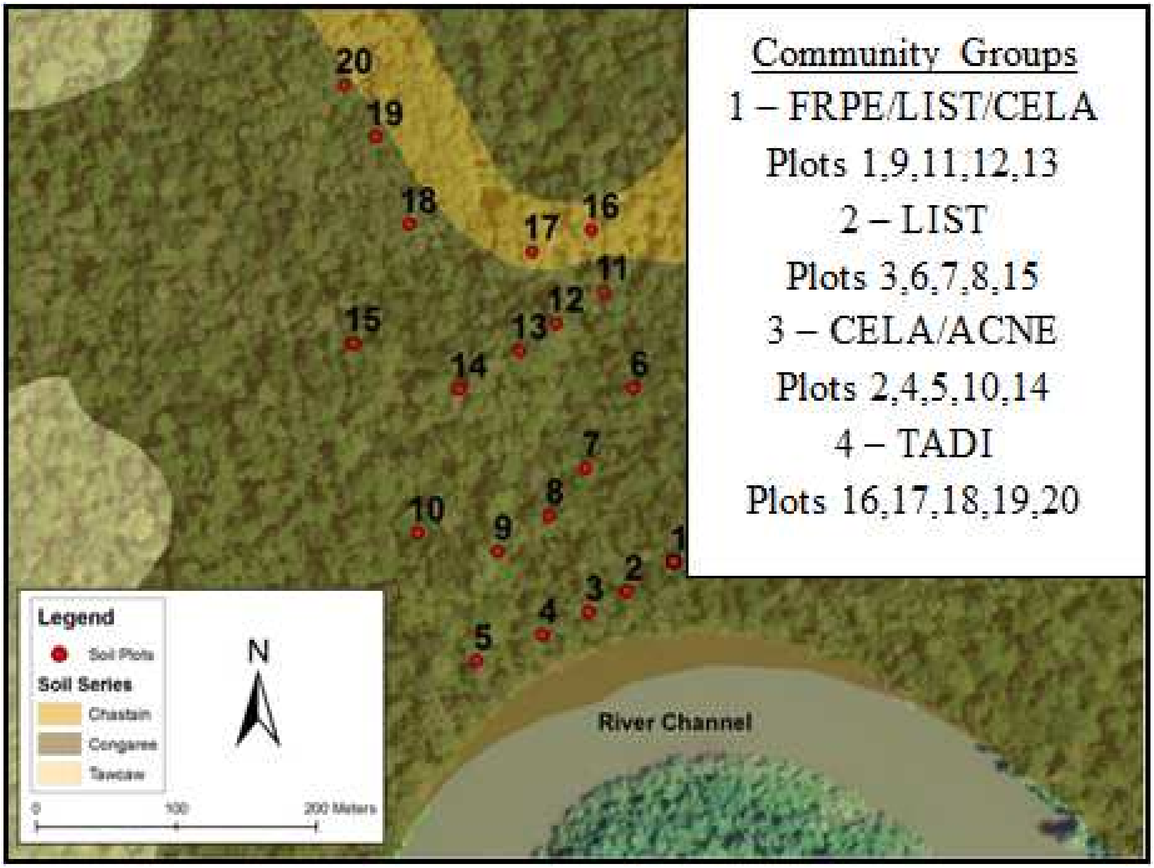


Figure 2.5. Scree plot of stress versus dimensionality (top) used to choose number of NMS dimensions and a plot of stress versus iteration number (bottom) used to assess stability of chosen NMS three-dimensional solution.

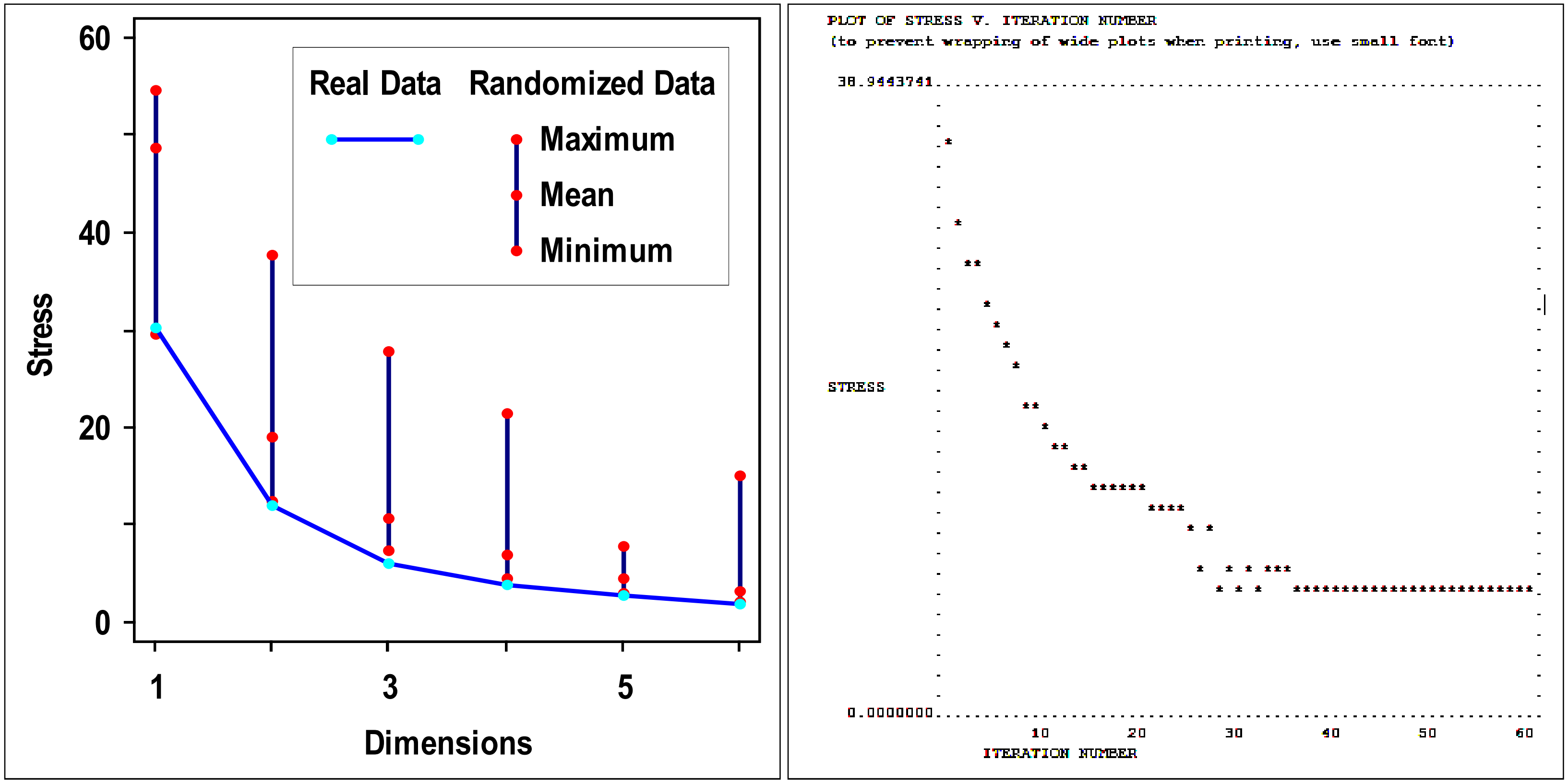
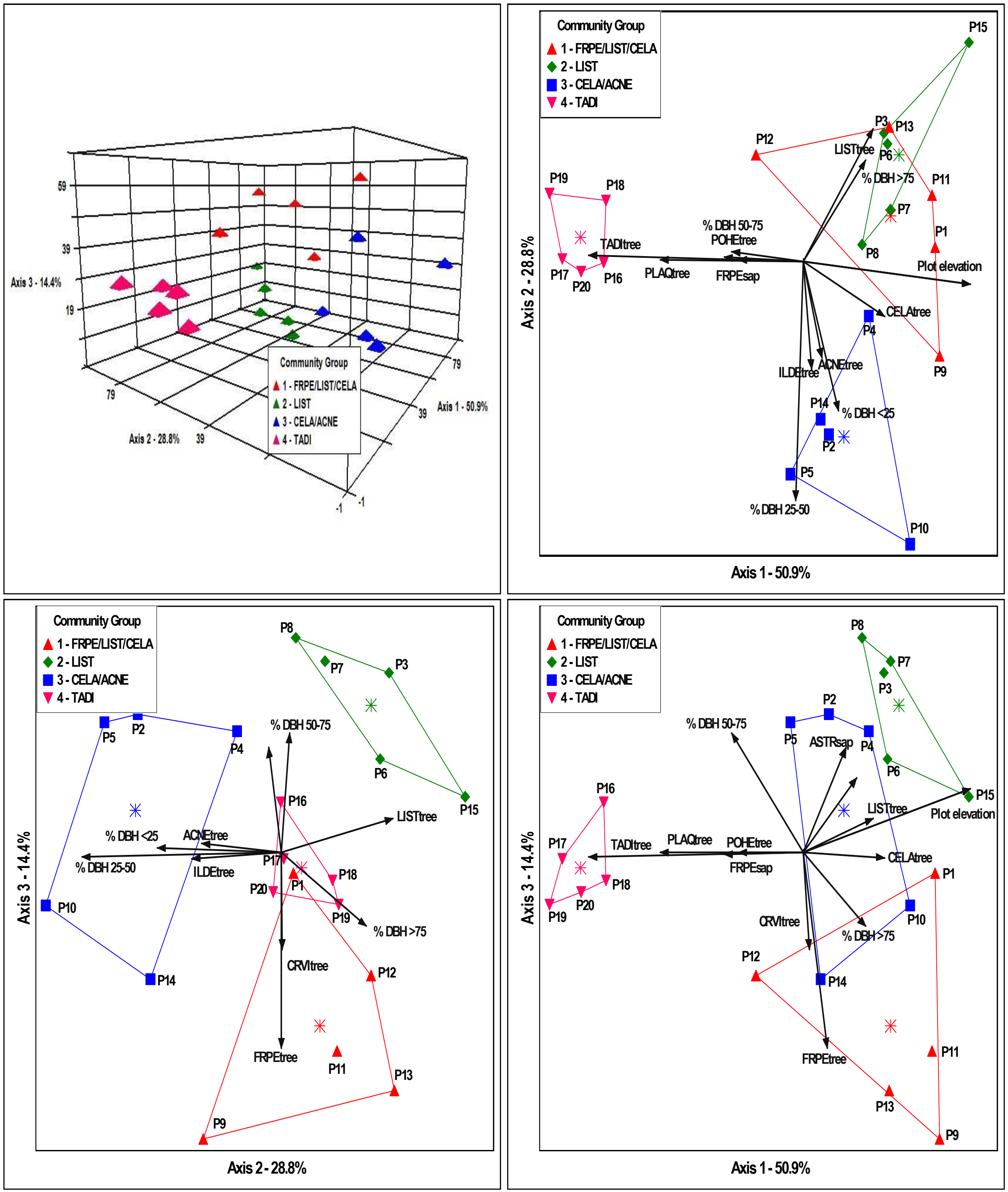


Figure 2.6. NMS ordination of sample plots in species space and separation within community groups.



Notes: Data source is a main matrix of 20 rows (plots) and 29 columns (basal area of 16 tree species, 9 sapling species, and % tree dry mass in four DBH classes). Asterisks are centroids defining community group space. Axes represent 94.2% of the total variation with a final stress of 6.09, instability < 10^{-5}, and Monte Carlo probability of $p = 0.004$. Joint plot cutoff is Pearson's correlation coefficient $r^2 \geq 0.250$.

CHAPTER THREE

ABOVEGROUND NET PRIMARY PRODUCTIVITY ACROSS AN ELEVATIONAL GRADIENT WITHIN A FLOODPLAIN FOREST OF THE CONGAREE RIVER, SOUTH CAROLINA, USA

Abstract. The interrelated dynamics of hydrology and sedimentation both help shape and interact with small scale elevational differences on southeastern floodplain forests to yield communities composed of species best suited to the characteristics of a given habitat. Productivity varies among community types across forested floodplains, and this variation can be attributed to the magnitude of, and spatial and temporal characteristics of, inundation and dry down patterns coupled with heterogeneity in both the rate and composition of deposited material. The integrity of hydrological connections, sedimentation dynamics, and flooding intensity and periodicity is necessary to maintain the diversity, composition, structure, and productivity rates within these systems. Unfortunately, anthropogenic activities have drastically changed the composition and volume of the alluvium deposited. Consequences of these changes are variable. In some instances, productivity has increased and in others decreased, and it is likely that changes to productivity will vary by species, community type, and position on the floodplain. Likewise, changes to the depth or timing of flood waters are widespread in forested wetland ecosystems due to flow control associated with dams, locks, and levees. Increases in water depth or length of inundation can decrease forest productivity considerably and may result in canopy tree mortality over time, while decreases in these parameters will favor less flood tolerant species and create a more hospitable environment for invasive species. Congaree National Park consists of a series of low relief fluvial landforms across the Congaree River floodplain representing gradients in sedimentation rates and inundation periodicity and depth. This study takes advantage of these gradients to assess whether differences in hydrology and sedimentation yield differential productivity rates within the Congaree floodplain forests. Four 20x25 m plots, blocked by *a priori* perceived elevation differences, were established in 2010 along each of five roughly parallel transects with a spacing of approximately 60 m between transects and oriented perpendicular to the river channel. *Post hoc* blocking was employed to refine blocking into ecologically meaningful community groups. Trees (stems ≥ 10 cm DBH) were inventoried by species, measured, tagged, and mapped within each plot. Saplings (stems ≥ 1m in height with a DBH or BD < 10 cm) were inventoried by species, measured, tagged, and mapped within a 5x25 m subplot within each plot. Littertraps were used to collect leaf and reproductive litterfall. Tree DBH was collected during the winter for five years, sapling DBH/BA was collected during the winter for three years, and litter was collected from litterboxes approximately every 4-6 weeks for two years. Annual ANPP was calculated as the sum of incremental wood mass gain of trees and saplings and annual leaf mass and reproductive mass retrieved from litter boxes.

Key words: aboveground net primary productivity; annual litter fall; old-growth; bottomland hardwood forest; bald cypress swamp; Congaree National Park

INTRODUCTION

Biological integrity and productivity of an ecosystem like the Congaree Swamp can be affected by both natural and anthropogenic forces. Naturally occurring agents of change influencing the ecology of Congaree Swamp over the past 250 years include floods, drought, fire, and powerful storms such as hurricanes and tornados (Conner et al. 1989). These selective forces, along with the dynamics of the river itself, have acted singly and in concert over many centuries and generations to produce a mosaic of community types across the floodplain. European settlement of the watershed brought into play additional agents of change with the potential to affect the biological integrity of the system, however these new anthropogenic forces, including development, climate change, agriculture, logging, invasive species, and alteration of the hydrologic regime, have only applied selective pressure on populations for limited generations compared to natural agents.

Floodwater characteristics (duration, intensity, frequency, timing) and groundwater levels determine the hydroperiod (or hydrologic regime) of a given area (Hupp 2000). The hydrologic regime of the Congaree River watershed remained mostly unaltered by humans until 1929 with the exception of scattered low head dams associated with mills (Conrads et al. 2008). Regulated streamflow of the Saluda River, which joins the Broad River to form the Congaree River, began in 1929 with operation of the Saluda Dam at Lake Murray (Patterson et al. 1985). Studies have indicated operation of the dam has affected the hydrologic regime within the Congaree Swamp; however parsing out to what extent dam operation is responsible for hydrologic and ecologic changes directly from the contributory effects of shifting precipitation patterns associated with climate change remains difficult (Patterson et al. 1985, Minchin and Sharitz 2007, Conrads et al. 2008). While operation of the dam has had no discernible effect on the probability that base flood stage would be equaled or exceeded in a given year (Patterson et al. 1985), the recurrence intervals of higher flood levels has increased by 6.1% for two year peak flows and 17.6% for 100 year peak flows (Conrads et al. 2008). The analysis by Conrads et al. (2008) comparing pre and post dam hydrologic regimes indicates the following: high water levels from December to May have been reduced; low water levels between June and November have increased; high ground water elevations have decreased and low ground water elevations have increased; minimum incremental gage heights have increased up to 23.9% and maximum values have decreased up to 7.2%. Along with the decrease in frequency and magnitude of larger floods associated with dam operation, the dynamics of flood pulse are shifted as the duration of inundated conditions associated with a given event has increased. Overbank flow has also been reduced leaving mainly backwater flooding through levee breaches contributory to backswamp inundation and limiting deposition to the levee and higher elevation flats (Patterson et al. 1985).

The study area (Figure 3.1) is located on a major alluvial floodplain associated with the Congaree River located at the interface of the lower piedmont and coastal plain and is predominantly forested except following major natural disturbances or anthropogenic activities (Messina and Conner 1998). The area is characterized by a wide floodplain with diverse topographic areas, which despite low relief, experience differential hydroperiods via overbank and backwater flooding (Sharitz and Mitsch 1993, Kellison et al. 1998). Backwater flooding can occur via channels known locally as “guts” which connect levee breeches to backwater swamps, thus allowing flooding of these swamps at flow levels below bank full (Shelley and Cohen 2010). The backwater swamp areas within the study area may be inundated for a majority of the year or may be free of standing water for much of the year, depending on annual fluctuations in rainfall amounts and timing (Sharitz and Mitsch 1993, Conner and Buford 1998).

It is often thought that red-water river floodplains and associated wetlands of the piedmont and upper coastal plain (like the Congaree floodplain) should be more productive compared to black-water systems of the lower coastal plain because of the greater nutrient subsidy associated with higher sediment loads and allochthonous organic matter transport, but this can be offset by the stress associated with prevalence of anaerobic conditions (Schilling and Lockaby 2005). Aboveground net primary productivity (ANPP) in southeast floodplain forests varies from 200-2000 g/m^2 per year (Conner 1994). ANPP may be affected via the stress-subsidy hypothesis from one growing season to the next or even within the same growing season via the physiological and growth rate differences related to anaerobic conditions, drought stress, and nutrient inputs associated with flooding, rainfall, and anthropogenic alterations to flow and flooding regimes (Megonigal et al. 1997).

In this study community groups were established post hoc based on numerous recorded community metrics and variables using ordination and Indicator Species Analyses to take all these parameters into consideration and define the most meaningful ecological groupings (Chapter 2). Differences in elevation and the associated differences in the frequency, duration, and intensity of flooding in conjunction with tree species composition were the defining gradients separating communities with additional refinement of communities defined by tree size classes. This study compares community groups across this elevational gradient to determine if productivity rates differ significantly and analyzes whether stand age/size affects productivity rates.

MATERIALS AND METHODS

The Congaree River begins at the confluence of the Broad and Saluda rivers near Columbia, South Carolina and ends at its confluence with the Wateree River to form the Santee River. For most of its length, the Congaree River occupies a broad floodplain bounded on the north by a complex of fluvial landforms and to the south by a steep bluff cut into upper coastal plain deposits (Shelley and Cohen 2010). The Congaree National Park (CONG) protects a vast, old growth floodplain forest in the lower Congaree River Valley (Figure 3.1) representing the last remaining major tract of mature bottomland hardwood forest in the southeastern United States (Gaddy et al. 1975, Shelley and Cohen 2010). Within the floodplain are spatially complex changes in elevation (generally < 75 cm) yielding microtopographic highs and lows which experience distinct flooding regimes, sedimentation processes, and soil drainage characteristics. This results in a complex spatial array of forest types which often differ in productivity (Conner et al. 2002).

Adjacent to the river channel and scattered farther from the river are the highest elevation areas which include the active natural levee and relict levees. Across the floodplain is a mosaic of flats abutting the levees at slightly lower elevations which experience intermediate inundation. The lowest areas, or backswamps, are oxbows and historic meander scars experiencing seasonal to semi-permanent flooding. A total of 20 data collection plots, blocked by *a priori* perceived elevation differences, were established in 2010 along five roughly parallel transects with a spacing of approximately 60 m between transects and oriented perpendicular to the river channel. Four 20x25 m plots (0.05 ha) were established along each transect with the transect azimuth bisecting the short sides of the rectangular plot; one plot in each of four perceived *a priori* elevation zones. Subplots and transects were established within each plot to facilitate collection of various data discussed below. After analysis of data, *post hoc* blocking of plots into community groups was executed. The plant nomenclature of Radford et al. (1968) was followed for all vegetation data collected in this study. Four letter codes (first two letters of genus and first two letters of specific epithet) were assigned to each species discussed in this study and these codes are used for brevity within tables; a species list is provided as Appendix 7.

Aboveground net primary productivity

Annual ANPP is often estimated via the sum of annual litterfall and annual incremental increase in stem tissue (Johnson and Risser 1974, Grier et al. 1981; Mitsch et al. 1991, Catchpole and Wheeler 1992, Schilling and Lockaby 2005). The biomass of stem, branch, and bark tissue at a given time can be estimated from diameter at breast height (DBH; 1.4 m) or basal diameter (BD) for a given species using specific gravity and allometric equations developed for a species or genus (Phillips 1981, Clark et al. 1985, Megonigal et al. 1997, Jenkins et al. 2003). The allometric equations of Jenkins et al. (2003) were used for all tree and sapling species with the following exceptions. The allometric equations used to estimate the biomass of bald cypress (*Taxodium distichum* [L.] Richard) follow those applied by Megonigal et al. (1997). Allometric equations to estimate the biomass of Chinese privet (*Ligustrum sinense* Lour.) follow those developed and used by Burton (Burton 2006, Burton and Samuelson 2008). These equations were also applied to two other large shrub species with very low frequency (buttonbush, *Cephalanthus occidentalis* L. and spicebush, *Lindera benzoin* [L.] Bloom) for which no equations could be found in the literature. Specific gravity values were taken from the extensive list provided in Woodall and Williams (2005) as required for a given allometric equation.

Trees were defined as all stems ≥ 10 cm DBH and were inventoried by species, measured, tagged, and mapped on a grid within each 20x25 m plot (each stem of multi-trunked individuals was inventoried as a separate stem for both trees and saplings). Saplings (stems ≥ 1m in height with a DBH or BD < 10 cm) were inventoried by species, measured, tagged, and mapped within a 5x25 m subplot within each plot. Stamped numerical, oval aluminum tags (approximately 2.5x5.0 cm) were attached with an aluminum nail for stems > 5 cm DBH; diameter was measured just below the bottom of the tag. When trees had noticeable buttresses, the tag was placed 0.5 m above buttress taper (Zhao et al. 2006). Stems smaller than 5 cm DBH had the tag attached with a nylon cable tie to avoid splitting and, as a backup, a pin flag bearing the tag number was placed at the base of the stem. A dot of tree paint was placed on the smaller stems where the initial diameter measurement is taken so additional measurements are taken at the same place. During collection of initial and subsequent diameter data the following was noted: tag number; species; conditions such as broken top, dead top, hollow, etc.; tool used - caliper or tape; DBH or BD measured; measured at tag or paint mark; and a description to insure measurements are repeatable (*e.g.*, fixed end of caliper placed under tag). These steps were taken to ensure consistency during annual measurements of DBH used to calculate ANPP.

Litterfall was collected for two years from five 0.25 m^2 littertraps per plot. One littertrap was placed near plot center and one littertrap was placed in each 5x5 m corner area of the plot. Littertraps were constructed from pressure treated wood with 1 mm fiberglass screen bottoms; screens were elevated 2.5 cm above a Styrofoam base. Each trap was mounted on a 60x60x6.25 cm thick section of Styrofoam so they would float during flooding and a nylon rope was used to tether traps to a nearby stem so they would not float away. The contents of each trap were collected approximately once a month (every 4-6 weeks; see Table 1 for collection dates), due to periods of low litterfall and extended inundation, collection intervals were variable. Only the portion within the trap perimeter was retained when material was located both in and out of trap (i.e., a branch resting across trap or a leaf folded over the trap edge). After oven drying at 70°C to constant mass, the contents of each trap was sorted into the following categories and weighed: (1) leaf biomass – leaves, leaflets, petioles, rachises, bud scales, stipules, lepidopteron frass (assumed to have been leaf material and thus a portion of ANPP); (2) reproductive biomass – seeds, fruit, flowers, cones; (3) wood such as twigs, bark and branches (assumed to be included in allometric equations); Spanish moss; and tissue from species other than trees, saplings, shrubs, and vines (this category was not weighed and thus not included in ANPP calculations (Megonigal et al. 1997)). Materials not in these categories such as insects or soil kicked into traps by rooting hogs were discarded.

Tree DBH was collected during the winter for five years, sapling DBH/BA was collected during the winter for three years, and litter was collected from litterboxes approximately every 4-6 weeks for two years (each "year" consisted of nine collections and covered a time period of 55 weeks; collection dates are given in Table 3.1). Annual ANPP was calculated as the sum of incremental wood mass gain of trees and saplings between annual measurements and annual leaf mass and reproductive mass retrieved from litter boxes (Megonigal and Day 1988). Only those tree and sapling stems which persisted over the sampling period (two years for saplings and four years for trees) were used in calculation of ANPP. "Shrinking growth" or when a DBH or BA measurement was less than that taken the previous year was treated as zero growth as opposed to negative values in analyses (Allen et al. 2005).

Classification of sample plots

The following is an abbreviated description of methodology used to classify sample plots; see Chapter 2 for a more detailed treatment. *Post hoc* blocking was employed to refine blocking into ecologically meaningful community groups based on numerous recorded community metrics and variables using cluster analysis, ordination, and Indicator

Species Analyses to take all these parameters into consideration and define the most meaningful ecological groupings. Differences in elevation and the associated differences in the frequency, duration, and intensity of flooding in conjunction with tree species composition were the defining gradients separating communities with additional refinement of communities defined by tree size classes. The main matrix used to classify plots within community groups consisted of 20 rows (sample plots) and columns for basal area of tree species, basal area of sapling species, and % tree dry mass within four DBH classes. After construction, all columns in the main matrix which had nonzero values for only one plot were deleted. Use of the distance measure Relative Sørensen applies relativization based on column total prior to analyses; therefore no data transformations or relativizations were deemed necessary (McCune and Grace 2002). Outlier analysis showed that plot 10 was a very slight outlier at 2.052 the standard deviation, but since the conventional cutoff is 2.0, the plot was retained. The resulting main matrix contained 20 rows and 29 columns. Cluster analysis was employed to yield the most ecologically significant grouping of sample plots based on plant species composition and DBH class. The mean indicator species *P* value was minimized at 0.334 and the number of significant species indicator values (IV) was maximized at 14 when the tree was pruned at 45% information remaining to yield four community groups (Dufrene and Legendre 1997, McCune and Grace 2002, Duberstein et al. 2014). Community group names are based on species representing ≥ 12% of tree basal area within the group (Table 3.2; Appendix 4).

Tree and sapling basal area data and tree DBH size classes were arranged along synthetic axes of sample plots in species space using the non-metric multidimensional scaling (NMS) technique (Kruskal 1964, Mather 1976) with relative Sørensen as the distance measure. The best solution was chosen by examining a scree plot of stress versus dimensionality and a plot of stress versus iteration number. The result was a three-dimensional ordination representing 94.2% of the total variation with a final stress of 6.09, final instability $< 10^{-5}$, and a Monte Carlo probability of $p = 0.004$ that a similar final stress could have been obtained by chance. The Monte Carlo test of significance was executed with a random start, 250 runs of real data and 250 runs of randomized data, and the final solution was truncated at 61 iterations by the program PC-ORD using the slow and thorough autopilot mode.

Data analysis

Repeated measures ANOVA utilizing standard least squares was used on ANPP values to determine if there was a significant interaction between community group and year and thus whether such an interaction would preclude interpretation and analysis of multiyear ANPP plot means in further analyses (Pierfelice et al. 2017). Parameters such as annual tree growth, detrital biomass, and annual litterfall involve collecting data on multiple occasions from the same experimental units (plots), and thus would be considered a repeated measures experimental design (Zhao et al. 2006). Although repeated measures ANOVA is commonly employed to test the hypothesis of no difference among group or subject means (community group and year in this study), the procedure involves assumptions which are commonly violated when applied to ecological data and are best reserved to assess whether significant interactions may prove detrimental to further analyses (McCune and Grace 2002). These assumptions include equality of group variances coupled with the characteristic of compound symmetry, where the correlation between the data of any possible pair of groups should be the same. Violation of this underlying conceptual assumption of repeated measures ANOVA, known as sphericity or circularity, is common, difficult to test for, and yields a type one error which exceeds the chosen significance level (Zar 1999). Alternative procedures which do not depend upon the sphericity assumption include the parametric multivariate analysis of variance (MANOVA), and the non-parametric procedures MRPP and perMANOVA (Zar 1999, McCune and Grace 2002) and were considered as alternatives. Therefore, it was necessary to examine the structure of the residuals of the collected data using descriptive statistics to determine whether the assumptions of a given procedure were met. The appropriate procedure(s) were applied based on assumption criteria for all repeated measure data collected. To test the hypothesis of no difference in variable means among community groups, both within a year and between years, ANOVA was employed; multiple comparisons used the Tukey test (includes Bonferroni correction for multiple comparisons (Rice 1989)). In cases where normality (Shapiro-Wilk W test) or equal variance (Brown-Forsythe test) assumptions on the residuals were not met at the $P = 0.05$ level, the data were subjected to the Kruskal Wallis test (rank sums); multiple comparisons following Kruskal Wallis test used Dunn’s method for joint ranking (includes Bonferroni correction for multiple comparisons (Rice 1989)). PC-ORD: multivariate analysis of ecological data (version 6.0, MjM Software Design, Gleneden Beach, Oregon; McCune and Mefford 2011) and JMP® Pro (Version 12.2.0, SAS Institute Inc., Cary, NC, 2015-2017) were used for statistical tests and graphs. The ≤ sign is used in the results section when several pairwise comparisons are significant and only the largest significant *P* value is reported.

RESULTS

Community groups 2 and 3 are mixed bottomland hardwood forests located at higher elevations on the active natural levee and on remnant levees separated by intervening intermediate elevation flats. Flooding occurs during overbank flooding, is of relatively short duration, and of limited depth. Canopy species composition in these two communities consists of sweetgum (*Liquidambar styraciflua* L.), sugarberry (*Celtis laevigata* Willd.), box elder (*Acer negundo* L.), American elm (*Ulmus americana* L.), laurel oak (*Quercus laurifolia* Michaux), green ash (*Fraxinus pennsylvanica* Marshall), water hickory (*Carya aquatic* [Michaux f.] Nuttall, Walter H.), and sycamore (*Platanus occidentalis* L.) and dominant sapling species include pawpaw (*Asimina triloba* [L.] Dunal.), possumhaw (*Ilex decidua* Walter), and the exotic shrub Chinese privet with proportions of these species differing between these two community groups (Table 3.2). Minor canopy and sapling species include laurel oak, sugarberry, red mulberry (*Morus rubra* L.), American holly (*Ilex opaca* Aiton), and ironwood (*Carpinus caroliniana* Walter). These groups are separated by the size class of trees with group 2 having 24.7% of trees > 50 cm DBH and group 3 with only 7.6% of trees this large. Community group 4 is a backswamp located in two adjoining, relatively shallow sloughs with a canopy dominated by bald cypress at 91.7% of tree basal area; the sapling layer is sparse and dominated by water elm (*Planera aquatic* Walter ex JF Gmelin) and possumhaw (Table

3.2). Other minor species within community group 4 include swamp cottonwood (*Populous heterophylla* L.), red maple (*Acer rubrum* L.), and sweetgum. Flooding occurs via overbank and backwater flooding with seasonal interaction with ground water. Duration of inundation is variable depending on amount and seasonality of rainfall, thus group 4 may experience several periods of inundation and dry down in a single year, and has an extended inundation maximum depth of 0.6 to 0.9 m. However, water marks on tree trunks indicate pulse inundation depths of 1.8 to 2.4 m do occur.

Community group 1 occupies an intermediate elevation as intervening flats located between the active levee and relict levees. Species composition is a mix of those species found in the other community groups due to a position intermediate in hydrologic regime and this community exhibits higher tree richness, evenness, and diversity compared to the other community groups. The canopy is dominated by green ash, sweetgum, sugarberry, overcup oak (*Quercus lyrata* Walter), and bald cypress with pawpaw, possumhaw, sugarberry, and water elm in the sapling layer (Table 3.2). Additional minor species include water hickory, green haw (*Crataegus virdis* L.) and parsley hawthorne (*Crataegus marshallii* Eggl.). Flooding in this community is intermediate in frequency and duration experiencing overbank flooding with occasional interaction with groundwater and receipt of water via backwater flooding. Extended inundation periods have a maximum depth of a 0.05 to 0.3 m, however, water marks on tree trunks indicate pulse inundation depths of 0.9 to 1.5 m do occur.

Tree density expressed as number of trees per hectare was greatest in community group 4 (504) which was significantly greater than the density in groups 2 and 3 (328 and

320, respectively; $F_{3, 16} = 4.56$, $P \leq 0.030$; Table 3.2). Tree basal area was significantly greater in community group 4 at 63.7 m²/hectare compared to groups 1 and 3 (36.4 and 20.6 m²/hectare, respectively; $F_{3, 16} = 7.20$, $P \leq 0.047$; Table 3.2). The percentage of trees within the < 25 cm DBH size class for each community group was 60.6%, 58.0%, 58.2%, and 37.3%, respectively (Table 3.2). The percent of total tree biomass within this DBH class was significantly greater for community group 3 compared to all other groups ($F_{3, 16} = 4.10$, $P \leq 0.049$; Table 3.2). The percentage of trees within the 25-50 cm DBH size class for each community group was 26.6%, 17.3%, 34.2%, and 34.9%, respectively (Table 3.2). Community group 3 has a significantly greater percent of total tree biomass within this DBH size class compared to groups 1 and 2 and group 4 was significantly greater than group 2 ($F_{3, 16} = 10.39$, $P \leq 0.048$; Table 3.2). The percentage of trees within the 50-75 cm DBH size class for each community group was 6.4%, 17.3%, 7.6%, and 26.2%, respectively (Table 3.2; Appendix 4). Community groups 4 and 2 have percent total tree biomass values within this DBH size class significantly greater than group 1 and values considerably greater, but not significant, compared to that of group 3 ($F_{3, 16} = 7.20$, $P \leq 0.048$; Table 3.2). The percentage of trees within the > 75 cm DBH size class for each community group was 6.4%, 7.4%, 0%, and 1.6%, respectively (Table 3.2). The percent of total tree biomass within this DBH class was significantly greater for community group 1 compared to groups 4 and 3 ($F_{3, 16} = 6.42$, $P \leq 0.018$; Table 3.2).

The number of sapling/shrub stems per hectare was significantly greater in community groups 2 and 3 (2848 and 5248, respectively) compared to a value of 384 in group 4 ($F_{3, 16} = 6.18$, $P \leq 0.024$; Table 3.2). Sapling basal area was significantly greater in community group 3 at 3.8 m²/ha compared to groups 1 and 4 (1.7 and 0.44 m²/ha, respectively) and group 2 (2.9) was significantly greater than group 4 ($F_{3,\,16} = 7.67$, $P \leq 0.048$; Table 3.2).

Sample plot elevation in meters above sea level based on the mean values of plots within each group showed significant differences (elevation data provided by Hupp, 2013). Mean elevations for each community group were 133.77, 134.43, 134.46, and 132.94 m, respectively (Table 3.2). Elevations of community groups 3 and 4 were significantly greater compared to groups 1 and 4 and group 1 was significantly greater than group 4 ($F_{3,\,16} = 30.33$, $P \leq 0.012$; Table 3.2).

Repeated measures ANOVA results on ANPP factors using community group and year as levels is presented in Table 3.3 (units for ANPP factor values in g/m² per year). There were no significant interactions between the levels community group and year for any of the ANPP factors analyzed ($F_{3,1,3} \leq 1.30$, $P \geq 0.292$; Table 3.3); therefore the use of multi-year means in further analyses is deemed legitimate. Independent significant differences in ANPP factors were present for the levels community group and year (Table 3.3).

The two year mean of total ANPP was significantly greater for community group 2 (1422 g/m²) compared to community groups 3 and 4 (1118 g/m² for both; $F_{3,1,3} = 3.69$, $P = 0.022$; Table 3.3); while community group 1 (1322 g/m²) did not differ significantly from the other groups. Total ANPP was significantly higher in 2011 compared to 2012 (1351 and 1140 g/m², respectively; $F_{3,1,3} = 7.10$, $P = 0.012$; Table 3.3). The two year mean of tree wood/stem ANPP was significantly greater for community group 2 (660 g/m²) compared to community groups 3 and 4 (402 and 381 g/m², respectively; $F_{3,1,3} = 3.35$, $P = 0.031$; Table 3.3); while community group 1 (597 g/m²) did not differ significantly from the other groups. Tree wood/stem ANPP was significantly higher in 2011 compared to 2012 (606 and 414 g/m², respectively; $F_{3,1,3} = 6.28$, $P = 0.018$; Table 3.3).

The four year mean of tree wood/stem ANPP did not differ significantly among community groups ($F_{3,3,9} = 2.18$, $P = 0.099$) nor among years ($F_{3,3,9} = 2.69$, $P = 0.055$; Table 3.3). The four year tree wood/stem ANPP was highest for community groups 1 and 2, intermediate for group 2, and least in group 4 (520, 530, 344, 462 g/m², respectively; Table 3.3). The annual tree wood/stem ANPP was highest in 2011 (606 g/m²) while the values for 2012, 2013, and 2014 were less, but nearly equivalent (414, 409, 427 g/m², respectively).

ANPP from the sapling wood/stem fraction was significantly greater within community groups 2 and 3 (72.6, 63.2 g/m², respectively) compared to community group 4 (5.5 g/m²) with community group 1 having an intermediate value of sapling wood production, but not differing significantly from the other groups (34.0 g/m²; $F_{3,1,3} = 7.14$, $P = 0.0008$; Table 3.3). Sapling wood production did not differ significantly between years 2011 and 2012 (40.2 and 47.4, respectively; $F_{3,1,3} = 0.41$, $P = 0.527$; Table 3.3).

The two year mean of total litterfall ANPP was significantly greater for community group 4 compared to group 3 (732 and 653 g/m², respectively), while the intermediate values of groups 1 and 2 did not differ significantly from the other groups (690 g/m² for both; $F_{3,1,3} = 3.00$, $P = 0.045$; Table 3.3). Total litterfall ANPP did not differ significantly between years 2011 and 2012 (705 and 678 g/m², respectively; $F_{3,1,3} = 2.17$, $P = 0.150$;

Table 3.3). The leaf fraction of litterfall ANPP was significantly greater in community group 4 (659 g/m²) compared to community groups 2 and 3 (599 and 578 g/m², respectively; $F_{3,1,3} = 5.09$, $P = 0.005$; Table 3.3); community group 1 was nearly identical to group 2; however group 1 did not differ significantly from any groups (601 g/m²; Table 3.3). Leaf production did not differ significantly between years 2011 and 2012 (609 and 610 g/m², respectively; $F_{3,1,3} = 0.01$, $P = 0.942$; Table 3.3). The reproductive fraction of total litterfall ANPP was fairly similar across community groups with no significant differences among groups (89.5, 90.9, 74.8, and 72.9 g/m², respectively; $F_{3,1,3} = 1.76$, $P = 0.174$; Table 3.3). Reproductive production was significantly greater in 2011 compared to 2012 (96.3 and 67.8 g/m², respectively; $F_{3,1,3} = 15.83$, $P = 0.0004$; Table 3.3). The difference is due in part to a mast year for the laurel oak and overcup oak in 2011 when oak reproductive mass was five times greater than in 2012; and 50% higher sweetgum fruit mass recovered in 2011 compared to 2012.

Baseline tree dry biomass (winter of 2010/11) among community groups ranged widely and showed considerable plot to plot variation with values of 26194, 33513, 11574, and 33199 g/m², respectively; community group 4 was significantly greater than group 3 ($H_{0.05,\,3} = 10.57$; $P \leq 0.023$; Table 3.4). Likewise, end of study tree biomass (winter 2014/15) showed the same relationships as baseline values (28273, 35633, 12950, and 35047, respectively; $H_{0.05,\,3} = 9.83$; $P \leq 0.038$; Table 3.4). Tree biomass gain over the four year sampling period also showed considerable plot variation and did not differ significantly among community groups (2079, 2120, 1316, and 1849 g/m², respectively; $F_{3,\,16} = 1.19$; $P = 0.34$; Table 3.4). The mean annual percent gain in tree biomass over four years exhibited less within group variation with community group 3 significantly greater compared to group (2.89 and 1.38%, respectively); community groups 1 and 2 exhibited similar values, but did not differ significantly from other groups (2.04 and 1.71%, respectively; $F_{3,\,16} = 3.54$; $P \leq 0.039$). Baseline sapling dry biomass (winter of 2010/11) showed considerable plot to plot variation within community groups and ranged widely with values of 392, 659, 823, and 110 g/m², respectively. Sapling baseline mass was highest in community groups 3 and 2 which were significantly greater than group 4 ($F_{3,\,16} = 6.89$; $P \leq 0.023$; Table 3.4). Likewise, end of study sapling biomass (winter 2012/13) showed the same relationships as baseline values (460, 804, 949, and 121 g/m², respectively; $F_{3,\,16} = 7.15$; $P \leq 0.015$; $P \leq 0.038$; Table 3.4). Sapling biomass gain over the two year sampling period showed considerable plot variation, but did show significant differences among community groups with community groups 2 and 3 greater than group 4 (68.0, 145.1, 126.4, and 10.9 g/m², respectively; $F_{3,\,16} = 4.88$; $P = 0.041$; Table 3.4). The mean annual percent gain in sapling biomass over two years exhibited a wide range of values, but due to excessive plot to plot variation, did not differ significantly among community groups. Mean sapling percent biomnass gain was highest in community groups 2 and 4 (12.2 and 12.0%, respectively) compared to the lower, but similar values of groups 1 and 3 (8.1 and 7.8%, respectively; $F_{3,\,16} = 0.39$; $P = 0.76$; Table 3.4).

Measured components of total ANPP (wood biomass, sapling biomass, leaf litter, reproductive litter) were calculated as mean percentages of the total for a two year period and comparisons were made by components among community groups (years 2011 and 2012, Figure 3.2; Table 3.4). The percentage of total ANPP represented by tree stem/wood production was higher for community groups 1 and 2 compared to groups 3 and 4, but did not exhibit significant differences among groups (43.1, 43.5, 35.1, and 33.1%, respectively; $F_{3, 16} = 1.82$; $P = 0.18$; Figure 3.2; Table 3.4). The percentage of total ANPP represented by sapling stem/wood production was highest for community groups 2 and 3 (5.9 and 5.7%, respectively) compared to group 4 (0.49%) while community group 1 had an intermediate value of 2.7% which did not differ significantly from the other groups ($H_{0.05, 3} = 11.72$; P ≤ 0.039; Figure 3.2; Table 3.4). Leaf litter represented the highest percentage of total ANPP for all community groups. Community group 4 had the highest percentage of litter production (59.9%) and was significantly greater than the percentages of groups 1 and 2 (47.2 and 44.1%, respectively) while the intermediate value of 52.6% within community group 3 did not differ significantly from the other groups ($F_{3, 16} = 5.26$; $P = 0.041$; Figure 3.2; Table 3.4). The percentage of total ANPP attributed to the reproductive litter fraction was very similar among community groups with no significant differences (7.0, 6.5, 6.7, and 6.6%, respectively; $F_{3, 16} = 0.10$; $P = 0.95$; Figure 3.2; Table 3.4).

We calculated a productivity efficiency ratio (two year mean total ANPP ÷ tree + sapling basal area) to compare community group production rates over different basal area values. Community group 3 showed the highest efficiency ratio of 46.9 and was significantly greater than group 4 (18.2); the ratio for group 1 (35.8) was also significantly greater than group 4. The group 2 ratio (32.9) did not differ significantly from the other groups ($F_{3, 16} = 9.41$; $P = 0.0024$; Table 3.4).

Over the course of the study there were trees and saplings that suffered mortality, sapling stems that grew into the tree class, and seedlings or ramets (clonal sprouts) which grew into the sapling class (Table 3.5). Tree mortality over a period of four years (2011-2014) was greatest in community group 2 (7 trees), intermediate in groups 1 and 3 (3 and 4 trees), and lowest in group 4 (2 trees; Table 3.5). Mass loss due to tree mortality was greatest in community group 2 (5124 kg), intermediate in groups 3 and 1 (2658 and 1144 kg, respectively), and least in group 4 (211 kg; Table 3.5). The percentage of tree loss mass over the course of the study within community groups was calculated as: {group tree loss mass ÷ (end of study tree biomass + group tree loss biomass)}*100; mortality mass was not included in ANPP calculations. The percentage of biomass loss due to tree mortality was highest in community group 3 at 7.6%, slightly less in group 2 (5.4%), and relatively lower in community groups 1 and 4 (1.6% and 0.24%, respectively). The tree mortality rate across community groups over a period of four years was 4.1% (382 trees originally tagged; 16 trees died; 11 saplings entered tree class).

Eleven saplings exceeded 10 cm in DBH during the course of the study and grew into the tree class; biomass for these species was included in ANPP calculations with biomass values being moved between categories. Five saplings grew into the tree class within community group 3, four in community group 2, and one each for groups 1 and 4 (Table 3.5). A total of 92 seedlings or ramets grew to one meter in height in the two year period of 2011 and 2012 and thus became included in the sapling class (sapling data was not collected in 2013 or 2014). Counts for stems growing into the sapling class were similar for community groups 1, 2, and 3 (24, 32, and 30, respectively; Table 3.5) while only five stems entered the sapling class in group 4. Pawpaw dominated sapling stem grow-in within groups 1 and 2, while community group 3 experienced codominant grow-in by pawpaw and Chinese privet. Green ash and swamp cottonwood stems were the only species to reach the sapling class in group 4. Sapling stem mortality over the two year period was 14 stems across all communities. Sapling stem mortality was highest at 6 stems within community group 2, intermediate in groups 1 and 3 (3 and 4, respectively; Table 3.5), and only one stem died in community group 4. The sapling mortality rate across community groups over a period of two years was 2.0% (618 originally tagged; 14 sapling stems died; 96 stems entered sapling class).

DISCUSSION

Annual differences in flooding, precipitation, and drought stress often leads to very large differences in year to year total ANPP values, introducing large variations making it difficult to compare years statistically (Megonigal et al. 1997). While researchers often find large year to year differences in wood biomass ANPP values, the differences in year to year contribution to ANPP from leaf and reproductive tissue shows much less variation. For example, Schilling and Lockaby (2005) reported the following values for ANPP along the Altamaha River in Georgia in two successive years (units are g/m^2): 1999 – litter range 560-600, tree wood range 640-800, total 1240-1440; 2000 – litter range 490-560, tree wood range 240-410, total 790-970. In this study, tree wood ANPP showed an annual mean range of 409-606 g/m^2 over a four year period (2011-2014) while total litterfall annual mean over a two year period (2011-2012) was 678 and 705 g/m^2, respectively and total ANPP was 1351 and 1140 g/m^2, respectively (Table 3.3). Leaf and reproductive tissue collected in litter boxes tend to account for a higher percentage of total ANPP compared to wood ANPP in southeastern forested wetlands. For example, Megonigal et al. (1997) reported a mean litter contribution of 62% to total ANPP, Ozlap et al. (2007) reported 63%. We found an average of 56% over a two year period (2011-2012) across all plots and suspect our value is slightly less because we included sapling wood in our calculation of total ANPP. In light of this, it seems studies should concentrate resources to extending annual DBH measures for as many years as practicable, even at the expense of reducing litterbox data, to produce a better estimate of long term ANPP and carbon storage and provide more accurate values to be used in long term models.

Our study shows similar values of tree basal area and ANPP compared to other regional studies in forested wetlands. Krauss et al. (2009) reported tree basal area values up to 87 m^2/ha for bald cypress dominated tidal freshwater swamps and freshwater floodplain backswamps in South Carolina, Georgia, and Louisiana. The range of tree basal area for bald cypress dominated freshwater floodplain backswamps in this study ranged from 45-94 m^2/ha. Ozlap et al. (2007) reported an ANPP range of 477-1117 g/m^2 (mean 743) for water tupelo/bald cypress dominated tidal freshwater wetlands on Bull Island, South Carolina, and Pierfelice et al. (2017) reported mean ANPP of 1061 g/m^2 in similar wetlands on the floodplain of the Waccamaw River in South Carolina.

Megonigal et al. (1997) measured ANPP over a two year period on the floodplain of the Savannah River with plots grouped across a flooding/elevation gradient. From the data presented in their paper, we calculated a productivity efficiency ratio (mean ANPP/tree basal area) of 33.2 for their “dry” category, 38.2 for their “intermediate” category, and 14.2 for their “wet” category. Since they did not include sapling wood and we did; our productivity efficiency ratio (Table 3.4) was recalculated excluding sapling wood. The values are remarkably similar with our higher elevation groups having a ratio of 36.8, intermediate plots at 35.3, and backswamp plots at 17.5. This ratio would be a useful tool to compare ANPP results reported in the literature, particularly when basal area of trees differs considerably among studies and for comparative purposes of carbon sequestration efficiency.

There have been many studies that have calculated ANPP in forested wetlands in the southeastern US using incremental increase in DBH and litterfall; however, there are other pools of potentially significant sources of aboveground ANPP that are not addressed. Most studies dismiss sapling wood (stems < 10 cm DBH) as insignificant and conclude that the majority of the sapling layer contribution to ANPP is within the contents of the littertraps (Whittaker et al. 1974, Megonigal et al. 1997, Schilling and Lockaby 2005, Ozlap et al. 2007, Pierfelice et al. 2017 are just a few examples). In our study, the range of sapling wood contribution to aboveground ANPP at the plot level was 0.02-18.7% and over a two year period accounted for a mean of 5.8% of total measured aboveground ANPP in community groups 2 and 3 (3.7% overall by plot mean for all community groups), suggesting that, at least in the areas experiencing occasional flooding of ephemeral duration with a moderate to dense sapling layer, sapling wood should be considered in ANPP calculations.

Another potentially significant source of ANPP within forested wetlands and floodplain forests in the southeast is the large, woody grass species cane (*Arundinaria gigantea* [Walt.] Muhl.). We could find no studies that calculated the contribution of cane to ANPP in these systems (although we cannot rule out that cane was included in the herbaceous layer calculations in some studies). While this study failed to include cane in calculations of ANPP as well, cane was included within point intercept data for woody vegetation within 2 m of ground surface (Chapter 2). Additionally, in this study, litter from cane was separated and not included in ANPP calculations; however, we cannot say whether similar studies of ANPP in these systems separated cane from litter box contents. Nelson et al. (2016) measured litterfall via littertraps over a year in cane-breaks in southern Illinois riparian zones and reported a mean plot value of 400 g/m²/year (dry weight) for cane litter (confirmed by personal communication; Amanda M. Nelson (09/20/17) that all mass reported was solely from cane). This value is significant and does not capture the mass of new culms produced annually from an extensive rhizome system. Ruangpanit (2000) measured primary productivity of the pygmy bamboo (*Arundinaria pusilla* A. Che.) within dry dipterocarp forests in Thailand. Aboveground ANPP (all living tissue) for pygmy bamboo based on the sum of positive increase in biomass ranged from 208-287 g/m² (dry weight) while the belowground ANPP was greater by an order of magnitude (mean of 2844 g/m² dry weight). Neither of these studies measured percent cover or density of cane culms, but it is assumed that culm density was very high. We found that cane represented 13.1, 30.1, 30.0, and 0.0% of all positive point intercept hits (community groups 1-4, respectively; Figure 3.3).

Observationally, cane was common in community groups 2 and 3 with a variable density from moderate to very dense. We conclude from our point intercept data, observations, and data from Nelson (2016) and Ruangpanit (2000) that our estimates of

ANPP on the Congaree River floodplain are underestimated (at least for community groups 2 and 3) and future work should address the contribution of cane to ANPP in forested wetlands, bottomland hardwood forests, and riparian zones.

Woody vines (lianas) are common on the Congaree floodplain and may also represent a potentially significant source of ANPP. Major vine species encountered in this study include pepper vine (*Ampelopsis arborea* [L.] Koehne), cross-vine (*Anisostichus capreolata* [L.] Bureau), trumpet vine (*Campsis radicans* [L.] Seemann), Virginia creeper (*Parthenocissus quinquefolia* [L.] Planchon), roundleaf greenbrier (*Smilax rotundifolia* Walter), poison ivy (*Toxicodendron radicans* L.), and muscadine grape (*Vitis rotundifolia* Michaux). We could find no reports of biomass or productivity measures or allometric equations in the literature for the woody vine species encountered at the study site. Woody vines exhibit a strong positive correlation with canopy openings and forest edges. Londre and Schnitzer (2006) reported vine stem densities were 4x greater within 15 m and 6x greater within 5 m of a forest edge in mixed hardwood forests in southern Wisconsin. Allen (2007) reported a strong inverse relationship between woody vine stem destinies and distance from the river channel on the Congaree River floodplain and a stem mortality rate much greater compared to shrubs, saplings, and trees. We did not measure DBH of woody vines in this study but did collect a relative density measure. We found that woody vines represented 35.3, 30.5, 27.0, and 15.5% of all positive point intercept hits (community groups 1-4, respectively; Figure 3.3).

Allen et al. (2005) reported mean densities of woody vine stems > 2.5 cm on the Congaree River floodplain of 56 stems/ha in backswamps to 215 stems/ha in bottomland hardwood forest plots (although DBH was recorded, no attempt was made to calculate biomass or productivity). Allen (2007) states that woody vine stems account for approximately 10% of all woody stems ≥ 2.5 cm DBH on the Congaree River floodplain. Comparatively, we found sapling and tree stem densities of 504 and 384 stems/ha in the backswamp (respectively) and maximums of 376 and 5248 stems/ha in bottomland hardwood forest plots, respectively (Table 3.2). Additionally, Allen et al. (2010) reported a maximum woody vine basal area of 0.50 m^2/ha on the Congaree River floodplain, while in our study the mean sapling basal area was 2.2 m^2/ha and sapling wood accounted for 3.7% of overall mean aboveground ANPP across all plots.

Allen (2007) and Allen et al. (2010) indicate that woody vine densities are increasing in the southeast, and this trend is likely to continue and accelerate due to increased forest fragmentation and increased atmospheric carbon dioxide and severe weather associated with climate change. Their literature reviews also indicate that the ratio of leaf area to stem area is 4-5 times greater compared to saplings and trees. Woody vine leaf and reproductive tissue was included in ANPP calculations in this study, and since the leaf/stem ratio of vines is so high, we conclude that inclusion of woody vine stem tissue would have little effect on our calculated ANPP values. If we extrapolate the maximum woody vine basal area of 0.50 m^2/ha given by Allen et al. (2010) based on our sapling results of 2.2 m^2/ha, vine wood would only contribute approximately an additional 0.84% to our ANPP values, even if we ignore the higher leaf/stem ratio of vines.

The herbaceous layer is also rarely included as a component of ANPP calculations in forested wetland studies. We followed herbaceous percent cover in this study; however, we did not measure herbaceous layer biomass. Two studies on the floodplain of the Waccamaw River shared plots in a tidal freshwater forested wetland with data overlapping for one year in 2012 (Ensign et al. 2013, Pierfelice et al. 2017). Compiling data from both papers, the herbaceous layer contributed 8.9% to total ANPP. Ensign et al. (2013) also collected the same data from a tidal freshwater forested wetland along the Savannah River where herbaceous layer annual production was measured as 187 g/m^2. Taking data from both papers and assuming that biomass from incremental DBH was equivalent to recorded litterfall (a conservative estimate), then the herbaceous layer could represent up to 25% of aboveground ANPP in these tidal freshwater forested wetlands. The list of plant species reported for the herbaceous layer from these studies was very similar to community group 4 in this study with some overlap to community group 1. We found mean percent herbaceous cover to be 12.2, 9.0, 14.4, and 15.7% in community groups 1-4, respectively, in our study (mean of three readings taken throughout 2011; see Chapter 2). Unfortunately, neither percent cover nor frequency data were reported in Ensign et al. (2013); therefore, we are unable, based on their work, to estimate what contribution the herbaceous layer may contribute to ANPP in our plots.

Studies have shown that the community composition and structure of the vegetation, and thus the productivity rate, in the Congaree Swamp is dependent upon the frequency, timing, and duration of saturated soil conditions and inundation, sedimentation dynamics, and microtopography (Patterson et al. 1985, Meitzen 2006). Seedling germination, recruitment, and survival are known to be sensitive to small changes in water levels with timing of inundation especially critical in southeastern floodplain forests like the Congaree Swamp (Sharitz et al. 1986, Walls et al. 2005). Dam release is often managed so as to keep impoundment levels as consistent as possible, leaving the downstream floodplain drier when precipitation is low and wetter when precipitation is high. The normal cycle of inundation and dry down is thus altered, leading to changes in productivity, increased seedling and sapling mortality, decreased recruitment, decline in the overstory, and a shift in community composition and structure (Wharton et al. 1982, Kellison et al. 1998, Ernest and Brook 2003). Changes to the hydrologic regime within the Congaree Swamp have shifted the seasonal ground water levels, altered root zone hydrology, and impacted microsite characteristics. Data indicate a community shift towards less flood tolerant tree species in the Congaree floodplain, at least in part, due to operation of the Saluda Dam, and this has most likely affected productivity (Minchin and Sharitz 2007).

Agriculture and development often is accompanied by changes to forested wetland hydrology – the main driving force of wetlands (Lockaby 2009, Ellis 2011). The increase in impervious surface associated with development can drastically increase runoff within a watershed, increase influx of pollutants, and overwhelm the capacity of wetlands to absorb sediment loads and buffer stormwater surges. Urbanization and agriculture are major sources of nutrient and pesticide runoff to watersheds, while wetlands are known to ameliorate the effects of these pollution sources, the capacity can be exceeded and species may be detrimentally affected decreasing productivity and/or a compositional shift may result (Galicki et al. 2002). Younger sediments and frequently flooded features such as point bars exhibit elevated concentrations of pollutants within the Congaree Swamp placing an additional stressor on productivity (Meitzen 2006). Sediment type and deposition rates strongly influence the productivity, composition, succession, and structure of the floristic community of bottomland forests (Hodges 1997, Cavalcanti and Lockaby 2005, Cavalcanti and Lockaby 2006, Hupp et al. 2008, Jolley et al. 2010), and these sediment dynamics have been altered substantially within portions of the Congaree watershed by flow control, development, agriculture, and logging. The rate of sediment transport and deposition increased greatly following European settlement of the Congaree watershed, although quantities have decreased somewhat in recent decades due to implementation of best management practices and abandonment of farm land (Patterson et al. 1985). The hydrologic regime can be said to have become more homogenous within the Congaree Swamp which improves habitat suitability for more generalist organisms and reduces establishment barriers for exotic plant species (Catford et al. 2011). Productivity varies among community types across forested floodplains, and this variation can be attributed to the magnitude or spatial and temporal characteristics of inundation and dry down patterns and to heterogeneity in both the rate and composition of deposited material. The integrity of hydrological connections, sedimentation dynamics, and flooding intensity and periodicity is necessary to maintain the diversity, composition, structure, and productivity rates within these systems.

The interrelated dynamics of hydrology and sedimentation both help shape and interact with small scale elevational differences on southeastern floodplain forests to yield communities composed of species best suited to the characteristics of a given habitat. Productivity varies among community types across forested floodplains, and this variation can be attributed to the magnitude of, and spatial and temporal characteristics of, inundation and dry down patterns coupled with heterogeneity in both the rate and composition of deposited material. We found that the annual percentage of mass gain for tree wood is greater at higher and intermediate elevations on the Congaree floodplain compared to the backswamp. Additionally, our results suggest that the percentage of tree wood gained annually is greater at a given elevation for plots having the majority of tree biomass in younger trees. These observations are best illustrated by our calculated metric - productivity efficiency ratio (Table 3.4). Even though the efficiency of tree mass gain is lower for areas having younger trees, the actual magnitude of mass gain and thus carbon sequestration is greater in areas having a larger proportion of very large trees. Sapling density and biomass is greatest at higher elevations on the floodplain and sapling wood should be considered in ANPP estimations, at least for areas that rarely flood. We also suggest that the contribution of cane to ANPP calculations may result in a considerable underestimation of productivity in floodplain forests. We conclude that topographic position, a surrogate for both hydrology and sedimentation, as well as stand age and size metrics result in differing productivity rates and thus carbon sequestration within forested floodplains of the southeast.

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Table 3.1. Timeline of data collection used to determine aboveground ANPP in this study.

Tree DBH	Sapling DBH/BA	Litter box collection Year 1	Litter box collection Year 2
Winter 2010/2011	Winter 2010/2011	Litter collection start = 12/14/2010	Litter collection start = 01/06/2012
Winter 2011/2012	Winter 2011/2012	02/16/2011	02/17/2012
Winter 2012/2013	Winter 2012/2013	03/24/2011	03/23/2012
Winter 2013/2014	N/A	05/07/2011	05/02/2012
Winter 2014/2015	N/A	06/07/2011	07/13/2012
		07/18/2011	09/05/2012
		09/13/2011	10/17/2012
		10/10/2011	11/12/2012
		11/18/2011	12/13/2012
		Final collection date 01/06/2012	Final collection date 01/29/2013

Table 3.2. Summary of species composition and structure of community groups within the study area on the Congaree River floodplain.

Parameters from winter 2010/2011 baseline data	Community Groups - sample plot group means (N=5 plots per group)			
	Group 1 FRPE/LIST/CELA	Group 2 LIST	Group 3 CELA/ACNE	Group 4 TADI
Basal area (m^2/hectare)				
Trees **4 > 1 = 3**	36.4 ± 3.6	44.8 ± 9.5	20.6 ± 2.5	63.7 ± 8.3
Saplings/shrubs **3 = 2 > 4; 3 > 1**	1.7 ± 0.4	2.9 ± 0.7	3.8 ± 0.7	0.44 ± 0.2
$F_{3,16} \geq 7.20$; $P \leq 0.048$				
Density of woody stems (stems/hectare)				
Trees	376	328	320	504
Saplings/shrubs	1392	2848	5248	384
Dominant tree species – based on % by species of total tree basal area (m^2) within community group	LIST 23.7% FRPE 23.2% CELA 12.6% QULY 9.2% TADI 7.7%	LIST 71.2% ULAM 8.2% CELA 7.3% ACNE 3.8% PLOC 2.9%	CELA 30.9% ACNE 25.5% LIST 10.2% ULAM 7.0% QULA 6.9% FRPE 6.8%	TADI 91.7% PLAQ 3.6% POHE 1.7% LIST 1.2% ACRU 1.1%
Dominant sapling species – based on % by species of total sapling basal area (m^2) within community group	ASTR 41.7% ILDE 33.7% CELA 17.7% PLAQ 4.4% LIST 2.42%	ASTR 67.5% QULA 8.6% ILOP 6.7% CELA 5.6% ACNE 3.6%	ASTR 41.1% LISI 31.0% ILDE 23.8% ULAM 2.3% PLOC 1.9%	PLAQ 53.8% ILDE 23.2% TADI 17.1% CEOC 2.8% QULA 1.2%
Mean elevation of community group (meters above sea level) **$F_{3,16} = 30.33$; $P \leq 0.012$; 3 = 2 > 1 > 4**	133.77 ± 0.23	134.43 ± 0.06	134.46 ± 0.07	132.94 ± 0.08
Qualitative flooding regime based on elevation differences and observations	Annual frequency and intermediate duration	Occasional frequency and ephemeral	Occasional frequency and ephemeral duration	Annual frequency and extended duration

Mean % biomass by tree DBH size class				
Trees < 25 cm DBH **3 > 1 = 2 = 4**	8.9 ± 1.4	7.4 ± 2.2	15.4 ± 3.0	5.2 ± 1.8
Trees 25-50 cm DBH **3 > 1 = 2; 4 > 2**	21.5 ± 4.9	11.6 ± 1.8	50.3 ± 6.3	32.5 ± 6.2
Trees 50-75 cm DBH **4 = 2 > 1**	18.9 ± 8.8	53.4 ± 10.3	34.3 ± 8.7	54.3 ± 3.0
Trees > 75 cm **1 > 4 = 3**	50.7 ± 6.9	27.6 ± 15.7	0.0	8.0 ± 5.2
$F_{3,16} \geq 4.10$; $P \leq 0.049$				
Mean % # of stems by tree DBH size class				
Trees < 25 cm DBH	60.6%	58.0%	58.3%	37.3%
Trees 25-50 cm DBH	26.6%	17.3%	34.2%	34.9%
Trees 50-75 cm DBH	6.4%	17.3%	7.6%	26.2%
Trees > 75 cm	6.4%	7.4%	0.0%	1.6%

Notes: Trees are stems ≥ 10 cm DBH; saplings are stems < 10 cm DBH/BA and > 1 meter in height. Values are the mean of five sample plots within each community group and are the baseline values collected during the winter of 2010/2011. Community groups were defined based on Cluster Analysis, Indicator Species Analysis, and Non-metric Multi-dimensional scaling as presented in Chapter 2. Elevation data provided by Hupp (2013).

Table 3.3. Repeated measures ANOVA results and multiple comparisons among community group and year for ANPP parameters across an elevational gradient on the Congaree River floodplain.

Net ANPP (g/m^2/year)	Source	Degrees of freedom	*F* statistic	*P*-value	Community Group (LSM) (g/m^2)					Year (LSM) (g/m^2)		
					1	2	3	4	SE	2011	2012	SE
Total ANPP (2011-2012)	community group	3	3.69	**0.022**	1322	1422	1118	1118	79.2	1351	1140	56.0
	year	1	7.10	**0.012**	**2 > 3 = 4**					**2011 > 2012**		
	group x year	3	0.81	0.499								
Tree wood/stem ANNP (2011-2012)	community group	3	3.35	**0.031**	597	660	402	381	76.2	606	414	53.9
	year	1	6.28	**0.018**	**2 > 3 = 4**					**2011 > 2012**		
	group x year	3	0.85	0.477								
Sapling wood/stem ANPP (2011-2012)	community group	3	7.14	**0.0008**	34.0	72.6	63.2	5.5	11.4	40.2	47.4	8.0
	year	1	0.41	0.527	**2 = 3 > 4**					no sig. difference		
	group x year	3	1.30	0.292								
Total litterfall ANPP (2011-2012)	community group	3	3.00	**0.045**	690	690	653	732	18.6	705	678	13.1
	year	1	2.17	0.150	**4 > 3**					no sig. difference		
	group x year	3	0.68	0.569								
Leaf litterfall ANPP (2011-2012)	community group	3	5.09	**0.005**	601	599	578	659	15.3	609	610	10.8
	year	1	0.01	0.942	**4 > 2 = 3**					no sig. difference		
	group x year	3	0.37	0.773								
Reproductive litterfall ANPP (2011-2012)	community group	3	1.76	0.174	89.5	90.9	74.8	72.9	7.2	96.3	67.8	5.1
	year	1	15.83	**0.0004**	no sig. difference					**2011 > 2012**		
	group x year	3	0.72	0.546								
Tree wood/stem ANNP (2011-2014)	community group	3	2.18	0.099	520	530	344	462	57.9	2011 = 606 2012 = 414 2013 = 409 2014 = 427 SE = 57.9 no sig. difference		
	year	3	2.69	0.055	no sig. difference							
	group x year	9	1.07	0.398								

Notes: Trees are stems $\geq$ 10 cm DBH; saplings are stems < 10 cm DBH/BA and > 1 meter in height. Community groups were defined based on Cluster Analysis, Indicator Species Analysis, and Non-metric Multi-dimensional scaling as presented in Chapter 2. Only tree data was collected for 2013 and 2014. Results are considered significant at $P < 0.05$. Multiple comparisons are among least square means and conducted using the Tukey Test; there were no significant interactions and those multiple comparisons are not presented.

Table 3.4. Results of analysis of variance and group comparisons conducted on community group means for biomass (dry weight) variables.

ANPP and associated variables	Analysis of variance test statistic and results of multiple comparisons	Community Groups (N = 5 plots per group)			
		Group 1 FRPE/LIST/CELA	Group 2 LIST	Group 3 CELA/ACNE	Group 4 TADI
		mean ± SE	mean ± SE	mean ± SE	mean ± SE
Baseline tree biomass winter 2010/11 (g/m²)	**4 > 3** **$H_{0.05, 3}$ = 10.57; $P \leq 0.023$**	26194 ±3077	33513 ±9204	11574 ±1411	33199 ±4720
End of study tree biomass winter 2014/15 (g/m²)	**4 > 3** **$H_{0.05, 3}$ = 9.83; $P \leq 0.038$**	28273 ±3081	35633 ±9464	12950 ±1505	35047 ±4991
Tree biomass gain over four years 2011-14 (g/m²)	$F_{3, 16}$ = 1.19; P = 0.34	2079 ±243	2120 ±380	1316 ±295	1849 ±318
Baseline sapling biomass winter 2010/11 (g/m²)	**3 = 2 > 4** **$F_{3, 16}$ = 6.89; $P \leq 0.023$**	392 ±101	659 ±153	823 ±141	110 ±56
End sapling biomass winter 2012/2013 (g/m²)	**3 = 2 > 4** **$F_{3, 16}$ = 7.15; $P \leq 0.015$**	460 ±121	804 ±188	949 ±153	121 ±59
Sapling biomass gain over two years 2011-12 (g/m²)	**2 = 3 > 4** **$F_{3, 16}$ = 4.88; $P \leq 0.041$**	68.0 ±21.5	145.1 ±42.4	126.4 ±27.1	10.9 ±4.9
Annual % tree mass gain (four year mean)	**3 > 4** **$F_{3, 16}$ = 3.54; $P \leq 0.039$**	2.04 ± 0.33	1.71 ± 0.23	2.89 ± 0.54	1.38 ± 0.15
Annual % sapling mass gain (two year mean)	$F_{3, 16}$ = 0.39; P = 0.76	8.14 ±0.62	12.19 ±2.84	7.75 ±1.24	12.01 ±7.02
Percent of total ANPP from tree wood	$F_{3, 16}$ = 1.82; P = 0.18	43.08 ±3.93	43.52 ±5.07	35.09 ±3.00	33.08 ±3.70
Percent of total ANPP from sapling wood	**2 = 3 > 4** **$H_{0.05, 3}$ = 11.72; $P \leq 0.039$**	2.69 ±0.89	5.90 ±1.99	5.65 ±1.22	0.49 ±0.23
Percent of total ANPP from leaf tissue	**4 > 2 = 1** **$F_{3, 16}$ = 5.26; $P \leq 0.041$**	47.24 ±3.07	44.08 ±2.95	52.59 ±2.80	59.87 ±3.21
Percent of total ANPP from reproductive tissue	$F_{3, 16}$ = 0.10; P = 0.95	7.00 ±0.85	6.50 ±0.64	6.67 ±0.63	6.57 ±0.69
Productivity efficiency ratio: (mean ANPP 2011-2012) ÷ (tree + sapling baseline BA)	**3 = 1 > 4** **$F_{3, 16}$ = 9.41; $P \leq 0.024$**	35.78 ±3.77	32.88 ±4.87	46.88 ±4.23	18.22 ±1.84

Notes: Groups are those defined via cluster analysis and Indicator species analysis; N = 5 sample plots for each group. F statistic with degrees of freedom from one-way ANOVA testing the hypothesis of no difference in means among groups; multiple comparisons used the Tukey test. In cases where normality (Shapiro-Wilk W test) or equal variance (Brown-Forsythe test) assumptions on the residuals were not met at the P = 0.05 level, the data were subjected to the Kruskal Wallis test (rank sums) and the H statistic with alpha level and degrees of freedom reported; multiple comparisons used Dunn's method for joint ranking. P values reported are either the highest significant value from multiple comparisons or from the analysis of variance when the groups did not differ. Trees are stems ≥ 10 cm DBH; saplings are stems < 10 cm DBH/BA and > 1 meter in height. Community groups were defined based on Cluster Analysis, Indicator Species Analysis, and Non-metric Multi-dimensional scaling as presented in Chapter 2.

Table 3.5. Tree mortality and sapling stem to tree grow-in over four years (2011-2014); sapling mortality and grow-in over two years (2011-2012).

Community Group	Tree mortality species code (dry mass kg)	Tree mass loss: group total mortality (kg)	Total living tree mass: end of study (kg)	% tree mass loss over course of study	Grow-in sapling to tree species code	Sapling grow-in: species code and quantity	Sapling mortality: species code and quantity
1 – FRPE/LIST/CELA	1 ACNE (707) 1 QULY (413) 1 ULAM (24)	1144	70683	1.59%	1 CELA	23 ASTR 1 LIST	2 ASTR 1 CACA
2 – LIST	1 ACNE (302) 3 CELA (218) 2 LIST (3897) 1 ULAM (707)	5124	89083	5.44%	2 ASTR 1 ILDE 1 QULA	29 ASTR 1 CELA 1 LISI 1 QULA	6 ASTR
3 – CELA/ACNE	3 ACNE (2216) 1 ULAM (442)	2658	32375	7.59%	2 ASTR 1 ILDE 1 LISI 1 QULA	18 ASTR 1 ILDE 11 LISI	1 ASTR 3 LISI
4 – TADI	2 PLAQ (211)	211	87619	0.24%	1 PLAQ	2 FRPE 3 POHE	1 FRPE

Notes: See Appendix 7 for conversion of species codes to species names. Mortality mass was excluded from ANPP calculations and all other analyses; grow-in mass was included. $N = 5$ sample plots for each group

Figure 3.1. Forest types in the Congaree National Park and location of the study area; inset shows plots by community groups.

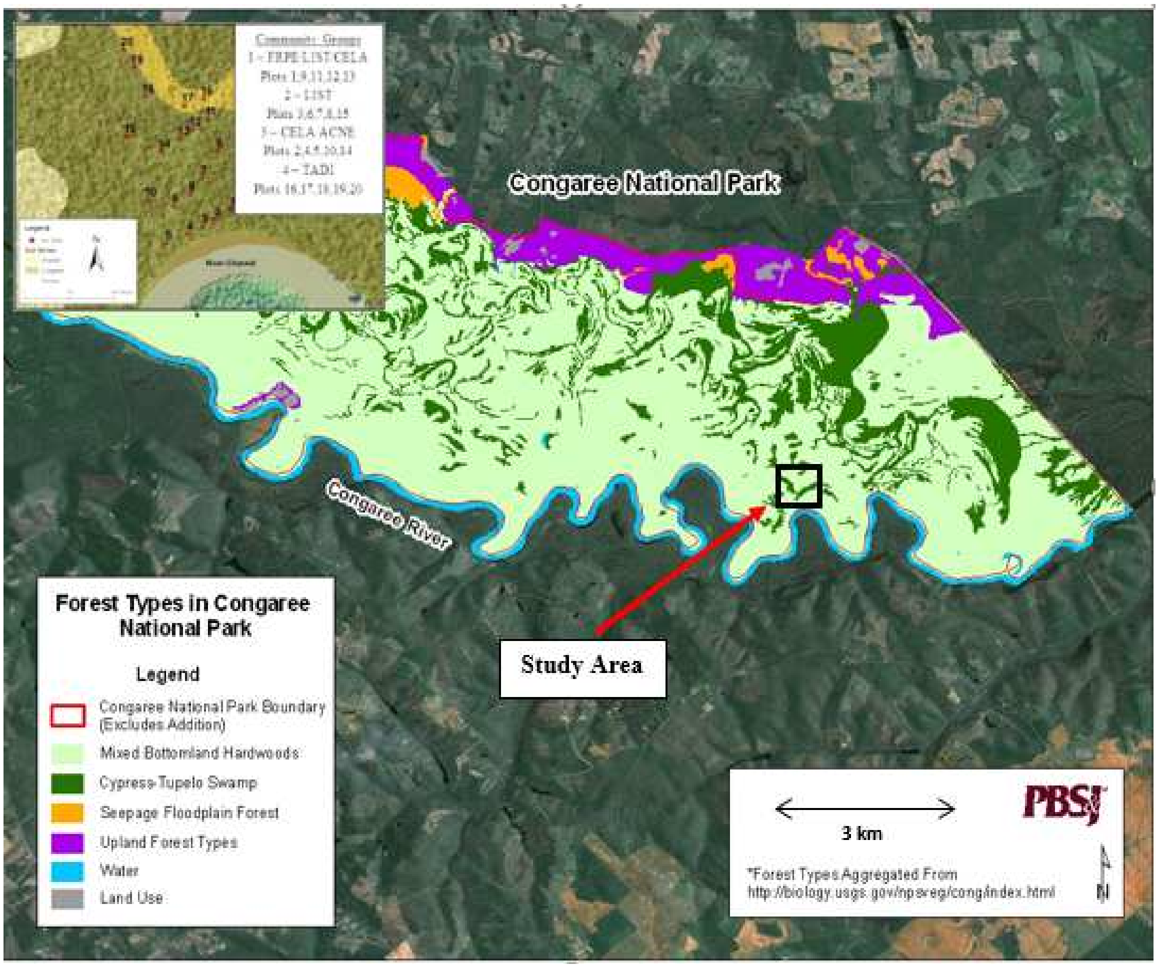


Figure 3.2. Percent of total ANPP by component over a two year period (2011-2012); bars are two year means with error bars SE of the mean.

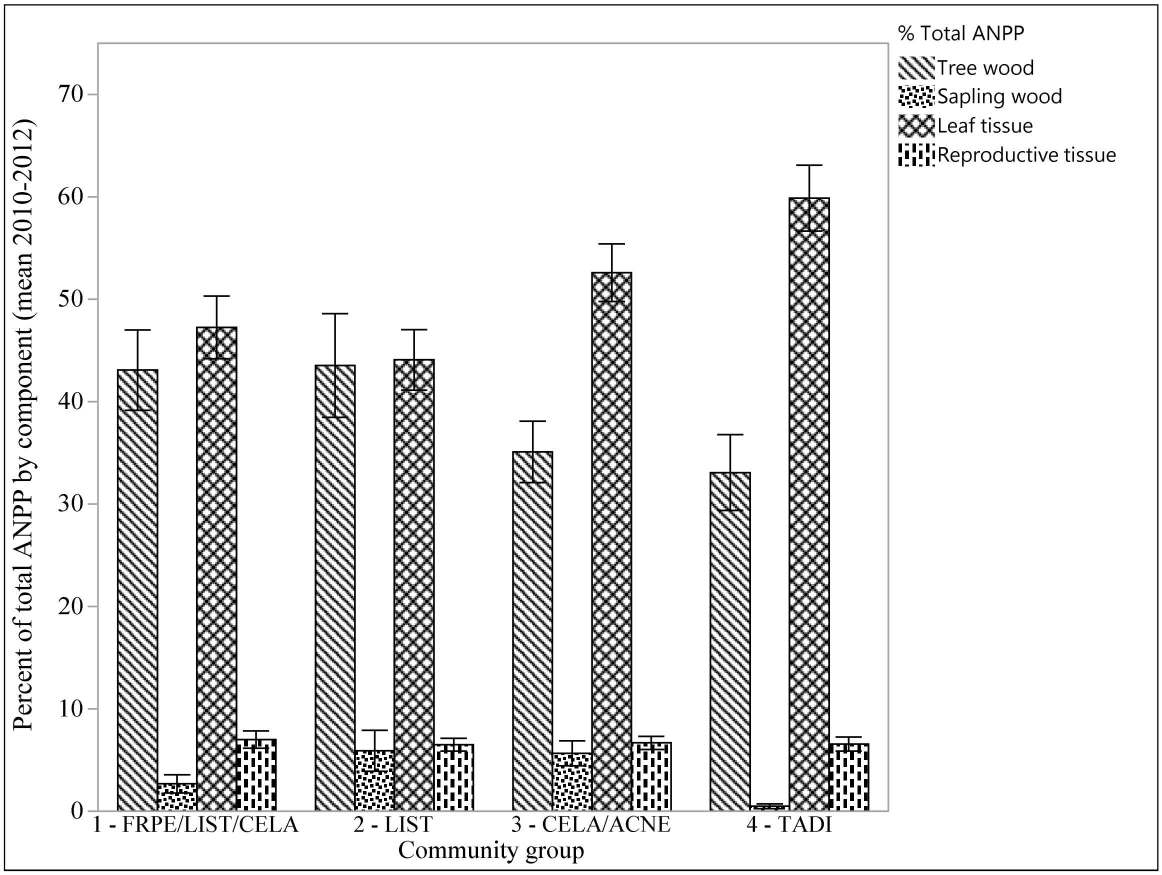
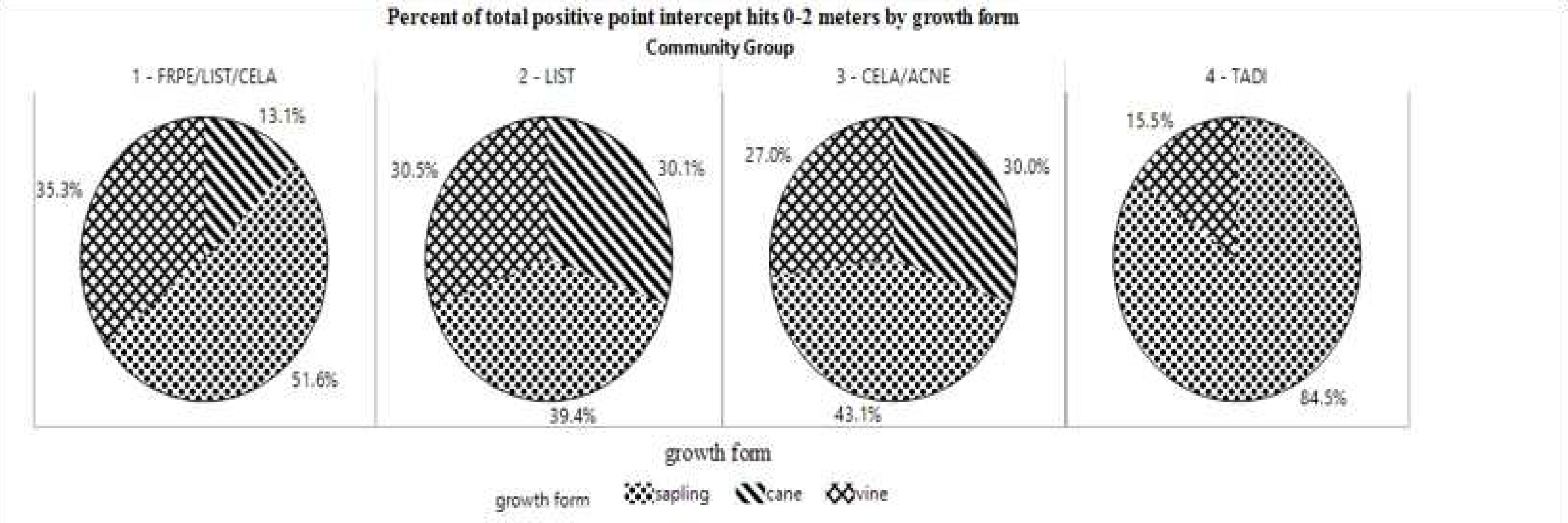


Figure 3.3. Percent of total positive point intercept hits by growth form across four 50 cm intervals from 0-2 meters.



Cumulative Point Intercept % positive 0-2.0 meters	**2 = 3 > 1 = 4** **$F_{3,16} = 8.08$; $P \le 0.047$**	35.36 ±8.09	122.72 ±23.69	100.32 ±22.19	25.76 ±3.44

Notes: See Chapter 2 for details and description of point intercept methods, analyses, and results; ANOVA table excerpt provided below graph.

CHAPTER FOUR

LITTER DECOMPOSITION RATES ACROSS AN ELEVATIONAL GRADIENT WITHIN A FLOODPLAIN FOREST OF THE CONGAREE RIVER, SOUTH CAROLINA, USA

Abstract. The decomposition of site specific, mixed species litter and single species litter was followed over a 100 week period from February 2011 to January 2013 employing the litterbag technique. Litterbags were installed in four communities on the floodplain of the Congaree River near the Orangeburg scarp separating the upper and middle coastal plain regions in South Carolina. The study area consists of a mosaic of low relief fluvial landforms across the floodplain subject to differential flood frequency, length of inundation, and the particle size and quantity of sediment deposited. Adjacent to the river channel and scattered farther from the river are the highest elevation areas which include the active natural levee and relict levees. Community groups 2 and 3 have similar species composition, but differ considerably in tree size distribution and are located within the levee areas. Across the floodplain is a mosaic of flats abutting the levees at slightly lower elevations subject to intermediate inundation (community group 1). The lowest areas are oxbows and historic meander scars experiencing seasonal to semi-permanent flooding known as backswamps (community group 4). Backwater flooding can occur via channels known locally as "guts" which connect levee breeches to lower flats and backwater swamps, thus allowing flooding of these areas at flow levels below bank full. Litter decomposition was rapid with turnover times of 64-80 weeks, but rates did not differ significantly among community groups or between litter types, although there were significant differences in both at given collection periods for percent of original mass remaining. All combinations of litter type and community groups showed an appreciable net accumulation of N, and all except mixed litter in group 1 showed an appreciable net accumulation of P. Accumulation occurred at some point between installation and collection week 22; a steady net mineralization occurred for both N and P after week 22. Litter decomposition rates in this study tended to be higher than those reported in other regional forested floodplain sites. Warm, moist, and humid conditions coupled with nutrient import associated with flooding events and the prevalence of species producing high quality litter appear to create an ideal decomposition environment and likely supports a diverse and dense decomposer community. Although it took 80 to 100 weeks for all initial mass to be reduced to < 2% mass remaining, the contents of the litter bags at week 64 showed little to no structure and would be more accurately described as humus. We conclude that litter decomposition and the cycling of the nutrient contents of the litter are comparatively rapid processes under the prevailing climatic conditions for the area of the Congaree River floodplain studied.

Key words: litter decomposition; litter nutrient cycling; old-growth; bottomland hardwood forest; bald cypress swamp; Congaree National Park

INTRODUCTION

Decomposition of litter is controlled by three main factors; the physiochemical environment, litter quality, and the decomposer community (Hattenschwiler et al., 2005). Leaf production accounts for an average of 43% of the annual aboveground primary productivity in southeastern floodplain forests and the decomposition rate of this litterfall is an important component of nutrient cycling and the composition and population dynamics of the bacteria, fungi, microinvertebrates, and macroinvertebrates that constitute the decomposer community (Conner, 1994). The decomposer community relies upon and processes litterfall into byproducts returning nutrients to the soil which perpetuates the productivity of the forest and helps shape the composition and structure of the floral community and the structure of the soil (Wharton et al., 1982; Hodges, 1997; Messina and Conner, 1998).

In general, at a broad spatial scale, litter decomposition rates are faster with increased temperature and increased precipitation, are maximized when consistent moisture and elevated temperature coincide, and exhibit variance dependent upon litter quality and forest type (Meetemeyer, 1978; Vogt et al., 1986; Zhang et al. 2008). At the local scale, even within the same floodplain, litter decomposition rates differ based on the litter quality of the specific community type, timing of leaf drop for community constituents (early drop coincides with warmer temperatures), nutrient content of deposited sediment, and the hydrologic regime (Groffman et al., 1996). While high quality litter will decay faster if other factors are held constant, litter decay rates are dependent upon numerous other factors at a given location at a given time.

Litter decomposition in southeastern alluvial forests, where length of inundation is low to moderate, is usually rapid due to higher temperatures and relatively consistent moisture with duff formation scant to nonexistent. With drought, litter decomposition slows due to insufficient moisture and suboptimal conditions for the decomposer community (Blair and Crossley, 1988; Hodges, 1997). Prolonged inundation can occur in deepwater swamps compared to alluvial floodplains, thus decomposition is hindered by anaerobic conditions, and organic matter accumulates to a much greater degree with soil organic matter contents of up to 36% (Wharton et al., 1982; Conner and Buford, 1998). Peat or muck accumulation may also occur with depth of deposits positively correlated with water depth and hydroperiod (Brinson, 1990).

Rates of litter decomposition and litter nutrient dynamics can vary significantly among and within forested wetlands subjected to differential flooding regimes. The length of inundation and the degree of flow versus stagnation can differ substantially, even at small spatial scales, resulting in unique balances of available nutrients, moisture and oxygen to drive the decomposition process (Conner and Day, 1991). While decomposition rates may be inversely related to the number and duration of flood events in one wetland, rates may be positively correlated in another indicating a complex interaction between hydrology and decomposition rate; long duration inundation may slow decomposition due to anaerobic conditions while frequent, short duration inundation may increase the decomposition rate by ameliorating moisture limitations (Megonigal and Day, 1988; Groffman et al., 1996; Baker et al., 2001). The communities of bacteria, fungi, microinvertebrates, and macroinvertebrates contribute to litter decomposition and nutrient flux processes and their activities peak with warmer conditions and consistent moisture while their efficacy is related to a sites hydrologic regime (Messina and Conner, 1998). Macrophages can be particularly important due to the fragmentation of litter which increases surface area of litter increasing leaching and the efficiency of bacteria, fungi, and microinvertebrates; additionally, macrophage fecal material diversifies food resources for the decomposer community and increases microbial richness (Conner and Day, 1991; Hattenschwiler et al., 2005).

Litter decomposition rates also vary widely among species (Adams and Angradi, 1996; Cornelissen, 1996). Single species replicates have been used in an attempt to more accurately assess decomposition rates among differing forested areas having different species composition. Replicates of single species with poor litter quality used in conjunction with site specific litter tend to exhibit slower decay rates when edaphic and hydrologic conditions are held constant (Baker et al., 2001). However, it has been shown that nitrogen fluxes and decomposer communities may differ substantially when mixed species and single species litterbags are compared on the same site and results from single species litter should not be extrapolated to site specific litter (Blair et al., 1990). The use of a standardized litter, such as single species litter, across sampling units may aid in isolating the effects of moisture and temperature on decomposition rates, but does little to address specifics of nutrient cycling or assessing the site specific decomposer community (Gingerich and Anderson, 2011). Thus, it is likely that following the decomposition of both mixed and single species litter maximizes the scope of data and information obtained.

Litter quality is most often defined by ratios of nutrients and recalcitrant compounds such as C:N, C:P, N:P, and lignin:N, as well the thickness of the cuticle layer and the toughness/thickness of the leaf structure (Meetemeyer, 1978; Baker et al., 2001; Hattenschwiler et al., 2005; Prescott, 2005). Litter with higher concentrations of nutrients and lower concentrations of recalcitrant components such as lignin, polyphenols, and inhibitory secondary metabolites tend to decompose more rapidly (Vogt et al., 1986). Although litter quality is considered the most important determinant factor controlling litter decay rates (Zhang et al., 2008), diversity of litter is also exceedingly important. In a review comparing litter decay rates for single species decay rates versus mixed species decay rates, Hattenschwiler et al. (2005) reported synergistic effects occurred in 50% of cases with mixed litter decaying up to 65% faster compared to the mean decay rate of component species, no effect was evident in 30% of the cases, and antagonistic effects occurred in 20% of cases with decay rates declining up to 22%. Litter diversity creates a more structurally complex litter layer which yields a diverse array of microclimatic and microhabitat niches supporting a more diverse decomposer community (Hattenschwiler et al., 2005).

Productivity and decomposition rates may be constrained in forested wetlands by N limitation, P limitation, or both with wide N:P ratios often indicating primary N limitation and secondary P limitation (Lockaby and Conner, 1999). Phosphorous is imported via the sediment suspended in flood water and is readily adsorbed by soil particles (particularly clay and organic matter) while water soluble N can be transported downward via percolation. Fine clay particles carry far more P via adsorption and only settle out of impounded or extremely slow moving water, thus deposition is non-uniform across the floodplain. Increases in N are often reported early in litter decomposition studies and is attributed to deposition via precipitation and flood waters, fixation of atmospheric N by microbial community, and the N content in the decomposer community colonizing the litter (Swift et al., 1979). Increases in the density of N fixing plant species has been shown to increase with increasing sedimentation rates (Jolley et al., 2010). When the C:N ratio is greater than 20 the decomposer community tends to immobilize N for growth (i.e. protein synthesis) while the substrate C content is released as carbon dioxide as a by-product of respiration; as the ratio drops below 20, N reaches a luxury level for the decomposer community and N is lost to the soil via mineralization (Bowden, 1987). A C:N ratio of approximately 16 and a C:P ratio near 200 are considered necessary by Brinson (1977) for complete decomposition of litter. A N:P ratio of 12 is considered optimum for the decomposer community to achieve efficient decomposition of litter in southeastern forested wetlands (Lockaby and Walbridge, 1998). As values depart in either direction, a nutrient limitation is placed on the decomposer community. Larger ratios are often associated with a prolonged hydroperiod and low P import while smaller ratios are indicative of shorter hydroperiods but greater P load in the flood water (Lockaby and Conner, 1999).

Evaluation of litter decomposition using open mesh litter bags has been a common technique for decades. Due to the importance of a diverse decomposer community, litter bags should have a suitable mesh size and have the open end loosely secured which will allow access to and egress from the litter (Blair and Crossley, 1988; Conner and Day, 1991). Prescott (2005) evaluated the technique and interpretations of related data and offered several caveats. Even though litter bags have openings, it is unlikely that there is not a degree of soil fauna exclusion which would likely yield erroneous estimates of decomposition rates. The practice of removing fecal excretions of decomposer community macrophages during processing of litter bag contents prior to evaluating mass remaining and subsampling for nutrient lab analyses over estimates loss of mass and mineralization of nutrients. Although the form has changed, it is erroneous to consider that the recalcitrant frass is truly mass loss and nutrients are truly mineralized. While the process of litter decomposition is of paramount importance to site productivity, the rate of the process itself has not been definitively proven to be critical to site productivity. Some studies have indicated that a maximum decomposition limit (or asymptote) is reached at which point the remaining mass in the bag is humus and a slower and different decay dynamic has begun (Prescott, 2005).

MATERIALS AND METHODS

Litter decomposition rates of mixed (site specific) and single species litter was monitored on the floodplain of the Congaree River within Congaree National Park (CONG) via the litter bag technique as part of a comprehensive study which also addressed community structure and annual aboveground primary productivity. A total of 20 data collection plots, blocked by a priori perceived elevation differences, were established in 2010 along five roughly parallel transects with a spacing of approximately 60 m between transects and oriented perpendicular to the river channel. Four 20x25 m plots (0.05 hectare) were established along each transect with the transect azimuth bisecting the short sides of the rectangular plot; one plot in each of four perceived a priori elevation zones (Figure 4.1). Subplots and transects were established within each plot to facilitate collection of various data. After analysis of community data post hoc blocking of plots into community groups was executed using nonparametric techniques (Table 4.1). The study area consists of a mosaic of low relief fluvial landforms across the floodplain subject to differential periods of inundation and sedimentation. Adjacent to the river channel and scattered farther from the river are the highest elevation areas which include the active natural levee and relict levees. Community groups 2 and 3 have similar species composition but differ considerably in tree size distribution and are located within these higher elevation areas (Table 4.1). Across the floodplain is a mosaic of flats abutting the levees at slightly lower elevations subject to intermediate inundation (community group 1). The lowest areas are oxbows and historic meander scars experiencing seasonal to semi-permanent flooding known as backswamps (community group 4). Backwater flooding can occur via channels known locally as “guts” which connect levee breeches to backwater swamps, thus allowing flooding of these swamps at flow levels below bank full (Shelley and Cohen, 2010). The plant nomenclature of Radford et al. (1968) was followed for all vegetation data collected in this study. Four letter codes (first two letters of genus and first two letters of specific epithet) were assigned to each species discussed in this study and these codes are used for brevity within tables; a species list table is provided as Appendix 7.

Decomposition of site specific litter mixtures and single species litter was monitored within each of the four community groups over a 100 week period from February 09, 2011 through January 29, 2013. Freshly fallen litter was collected in suspended hammocks constructed of 1.25 cm PVC pipe and 1 mm fiberglass screen between October 01 and December 15, 2010 (Table 4.2). Three hammocks were placed in each community group to obtain site specific litter mixtures (Figure 4.1; Table 4.1). Single species litter was collected from three hammocks placed under a mature, isolated white oak (*Quercus alba* L.) at the lead author's home in Asheville, North Carolina. Collected litter was air dried at room temperature, pooled by collection site, sorted to remove all non-leaf material, and sorted by species. Each litter bag contained 20 g of air-dried litter. Mixed species litter bags contained site specific proportions by mass of the major species and a minor species pool (Table 4.1). The 30 cm X 45 cm litter bags are constructed of nylon with mesh openings of 6 mm on the top and 2 mm on the bottom (Blair et al., 1990). The open end of litter bags was closed using a single 20 cm cable tie inserted through an aluminum tag bearing a stamped, sequential identification number in the middle and two 10 cm cable ties on each side of center leaving sufficient gaps for arthropod entry and exit. On February 09, 2011, litterbags were placed flat in the locations where site specific litter was collected and secured to the ground using three 15 cm X 2.5 cm #11-gauge sod staples to prevent movement during flooding and minimize the impact of wild hog activity. A pin flag bearing the tag number was inserted near bag center to facilitate location during subsequent collection.

A total of 360 litter bags were constructed (2 litter composition types * 4 community groups * 3 replicates * 15 samples). Litter bags were collected in triplicate by tag number using a random number generator. The first sample of 24 bags was oven dried at 70°C for 48 hours to obtain a correction factor for air versus oven dried weight. The fourteen remaining samples were collected, as near as practicable, at the following intervals: 0-2-4-6-8-12-16-22-28-38-48-64-80-100 weeks (Table 4.2). The 0-week collection was used to obtain a correction factor for handling loss during installation of the litter bags and to establish a mass and nutrient baseline. Three single species and three mixed species litter decomposition bags were collected from each community group at each collection period (Table 4.2). Within each litter type, bags were collected by tag number and each bag was assigned to a replicate (A, B, or C) based on a random number generator. Collected litter decomposition bags were inserted into 2 gallon Ziploc bags and stored at -20°C in a manual defrost freezer until further processing.

The litter from each bag was sorted to remove extraneous debris such as twigs, sediment, reproductive parts, invertebrates, etc. which had entered the bag. Distilled water and a progressive sieve stack were used to assist in removal of sediment prior to oven drying of sample. Litter was oven dried at 70°C for 48 hours and weighed to obtain oven-dried weight. The contents of each bag was ground and collected through a 20-mesh sieve in preparation for lab analyses. The three replicates for each litter type within each collection period were pooled and stored at -20°C in whirl-pack bags. Replicates were pooled as opposed to being analyzed individually due to funding constraints. Subsamples were sent to Dr. Lockaby's lab at Auburn University to determine nitrogen, phosphorous, and carbon concentrations and ash content as described in Baker et al. (2001). All values were reported are on an ash-free basis.

Moisture regime and temperature are well established parameters which affect the rate of litter decomposition rates around the world (Zhang et al., 2008). For this study, there was not enough funding to employ water level, precipitation, or temperature sensors; therefore, relevant information was obtained from online data from USGS (2018; gage levels, information accessed 02/15/2018) and NOAA (2018; precipitation and temperature, information accessed 02/15/2018) and interpreted in conjunction with field observations over four years of field data collection. Temperature and precipitation data were retrieved from NOAA station # USC0038675 near Pelion, SC located approximately 40 kilometers due west from the study site; this is the closest station having complete data for the period in which decomposition bags were in the field. Two USGS gage stations were monitored over the four years during which field work was conducted at the study site (2010-2014). The Cedar Creek station (USGS gage station #02169672 – Cedar Creek at Congaree National Park near Gadsden, SC) is located 9 kilometers WNW of study area and 3 kilometers upstream of the confluence of Cedar Creek and the Congaree River within CONG. Levels of this gage were an excellent predictor of backwater flooding for lower elevation community groups with levels of 1.45 and 1.68 m indicating the onset of inundation for community groups 4 and 1, respectively. The Congaree River station (USGS gage station #02169625 – Congaree River at CONG near Gadsden, SC) is located

13 kilometers WNW and upstream of the study area at the western boundary of CONG. Levels of this gage at or exceeding 4.27 m indicated that overbank flooding of the Congaree River had begun at the study site resulting in inundation for all community groups. Levels in excess of 3.51 m were indicative that guts (connected to river channel via levee breaches) would convey water via backwater flooding to community group 4. These flows may also inundate lower flats (group 1) once the backswamps have filled and inflow outpaces outflow.

The single negative exponential decay model (Olson, 1963) was used to calculate annual decay rates for mixed and single species litter types within each community group. Decomposition rate (*k*) was calculated in JMP Pro 12.0 (SAS Institute, 2015) using the first order decay kinetics equation from the nonlinear model library adjusted to execute Olson's (1963) model, $X/X_0 = e^{-kt}$. Mixed, site specific litter and single species litter were analyzed separately by community group and compared within community group. Analysis of variance (ANOVA) followed by pairwise or multiple comparisons employing the Tukey test with community group and litter composition as factors was used to analyze decay rates and the percent dry mass remaining at each collection period. The significance level was set at $P < 0.05$. Nutrient content values are presented in tabular and graphic form, but were not subjected to ANOVA as pooling of the replicates for lab procedures precludes the replication required to perform statistical analyses. Litter nutrient content, decay rate, and mass remaining are expressed and were calculated on an ash-free basis.

RESULTS

Temperature, precipitation, and flooding

Due to the close proximity of the community groups within the study area it can be assumed that both temperature and precipitation were identical among community groups; however as elevation differences exist among groups (Table 4.1), differential flooding may have affected decay rates. Monthly high temperature means and precipitation totals during the period decomposition bags were in the field and the 1981-2010 average monthly means for these values are shown in Figure 4.2. Monthly high temperature averages during the study were similar or higher compared to the averages for the previous 30 years. Spring and fall temperatures were nearly identical to the 30 year average while summer and winter temperatures during the study tended to be higher. Higher than average temperatures prevailed throughout the summer of 2011 while only July was above average during the 2012 summer. The winter months of December, January, and February exhibited higher than average temperatures throughout the decomposition study compared to 30 year averages. Precipitation by month deviated from the monthly averages compared to the preceding 30 years. The decomposition study began with lower than normal rainfall in February 2011 followed by above average precipitation for March and April of 2011. A long period of below average rainfall began in June 2011 and persisted through February 2012. Near normal precipitation ensued during the spring and summer of 2012 excepting above average rainfall in May and August. Lower than normal rainfall returned for the remainder of the decomposition study from September 2012 through January 2013 with the exception of December when rainfall was near the 30 year average.

Flooding events during the decomposition study were estimated based on level data from two USGS gage stations and four years of field observations (Figure 4.3; Table 4.3). These events do not necessarily coincide with higher than normal precipitation in the study area. Major precipitation events far upstream in the watershed, in conjunction with flow controls may yield water levels producing backwater flooding via guts and/or overbank flooding despite local precipitation. Conversely, backwater flooding from adjacent streams and wetlands located on the river floodplain may occur in association with heavy local precipitation with only a nominal increase in levels at the Congaree River gage station. The higher elevation communities (groups 2 and 3) received low level, ephemeral inundation via short lived overbank flooding on three occasions during the decomposition study (April 2011, May 2012, and December 2012 – Congaree River gage 4.27-4.57 m; Figure 4.3). The overbank flooding in January 2013 at a gage level of 5.18 m likely produced a flooding event of moderate level and marginally longer duration. All four of these events would have caused inundation in the lower elevation community groups 1 and 4 by both overbank and backwater flooding. However, because these communities are located within depression areas lower in elevation than the inflow and outflow drainage patterns and guts connecting them to surface waters on the floodplain, inundation would be more persistent, remaining until the water table receded and ponded water either percolated into the soil or evaporated. The late March/early April 2011 event reached levels just short of overbank flooding, thus community groups 2 and 3 were not inundated. The lead author was in the field during this event and observed the following: the mouth of a gut beginning at a levee breach approximately 500 meters downstream of the study area was conveying water from the river into the floodplain. Upon following the gut and associated smaller drainage patterns, water was found to be flowing into community groups 1 and 4 with depth controlled by outlets of higher elevation.

The two events occurring in January and March 2012 are examples of when high levels of precipitation within the watershed, but much lower local precipitation produced a flooding event in the study area; this is evidenced by high levels at the river gage, but nominal change in the Cedar Creek gage. The proximal down river gut begins to receive river flow when the river gage reaches a level of approximately 3.51 m; thus community group 4 receive backwater flooding during these events, but intermediate elevation community group 1 does not receive this flow until the river gage reaches approximately 3.96 m and was not inundated during these two events. The remaining three events resulted in backwater flooding within community group 4 only (May 2011, June 2012, and August 2012). We are unsure of what drives these events, but group 4 receives low level inundation whenever the Cedar Creek gage exceeds 4.75 m, regardless of the Congaree River gage level. The most likely explanation is a thunderstorm producing heavy rainfall over a small area causing a pulse in the level of tributaries that flow through the river floodplain and a portion is conveyed to depressional areas via the complex network of guts and drainage patterns on the floodplain.

Decay rates and mass change over time

Decomposition rates showed no significant differences either between litter types or among community groups (Figure 4.4). The variance among replicates produced high standard errors and in conjunction with a small sample size yielded non-significant

ANOVA results for the calculated decay rate (k) (Tables 4.4 and 4.5). Mixed species litter showed a relatively greater decay rate in higher elevation community groups 2 and 3 (1.57 and 1.53, respectively) compared to values of 1.41 for community group 1 and 1.44 for group 4 (Table 4.4). Conversely, the single species litter decay rate tended to be lower at 1.33 and 1.40 in community groups 2 and 3 in relation to intermediate elevation group 1 (1.44) and low elevation group 4 (1.49; Table 4.4). Decay rates showed little separation based on litter type within community groups 1 and 4 ($\Delta = 0.03$ and 0.05, respectively) while litter type differences were more pronounced in groups 2 and 3 ($\Delta = 0.24$ and 0.13, respectively; Table 4.4).

The percent mass remaining for single species and mixed species litter over time within community groups is shown graphically in Figure 4.5. The graphed curves of all community groups for single species litter over time are very similar. Percent mass remaining for single species litter is significantly greater for groups 2 and 3 compared to groups 1 and 4 during weeks four through twelve (Figure 4.5; Table 4.5). Mass differences become less pronounced after this point and increasing replicate variance leads to non-significant ANOVA results. At collection week 64, single species percent mass remaining is low and very similar across community groups, very low at collection week 80, and essentially there is no single species litter remaining at collection week 100. The percent mass remaining curves for mixed species litter over time show that community groups are similar through week 6, significantly divergent for weeks 8 through 64 with the exception of week 38, and again become very similar at weeks 80 and 100 (Figure 4.5; Table 4.5). The divergence between weeks 8 and 64 show that the higher elevation community groups

2 and 3 remain almost identical and exhibit a significantly faster mass loss rate over this period compared to groups 1 and 4 which are very similar. As with single species litter, there is limited mixed species litter mass remaining at week 64, very low at week 80, and essentially gone at week 100.

Nutrient ratios over time

The percent C remaining over time showed a markedly similar trend across both litter types and community groups (Figure 4.6; Table 4.6) and C loss patterns appear to be closely linked to overall mass loss. The most rapid loss of C occurred during the late spring through fall of 2011 between weeks 12 and 38. Continuous mineralization of C occurred throughout the study suggesting deposition/accumulation of this element is not a part of above ground litter decay processes in the study area, at least during the time period when litter decomposition bags were in the field.

All combinations of litter type and community groups, except mixed litter in group 1 showed an appreciable net accumulation of P at some point between installation and collection week 16 (Figure 4.6; Table 4.6). Percent P remaining patterns were very similar among community groups for single species litter with rather rapid initial mineralization from installation through collection week 4 for groups 1, 3, and 4 and through week 6 for group 2 (Table 4.6). After this initial decrease, percent P remaining increased for single species litter in association with two flood events between weeks 4 and 8. The increase in P was greatest for community group 4 at 29.1% while being similar for groups 1, 2, and 3 (11.7, 14.4. and 14.7%, respectfully). Percent P remaining in single species litter then entered a relatively steady state from weeks 6 through 16 in community groups 1 and 3, weeks 8 through 16 for group 2, and weeks 6 and 8 within group 4. Following the period of P equilibrium, steady mineralization from single species litter prevailed for the remainder of the study with the exception of minor accumulation between weeks 22 and 28 in community group 3 and between weeks 28 and 38 in group 4 (Table 4.6).

Percent P remaining patterns for mixed species litter was more variable among community groups compared to single species litter (Figure 4.6; Table 4.6). Although mixed litter for group 1 only exhibited an increase in net P of 5.1% from collection week 4 to 6, percent P remaining did show a steady state from collection weeks 8, 12, and 16, suggesting a period where mineralization and accumulation were in equilibrium. Mineralization of P followed in community group 1 from week 22 through 100 comparable to mass and C declines (only litter bags with QULY leaves – 22.8%). In community group 2, there was an immediate 18.3% increase in P following installation followed by steady mineralization through week 100; steady state was not apparent in this community for mixed species litter. Groups 3 and 4 exhibited a decrease in % P remaining from installation to week 2 collection (22.1 and 17.5%, respectively) followed by a period of equilibrium. A steady state for P persisted in community group 3 from week 2 through week 6, followed by a 34.5% increase between weeks 6 and 8, then a steady decline through week 100. Community group 4 also exhibited equilibrium in percent P remaining from weeks 2 through 6, showed a 14.2% decrease from week 6 to 8, a 29.8% increase from week 8 to 12, and a steady decline in % P remaining from week 12 through week 100.

Percent N remaining also showed periods of accumulation during the decomposition study with the greatest accumulation occurring for single species litter within community group 2 (Figure 4.6; Table 4.6). The % N remaining in group 1 single litter vacillated between +15% and - 3% of the installation value through collection week 22 followed by a steady mineralization of N until none remained at week 100; except for a steady state between weeks 38 and 48 (late fall/winter 2011-2012). In community group 2 percent N vacillated from +40.7% and -9.3% of the installation value through collection week 16 followed by a steady decline to only 1.3% at week 100. Percent N also vacillated in single species litter within community group 3 up to collection week 16 ranging from +12% to -8.6% of the original mass; steady mineralization ensued until less than 1% of the original N mass remained at week 100. In community group 4 percent N dropped by 7.2% from installation to week 2 then remained at a relative steady state from week 2 through week 12. This was followed by a steady decline to only 2.6% of the original N remaining at week 100, although there was essentially no change in % N between weeks 28 and 38 (fall 2011).

Percent N remaining values remained elevated for the longest period of time for mixed species litter in community group 1. There was an initial drop of 13.2% between installation and week 2 followed by a period of vacillation where the N mass varied from +6.8% to -14.0% of the original mass between collection weeks 2 and 22. Nitrogen mass followed a steady trend of mineralization from week 22 to week 100 when only 2.8% of the original mass remained in group1 (Figure 4.6; Table 4.6). Percent N remaining in mixed litter vacillated between +7.4% and -0.3% between installation and collection week 12 in community group 2. This was followed by a steady decline in N mass until less than 1% of the original mass remained at week 100. Mixed litter N in community group 3 showed a vacillating range of +6.6% to -11.4% compared to installation mass followed by a steady trend of mineralization from week 12 until no mass remained at week 100; however there was essentially no change in N mass between weeks 28 and 38. In community group 4 mixed species litter there was an initial drop of 14.6% between installation and week 2. A period of vacillation ensued between collection weeks 2 and 16 with N mass varying between +9.8% and -12.0% of original mass. Nitrogen mass declined steadily after week 16 and no mass remained in the 100 week collection.

Initial C:N ratios for mixed species litter were nearly identical among community groups (41.9-42.1) and all groups showed a gradual decline in the C:N ratio over time through week 64 (Table 4.7, Figure 4.7). The mixed species litter C:N ratio showed a more rapid decline for lower elevation groups 1 and 4 (22.3 and 22.4) when week 64 values are compared to higher elevation groups 2 and 3 (32.9 and 30.8). Single species litter C:N ratios unexpectedly exhibited a much wider range for initial C:N ratios than mixed species litter among community groups (46.4-61.6; Table 4.7). After installation single species litter C:N ratios declined for all community groups and by week 16 were nearly identical with a range of 33.7 to 36.0. At week 64 single species litter C:N ratios showed a similar, but less pronounced, difference among community groups compared to mixed species litter. Week 64 values were 25.0 and 26.2 for lower elevation community groups 1 and 4 while groups 2 and 3 showed single species C:N ratios of 29.6 and 33.3. Overall, with the exception of higher initial values for single species litter in groups 1 and 2, the graphed C:N ratio overtime was similar for all combinations of community group and litter type (Figure 4.7).

Initial C:P ratios showed a wide range among community groups for both litter types with single species litter values higher (range 296-427) compared to mixed species litter (range 105-258; Table 4.7). The ratio among community groups still exhibited a relatively wide range of 133 to 203 for mixed species litter at week 64 while C:P ratios remained higher for single species litter, but the range had narrowed considerably (208 to 233). In general, the C:P ratio tended to be higher for single species litter across community groups through time compared to mixed species litter and all combinations of group and litter type showed a period where the C:P ratio increased sharply, although increases in group 4 were much less pronounced (Figure 4.7). Litter type C:P ratios were the most similar within community group 1, most likely due to the overcup oak leaves being a major component of group 1 mixed litter and probable similarity to white oak leaves used as single species litter. Mixed species litter values are very similar for community groups 2 and 3 and reflective of the similar species composition for these two groups (Table 4.1). C:P ratios remained the most consistent in community group 4 over time for both litter types suggesting possible depositional effects for P.

At installation the N:P ratio ranged from 4.8 to 9.2 for single species litter and 2.5 to 6.1 for mixed species litter (Table 4.7). Initial ratios were considerably lower in the mixed species litter of community groups 2 and 3 (3.2 and 2.5, respectively) compared to 4.9 and 6.1 in groups 1 and 4. Once again the initial values for single species litter showed a wider than expected range of 4.8 to 9.2 among community groups. The N:P ratio increased over time from week 0 to week 64 for single species litter by 44% in community group 1 and 65% for group 2 while a decrease of 14% and 7% were observed for groups 3 and 4, respectively. During this same period, N:P ratios increased considerably for all mixed species litter with community groups 2 and 3 showing a larger increase (78 and 72%, respectively) compared to groups 1 and 4 (57 and 49%, respectively). This may be due to more rapid mineralization of P in groups 2 and 3 and/or supplemental P via deposition in groups 1 and 4. In general, the N:P ratio of single species litter remained higher through week 64 compared to mixed species litter across community groups; however the mixed species litter ratio was mostly higher than single species in group 1 from week 12 to week 38 (Table 4.7; Figure 4.7).

DISCUSSION

Litter quality varies widely among species and has been estimated to account for up to 70% of the variation in reported decay rates in the literature (Hattenschwiler et al., 2005; Zhang et al., 2008). Species comprising 89.6 and 96.1% of the mass in mixed species litter within community groups 2 and 3 are considered high quality litter based on reviewed literature (Webster and Benfield, 1986 (family level assessment); Conner and Day, 1991; Mehring et al., 2014; Midgley et al., 2015). These species producing high quality litter include: sweetgum (*Liquidambar styraciflua* L.), box elder (*Acer negundo* L.), American elm (*Ulmus americana* L.), sugarberry (*Celtis laevigata* Willd.), and pawpaw (*Asimina triloba* L. (Dunal.)). In community group 1 mixed litter, high quality species (sweetgum, American elm, and sugarberry) represented 34.3% of the mass. Two additional species producing high quality litter, green ash (*Fraxinus pennsylvanica* Marshall) and bald cypress (*Taxodium distichum* (L.) Richard), accounted for an additional 29.4% of the mass in group 1 mixed species litter bags (Webster and Benfield, 1986 (family level assessment); Conner and Day, 1991). Overcup oak (*Quercus lyrata* Walter) and sycamore (*Platanus occidentalis* L.) accounted for 31.3% of community group 1 mixed litter mass; these two species are considered low quality litter (Webster and Benfield, 1986 (family level assessment); Leroy and Marks, 2006; Mehring et al., 2014; Midgley et al., 2015). High quality litter from bald cypress (83.6%) and green ash (6.2%) were the species contributing the most mass to mixed species litter in community group 4. An additional 5.9% of mass for group 4 came from two additional species, red maple (*Acer rubrum* L.) and swamp cottonwood (*Populous heterophylla* L.), producing high quality litter (Webster and Benfield, 1986 (family level assessment); Mehring et al., 2014; Midgley et al., 2015).

In this study white oak (*Quercus alba* L.) was used in single species litter. Oak species and the family Fagaceae overall are considered to produce low quality litter (Webster and Benfield, 1986; Mehring et al., 2014). Midgley et al. (2015) used white oak in single species litter bags as well and reported initial values of 46.6 for percent C, 0.69 for percent N, and a C:N ratio of 67.4 for leaves collected in an upland mixed hardwood forest. Our values were similar at 45.6% C, 0.87% N, and a C:N ratio of 53.1; the higher N value is likely due to the location of the white oak tree in a managed yard and this elevated N level may indicate that the leaves we used are a higher quality litter than that of oaks growing in natural forests. We saw considerable variance in initial nutrient ratio values from lab analysis of the single species litter. White oak leaves have a very prolonged senescence and leaf drop period which likely has an effect on the nutrient content of a given temporal cohort of collected leaves. No measures were taken to compensate for this during processing and litter bag assembly and it is likely stochastic effects yielded excessive variation in initial nutrient values.

Brinson (1990) reported an average decay rate of 1.01 in temperate riverine forests; our results were well above average with mean decay rate values 1.49 for mixed litter and 1.41 for single species litter. The closest corollary to this study as a point of comparison is one conducted by Baker et al. (2001) which followed decomposition of mixed (site specific) litter, single species litter (cherrybark oak - *Quercus falcata* var. *pagodaefolia* Ell.), and popsicle sticks over a 100 week period in four forested floodplain communities subject to differing hydrologic regimes in the southeast. The communities studied by Baker et al. (2001) exhibited similar precipitation and temperature and were roughly analogous to our communities in regard to hydrologic regime, although the percent of high quality litter in mixed species litter was considerably lower in their communities and inundation duration tended to be longer. Additionally, they also used a low quality oak litter as their single species litter, although they did not install single species litter in their SCwet group, but did install popsicle sticks. The LA group (cherrybark oak community along Iatt Creek in central Louisiana) studied by Baker et al. (2001) showed hydrology nearly identical to our community groups 2 and 3; however the content of high quality litter in our mixed bags was > 90% while theirs was only 27%. They found an annual decay rate (% mass remaining) of 1.27 (5.2%) for mixed litter and 1.33 (6.9%) for single species litter while our results were 1.55 (< 1%) for mixed litter and 1.37 (< 1%) for single species litter; this would seem to indicate that our faster decay rate for mixed litter may be attributed to higher litter quality, greater nutrient import via flood water, and/or more conducive edaphic conditions. Baker et al. (2001) SCdry group (laurel oak - *Quercus laurifolia* Michaux community along Coosawhatchie River in southeast South Carolina) showed a similar hydrologic regime to our community group 1, but experienced three more flooding events and likely was subjected to more days of inundation. SCdry mixed litter contained only 37% high quality litter while our group 1 contained 63.7%. Their SCdry group showed a decay rate (% mass remaining) of 0.84 (17.8%) for mixed litter and 0.79 (15.8%) for single species litter while our community group 1 had values of 1.41 (1.7%) and 1.44 (0%), respectively. A combination of factors may have contributed to our faster decay rates including: higher quality litter for our mixed species litter; the Congaree headwaters are in the piedmont and mountains and floodwaters (red water river) likely deposited more nutrients compared to the Coosawhatchie – a black water river; and our community likely experienced shorter duration periods of inundation. Baker et al. (2001) SCwet group (sweetgum – swamp tupelo [*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.] community along Coosawhatchie River) is similar hydrologically to our community group 4; however SCwet flooded on 17 occasions while our bald cypress backswamp is estimated to have flooded on 10 occasions and is thus likely to have been inundated for less days. Our community group 4 contained 97% high quality litter by mass while SCwet contained 67%. We found a decay rate (% mass remaining) of 1.44 (0%) for mixed species litter and 1.48 (1.7%) for single species litter while values of SCwet were reported as 1.00 (8.1%) for mixed litter and 0.91(9.4%) for popsicle sticks (single species litter not installed in this community). Possible factors for our faster decay rates are the same as those listed above for community group 1 – Scdry comparison.

The % C remaining over time for both litter types across communities closely followed the trend of % mass remaining and this relationship has been observed in other decomposition studies in forested wetlands in the southeast (Baker et al., 2001; Ozlap et al., 2007). Percent P and N remaining tended to vacillate between periods of net loss and net gain early on for all combinations of litter and community group followed by rapid loss near the end of the study; this trend has been reported in other studies following decomposition in regional forested wetlands (Conner and Day, 1991; Baker et al., 2001; Ozlap et al., 2007). Baker et al. (2001) found single species overall means for the C:N ratio of 45.8 initially and 24.5 at 100 weeks (analogous communities only). In our study the initial C:N ratio across all groups was 52.5 for single species litter and the mean of last samples containing mass was 15.7 (either 80 or 100 week). While they began with a narrower C:N ratio, our ending value suggests less N limitation in our communities possibly due to greater N deposition, higher rate of N fixation by microbial community, and/or higher available soil N. Analogous community means in the Baker et al. (2001) study for single species litter (initial/final) was 8.3/7.7 for the N:P ratio and 369/189 for the C:P ratio. Our initial values of 7.2 and 368 are similar; however, our final values of 4.9 and 115 indicate our communities may receive more P via deposition and/or have more P rich soils. Mixed species litter nutrient ratios for SCdry (Baker et al., 2001) were C:N - 68.1/29.9, N:P - 4.8/6.5, and C:P - 325/194 (initial/final) while our community group 1 had values of 41.9/15.0, 4.9/5.4, and 204/121, respectfully indicating that we began with higher litter quality and experienced less nutrient limitation during decomposition. Mixed species litter nutrient ratios for SCwet (Baker et al., 2001) were C:N – 57.3/23.3, N:P – 6.1/5.6, and C:P – 330/130 while our community group 4 had values of 42.0/21.1, 6.1/9.3, and 258/196, respectfully. The values in this comparison indicate we began with slightly higher quality litter, but our community appears to have been subjected to higher levels of both N and P limitation; SCwet experienced more inundation events and longer inundation periods suggesting greater nutrient deposition, but due to longer anaerobic periods, a slower decay rate. Mixed species litter nutrient ratios for LA (Baker et al., 2001) were C:N – 46.0/24.5, N:P – 7.8/7.6, and C:P – 358/186 while our community groups 2 and 3 had values of 42.1/9.2, 2.9/1.6, and 120/42.4, respectfully. These values suggest N limitation was the restricting factor to decomposition in our groups 2 and 3 while P was more limiting in their LA group.

Three flood events occurred in our study area in the spring of 2011 (between collection weeks 4 and 12); one of which inundated all community groups. Import of nutrients associated with the flood events are likely the reason for the accumulation of P and N found in samples between weeks 4 and 16 across communities and litter types. The subsequent steady state in nutrient content which followed may be due, at least in part, to immobilization of nutrients by the decomposer community as decomposer populations enter a rapid period of growth and proliferation as temperatures warm requiring rapid nutrient assimilation. As the decomposer community population reaches a seasonal high, immobilization declines as nutrient needs are reduced and mineralization of nutrients ensues as carbon respiration outpaces the need for nutrient assimilation by the decomposer community. While this sequence may be a reasonable deduction from collected data for

2011, the increasingly wide collection intervals does not allow the same postulate to be applied to spring and summer of 2012.

Nelson et al. (2016) measured litterfall via littertraps over a year in cane-breaks in southern Illinois riparian zones and reported a mean plot value of 400 g/m^2/year (dry weight) for litter solely from the large, woody grass species cane (*Arundinaria gigantea* (Walt.) Muhl.). They also reported an initial C:N ratio of 24.2 for the cane litter; much closer to the optimal value to complete decomposition of 16 suggested by Brinson (1977) and much narrower than the initial range of 41.9 to 42.1 for mixed litter calculated in this study. We found that cane represented 13.1, 30.1, 30.0, and 0.0% of all positive point intercept hits from ground level to a height of two meters (community groups 1-4, respectively; Chapter 2). Additionally, in this study, litter from cane was separated and discarded from litter collection prior to assembling litter bags. It may be assumed due to the density of cane in community groups 2 and 3 and the narrow C:N ratio of cane reported by Nelson et al. (2016) that inclusion of cane in mixed species litter would likely affect the decay rate and nutrient dynamics for these community groups.

A study by Mitchell et al. (2011) addressed the effects on litter decomposition and nutrient dynamics of the exotic shrub Chinese privet (*Ligustrum sinense* Lour.) in a southeastern riparian forest. They reported an increase in the decay rate, narrowing of the C:N ratio, and an increase in nitrogen mineralization of N as larger percentages of Chinese privet litter was added to the litter mix. These results were attributed to the high quality of privet litter having lower lignin, higher N concentration, and a lower C:N ratio compared to native species and indicate invasion can substantially alter decomposition rates and soil nutrient dynamics. Chinese privet occurred in our study site at different densities (Chapter 2). Privet was absent in community group 4, a minor component in group 1 (0.9% of sapling basal area), and a significant component in community groups 2 and 3 (5.0% and 18.3% of sapling basal area, respectfully). Our litter collection hammocks were installed at a height of approximately two meters above ground surface; a height too great to allow for effective collection of Chinese privet litter and thus the direct effects of this litter within the site specific litter mixes were not addressed. However, naturally falling Chinese privet litter was present where litter bags were installed in community groups 2 and 3 thus there may have been an indirect affect via edaphic nutrient levels on the decay rate and nutrient ratios for mixed species litter in these groups. Considering the results of Midgely et al. (2015) where it was demonstrated that adding N to a site or installing low quality litter to a site where species producing high quality litter dominated had no effect on decomposition rates of low quality litter (i.e. our single species white oak litter), but the decomposition rate of high quality litter was significantly increased when N was added to a site and depressed when high quality litter was installed in sites dominated by species producing low quality litter. Midgely et al. (2015) concluded that due to the secondary compounds and recalcitrant structure of low quality litter, the decomposition rate is sufficiently restrained regardless of nutrient availability or the quality of the surrounding litter matrix on site. Accordingly, Chinese privet litter may have accelerated the decay rate of mixed species litter in community groups 2 and 3, but it is unlikely to have affected decomposition of single species litter in these groups. The study by Midgely et al. (2015) also found that the litter decay rate in stands dominated by species which primarily form arbuscular mycorrhizal relationships tended to be significantly higher than in stands where the dominant species primarily form ectomycorrhizal relationships. This finding may enhance decomposition on the Congaree floodplain as fruiting bodies of ectomycorrhizal fungi were never observed over four years of field work.

Litter decomposition rates in this study tended to be higher than those reported in other regional forested floodplain sites. Observationally, this is reinforced by, for the most part, the absence of a duff layer, lack of a soil O horizon, and a thin, discontinuous litter layer (except for a short period following maximum leaf fall). Despite these observations being common to forested floodplains of the southeast, we found rather high litter decomposition rates suggesting an optimal decomposition environment for the study area. In scattered depressions and in association with localized structure which concentrates litter (i.e. coarse woody debris, dense cypress knees); duff, humus, and partially decomposed litter did accumulate, but these areas represented less than 5% of the study area. Although it took 80 to 100 weeks for all initial mass to be reduced to < 2% mass remaining, the contents of the litter bags at week 64 showed little to no structure and would be more accurately described as humus; here the decay function would have reached an asymptote referred to as the maximum decomposition limit and entered into a much slower rate of decay with differing dynamics associated with the decomposition of humus (Prescott, 2005). At this point it is likely the humus in the bag would have exited through the mesh with precipitation, not necessarily have decomposed. The concentration of the humus itself may be considered an artificial event dictated by the litter bag and is unlikely to occur naturally due to dispersion and mixing associated with rain, percolation, flooding, feral hog rooting activity, and macroinvertebrate activity. We conclude that litter decomposition and the cycling of the nutrient contents of the litter are comparatively rapid processes under the prevailing climatic conditions on the area of the Congaree River floodplain studied. Warm, moist, and humid conditions coupled with nutrient import associated with flooding events and the prevalence of species producing high quality litter appear to create an ideal decomposition environment and likely supports a diverse and dense decomposer community. With the low quality oak litter showing only a slightly lower decomposition rate than the high quality site specific mixed litter, it is suggested that the rapid cycling of high quality litter has created edaphic nutrient content that buffers nutrient limitation regardless of litter quality. However, it is likely this would change over time if dominance shifted to species producing low quality litter. Relatively faster decay of single species litter in lower elevation areas compared to groups 2 and 3 suggests periodic inundation ameliorates moisture limitations and aids in the decomposition of recalcitrant lower quality litter such as white oak. It is probable that extended drought or extended inundation could result in litter accumulation, but unless these conditions become a long term trend, the prevailing decomposition environment will prevent the formation of a continuous litter layer, duff layer, or organic soil horizon.

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Table 4.1. Species composition and proportion of mass of litter used in litter decomposition bags within floodplain community groups and a summary of species composition and structure of community groups.

	Group 1 – FRPE/LIST/CELA plots: 1, 9, 11, 12, 13 litter collected b/w plots 12&13	Group 2 – LIST plots: 3, 6, 7, 8, 15 litter collected b/w plots 7&8	Group 3 – CELA/ACNE plots: 2, 4, 5, 10, 14 litter collected behind plot 4	Group 4 – TADI plots 16, 17, 18, 19, 20 litter collected b/w plots 17&18	Single species litter
Composition of litter collected and used in litter decomposition bags	FRPE – 21.4% QULY – 22.8% LIST – 13.5% CELA – 12.2% ULAM – 8.6% PLOC – 8.5% TADI – 8.0% minor spp. mix – 5.0%	LIST – 44.2% CELA – 16.4% ULAM – 16.0% ACNE – 7.5% ASTR – 5.5% minor spp. mix – 10.4%	CELA – 18.5% ACNE – 20.4% LIST – 27.2% ULAM – 17.8% ASTR – 12.2% minor spp. mix – 3.9%	TADI – 83.6% FRPE – 6.2% ACRU – 4.8% POHE – 2.1% minor spp. mix – 3.3%	QUAL – 100% Collected under single, isolated white oak (*Quercus alba* L.)
Mean elevation (m above sea level)	133.77	134.43	134.46	132.94	728
Qualitative flooding regime based on elevation & observations	Annual frequency and intermediate duration	Occasional frequency and ephemeral duration	Occasional frequency and ephemeral duration	Annual frequency and extended duration	none
Dominant tree species – based on % total tree basal area (m²) within community group	LIST 23.7% FRPE 23.2% CELA 12.6% QULY 9.2% TADI 7.7%	LIST 71.2% ULAM 8.2% CELA 7.3% ACNE 3.8% PLOC 2.9%	CELA 30.9% ACNE 25.5% LIST 10.2% ULAM 7.0% QULA 6.9% FRPE 6.8%	TADI 91.7% PLAQ 3.6% POHE 1.7% LIST 1.2% ACRU 1.1%	N/A
Dominant sapling species – based on % total sapling basal area (m²) within community group	ASTR 41.7% ILDE 33.7% CELA 17.7% PLAQ 4.4% LIST 2.42%	ASTR 67.5% QULA 8.6% ILOP 6.7% CELA 5.6% ACNE 3.6%	ASTR 41.1% LISI 31.0% ILDE 23.8% ULAM 2.3% PLOC 1.9%	PLAQ 53.8% ILDE 23.2% TADI 17.1% CEOC 2.8% QULA 1.2%	N/A

Mean aboveground net primary productivity (ANPP) (g dry mass/m²/year) (2011-2012)	1322	1422	1118	1118	N/A
Mean (g dry mass/m²/year) and % of total ANPP from leaf tissue (2011-2012)	601 47.24%	599 44.08%	578 52.59%	659 59.87%	N/A
Mean % biomass within community group					
Trees < 25 cm DBH	8.9%	7.4%	15.4%	5.2%	N/A
Trees 25-50 cm DBH	21.5%	11.6%	50.3%	32.5%	
Trees 50-75 cm DBH	18.9%	53.4%	34.3%	54.3%	
Trees > 75 cm	50.7%	27.6%	0.0%	8.0%	

Notes: Percentages shown are on a dry mass basis for all litter collected in litter collection hammocks; mixed species litter decomposition bags were assembled to a dry mass content of 20 grams using these species percentages. The use of a single individual of a single species attempts to more accurately assess decomposition rates among differing forested areas independent of litter derived from differing species composition and frequencies (i.e. a control); the white oak is in the front yard of lead author in Asheville, NC. See Appendix 7 for conversion of four letter species codes to species names. Community groups were defined based on Cluster Analysis, Indicator Species Analysis, and Non-metric Multi-dimensional scaling as presented in Chapter 2. Trees are stems ≥ 10 cm DBH; saplings are stems < 10 cm DBH/BA and > 1 meter in height. Values are the mean of five sample plots within each community group and are the baseline values collected during the winter of 2010/2011. ANPP data is from Chapter 3. Elevation data provided by Hupp (2013).

Table 4.2. Timeline for installation and collection of litter decomposition bags and litter collection hammocks in this study.

Litter bag collection date	Litter bag collection week	Mixed species litter collection
02/09/2011 - install	0	collection hammocks installed – 10/01/2010
02/23/2011	2	litter collection – 10/29/2010
03/09/2011	4	litter collection – 11/19/2010
03/24/2011	6	litter collection & hammock removal – 12/14/2010
04/06/2011	8	
05/07/2011	12	Single species litter collection
06/07/2011	16	
07/18/2011	22	collection hammocks installed – 10/01/2010
09/13/2011	28	litter collection – 10/30/2010
11/18/2011	38	litter collection – 11/20/2010
01/27/2012	48	litter collection & hammock removal – 12/15/2010
05/25/2012	64	
09/05/2012	80	*Notes:* All litter bags were installed in the field on 02/09/2011; the week 0 collection was used to correct for handling loss. Three mixed species and three single species litter bags were randomly selected and collected on each collection date.
01/29/2013 – final collection	100	

Table 4.3. Flooding events by community groups for the period during which litter decomposition bags were in the field.

Flooding event	Group 1 – FRPE/LIST/CELA	Group 2 – LIST	Group 3 – CELA/ACNE	Group 4 – TADI
March, 2011	low level backwater flooding	none	none	moderate backwater flooding
April, 2011	moderate backwater and overbank flooding	low level overbank flooding	low level overbank flooding	high backwater and overbank flooding
May, 2011	none	none	none	low level backwater flooding
January, 2012	none	none	none	low level backwater flooding
March, 2012	none	none	none	low level backwater flooding
May, 2012	moderate backwater and overbank flooding	low level overbank flooding	low level overbank flooding	high backwater and overbank flooding
June, 2012	none	none	none	low level backwater flooding
August, 2012	none	none	none	low level backwater flooding
December, 2012	low level backwater and overbank flooding	low level overbank flooding	low level overbank flooding	moderate backwater and overbank flooding
January, 2013	high backwater and overbank flooding	moderate level overbank flooding	moderate level overbank flooding	high backwater and overbank flooding

Notes: Assessment based on data from USGS gage station 02169672 – Cedar Creek at Congaree National Park near Gadsden, SC and USGS gage station 02169625 – Congaree River at Congaree National Park near Gadsden, SC in conjunction with four years of field observations.

Table 4.4. ANOVA results for decay rate and % mass remaining by litter type within community groups for each litter bag collection period.

Weeks in the field & collection date	Community Groups ($N = 3$ litter bag replicates per group for each litter type)							
	Group 1 FRPE/LIST/CELA		Group 2 LIST		Group 3 CELA/ACNE		Group 4 TADI	
	Mixed species mean ± SE	Single species mean ± SE	Mixed species mean ± SE	Single species mean ± SE	Mixed species mean ± SE	Single species mean ± SE	Mixed species mean ± SE	Single species mean ± SE
Decay rate (k)	1.41 (0.22)	1.44 (0.04)	1.57 (0.09)	1.33 (0.47)	1.53 (0.10)	1.40 (0.22)	1.44 (0.08)	1.48 (0.25)
	$F_{1,4} = 0.02$; $P = 0.89$		$F_{1,4} = 0.26$; $P = 0.64$		$F_{1,4} = 0.31$; $P = 0.61$		$F_{1,4} = 0.04$; $P = 0.86$	
Week 2 02/23/2011	100.73 (0.16)	99.91 (0.11)	100.17 (0.16)	100.46 (0.07)	97.26 (1.13)	99.56 (0.23)	99.94 (0.12)	99.21 (0.30)
	$F_{1,4} = 17.38$; $P = 0.014$ **M > S**		$F_{1,4} = 2.72$; $P = 0.174$		$F_{1,4} = 3.96$; $P = 0.118$		$F_{1,4} = 5.27$; $P = 0.083$	
Week 4 03/09/2011	99.87 (0.64)	95.35 (0.17)	98.50 (0.07)	99.80 (0.03)	96.05 (0.78)	99.59 (0.05)	95.10 (1.72)	94.76 (0.06)
	$F_{1,4} = 137.0$; $P = 0.0003$ **M > S**		$F_{1,4} = 273.6$; $P < 0.0001$ **S > M**		$F_{1,4} = 20.66$; $P = 0.011$ **S > M**		$F_{1,4} = 0.04$; $P = 0.850$	
Week 6 03/24/2011	95.57 (0.25)	92.92 (0.48)	94.12 (0.40)	95.69 (0.50)	95.51 (1.65)	96.42 (0.27)	94.39 (0.98)	90.45 (0.81)
	$F_{1,4} = 23.48$; $P = 0.008$ **M > S**		$F_{1,4} = 6.11$; $P = 0.069$		$F_{1,4} = 5.46$; $P = 0.080$		$F_{1,4} = 9.55$; $P = 0.037$ **M > S**	
Week 8 04/06/2011	93.52 (1.02)	89.23 (1.12)	86.76 (0.66)	93.78 (0.44)	90.53 (0.31)	93.41 (0.24)	90.85 (1.28)	85.78 (0.97)
	$F_{1,4} = 8.07$; $P = 0.047$ **M > S**		$F_{1,4} = 78.82$; $P = 0.0009$ **S > M**		$F_{1,4} = 54.41$; $P = 0.002$ **S > M**		$F_{1,4} = 9.96$; $P = 0.034$ **M > S**	
Week 12 05/07/2011	88.49 (0.59)	82.84 (0.54)	74.78 (1.798)	88.31 (0.81)	76.20 (3.29)	87.64 (0.65)	84.95 (0.50)	83.13 (0.56)
	$F_{1,4} = 49.87$; $P = 0.002$ **M > S**		$F_{1,4} = 47.70$; $P = 0.002$ **S > M**		$F_{1,4} = 11.62$; $P = 0.027$ **S > M**		$F_{1,4} = 5.86$; $P = 0.073$	
Week 16 06/07/2011	79.75 (1.40)	71.81 (0.99)	55.87 (1.37)	80.82 (1.51)	57.07 (1.23)	74.29 (1.85)	77.53 (1.71)	67.42 (4.29)
	$F_{1,4} = 21.54$; $P = 0.010$ **M > S**		$F_{1,4} = 159.4$; $P = 0.0002$ **S > M**		$F_{1,4} = 60.05$; $P = 0.002$ **S > M**		$F_{1,4} = 4.78$; $P = 0.094$	
Week 22 07/18/2011	64.35 (0.76)	60.62 (7.79)	32.19 (0.36)	66.76 (6.00)	35.30 (3.20)	55.05 (3.76)	57.19 (5.77)	58.67 (2.77)
	$F_{1,4} = 0.23$; $P = 0.66$		$F_{1,4} = 33.08$; $P = 0.005$ **S > M**		$F_{1,4} = 16.00$; $P = 0.016$ **S > M**		$F_{1,4} = 0.54$; $P = 0.83$	
Week 28 09/13/2011	53.99 (1.35)	38.29 (4.83)	21.33 (3.64)	43.66 (1.86)	20.89 (2.93)	43.91 (3.73)	42.82 (2.03)	33.75 (6.59)
	$F_{1,4} = 9.78$; $P = 0.035$ **M > S**		$F_{1,4} = 30.13$; $P = 0.005$ **S > M**		$F_{1,4} = 23.55$; $P = 0.008$ **S > M**		$F_{1,4} = 1.73$; $P = 0.26$	

Week 38 11/18/2011	41.51 (0.40)	16.60 (2.37)	17.34 (3.14)	30.53 (4.96)	19.19 (2.30)	27.88 (2.48)	27.06 (6.49)	30.70 (5.29)
	$F_{1,4} = 107.8$; $P = 0.0005$ **M > S**		$F_{1,4} = 5.05$; $P = 0.088$		$F_{1,4} = 6.62$; $P = 0.062$		$F_{1,4} = 0.56$; $P = 0.49$	
Week 48 01/27/2012	17.39 (0.58)	15.73 (1.55)	11.89 (1.04)	24.12 (0.42)	9.71 (0.87)	21.98 (4.20)	17.03 (3.68)	17.59 (7.34)
	$F_{1,4} = 1.00$; $P = 0.37$		$F_{1,4} = 118.3$; $P = 0.0004$ **S > M**		$F_{1,4} = 8.18$; $P = 0.046$ **S > M**		$F_{1,4} = 0.005$; $P = 0.95$	
Week 64 05/25/2012	11.70 (2.34)	12.61 (2.31)	9.54 (1.08)	16.69 (1.91)	3.47 (0.58)	17.67 (1.70)	5.64 (0.71)	12.76 (2.04)
	$F_{1,4} = 0.08$; $P = 0.80$		$F_{1,4} = 10.64$; $P = 0.031$ **S > M**		$F_{1,4} = 62.19$; $P = 0.001$ **S > M**		$F_{1,4} = 10.90$; $P = 0.030$ **S > M**	
Week 80 09/05/2012	7.17 (0.38)	4.18 (1.96)	1.54 (0.22)	0.62 (0.46)	0.58 (0.58)	4.84 (1.54)	2.66 (0.86)	8.22 (0.85)
	$F_{1,4} = 2.24$; $P = 0.21$		$F_{1,4} = 1.94$; $P = 0.24$		$F_{1,4} = 6.69$; $P = 0.061$		$F_{1,4} = 21.30$; $P = 0.010$ **S > M**	
Week 100 01/29/2013	1.71 (1.02)	0	0.49 (0.49)	0.62 (0.62)	0	0.61 (0.61)	0	1.71 (1.61)
	$F_{1,4} = 2.82$; $P = 0.17$		$F_{1,4} = 0.02$; $P = 0.88$		$F_{1,4} = 1.00$; $P = 0.37$		$F_{1,4} = 3.35$; $P = 0.14$	

Notes: F statistic with degrees of freedom from one-way ANOVA testing the hypothesis of no difference in litter type means within community groups; pairwise comparisons used the Tukey test at the alpha = 0.05 level. Mixed species litter was collected within each community group and single species litter was collected from a single, isolated white oak tree. All litter bags were installed on 02/09/2011. Each mean is derived from three replicate litter decomposition bags for each litter type on each collection date; % dry mass remaining is calculated on an ash-free basis. The decay rate is calculated according to Olson's (1963) model ($X/X0 = e^{-kt}$). Community groups were defined based on Cluster Analysis, Indicator Species Analysis, and Non-metric Multi-dimensional scaling as presented in Chapter 2.

Table 4.5. ANOVA results for decay rate and % mass remaining by community group within litter type for each litter bag collection period.

Collection date	Community Groups ($N = 12$; three litter bag replicates by four groups for each litter type; values are mean (SE))				
	Litter type: ANOVA results	1 - FRPE/LIST/CELA	2 - LIST	3 - CELA/ACNE	4 - TADI
Decay rate (k)	Mixed: $F_{3,8} = 0.32$; $P = 0.80$	1.41 (0.22)	1.57 (0.09)	1.53 (0.10)	1.44 (0.08)
	Single: $F_{3,8} = 0.05$; $P = 0.98$	1.44 (0.04)	1.33 (0.46)	1.40 (0.22)	1.49 (0.25)
Week 2	Mixed: $F_{3,8} = 7.07$; $P = 0.012$; **1 = 2 = 4 > 3**	100.73 (0.16)	100.17 (0.16)	97.26 (1.13)	99.40 (0.12)
02/23/2011	Single: $F_{3,8} = 7.26$; $P = 0.011$; **2 > 3 = 4**	99.91 (0.11)	100.46 (0.07)	99.56 (0.23)	99.21 (0.30)
Week 4	Mixed: $F_{3,8} = 5.18$; $P = 0.028$; **1 > 4**	99.87 (0.37)	98.50 (0.07)	96.05 (0.78)	95.10 (1.72)
03/09/2011	Single: $F_{3,8} = 21.76$; $P < 0.0001$; **2 = 3 > 1 > 4**	95.35 (0.10)	99.80 (0.03)	99.59 (0.05)	94.76 (0.06)
Week 6	Mixed: $F_{3,8} = 1.62$; $P = 0.26$	95.57 (0.25)	94.12 (0.40)	92.51 (1.65)	94.39 (0.98)
03/24/2011	Single: $F_{3,8} = 24.71$; $P = 0.0002$; **3 = 2 > 1 = 4**	92.92 (0.48)	95.69 (0.50)	96.42 (0.27)	90.45 (0.81)
Week 8	Mixed: $F_{3,8} = 9.69$; $P = 0.005$; **1 = 4 > 2**	93.52 (1.02)	86.76 (0.66)	90.53 (0.31)	90.85 (1.28)
04/06/2011	Single: $F_{3,8} = 23.48$; $P = 0.0003$; **2 = 3 > 1 = 4**	89.23 (1.12)	93.78 (0.44)	93.41 (0.24)	85.78 (0.97)
Week 12	Mixed: $F_{3,8} = 12.15$; $P = 0.002$; **1 = 4 > 3 = 2**	88.49 (0.60)	74.78 (1.79)	76.20 (3.29)	84.95 (0.50)
05/07/2011	Single: $F_{3,8} = 20.07$; $P = 0.0004$; **2 = 3 > 4 = 1**	82.84 (0.55)	88.31 (0.81)	87.64 (0.65)	83.13 (0.56)
Week 16	Mixed: $F_{3,8} = 82.81$; $P < 0.0001$; **1 = 4 > 3 = 2**	79.75 (1.40)	55.09 (1.37)	57.07 (1.23)	77.53 (1.71)
06/07/2011	Single: $F_{3,8} = 4.99$; $P = 0.031$; **2 > 4**	71.81 (0.99)	80.82 (1.51)	74.29 (1.85)	67.42 (4.29)
Week 22	Mixed: $F_{3,8} = 22.94$; $P = 0.0003$; **1 = 4 > 3 = 2**	64.35 (0.76)	32.19 (0.36)	35.30 (3.20)	57.19 (5.77)
07/18/2011	Single: $F_{3,8} = 0.81$; $P = 0.52$	60.62 (7.79)	66.76 (6.00)	55.05 (3.76)	58.67 (2.77)
Week 28	Mixed: $F_{3,8} = 38.83$; $P < 0.0001$; **1 = 4 > 2 = 3**	53.99 (1.35)	21.23 (3.64)	20.89 (2.93)	42.82 (2.03)
09/13/2011	Single: $F_{3,8} = 1.12$; $P = 0.40$	38.29 (4.83)	43.66 (1.86)	43.91 (3.73)	33.75 (6.59)
Week 38	Mixed: $F_{3,8} = 16.51$; $P = 0.0009$; **1 > 4 = 3 = 2**	41.51 (0.40)	17.34 (3.14)	19.19 (2.30)	27.06 (3.75)
11/18/2011	Single: $F_{3,8} = 3.90$; $P = 0.055$	16.60 (2.37)	30.53 (4.96)	27.89 (2.47)	30.70 (3.06)
Week 48	Mixed: $F_{3,8} = 3.69$; $P = 0.062$	17.39 (1.01)	11.89 (1.80)	9.71 (1.51)	17.03 (6.37)
01/27/2012	Single: $F_{3,8} = 0.85$; $P = 0.53$	15.73 (1.55)	24.12 (0.42)	21.98 (4.20)	17.56 (7.36)
Week 64	Mixed: $F_{3,8} = 7.40$; $P = 0.011$; **1 > 3**	11.70 (2.34)	9.54 (1.08)	3.47 (0.58)	5.64 (0.71)
05/25/2012	Single: $F_{3,8} = 1.79$; $P = 0.23$	12.61 (2.31)	15.78 (1.08)	17.67 (1.70)	12.76 (2.04)
Week 80	Mixed: $F_{3,8} = 26.89$; $P = 0.0002$; **1 > 4 = 2 = 3**	7.17 (0.38)	1.54 (0.22)	0.58 (0.58)	2.66 (0.86)
09/05/2012	Single: $F_{3,8} = 5.31$; $P = 0.026$; **4 > 1**	4.18 (1.96)	0.62 (0.62)	4.84 (1.54)	8.22 (0.85)
Week 100	Mixed: $F_{3,8} = 2.04$; $P = 0.19$	1.71 (1.02)	0.49 (0.49)	0	0
01/29/2013	Single: $F_{3,8} = 1.25$; $P = 0.36$	0	0.62 (0.62)	0.61 (0.61)	1.71 (0.93)

Notes: F statistic with degrees of freedom from one-way ANOVA testing the hypothesis of no difference in community group means by litter type; multiple comparisons used the Tukey test at the alpha = 0.05 level. Mixed species litter was collected within each community group and single species litter was collected from a single, isolated white oak tree. All litter bags were installed on 02/09/2011. Each mean is derived from three replicate litter decomposition bags per community group for each litter type on each collection date; % dry mass remaining is calculated on an ash-free basis. The decay rate is calculated according to Olson's (1963) model ($X/X0 = e^{-kt}$).

Table 4.6. Percent of original phosphorous, carbon, and nitrogen remaining in single and mixed litter at each collection period by community group.

Community Group	Weeks in the field	% P single	% C single	% N single	% P mixed	% C mixed	% N mixed
1 - FRPE/LIST/CELA	0	100.00	100.00	100.00	100.00	100.00	100.00
	2	81.05	101.64	97.64	86.00	103.07	86.84
	4	73.81	95.95	110.18	63.77	102.96	101.80
	6	82.48	93.63	108.64	67.00	95.83	85.96
	8	82.55	85.56	115.56	55.51	94.12	86.33
	12	79.64	77.89	97.03	56.33	89.99	98.89
	16	79.77	64.66	106.29	54.27	81.19	106.82
	22	73.88	52.58	101.36	49.20	62.38	98.30
	28	56.85	32.42	78.86	45.89	48.62	75.28
	38	25.23	12.37	30.14	36.22	39.03	64.25
	48	19.85	13.45	30.70	15.94	15.12	27.25
	64	18.20	11.74	26.51	12.46	10.52	19.78
	80	7.57	3.32	8.43	7.42	6.01	12.34
	100	0.00	0.00	0.00	1.69	1.50	2.78
2 - LIST	0	100.00	100.00	100.00	100.00	100.00	100.00
	2	88.65	101.76	105.98	118.33	102.19	100.29
	4	75.41	99.32	90.75	102.59	99.84	105.84
	6	69.45	94.48	109.80	91.18	90.54	107.39
	8	79.45	91.35	106.64	80.08	85.00	103.41
	12	77.61	86.31	135.32	66.95	72.26	99.73
	16	80.69	78.92	140.73	34.43	53.32	57.91
	22	64.70	61.98	100.41	22.04	31.37	38.44
	28	52.97	39.80	91.23	15.45	20.45	28.97
	38	36.13	27.88	62.17	11.60	16.11	25.28
	48	27.84	21.06	50.80	7.44	11.24	15.41
	64	18.00	14.16	29.47	6.72	9.40	12.03
	80	0.68	0.46	1.33	1.14	1.44	2.15
	100	0.75	0.51	1.31	0.37	0.40	0.62
3 - CELA/ACNE	0	100.00	100.00	100.00	100.00	100.00	100.00
	2	77.88	99.08	93.66	77.87	95.42	106.61
	4	77.72	98.97	96.96	84.53	93.70	99.93
	6	89.16	93.57	111.96	75.17	90.82	88.57
	8	86.59	91.09	95.20	101.07	89.48	102.83

	12	71.77	84.64	91.39	60.15	70.97	91.92
	16	76.75	68.58	97.48	36.42	52.56	64.76
	22	58.83	50.03	72.00	17.16	33.22	41.21
	28	61.25	39.11	56.33	12.81	17.72	22.23
	38	35.97	25.84	41.99	12.92	16.79	24.22
	48	25.11	19.90	31.46	4.37	9.02	11.86
	64	27.61	16.39	23.55	1.96	2.47	3.38
	80	6.95	3.93	7.91	0.35	0.37	0.54
	100	0.92	0.48	0.89	0.00	0.00	0.00
4 - TADI	0	100.00	100.00	100.00	100.00	100.00	100.00
	2	94.92	99.13	92.84	82.48	96.96	85.38
	4	82.35	93.84	94.01	84.81	94.29	88.01
	6	106.34	87.29	97.49	89.89	89.52	104.42
	8	101.05	80.93	94.30	77.15	88.05	98.62
	12	90.65	78.45	92.89	100.15	78.99	98.79
	16	82.44	63.87	82.30	83.67	71.60	109.75
	22	76.79	55.73	73.02	59.33	52.05	78.00
	28	42.76	30.58	47.12	46.12	39.50	61.03
	38	49.82	28.58	51.07	33.24	21.64	38.37
	48	24.54	14.79	24.65	19.68	13.96	24.14
	64	21.67	11.41	20.20	6.53	5.14	9.63
	80	13.96	7.35	12.77	3.08	2.34	4.65
	100	3.19	1.40	2.65	0.00	0.00	0.00

Notes: Three replicates were collected for each litter type at each collection period; values are the mean of the replicates calculated based on lab results, original mass, and mass at collection. Material from the three replicates was combined and a single pooled subsample was subjected to lab analyses; therefore statistical analyses would be invalid due to pseudo-replication.

Table 4.7. Nutrient ratios by litter type within community groups over time on the floodplain of the Congaree River.

	Community group - single species litter bags											
	1 - FRPE/LIST/CELA			**2 - LIST**			**3 - CELA/ACNE**			**4 - TADI**		
Weeks in the field	**C:N ratio**	**C:P ratio**	**N:P ratio**	**C:N ratio**	**C:P ratio**	**N:P ratio**	**C:N ratio**	**C:P ratio**	**N:P ratio**	**C:N ratio**	**C:P ratio**	**N:P ratio**
0	56.4	352.6	6.3	61.6	295.6	4.8	47.9	350.9	7.3	46.4	427.3	9.2
2	58.8	442.2	7.5	59.1	339.3	5.7	50.7	446.5	8.8	49.6	446.3	9.0
4	49.2	458.4	9.3	67.4	389.3	5.8	48.9	446.8	9.1	46.4	486.9	10.5
6	48.6	400.3	8.2	53.0	402.1	7.6	40.0	368.3	9.2	41.6	350.8	8.4
8	41.8	365.5	8.8	52.8	339.9	6.4	45.8	369.2	8.1	39.9	342.3	8.6
12	45.3	344.9	7.6	39.3	328.8	8.4	44.3	413.8	9.3	39.2	369.8	9.4
16	34.3	285.8	8.3	34.5	289.1	8.4	33.7	313.5	9.3	36.0	331.1	9.2
22	29.3	251.0	8.6	38.0	283.2	7.5	33.3	298.4	9.0	35.5	310.2	8.8
28	23.2	201.1	8.7	26.9	222.1	8.3	33.3	224.1	6.7	30.1	305.6	10.1
38	23.2	172.9	7.5	27.6	228.1	8.3	29.5	252.1	8.6	26.0	245.1	9.4
48	24.7	239.0	9.7	25.5	223.6	8.8	30.3	278.2	9.2	27.9	257.6	9.2
64	25.0	227.4	9.1	29.6	232.6	7.9	33.3	208.3	6.3	26.2	225.0	8.6
80	22.2	154.8	7.0	7.1	66.5	3.1	23.8	198.2	8.3	26.7	225.0	8.4
100	*	*	*	8.1	67.5	2.8	8.7	61.0	2.4	16.4	125.4	5.1
	Community group - mixed species litter bags											
	1 - FRPE/LIST/CELA			**2 - LIST**			**3 - CELA/ACNE**			**4 - TADI**		
Weeks in the field	**C:N ratio**	**C:P ratio**	**N:P ratio**	**C:N ratio**	**C:P ratio**	**N:P ratio**	**C:N ratio**	**C:P ratio**	**N:P ratio**	**C:N ratio**	**C:P ratio**	**N:P ratio**
0	41.9	204.2	4.9	42.1	134.7	3.2	42.1	105.2	2.5	42.0	257.9	6.1
2	49.7	244.8	4.9	42.9	116.3	2.7	37.7	128.9	3.4	47.7	303.2	6.4
4	42.3	329.8	7.8	39.7	131.1	3.3	39.5	116.6	3.0	45.0	286.7	6.4
6	46.7	292.1	6.3	35.5	133.8	3.8	43.2	127.1	2.9	36.0	256.8	7.1
8	45.7	346.3	7.6	34.6	143.0	4.1	36.7	93.1	2.5	37.5	294.3	7.9
12	38.1	326.3	8.6	30.5	145.4	4.8	32.5	124.1	3.8	33.6	203.4	6.1
16	31.8	305.6	9.6	38.8	208.6	5.4	34.2	151.8	4.4	27.4	220.7	8.1
22	26.6	259.0	9.7	34.4	191.7	5.6	34.0	203.6	6.0	28.0	225.9	8.1
28	27.0	216.4	8.0	29.7	178.3	6.0	33.6	145.5	4.3	27.2	220.9	8.1
38	25.4	220.1	8.7	26.9	187.2	7.0	29.2	136.7	4.7	23.7	167.9	7.1
48	23.2	193.8	8.3	30.7	203.7	6.6	32.1	217.0	6.8	24.3	182.9	7.5
64	22.3	172.5	7.7	32.9	188.3	5.7	30.8	132.5	4.3	22.4	203.3	9.1
80	20.4	165.5	8.1	28.1	169.2	6.0	9.5	36.2	1.3	21.1	195.6	9.3
100	15.0	121.1	5.4	8.9	48.5	1.8	*	*	*	*	*	*

Notes: Values obtained from lab test on a subsample taken from a pooled sample from three litter bags; ratios are based on ash-free dry mass. * Indicates complete decomposition of litter or remaining litter insufficient amount to conduct lab analyses.

Figure 4.1. Location of the study area; inset shows plots by community groups and field location of litter decomposition bags.

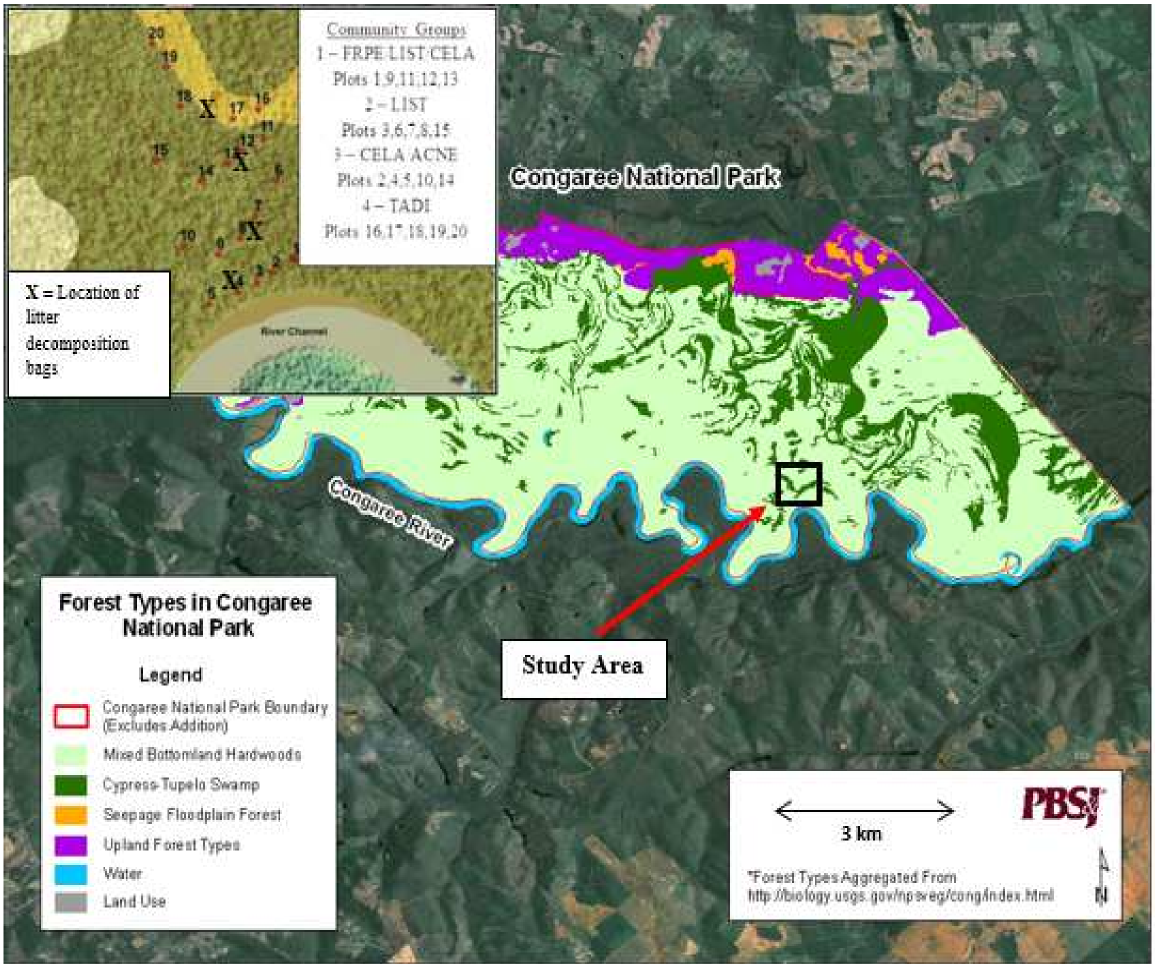
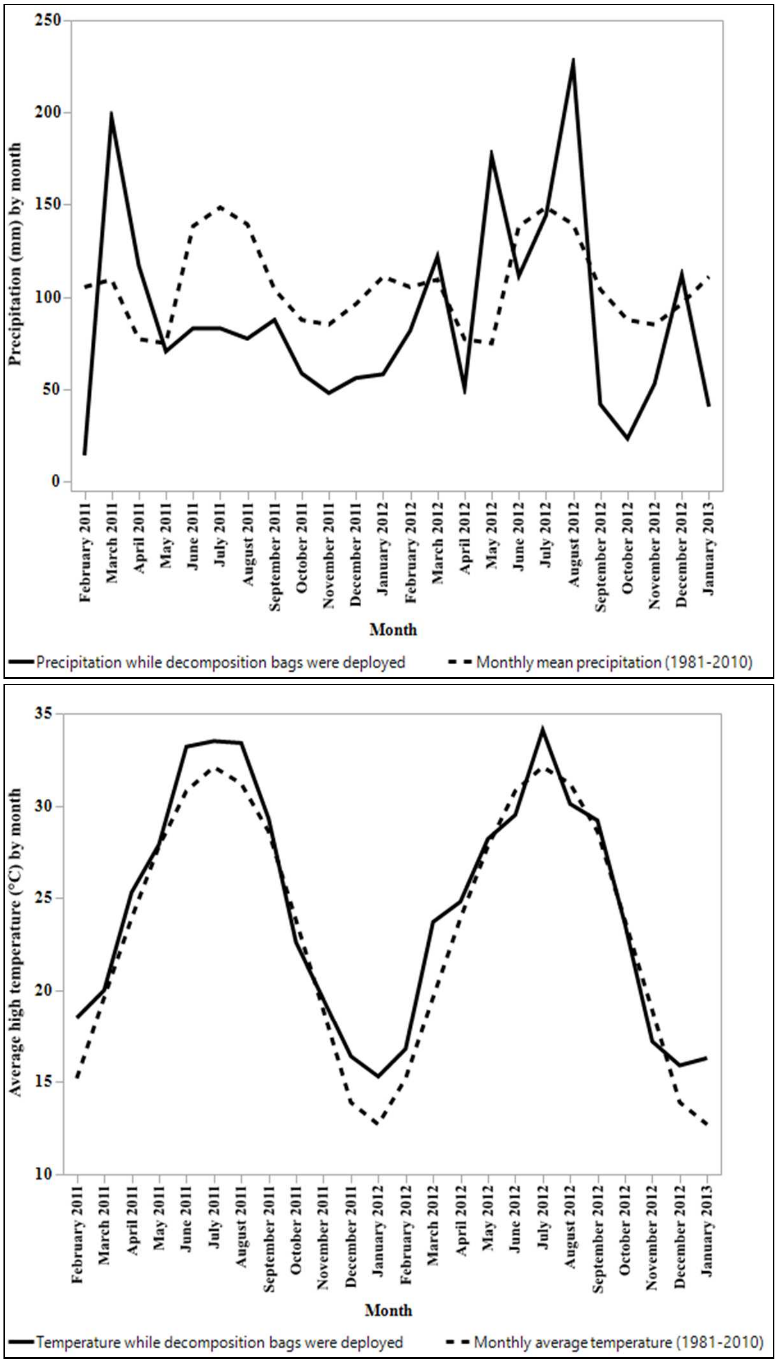
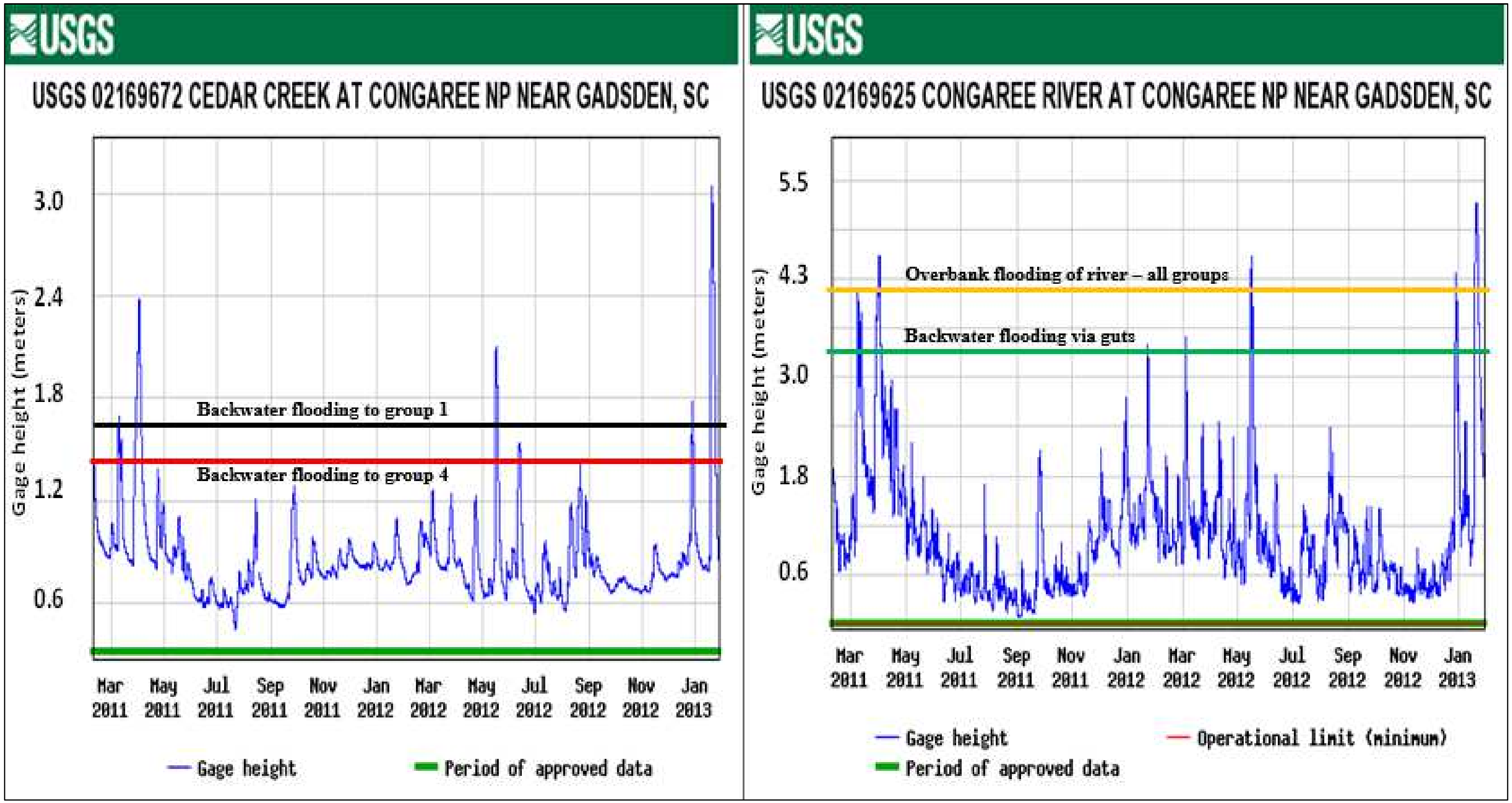


Figure 4.2. Monthly means for precipitation (top) and daily high temperature (bottom) while litter decomposition bags were in the field.



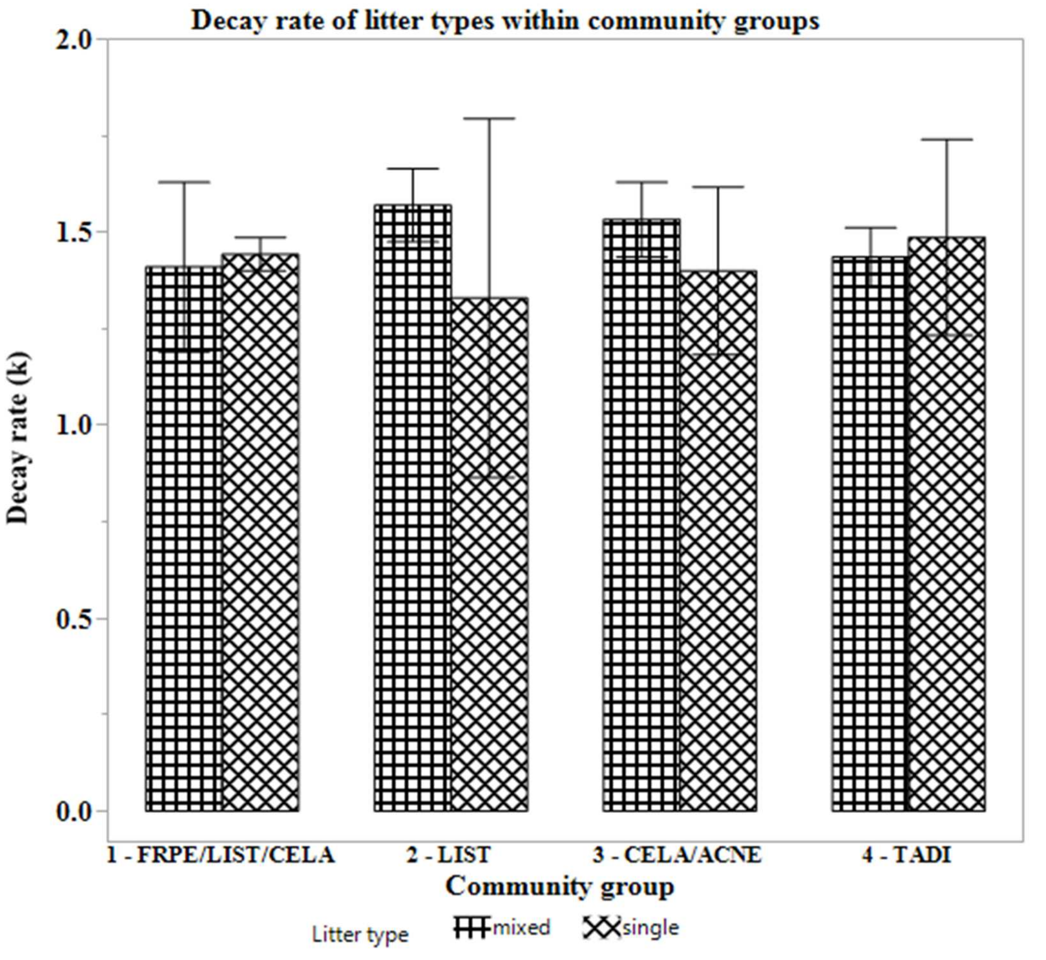
Notes: Monthly means and the 30 year averages preceding litter bag installation (data from NOAA, 2018)

Figure 4.3. Daily maximum gage heights and gage levels producing flood events while decomposition bags were in the field.



Notes: Graphs show levels at USGS (2018) gage stations proximate to the study area for the period during which litter decomposition bags were present in the field; graphed as daily maximum gage height in meters (02/09/2011–01/29/2013).

Figure 4.4. Decomposition rate (*k*) of litter types within community groups calculated for the 100 week period of decomposition study.



Notes: Bars are the mean of three replicates; error bars are the standard error of the means (there were no significant differences at the $P < 0.05$ level).

Figure 4.5. Percent ash-free dry mass remaining for single species (top) and mixed species (bottom) litter over time within community groups.

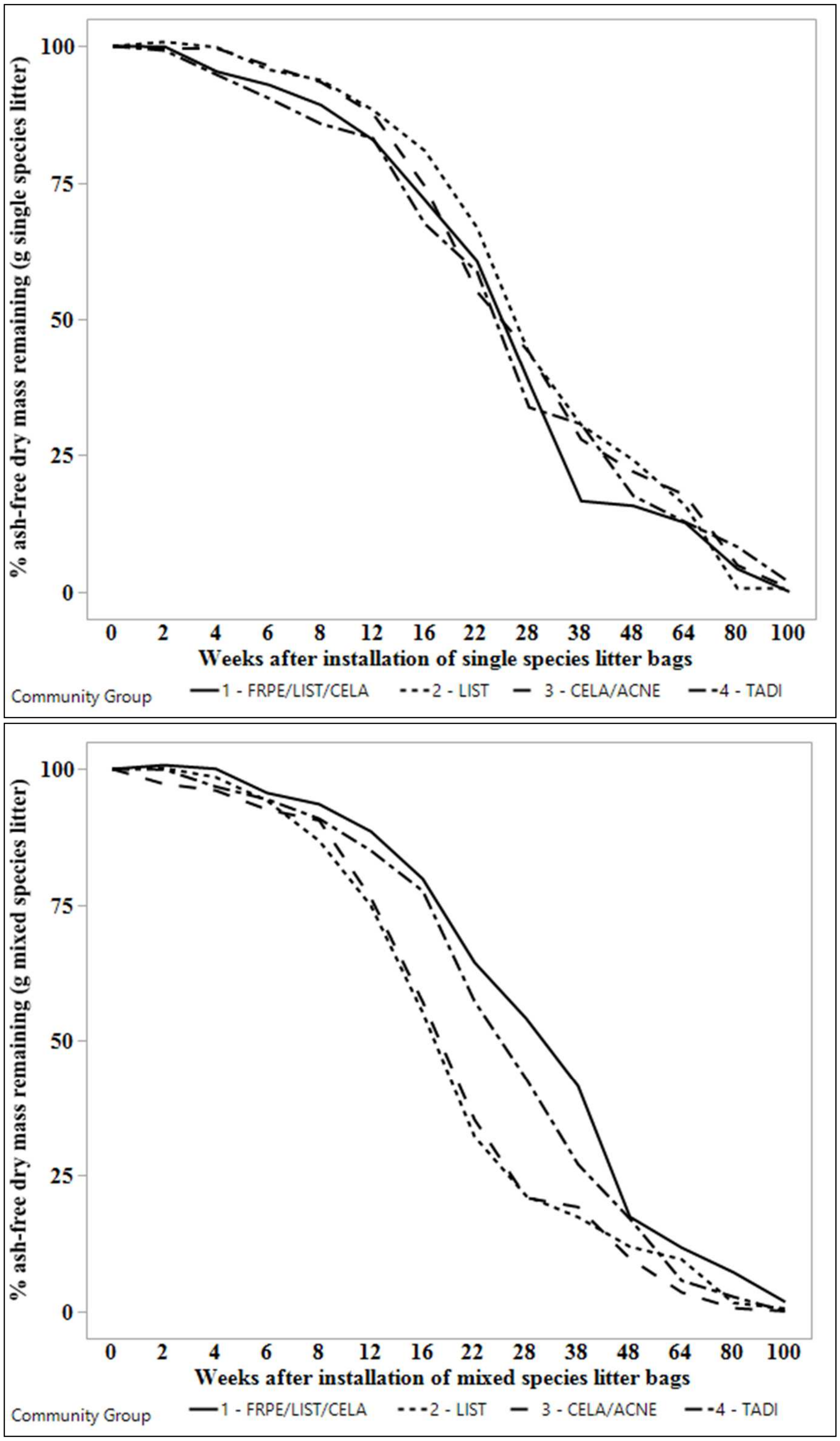


Figure 4.6. Percent of mass remaining for the elements phosphorous, carbon, and nitrogen over time for single and mixed litter types by community group.

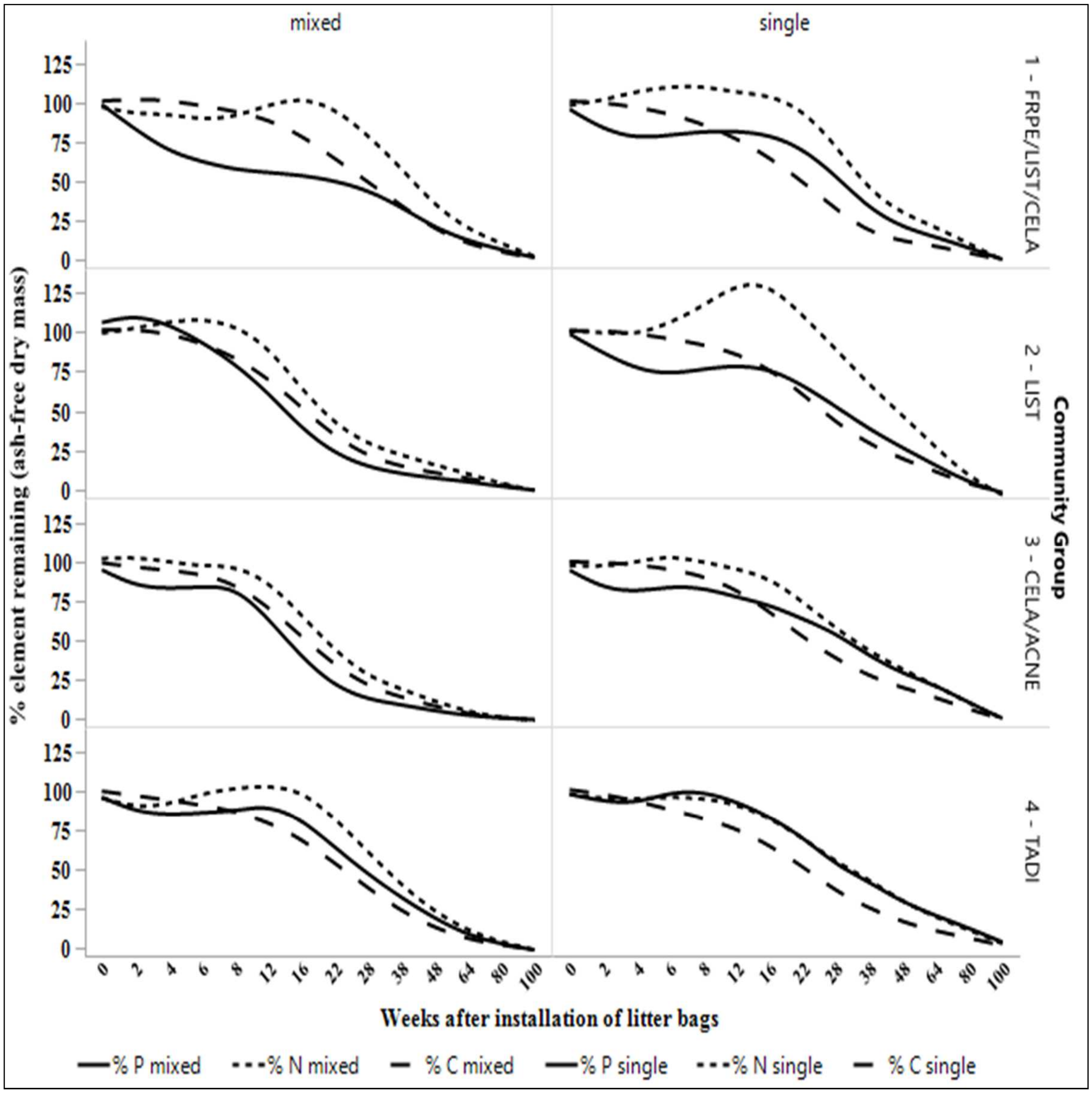
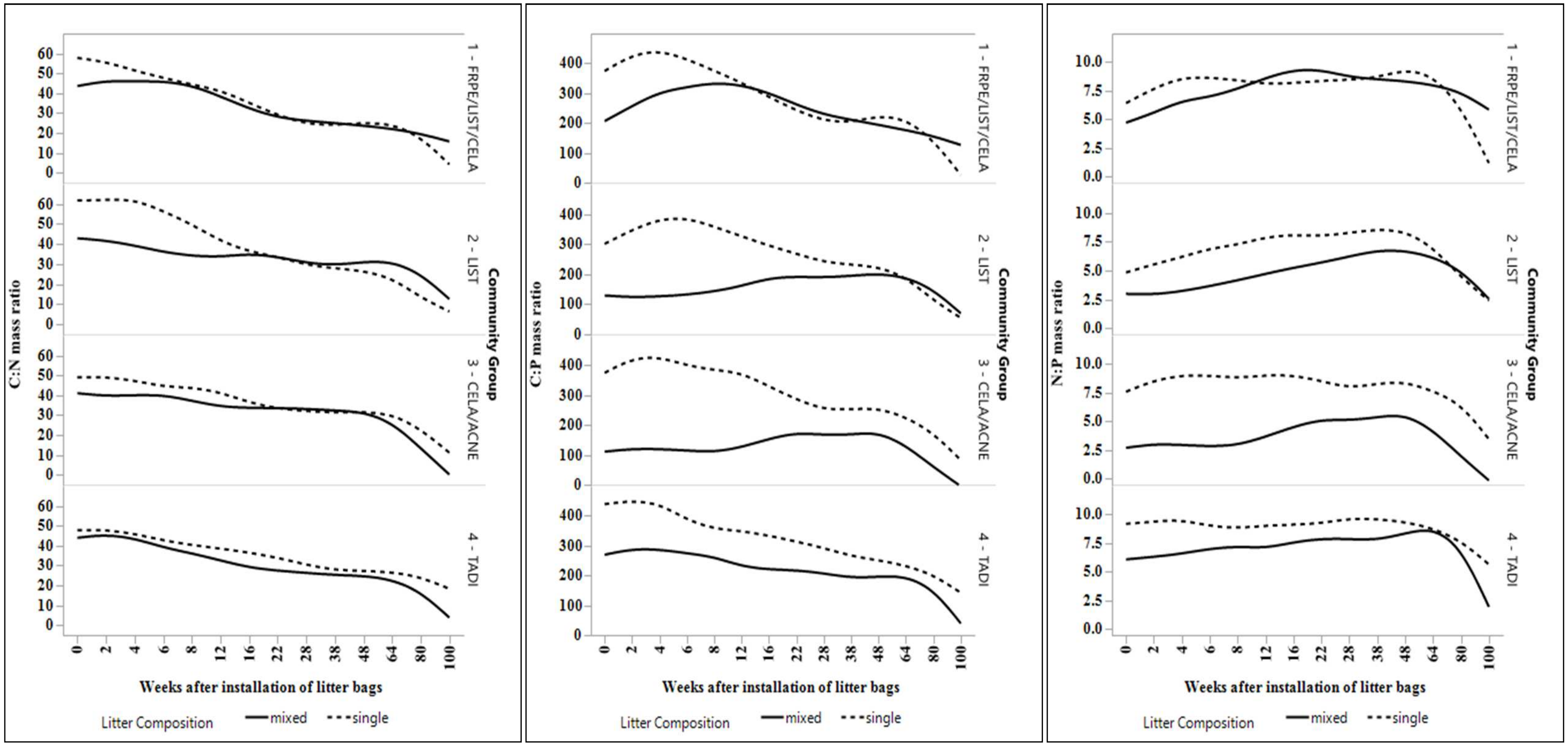


Figure 4.7. Nutrient ratios for the elements phosphorous, carbon, and nitrogen over time for single and mixed litter types within community groups.



CHAPTER FIVE

WOODY DETRITUS BIOMASS AND ABOVEGROUND CARBON POOLS ACROSS AN ELEVATIONAL GRADIENT WITHIN A FLOODPLAIN FOREST OF THE CONGAREE RIVER, SOUTH CAROLINA, USA

Abstract. The quantity, volume, and dry mass of woody detrital biomass was recorded, measured, and calculated on the floodplain of the Congaree River. Stands studied included three mixed bottomland hardwood communities and a bald cypress swamp. The objectives of the study were to categorically quantify aboveground biomass (and thus pools of stored carbon), calculate the percent of stored carbon contained in living wood and woody detritus pools, determine whether these pools differed along an elevation gradient, determine if these pools differed among stands having different age/size class structure, and compare species composition of dead wood and living wood. For all pools of aboveground sequestered carbon measured in this study, downed dead wood, standing dead wood, and live tree, sapling, and shrub wood, we found cumulative values of 14840, 18878, and 7460 grams C/m^2 for bottomland hardwood forest and 19076 grams C/m^2 for the bald cypress swamp. Sequestered carbon mass ranged from 77.6-88.8% in tree wood, 0.3-5.5% in sapling and shrub wood, 1.6-4.6% in fine woody debris, 2.8-7.0% in coarse woody debris, and 3.1-5.9% in snags and stumps. Results indicate that the mass and sequestered C in both live and dead wood are at the high end of both measured and modeled ranges reported in the literature for U.S. forests in general and within the range for regional floodplain forests specifically. As such the forests on the floodplain of the Congaree River represent a substantial and important store of sequestered C. The data indicate that differences in carbon stocks within a given pool are more strongly related to a stand's tree age/size distribution than to elevation. Our comparison of species composition, wood mass and volume, and unit quantities between the dead and live wood fractions, in conjunction with decay class of dead wood used as a temporal proxy, suggests there are ongoing shifts in both the canopy and understory in the bottomland hardwood forest stands while the cypress swamp appears to be stable. It appears that sweetgum, box elder, and bald cypress are declining and sugarberry, green ash, and laurel oak are increasing as canopy components of the elevation gradient we studied. Invasive Chinese privet is also likely to increase and expand within the understory of higher elevation bottomland hardwood forests, particularly in canopy gaps left by senescence of sweetgum and box elder.

Key words: Carbon pools; woody debris; old-growth; bottomland hardwood forest; bald cypress swamp; Congaree National Park

INTRODUCTION

Forested wetland and floodplain communities are among the most effective ecosystems at sequestering atmospheric carbon (C) in addition to numerous other benefits such as improved water quality, protection from storm surge and high tides, and flood mitigation (Mitsch et al., 2013). Globally, forests contain approximately 45% of terrestrial sequestered C within four main pools: living plant material; woody detritus; forest floor – litter, senesced herbaceous vegetation, duff, and soil O horizon; and soil organic C stored in mineral horizons (Bradford et al., 2009). Tree mortality introduces important structural and functional components into these forested ecosystems in the form of both standing and fallen dead wood yielding important microclimates and spatial complexity (Jenkins et al., 2004). Dead woody material provides critical habitat elements for a myriad of plant, animal, and microbial species such as refugia, foraging, recruitment, den/nest sites, and protection (Woodall and Nagel, 2006).

Although the bulk of aboveground sequestered C in these systems is found in living trees and the litter layer, woody detritus in the form of snags, stumps, fine woody debris, and coarse woody debris account for, on average, 16% of the aboveground C pool in U.S. forests (Turner et al., 1995) and consideration of detrital biomass as a C pool is often absent from many studies and inventories (Bradford et al., 2009). Components within this pool may represent long-term sequestration as in large snags and coarse woody debris that may persist for over a century or short-term sequestration in fine woody debris that persists for only 1 to 10 years depending on the decay rate of the site (Jenkins et al., 2004; Fasth et al., 2011; Sain et al., 2012; Sutfin et al., 2016). Although fine woody debris accounts for on average ≤ 4% of aboveground C, due to more rapid decay rate compared to coarse woody debris, it may contribute up to three times the percentage of heterotrophic respiration (Fasth et al., 2011).

Accurately estimating aboveground sequestered C in forested ecosystems involves not only estimating living biomass, but detrital biomass as well (Sutfin et al., 2016). Aboveground detrital biomass includes duff, litter, and dead woody material consisting of materials usually classed as fine woody debris (FWD, < 7.5 cm diameter), coarse woody debris (CWD, > 7.5 cm in diameter), and standing dead wood (SDW, snags and stumps). It has been shown that dead woody material can account for 14 to 17% of aboveground C (Fahey et al., 2005; Woodall and Liknes, 2008; Bradford et al., 2009). It has also been shown that old growth sites generally have a higher dead tree/live tree ratio and the unit volume of dead wood increases with productivity of the site (Spetich et al., 1999).

As southern bottomland forests are, in general, highly productive and the Congaree National Park (CONG) floodplain forest contains old growth areas or mature secondary growth, detrital biomass is likely a major contributor to aboveground sequestered C in this system. This in turn has carbon budget implications related to climate change. While FWD remains more balanced when using latitude as a proxy for increasing temperature, the decay rate of CWD increases substantially with decreasing latitude suggesting the liberation of C from CWD will accelerate with global warming and may potentially shift this biomass pool to a net CO2 emitter (Woodall and Liknes, 2008).

Comparing the volume, quantity, and species composition of standing and down dead wood to that of living trees may be used to analyze forest stand dynamics such as successional trends or species shifts due to environmental changes driven by disease and pathogens, climate change, pollution, hurricanes, floods, and urbanization (Woodall and Nagel, 2006). Distribution, unit density, and mass of dead wood by species within decay class categories may provide additional insight into the temporal and spatial extent of mortality rate changes and community shifts (Sain et al., 2012). Of particular concern in forested wetlands such as that of the CONG floodplain are shifts in community composition via differential mortality and recruitment due to changes in water quality, sedimentation rates and flood regimes associated with land use and water level manipulation in rapidly developing watersheds (Jolley et al., 2010; Jones et al., 1994; Walls et al., 2005; Zimmerman et al., 2008).

Community groups were established post hoc based on numerous recorded community metrics and variables using ordination and Indicator Species Analyses to take all these parameters into consideration and define the most meaningful ecological groupings (Chapter 2). Differences in elevation and the associated differences in the frequency, duration, and intensity of flooding in conjunction with tree species composition were the defining gradients separating communities with additional refinement of communities defined by tree size classes. The quantity, volume, and dry mass of woody detrital biomass was recorded, measured, and calculated on the floodplain of the Congaree River using established protocols as part of a comprehensive study which also addressed community structure, litter decomposition, and annual aboveground net primary productivity. Litter and duff can also represent a significant source of detrital biomass; however litter decomposition results suggest that mass cycling of litter is an annual cycle under the prevailing climatic conditions for the area of the Congaree River floodplain studied with duff formation and litter accumulation scant to nonexistent (Chapter 4). The objectives of the study were to quantify aboveground biomass (and thus stored C) and the percent of stored C contained in woody detritus, determine whether this fraction differed along an elevation gradient, determine if the fraction differed among stands having different age/size class structure, and compare species composition of dead wood and living wood.

MATERIALS AND METHODS

The Congaree River begins at the confluence of the Broad and Saluda rivers near Columbia, South Carolina and ends at its confluence with the Wateree River to form the Santee River. For most of its length, the Congaree River occupies a broad floodplain bounded on the north by a fluvial complex and to the south by a steep bluff cut into upper coastal plain deposits (Shelley and Cohen, 2010). The CONG protects a vast, old growth floodplain forest in the lower Congaree River Valley (Figure 5.1) representing the last remaining major tract of mature bottomland hardwood forest in the southeastern U.S. (Gaddy et al., 1975; Shelley and Cohen, 2010). Within the floodplain are spatially complex changes in elevation (generally < 75 cm) yielding micro high and low areas resulting in distinct flooding regimes, sedimentation processes, and soil drainage characteristics. The spatially variable geomorphic landscapes of southern floodplains result in complex spatial arrays of forest types which often differ in productivity (Conner et al., 2002).

The study area consists of a mosaic of low relief fluvial landscapes across the floodplain subject to differential periods of inundation and sedimentation. Adjacent to the river channel and scattered farther from the river are the highest elevation areas which include the active natural levee and relict levees. Across the floodplain is a mosaic of flats and sloughs (topographic highs and lows) abutting the levees at slightly lower elevations subject to intermediate inundation (community group 1). Community groups 2 and 3 have similar species composition, but differ considerably in tree size distribution and are located within these higher elevation areas (Table 5.1). The lowest areas are oxbows and historic meander scars with seasonal to semi-permanent flooding (community group 4). Backwater flooding can occur via channels known locally as “guts” which connect levee breeches to lower flats and backwater swamps, thus allowing flooding of these areas at flow levels below bank full (Shelley and Cohen, 2010).

Twenty data collection plots, blocked by a priori perceived elevation differences, were established in 2010 along five roughly parallel transects oriented perpendicular to the river channel. Four 20x25 m plots (0.05 ha) were established along each transect with the transect azimuth bisecting the short sides of the rectangular plot; one plot in each of four perceived elevation zones (Figure 5.1). Due to high data variability, a paired 20x25 m plot was added adjacent to each original plot in 2012; each pair was treated as a single 0.10 ha plot for analyses.

Protocols and equations of the Forest Inventory Analysis (FIA) Program (United States Department of Agriculture - Forest Service) were used as a basis for data collection and to calculate volume, biomass, and C mass per unit area for downed and standing dead wood (Brown, 1974; Woodall and Williams, 2005). Downed woody debris (DWD) included fine woody debris (FWD, < 7.5 cm diameter large end) and coarse woody debris (CWD, ≥ 7.5 cm in diameter large end; Brown, 1974) and was summed at plot level using four 25 m transects within each plot pair (long sides of plot pair perimeter). However, DWD transects were parallel rather than intersecting as in the FIA protocol; parallel was more conducive to plot pair shape and the intersecting arrangement does not improve precision (Woldendrop et al., 2004). Standing dead wood (SDW) having a basal diameter ≥ 2.5 cm included stumps (< 2 m in height) and snags (≥ 2 m in height) was mapped within each 0.1 ha plot pair and sufficient data to calculate volume of each unit was recorded. The use of a laser hypsometer and a 2.5 meter ladder was employed to collect upper diameter values and heights for SDW.

Volume of FWD was calculated at plot level according to the methods and formulas contained within Woodall and Williams (2005) with horizontal lean angle correction factor and slope correction factor both set at 1.0 due to the flat topography. A community specific density was calculated and employed in formulas for FWD based on tree and sapling species basal area percentages and species-specific gravity values within community groups. Volume of coarse dead wood was calculated based on the formula for a frustum of a right circular cone (Equation 1; Smalian's formula; Waddell, 2002) as it is more accurate compared to recording only diameter at point of intersection or large end diameter and calculating as the volume of a cylinder (Woodall et al., 2008; Bates et al., 2009). Two diameters for SDW were recorded and the same decay class corrections as those for CWD were used. The first was at or near the base and the second at the top or as high up the bole as possible using a ladder. It was then possible to calculate a taper (Equation 2) to derive the diameter at the top of the snag (Equation 3) followed by application of Equation 1. Hollows in dead wood having a diameter greater than 7.5 cm were volume corrected by subtracting volume of the void using void diameters. Volumes of CWD units were converted to a volume per unit area basis using equation 4 and the results were summed at the plot level prior to analyses.

Equation 1: Volume of piece of dead wood (m^3) = $(\pi/8)*(DLE^2 + DSE^2)$*length or height

Equation 2: Taper constant = (lower diameter – upper diameter) / (distance between diameters)

Equation 3: Calculated DSE for SWD top diameter = DLE – (taper constant*height)

Equation 4: CWD volume m^3/hectare = [π/(2*transect length]*(CWD volume/length of CWD)*(10,000m^2/hectare)

Note: Equation results for each CWD piece summed to plot level prior to analyses

Equation 5: Dry mass of piece of dead wood (g) = (Volume m^3)*(10^6 grams/m^3)*(specific gravity)*(decay class reduction factor)

Where: DLE = diameter large end for CWD or lower diameter for SDW

DSE = diameter small end for CWD or measured/calculated diameter at top for SDW

CWD = coarse woody debris

SDW = standing dead wood

Note: All diameters, lengths, and heights in meters; equations based on those in Waddell (2002).

Dry mass of dead wood was calculated according to standard procedures employing decay class reduction factors and specific gravity values by species to obtain dry mass (Equation 5). A decay class (1 through 5) was assigned to each unit of dead wood and the corresponding decay class reduction factor was used in calculation of dry mass (Waddell, 2002). Published species specific gravity values were obtained from Jenkins et al. (2003) and Woodall and Williams (2005). Carbon mass was assumed to be 50% of dry mass for all woody plant material as a general comparative estimate among community types (Fahey et al., 2005; Shoch et al., 2009; Moerschbaecher et al., 2016).

The dry mass of standing dead trees and recent blow downs with intact canopy (decay class 1 – fine twigs still intact) was calculated differently than described above. The allometric equations for live tree biomass were used (Chapter 3). The biomass of these was estimated from diameter at breast height (DBH; 1.4 m) for a given species using specific gravity and allometric equations developed for a species or genus (Phillips, 1981; Clark et al., 1985; Megonigal et al., 1997; Jenkins et al., 2003). The allometric equations of Jenkins et al. (2003) were used for all tree and sapling species with the following exceptions. The allometric equations used to estimate the biomass of bald cypress (Taxodium distichum [L.] Richard) follow those applied by Megonigal et al. (1997). Allometric equations to estimate the biomass of Chinese privet (Ligustrum sinense Lour.) follow those developed and used by Burton (Burton, 2006; Burton and Samuelson, 2008). These equations were also applied to the large shrub species buttonbush (Cephalanthus occidentalis L.) for which no equations could be found in the literature. Specific gravity values were taken from the extensive list provided in Woodall and Williams (2005) as required for a given allometric equation.

After analysis of community data, post hoc blocking of plots into community groups was executed using non-parametric techniques (Chapter 2). Statistical analyses employed the program JMP Pro 12.0 (SAS Institute, 2015). To test the hypothesis of no difference among community groups, one-way analysis of variance (ANOVA) was employed; multiple comparisons used the Tukey test (corrects for multiple comparisons). In cases where normality (Shapiro-Wilk W test) or equal variance (Brown-Forsythe test) assumptions on the residuals were not met at the $P = 0.05$ level, the data were subjected to the Kruskal Wallis test (rank sums); multiple comparisons following Kruskal Wallis test used Dunn's method for joint ranking (corrects for multiple comparisons). The $\leq$ sign is used in the results section when several pairwise comparisons are significant and only the largest P value is reported. The plant nomenclature of Radford et al. (1968) was followed for all vegetation data collected in this study. Four letter codes (first two letters of genus and first two letters of specific epithet) were assigned to each species discussed in this study and these codes are used for brevity within tables; a species list table is provided as Appendix 7.

RESULTS

Woody detritus within community groups

Total aboveground woody detritus and component mass per unit area values exhibited high variation from plot to plot within community groups and among community group means yielding no significant differences in many instances. Total dead wood did not differ significantly among community groups, but showed the same ranking as total live wood; these differences seem to be more related to tree size than elevation. Total living wood was lowest, and significantly less than group 4, in higher elevation community group 3 at 12397 g/m^2; group 3 also had the lowest number of trees $\geq$ 50 cm DBH at 7.6%, lowest tree basal area of 20.6 m^2/ha, and the lowest mass of dead wood at 2523 g/m^2 (Tables

5.1 and 5.2). Community group 2 occurs at the same elevation, on same soil type, and has the same canopy dominants as group 3, but a much higher basal area of 44.8 m²/ha and 24.7% of trees having a DBH ≥ 50 cm (Table 5.2). Total living and dead wood biomass were also considerably larger in group 2 compared to group 3 (34172 and 3583 g/m², respectfully, Table 5.2). Community group 4 is the lowest elevation group, occurs on the Chastain soil series, and had the highest basal area and percent of trees ≥ 50 cm DBH (63.7 m²/ha and 27.8%, respectfully; Tables 5.1 and 5.2). Total living wood in group 4 (33308 g/m²) is significantly greater than group 3 (12397 g/m²; $P = 0.033$) and essentially identical to group 2 (34172 g/m²; Table 5.2). Total dead wood mass was greatest in group 4 at (4843 g/m²), but this value was not significantly greater compared to the other community groups (Table 5.2; $P = 0.32$). Intermediate in elevation and species composition and located at the interface of the Congaree and Chastain soil series is community group 1 (Table 5.1). Group 1 also exhibited intermediate values for basal area, percent of trees ≥ 50 cm DBH, total living wood mass, and total dead wood mass (36.4 m²/ha, 12.8%, 26586 g/m², and 3094 g/m², respectfully; Tables 5.1 and 5.2).

The FWD component of aboveground dead wood dry mass did not differ significantly among community groups, although group means ranged from 478 to 989 g/m² (Table 5.2). Community group 4 showed the highest FWD mass at 989 g/m²; however this is the only group regularly receiving flood waters of sufficient velocity to transport woody debris; as such this value may be inflated by exogenous material. Values for community groups 2 and 3 were very similar (758 and 691 g/m²; respectfully), which may be related to similar species composition, although tree size/age structure differ considerably. Community group 1 had the lowest FWD dry mass at 478 g/m²; which could be due to occasional flood water transport to adjacent group 4. The mean annual input of FWD based on litter box data in 2011 and 2012 did not differ significantly among community groups with a range of 116 to 138 g/m²/year (Table 5.2; litter box data from Chapter 3). Annual FWD input was highest in community group 2 at 138 while being nearly identical for other groups (116-122 g/m²/year).

Community groups 2 and 3 were also nearly identical for dry mass of CWD (1039 and 1040 g/m², respectfully; Table 5.2). This would be expected with similar species composition and landscape position, but seems unusual when differences in age and size structure are considered. Group 4 had the highest CWD dry mass of 2366 g/m², which is likely related to having the highest tree density and greatest tree basal area among groups. A portion of this could be due to transport of exogenous material, but it is unlikely larger pieces are routinely imported due to high tree density and bald cypress knee density restricting floating debris. Community group 1 exhibited an intermediate CWD dry mass of 1723 g/m², which seems most likely attributable to a mixed species composition. Like FWD, the CWD component of aboveground dead wood dry mass did not differ significantly among community groups, although group means exhibited a wide range.
Dry mass of total dead wood within the snag component ranged from 782 to 1766 g/m² among community groups, but due to high plot to plot variance no statistically significant differences were apparent. Snag dry mass was greatest in community groups 2 and 4 (1766 and 1406 g/m², respectfully; Table 5.2) having the highest percent of trees ≥ 50 cm DBH (24.7 and 27.8%, respectfully; Table 5.1); this would appear intuitive as larger trees result

in larger snags. Snag dry mass was considerably less in community groups 1 and 3 (846 and 782 g/m², respectfully; Table 5.2) and is likely related to the smaller proportion of larger trees (12.8 and 7.6% of trees ≥ 50 cm, respectfully; Table 5.1).

The stump fraction dry mass represented the smallest aboveground dead wood mass component with a range of 10.4 to 81.4 g/m² (Table 5.2). The higher elevation groups 2 and 3 showed the least amount of dead wood dry mass in stumps (20.6 and 10.4 g/m², respectfully; Table 5.2). The highest stump dry mass was recorded for community group 4 (81.4 g/m²), which had the highest tree density and highest tree basal area. Community group 1 was intermediate in stump dry mass at 47.1 g/m². Community group 4 stump dry mass was significantly greater than group 1 mass ($P = 0.025$; Table 5.2). Bald cypress, a more rot resistant species, was only present at a significant level in both dead and live wood fractions within community groups 1 and 4 and may be responsible, in part, for the higher stump and CWD mass values in those groups.

Species composition of living and dead wood

The species composition of dead wood mass (percent of total mass) and dead wood units (percent of total recorded units with a diameter ≥ 7.5 cm) were compared to the species composition of live wood based on percent of basal area of living trees and saplings (Tables 5.1 and 5.3). In some cases, a species appeared to be proportionally represented in live and dead wood, while in other cases was either over represented or under represented within dead wood compared to live wood values. Percent dry mass within dead wood decay class (Table 5.4) was also considered as a temporal surrogate; large differences in decay class mass may reveal episodic changes in mortality rates.

The sapling layer in community group 1 is dominated by pawpaw (Asimina triloba [L.] Dunal) and possumhaw (Ilex decidua Walter; 41.7 and 33.7% of basal area, respectfully; Tables 5.1 and 5.3). Pawpaw represented 7.3% and possumhaw 15.9% of dead wood units within group 1, while both species accounted for only approximately 0.5% each of dead wood dry mass. These values suggest these species are most likely stable sapling components, although possumhaw appears to have higher stem mortality due to its multi-stemmed habit compared to pawpaw. Sweetgum (Liquidambar styraciflua L.) accounted for 23.7% of the basal area, 18.8% of the dead wood units, and 46.0% of the dead wood mass within community group 1 (Tables 5.1 and 5.3; Chapter 2 – Appendix 4). Based on these values and a sapling basal area of only 2.4%, it appears that sweetgum is in decline within this community with mortality skewed to larger individuals. Bald cypress also appears to be in decline within this community with a tree basal area of 7.7%, 20.3% of dead wood units, and 35.5% of dead wood mass, while being absent from the sapling layer (Tables 5.1 and 5.3; Chapter 2 – Appendix 4). American elm (Ulmus americana L.) and sycamore (Platanus occidentalis L.) are minor canopy components and appear in equilibrium with basal areas of 5.8 and 5.5%, dead wood units at 7.3 and 2.9%, and dead wood mass at 1.9 and 6.0%; both are absent from the sapling layer. Box elder (Acer negundo L.) also appears to be a relatively stable minor component representing 6.7% of basal area, absent from sapling layer, 14.5% of dead wood units, and 3.3% of dead wood mass. Overcup oak (*Quercus lyrata* Walter) accounts for 9.2% of tree basal area in community group 1, but was not recorded in the sapling layer or dead wood inventory. Green ash (Fraxinus pennsylvanica Marshall) and sugarberry (Celtis laevigata Willd.)

exhibit values suggesting these two species may be on the increase, although neither was present within the sapling layer. Green ash represents 23.2% of tree basal area while accounting for only 4.4% of dead wood units and 3.2% of dead wood mass. Sugarberry also represents 4.4% of dead wood units and only 2.8% of the mass, but accounts for 12.6% of tree basal area.

The canopy of community group 2 is dominated by very large sweetgum trees accounting for 71.2% of tree basal area, 29.9% of dead wood units, and 80.6% of dead wood mass; sweetgum is absent from the sapling layer (Tables 5.1 and 5.3; Chapter 2 – Appendix 4). These values suggest sweetgum is at a climax seral stage, but is likely approaching a point of decline as the oldest, largest trees begin to die with no recruitment to the sapling layer. Box elder represented 15.6% of dead wood mass and 31.0% of the units while only accounting for 3.8% and 3.6% of tree and sapling basal area indicating this species is also in decline within community group 2. Laurel oak (*Quercus laurifolia* Michaux) only accounts for 2.3% of tree basal are, but 8.6% of sapling basal area and is absent from the dead wood inventory indicating this species may be a future canopy dominant within community group 2. American elm represents 8.2% of the tree basal area, 2.9% of the sapling layer, 3.5% of dead wood units, and 1.7% of dead wood mass indicating this species is either in stasis or may represent a larger canopy component in the future. Sugarberry also appears in equilibrium or increasing with a tree basal area of 7.3%, sapling basal area of 5.6%, while only accounting for 1.2% of dead wood units and 0.08% of dead wood mass. Pawpaw dominates the sapling layer at 67.5% of the basal area and appears stable or ascendant at 1.0% of dead wood mass and 18.4% of dead wood units. American holly (*Ilex opaca* Aiton) is 6.7% of sapling basal area, but absent from the dead wood inventory suggesting this species may increase over time while the deciduous holly, possumhaw, appears to be in stasis as a minor component of the sapling layer (basal area 3.0%, dead wood mass 0.2%, dead wood units 10.3%).

Overall, community group 3 has the lowest tree basal area and the lowest percent of trees ≥ 50 cm DBH indicating it is the youngest group. Two of the present canopy dominants, box elder and sweetgum, accounting for 25.5 and 10.2% of tree basal area appear to be in decline with percent dead wood mass values of 34.0 and 34.3% and percent of dead wood units at 34.7 and 5.1% (Tables 5.1 and 5.3; Chapter 2 – Appendix 4). Neither species is present within the sapling layer and sweetgum mortality appears skewed towards larger individuals. American elm accounts for 7.0% of tree and 2.3% of sapling basal area, 12.2% of dead wood units, and 9.6% of dead wood mass and would appear to be at stasis. Green ash and water hickory (*Carya aquatica* (Michaux f.) Nuttall, Walter H.) are absent from the sapling layer and may be at stasis or in slight decline; tree basal areas are 6.8 and 4.2%, dead wood units 2.0 and 1.0%, and dead wood mass 11.4 and 6.0%. Sugarberry, red maple (Acer rubrum L.), and laurel oak (tree basal area 30.9, 5.9 and 6.9%, absent from sapling layer) are likely increasing canopy components with dead wood units at 4.1, 1.0 and 1.0% and mass 2.2, 0.4 and 0.4%. The understory in community group 3 is dominated by pawpaw, possumhaw, and Chinese privet (*Ligustrum sinense* Lour.) with basal areas of 41.1, 23.8, and 31%, respectfully. Both pawpaw and possumhaw represent 17.4% of dead wood units, but only 1.3 and 0.7% of dead wood mass indicating stable understory components; possumhaw appears to have higher stem mortality due to its multi-stemmed habit compared to pawpaw. The exotic shrub Chinese privet appears it will increase in the understory as the species accounts for only 4.1% of dead wood units and 0.07% of mass.

Community group 4 appears the most stable group with a canopy dominated by bald cypress and a sparse understory of water elm (*Planera aquatic* Walter ex JF Gmelin) and possumhaw. Bald cypress accounts for 91.7% of tree basal area, 17.1% of sapling basal area, 76.5% of dead wood units, and 92.8% of dead wood mass indicating a stable canopy dominant with sufficient sapling recruitment to continue stasis. Water elm is a minor component of tree class at 3.6% of basal area, but is prevalent and appears stable in the understory at 53.8% of basal area; dead wood mass is 1.9% and units 5.3%. Swamp cottonwood (*Populous heterophylla* L.) is a minor canopy component at 1.7%, is absent from the sapling layer, but was the most common seedling encountered in group 4; dead wood units were 15.2% and mass 0.9% with most of the dead units being ramets arising from stumps and snags. Sweetgum is also a minor component at 1.2% of tree basal area and 0.9% sapling basal area while accounting for 1.5% dead wood units and 4.4% of mass; it is likely this species is in decline. Buttonbush (*Cephalanthus occidentalis* L.) and possumhaw appear to be stable components of the understory (basal areas 2.8 and 23.2%) and collectively accounted for only 0.02% of dead wood mass and 0.8% of dead wood units.

The percent of total dead wood dry mass by woody detritus type and the decay class assigned to CWD, snags, and stumps by community group is shown in Table 5.4. Mass of dead wood in the most advanced decay class 5 is comparatively insignificant with a range of 0.15 to 2.4% across community groups. Decay classes 1 and 2 represent the most recent additions to total dead wood mass and collectively contain 65.5% of mass in community group 2 which also has the highest snag fraction at 49.2% (Table 5.4). This indicates a recent increase in mortality for standing sweetgum and box elder (80.6 and 15.6% dead wood mass; Table 5.3). The majority of dead wood mass (61.3%) was classified as decay class 3 with 41.2% as CWD and 31.0% as snags in community group 3 indicating a discreet period of increased mortality (Table 5.4). Sweetgum and boxelder represent 81.3% of dead wood mass in decay class 3 and appear to be responsible for this mortality pulse. The majority of dead wood mass within community group 1 occurs in decay classes 2 and 3 (39.2 and 36.2%) and in the CWD fraction (55.7%; Table 5.4). Sweetgum and bald cypress account for 79.5% of mass in decay class 2 and 88.4% in decay class 3 within group 1. It appears these two species suffered an historical, episodic increase in mortality. It is possible that group 1 is marginal habitat for these two species with periods of environmental parameters outside the species' tolerance range likely. Bald cypress dominates both live and dead biomass in community group 4, but appears to have suffered elevated mortality in the time span that coincides with decay class 3 (Table 5.4).

Aboveground woody carbon pools

Total aboveground C in woody material ranged from 7460 to 19076 grams C/m^2. The largest pool of sequestered C is living tree biomass ranging from 5787 to 16757 g C/m^2 (77.6-88.8% total C; Table 5.5) which is directly proportional to both tree basal area and the percent of trees ≥ 50cm DBH (Tables 5.1 and 5.2). Carbon in living sapling and shrub wood is a substantial pool in younger community group 3 (5.5%; 412 g/m^2), but less so in other community groups (0.3-1.7%; 55-330 g/m^2; Table 5.5). FWD was also a more important C pool in group 3 (4.6%; 346 g/m²) compared to other groups (1.6-2.6%; 239-495 g/m²). Carbon stored in the stump fraction of dead wood was insignificant across community groups (0.05-0.2%; 5.2-41 g/m²; Table 5.5). The percent C within the CWD carbon pool was lowest in community group 2 (2.8%) and ranged from 5.8 to 7.0% in other groups with C mass ranging from 520 to 1183 g/m² across all community groups. Snag C mass ranged from 391 to 883 g/m² and accounted for 2.9% to 5.2% of aboveground carbon (Table 5.5).

DISCUSSION

Dead wood volumes in forest communities exhibit a very high spatial variability which requires a requisite high sampling effort to obtain a reasonable coefficient of variation that does not obscure significant differences among sites or communities, particularly for CWD (Woldendorp et al., 2004). This threshold is difficult to obtain in practice due to funding and time constraints, especially for multifaceted studies where dead wood is only one component. Although we doubled our sampling effort, variation in our woody debris variables remained excessive from plot to plot and yielded high standard deviation values at the community group level. For example, we found a transect CWD volume range of 10 to 208 m³/ha for 80 25-m transects across 20 plots and a range of 40.4 to 87.8 for community group means. Wohl et al. (2011) found a transect level range of 1.4 to 178.5 m³/ha for CWD volume across 46 100-m transects, 6 200-m transects, and 3 500-m transects located on 11 sites within the CONG. While our CWD volume ranges are very similar, the results of CWD decay class distribution between studies were highly divergent.

Wohl et al. (2011) assigned CWD units to three decay classes and reported that 95% of in channel and 80% of floodplain CWD units were placed in their most advanced decay category 3. We followed the five level decay class system of Waddell (2002) with decay class 5 being the most advanced. Across all plots we found the distribution of CWD units within assigned classes to be: 8% in class 1; 28% in class 2; 41% in class 3; 21% in class 4; and 2% in class 5. This difference suggests that there is a comparative and relatively recent substantial increase in CWD input in our study area, although the difference may also be artificially inflated by interpretation bias associated with researchers. The difference in percent of CWD in the most advanced decay class between this study and results reported by Wohl et al. (2011) may also be associated with differences in feral pig (Sus scrofa) activity. Zengel (2008) reported that recent rooting activity by feral pigs was 3.5 times greater in sample quadrats associated with CWD within CONG.

Harmon et al. (1986) reported a mass range of 1100 to 3800 g/m² for CWD in temperate deciduous forests. We found similar values of 1039 to 2366 g/m² for CWD within floodplain community groups in the CONG. Our higher values of 1723 and 2366 g/m² for community groups 1 and 4 are similar to the mean of 2180 g/m² reported by Muller (2003) for old growth deciduous forests in Kentucky. We found a CWD mass of 1040 g/m² for higher elevation younger stands (community group 3) and 1039 g/m² for higher elevation old growth stands (community group 2); considerably higher than the 660 g/m² value reported by Polit and Brown (1996) for a floodplain forest in Illinois. Jenkins et al. (2004) reported a CWD volume range of 10.8 to 22.4 m³/ha for 34 stands in mixed hardwood forests in Indiana (stands 75-105 years old). Spetich et al. (1999) reported a mean of 60.4 and a range of 24 to 111 m³/ha for CWD volume in upland, old growth, mixed hardwood forests within Indiana, Missouri, Illinois, and Iowa based on 328 plots across 12 sites. We found a CWD volume range of 40.4 to 87.8 m³/ha as community group means. Comparatively, CWD stocks on the floodplain of the Congaree River are variable, but overall appear to be above average; even though the decay rate of CWD is likely considerably faster at our study site compared to the geographic areas referenced above, elevated inputs of dead wood volume is a common characteristic of old growth forests (Spetich et al., 1999). Rice et al. (1997) reported much higher CWD mass for mixed bottomland hardwood forests in the Atchafalaya Basin in Louisiana following damage associated with the passage of Hurricane Andrew. They found a mean CWD mass of 6600 g/m² for less damaged areas having a canopy closure of 70-75% and 12500 g/m² for heavily damaged areas with 25-30% canopy closure illustrating how such events can dramatically increase volumes of dead wood. Our study plots exhibited summer canopy closure values $\geq$ 95% (Chapter 2) and the last major hurricane disturbance in the study area causing widespread damage to trees occurred in 1989 with the passage of Hurricane Hugo. Rice et al. (1997) reported relatively high CWD decay rates (0.050-0.081) compared to other studies, but similar to values reported for other floodplain forests. We suspect CWD decay rates in our study area would be similar to those of Rice et al. (1997) as both areas have a warm and moist decomposition environment with periodic inundation which reduces moisture limitations.

Fasth et al. (2011) reported the wood turnover rate of a variety of species and size classes of FWD in a North Carolina mixed hardwood/pine forests ranged from 4 to 10 years. Ricker et al. (2016) evaluated woody debris decay rates at the same study plots used in this study. They placed red maple pieces and wooden dowels 3.0-4.5 cm in diameter on the soil surface and through periodic collection and analyses calculated a wood turnover rate of 4.9 years for this homogenous and intermediate FWD. They also observed infestation of red maple pieces by the exotic red fire ant (*Solenopsis invicta* Buren) which may have accelerated the decay rate (Ricker et al., 2016). We used litter box data from 2011 and 2012 (Chapter 3) and FWD mass calculated in this study (Table 5.2) to estimate the turnover rate of FWD within community groups. Our estimates of FWD turnover rate are 8.5 years for low elevation community group 4, 3.9 years for intermediate elevation group 2, and 5.5-5.7 years for highest elevation groups 2 and 3; these estimates are similar to those reported in the two studies referenced above.

For all pools of aboveground sequestered C measured in this study, downed dead wood, standing dead wood, and live tree, sapling, and shrub wood, we found cumulative values of 14840, 18878, 7460, and 19076 gC/m^2 for community groups 1-4. Ricker and Lockaby (2015) found mean soil organic C stored in the top 100 cm of soil in the CONG to be 10900 and 19300 gC/m^2 for the Congaree and Chastain soil series, respectively. Using our data, their data, and the mapped boundaries of the soil series, we can estimate mean sequestered C values of 28540, 29778, 17460, and 38376 gC/m^2 for community groups 1-4. Other C pools for which we do not have a data source include dead and living roots and the herbaceous layer, particularly the large, woody grass species cane (Arundinaria gigantea [Walt.] Muhl.). We found that cane represented 13.1, 30.1, 30.0, and 0.0% cover (community groups 1-4, respectively; Figure 3.3; Chapter 3). It is likely these additional sources would increase our sequestered C estimates by at least 15-20%.

Woodall and Liknes (2008) reviewed the literature to examine how C stocks in aboveground dead wood varied across latitude within the U.S. They reported mean values of 388 and 243 gC/m² for the CWD and FWD pools at latitudes < 33°N and 307 and 302 gC/m for a latitude range of 33-37°N. The approximate center of our study site within CONG is at 33°46′14.3″N, 80°43′40.6″W; at the interface of their latitude classes. Across our four community groups we calculated a range of 520-1183 gC/m² and 239-495 gC/m² for CWD and FWD C pools, respectfully, indicating these C stocks are substantially greater than the mean values of sites at similar latitudes. One of the few studies reporting SDW and DDW C pools separately comes from the long-term research and monitoring program at the Hubbard Brook Experimental Forest in New Hampshire. Fahey et al. (2005) reported mean estimates of 657 and 468 gC/m² for SDW and DDW accounting for 10.6% of aboveground C for stands with a mean of 9495 gC/m² in live tree wood. SDW was similar in CONG with snags and stumps showing a C stock range of 396-893 gC/m² while our DWD means were 2 to 3.5 times (866-1678 gC/m²) the mean reported for Hubbard Brook Experimental Forest. The percent of aboveground C found in SDW and DDW in our community groups ranged from 9.5-16.9% with C stocks in live tree wood ranging from 5787 to 16757 gC/m². Results in our study for dead wood C stocks are similar to the range reported by Bradford et al. (2009) for three regional temperate upland forests types (northern hardwood forests in New Hampshire, mixed forests in Minnesota, and subalpine Rocky Mountain forests in Wyoming and Colorado). They reported a total dead wood C pool range of 1750-2750 gC/m² representing 16-20% of aboveground woody C. Our total dead wood C pool range of 1262-2422 gC/m² at 9.5-16.9% of the total aboveground C pool are comparatively less and likely due to an appreciably faster dead wood decay rate at our study area.

Shoch et al. (2009) used data from multiple sources to develop a fitted model to estimate C storage in mixed hardwood bottomland forests in the lower Mississippi Valley of Arkansas, Mississippi, and Louisiana for naturally regenerated stands 0 to 140 years after harvest. The model estimates total aboveground and belowground C in live tree wood for bottomland stands in the region to range from 12000 to 18000 gC/m² for stands 40 to 140 years old. We found a range of C sequestered in aboveground living tree wood of 5787 to 16757 gC/m², which would appear somewhat greater than their model as we did not calculate below ground tree mass. Moerschbaecher et al. (2016) estimated C stocks in mixed age stands of bottomland hardwood forests in south Louisiana and, based on literature review and their results, concluded living trees account for 69-94% of total aboveground biomass in natural bottomland hardwood forests and that 50% of that mass is generally found in a small number of the largest trees within a sample unit. Our results are congruent with these conclusions with 77.6-88.8% of aboveground biomass within living tree wood across community groups. In community groups 1,2, and 4, trees ≥ 50 cm DBH were 12.8, 24.7, and 27.8% of trees which accounted for 69.6, 81.0, and 62.3% of total tree biomass, respectfully. Moerschbaecher et al. (2016) reported a seven year mean annual C assimilation rate range of 190-340 gC/m² for bottomland hardwood forest studied (all stems > 3 cm DBH). Based on four years of tree data and 2 years of sapling data we found mean annual C assimilation rates of 277, 301, and 204 gC/m² for bottomland hardwood forest (community groups 1-3) and 234 gC/m² for a bald cypress stand (Chapter 3; C calculated as 50% of dry mass). Their values are from stands having a basal area range of 21.2-32.5 m²/ha and C stock of 6300-14000 gC/m² for stems > 3 cm. In our study, community group values for trees and saplings exhibited a basal area range of 24.4-47.7 m²/ha and C stock range of 6199-17087 gC/m² for bottomland hardwood forest; values for bald cypress (community group 4) were 64.1 m²/ha and 16655 gC/m². Our C assimilation rates and stored C mass results closely match those of Moerschbaecher et al. (2016).

Woody detritus at a given site affects fire behavior and severity and fine fuels greatly elevate the possibility of ignition. FWD promotes ignition and volumes can change rapidly in the wake of disturbances such as hurricanes, ice and snow storms, insect outbreaks (i.e. cicada years), and timber harvest (Fasth et al., 2011). Volumes of woody detritus within CONG are likely elevated due to greater volumes associated with old growth forests (Harmon et al., 1986; Spetich et al., 1999) and episodic elevated input associated with hurricanes in the southeast (Putz and Sharitz, 1991; Allen et al., 2005). Fire danger increases following a hurricane, even in mesic sites considered immune to fire prior to the disturbance. Potential fuel increases include CWD (dead limbs stored in canopy, broken canopy limbs, broken boles, windthrown trees, and tree mortality related to saline storm surge); FWD, leaves, and vines stripped from trees by wind; and additional herbaceous surface fuels associated with increased light (Myers and van Lear, 1998; Gagnon, 2009).

The study area on the river floodplain within CONG has some old growth trees, but is unlikely a large contiguous block of old growth forest having been somewhat fragmented by historic bouts of selective logging. Although there are scattered large bottomland oaks, the higher density of very large sweetgum and prevalence of sweetgum suggest selective logging was practiced. Woodall and Nagel (2006) suggest that the species composition of dead wood may indicate temporal trends in canopy species composition and succession based on data review from 378 upper Midwest forested sites. They reported that 48% of sites showed appreciable differences in dominant living species and dominant dead wood species. However, they were unable to find an overall trend or predictive model explanatory, concluding that species shifts seen when comparing composition of live and dead wood seemed dependent on unique combinations of stand history, structure, composition, and site attributes. This is likely amplified in Congaree National Park due to periodic wide scale, but spatially complex degree of hurricane damage common to the region (Putz and Sharitz, 1991; Allen et al., 2005).

Our comparison of species composition, wood mass, and units between the dead and live wood fractions suggest there are ongoing shifts in both the canopy and understory in the community groups studied. The understory appears more stable than the canopy when comparing dead and live wood fractions. Pawpaw and possumhaw appear stable and will continue to be major understory components across much of the floodplain. It seems that American holly will remain a minor component of the understory at higher elevations and is likely to increase slightly. The most disturbing apparent shift in the study area is the likely increase of the exotic shrub Chinese privet. Data indicate this species will increase in the youngest stands represented by community group 3 and will likely spread rapidly into canopy gaps resulting from the apparent decline of large sweetgum and box elder at higher elevations.

It appears that sweetgum is now in decline across all community groups and may be replaced as a canopy dominant at higher and intermediate elevations or be eliminated as a minor component at lower elevations in coming decades. This trend is supported by snag/ live ratios of 0.32 to 0.53 in our community groups 1, 2, and 3 where 60-80% of all snags are sweetgum. Spetich et al. (1999) reported a snag/tree ratio range of 0.07 to 0.12 for 12 old growth mixed hardwood forests across Indiana, Missouri, Illinois, and Iowa. Box elder appears to be in decline as a major canopy component at higher elevations, but is stable as a minor component at intermediate elevations. Bald cypress is essentially absent from higher elevation community groups 2 and 3, is stable in low elevation group 4, but appears to be declining in intermediate elevation group 1. Green ash data suggests this species will increase in the canopy at intermediate elevations and is a stable minor component elsewhere. Comparisons indicate that sugarberry will increase in the canopy of higher and intermediate elevations while remaining absent from community group 4. Red maple appears to be increasing in the youngest stands of community group 3, but will likely remain insignificant in other groups. Data comparisons indicate American elm may either increase slightly or remain a stable canopy component at higher elevations. It appears that laurel oak is increasing at higher elevations and is likely to become a more important canopy component in the future; however selective seedling predation by feral pigs can severely depress oak and hickory recruitment (Mayer et al., 2000). Feral pigs are common in the study area, were often seen during field work, and excessive soil disturbance causing very high seedling mortality was observed related to rooting associated with foraging.

Results indicate that the mass and sequestered C in both live and dead wood are at the high end of both measured and modeled ranges reported in the literature for U.S. forests in general and within the range for regional floodplain forests specifically. As such the forests on the floodplain of the Congaree River represent a substantial and important store of sequestered C. The data indicate differences in C stocks within a given pool are more strongly related to a stand's tree age/size distribution than to elevation. Spatial complexity of old growth remnants and old growth mortality associated with episodic disturbances such as hurricanes and strong thunderstorms/microbursts are likely determinant reasons for comparatively high mass as well as very high spatial variation in dead wood units in CONG. The importance of old growth characteristics to higher dead wood loads in CONG is made apparent by a relatively higher decay rate for the study area compared to the majority of studies referenced. Our results also reinforce the trend of increasing dead wood mass with increasing stand age and productivity observed by other researchers. Our comparison of species composition, wood mass and volume, and unit quantities between the dead and live wood fractions, in conjunction with decay class of dead wood used as a temporal proxy, suggests there are ongoing shifts in both the canopy and understory in the bottomland hardwood forest stands while the bald cypress swamp appears to be stable. It appears that sweetgum, box elder, and bald cypress are declining and sugarberry, green ash, and laurel oak are increasing as canopy components of bottomland hardwood forests and that Chinese privet is likely to increase and expand within the understory of higher elevation bottomland hardwood forests, particularly in canopy gaps left by senescence of sweetgum and box elder. Although our data suggests green ash is increasing, this species is susceptible to the invasive beetle emerald ash borer (*Agrilus planipennis* Fairmaire). The emerald ash borer was first detected in the neighboring states of North Carolina and Georgia in 2003 and after over a decade of trap monitoring the invasive beetle was detected in South Carolina in August 2017 (Veit, 2017).

The future of CWD as a significant carbon pool in the study area may be affected both directly and interactively by human induced factors such as spread of invasive species, hydrology manipulations, and climate change. As the mean temperature increases in association with climate change it is likely the decay rate of dead wood carbon pools will accelerate resulting in a decrease in importance of woody detritus as a C sequestration pool in this system. However; if the prediction of increasing frequency and intensity of severe weather events such as hurricanes is born out, there may be an appreciable shift of stored organic C from the live wood pool to the dead wood pool – a shift that would decrease C storage time. Human flow manipulations and/or climate change induced precipitation patterns may affect CWD decay rates via inundation patterns; increased duration of inundation may depress decomposition via anaerobic conditions or may increase the decay rate by removing moisture limitations when frequency increases but duration is not limiting. The rooting and foraging of feral pigs often fragments advanced decay class CWD which is likely to speed decomposition and shorten the residence time of C within this pool. Spread and infestation by emerald ash borer has the potential to eliminate green ash as a canopy component and cause a spike in dead wood volume within the study area, which in conjunction with the probable increase of decomposition rates associated with climate change will reduce the residence time of C stored within green ash.

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Table 5.1. Species composition by dead wood mass and unit quantity within floodplain community groups and a summary of community attributes of those groups within the study area on the Congaree River floodplain.

	Group 1 – FRPE/LIST/CELA plots: 1, 9, 11, 12, 13	Group 2 – LIST plots: 3, 6, 7, 8, 15	Group 3 – CELA/ACNE plots: 2, 4, 5, 10, 14	Group 4 – TADI plots 16, 17, 18, 19, 20
Percent of total recorded dead wood pieces/units by species (CWD, snags, and stumps; for pieces having the largest diameter recorded ≥ 7.5 cm)	TADI 20.3% LIST 18.8% ILDE 15.9% ACNE 14.5% ULAM 7.3% ASTR 7.3% CELA 4.4% FRPE 4.4%	ACNE 31.0% LIST 29.9% ASTR 18.4% ILDE 10.3% ULAM 3.5%	ACNE 34.7% ASTR 17.4% ILDE 17.4% ULAM 12.2% LIST 5.1% CELA 4.1% LISI 4.1%	TADI 76.5% POHE 15.2% PLAQ 5.3% LIST 1.5%
Percent of total dead wood dry mass by species (CWD, snags, and stumps)	LIST 46.0% TADI 35.5% PLOC 6.0% ACNE 3.3% FRPE 3.2%	LIST 80.6% ACNE 15.6% ULAM 1.7% ASTR 1.0%	LIST 34.3% ACNE 34.0% FRPE 11.4% ULAM 9.6% CAAQ 6.0%	TADI 92.8% LIST 4.4% PLAQ 1.9% POHE 0.9%
Dominant tree species – based on % total tree basal area (m²) within community group	LIST 23.7% FRPE 23.2% CELA 12.6% QULY 9.2% TADI 7.7%	LIST 71.2% ULAM 8.2% CELA 7.3% ACNE 3.8% PLOC 2.9%	CELA 30.9% ACNE 25.5% LIST 10.2% ULAM 7.0% QULA 6.9% FRPE 6.8%	TADI 91.7% PLAQ 3.6% POHE 1.7% LIST 1.2% ACRU 1.1%
Dominant sapling species – based on % total sapling basal area (m²) within community group	ASTR 41.7% ILDE 33.7% CELA 17.7% PLAQ 4.4% LIST 2.4%	ASTR 67.5% QULA 8.6% ILOP 6.7% CELA 5.6% ACNE 3.6%	ASTR 41.1% LISI 31.0% ILDE 23.8% ULAM 2.3% PLOC 1.9%	PLAQ 53.8% ILDE 23.2% TADI 17.1% CEOC 2.8% QULA 1.2%

	Group 1 – FRPE/LIST/CELA plots: 1, 9, 11, 12, 13	Group 2 – LIST plots: 3, 6, 7, 8, 15	Group 3 – CELA/ACNE plots: 2, 4, 5, 10, 14	Group 4 – TADI plots 16, 17, 18, 19, 20
Mean % biomass within community group				
Trees < 25 cm DBH	8.9%	7.4%	15.4%	5.2%
Trees 25-50 cm DBH	21.5%	11.6%	50.3%	32.5%
Trees 50-75 cm DBH	18.9%	53.4%	34.3%	54.3%
Trees > 75 cm	50.7%	27.6%	0.0%	8.0%
Mean % # of stems by tree DBH size class				
Trees < 25 cm DBH	60.6%	58.0%	58.3%	37.3%
Trees 25-50 cm DBH	26.6%	17.3%	34.2%	34.9%
Trees 50-75 cm DBH	6.4%	17.3%	7.6%	26.2%
Trees > 75 cm	6.4%	7.4%	0.0%	1.6%
Tree and sapling wood fraction of ANPP 2011-2012 (g dry mass/m²/year)	554	603	407	468
Ratio ANPP to total dead wood mass (years to produce equivalent mass)	5.6	5.9	6.2	10.3
Mean elevation of community group (m above sea level)	133.77	134.43	134.46	132.94
Qualitative flooding regime based on elevation & observations	Annual frequency and intermediate duration	Occasional frequency and ephemeral duration	Occasional frequency and ephemeral duration	Annual frequency and extended duration
Soil series	Chastain and Congaree interface	Congaree	Congaree	Chastain

Notes: Elevation data provided by Hupp (2013); soil series information from Ricker and Lockaby (2015); tree, sapling, ANPP, and flooding regime from Chapters 2-4.

Table 5.2. Results of ANOVA for community group means of woody biomass and related variables.

Woody biomass variables	Analysis of variance test statistic and results of multiple comparisons	Community Groups			
		Group 1 FRPE/LIST/ CELA	Group 2 LIST	Group 3 CELA/ACNE	Group 4 TADI
		mean ± SE	mean ± SE	mean ± SE	mean ± SE
Tree biomass winter 2010/11 (g/m²)	**4 > 3** **$H_{0.05,\,3} = 10.57$; $P \le 0.023$**	26194 ±3077	33513 ±9204	11574 ±1411	33199 ±4720
Sapling biomass winter 2010/11	**3 = 2 > 4** **$F_{3,\,16} = 6.89$; $P \le 0.023$**	392 ±101	659 ±153	823 ±141	110 ±56
Total living wood (g/m²)	**4 > 3** **$H_{0.05,\,3} = 10.38$; $P \le 0.033$**	26586 ±3064	34172 ±9055	12397 ±1284	33308 ±4768
CWD dry mass (g/m²)	$H_{0.05,\,3} = 4.63$; $P = 0.201$	1723 ±929	1039 ±240	1040 ±342	2366 ±585
CWD volume m³/hectare	$H_{0.05,\,3} = 3.23$; $P = 0.358$	64.75 ±36.36	40.44 ±9.48	40.92 ±12.97	87.78 ±22.34
FWD dry mass (g/m²)	$F_{3,\,16} = 2.25$; $P = 0.12$	478 ±103	758 ±190	691 ±60	989 ±169
FWD mean annual dry mass from litter boxes 2011-12	$F_{3,\,16} = 0.50$; $P = 0.69$	122 ±16	138 ±7.2	122 ±17	116 ±10
Down dead wood (FWD+CWD) dry mass (g/m²)	$H_{0.05,\,3} = 4.22$; $P = 0.24$	2201 ±889	1797 ±404	1731 ±298	3355 ±729
Snag dry mass (g/m²)	$F_{3,\,16} = 0.57$; $P = 0.64$	846 ±368	1766 ±977	782 ±441	1406 ±516
Stump dry mass (g/m²)	**4 > 3** **$F_{3,\,16} = 4.13$; $P \le 0.025$**	47.10 ±15.05	20.58 ± 7.65	10.41 ±3.02	81.39 ±26.08
standing dead wood dry mass (g/m²)	$F_{3,\,16} = 0.58$; $P = 0.63$	893 ±357	1786 ±974	792 ±440	1488 ±531
Total dead wood dry mass (g/m²)	$F_{3,\,16} = 1.26$; $P = 0.32$	3094 ±986	3583 ±1132	2523 ±400	4843 ±833
Total wood dry mass dead and alive	**4 = 2 > 3** **$H_{0.05,\,3} = 11.45$; $P \le 0.048$**	29680 ±3237	37756 ±9316	14920 ±972	38151 ±5404
% dry mass in dead wood	$F_{3,\,16} = 0.80$; $P = 0.51$	10.4 ±2.9	9.5 ±5.1	16.9 ±3.6	12.7 ±1.6
Tree basal Area winter 2010/11	**4 > 1 = 3** **$F_{3,\,16} = 7.20$; $P \le 0.047$**	36.37 ±3.58	44.76 ±9.53	20.61 ±2.49	63.70 ±8.32
Sapling basal area winter 2010/11	**3 = 2 > 4; 3 > 1** **$F_{3,\,16} = 7.67$; $P \le 0.048$**	1.67 ±0.41	2.94 ±0.68	3.77 ±0.66	0.44 ±0.21

Notes: Groups are those defined via cluster analysis and Indicator species analysis; N = 5 sample plots for each group. F statistic with degrees of freedom from one-way ANOVA testing the hypothesis of no difference in means among groups; multiple comparisons used the Tukey test. In cases where normality (Shapiro-Wilk W test) or equal variance (Brown-Forsythe test) assumptions on the residuals were not met at the $P = 0.05$ level, the data were subjected to the Kruskal Wallis test (rank sums) and the H statistic with alpha level and degrees of freedom reported; multiple comparisons used Dunn's method for joint ranking. P values reported are either the highest significant value from multiple comparisons or from the analysis of variance when the groups did not differ. Community groups were defined based on Cluster Analysis, Indicator Species Analysis, and Non-metric Multi-dimensional scaling as presented in Chapter 2**;** tree and sapling mass and litter box data from Chapter 3.

Table 5.3. Percent of total dead wood pieces and percent of dead wood dry mass by species calculated within community groups.

	Percent of total dead wood pieces by species (CWD, snags, and stumps; pieces having the largest diameter recorded ≥ 7.5 cm)				Percent of total dead wood dry mass (CWD, snags, and stumps; includes snags and stumps with large diameter ≥ 7.5 cm)			
	Community groups				Community groups			
Species Code	1 - FRPE/LIST/CELA	2 - LIST	3 - CELA/ACNE	4 - TADI	1 - FRPE/LIST/CELA	2 - LIST	3 - CELA/ACNE	4 - TADI
ACNE	14.49%	31.03%	34.69%	0.00%	3.29%	15.63%	34.03%	0.00%
ACRU	1.45%	0.00%	1.02%	0.00%	0.16%	0.00%	0.04%	0.00%
ASTR	7.25%	18.39%	17.35%	0.00%	0.40%	1.03%	1.26%	0.00%
CAAQ	0.00%	0.00%	1.02%	0.00%	0.00%	0.00%	5.99%	0.00%
CACA	1.45%	0.00%	0.00%	0.00%	0.07%	0.00%	0.00%	0.00%
CELA	4.35%	1.15%	4.08%	0.00%	2.82%	0.08%	2.21%	0.00%
CEOC	0.00%	0.00%	0.00%	0.76%	0.00%	0.00%	0.00%	0.02%
FRPE	4.35%	0.00%	2.04%	0.00%	3.15%	0.00%	11.37%	0.00%
ILDE	15.94%	10.34%	17.35%	0.00%	0.49%	0.15%	0.68%	0.00%
LISI	0.00%	0.00%	4.08%	0.00%	0.00%	0.00%	0.07%	0.00%
LIST	18.84%	29.89%	5.10%	1.52%	46.02%	80.59%	34.26%	4.36%
PLAQ	1.45%	2.30%	0.00%	5.30%	0.14%	0.29%	0.00%	1.88%
PLOC	2.90%	0.00%	0.00%	0.00%	6.04%	0.00%	0.00%	0.00%
POHE	0.00%	0.00%	0.00%	15.15%	0.00%	0.00%	0.00%	0.91%
QULA	0.00%	0.00%	1.02%	0.00%	0.00%	0.00%	0.44%	0.00%
TADI	20.29%	1.15%	0.00%	76.52%	35.53%	0.04%	0.00%	92.82%
ULAM	7.25%	3.45%	12.24%	0.76%	1.89%	1.62%	9.64%	0.01%
VIRO	0.00%	2.30%	0.00%	0.00%	0.00%	0.58%	0.00%	0.00%

Notes: See Appendix 7 for conversion of species code to species name.

Table 5.4. Percent dry mass by community group for dead wood type and decay class.

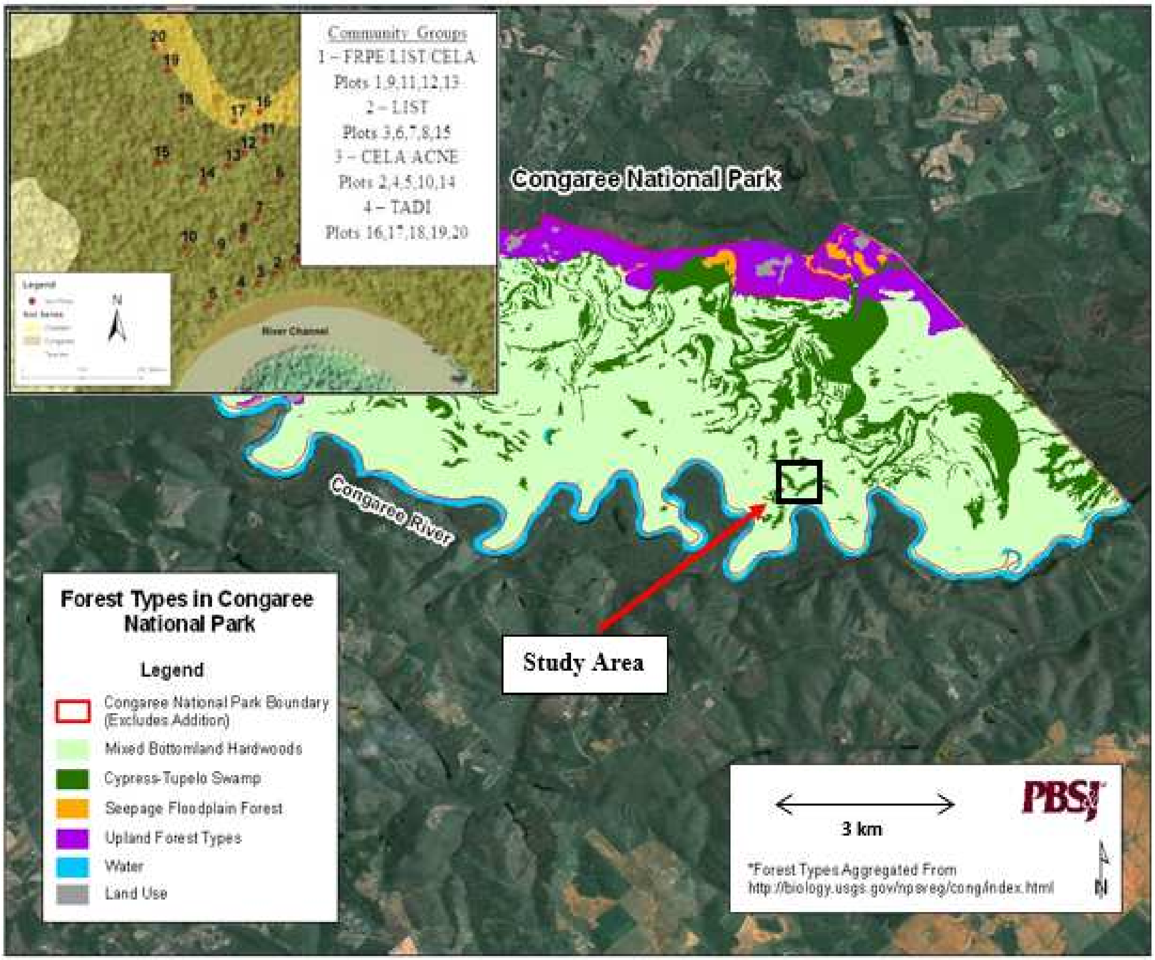
	Community group			
	1 - FRPE/LIST/CELA	2 - LIST	3 - CELA/ACNE	4 - TADI
Dead wood type				
FWD	15.4	21.2	27.4	20.4
CWD	55.7	29.0	41.2	48.9
snag	27.3	49.2	31.0	29.0
stump	1.6	0.6	0.4	1.7
Decay Class – CWD, snags, & stumps				
1	1.27%	16.60%	9.11%	1.95%
2	39.22%	48.92%	19.36%	25.08%
3	36.23%	21.56%	61.29%	52.54%
4	22.60%	12.77%	10.09%	18.02%
5	0.68%	0.15%	0.15%	2.41%

Table 5.5. Mass of aboveground carbon pools and percent of aboveground carbon sequestered within each pool by community group.

Carbon pool	Group 1 – FRPE/LIST/CELA mass(g/m²) % of total	Group 2 – LIST mass(g/m²) % of total	Group 3 – CELA/ACNE mass(g/m²) % of total	Group 4 – TADI mass(g/m²) % of total
FWD	239 1.6%	379 2.0%	346 4.6%	495 2.6%
CWD	862 5.8%	520 2.8%	520 7.0%	1183 6.2%
snags	423 2.9%	883 4.7%	391 5.2%	703 3.7%
stumps	24 0.16%	10 0.05%	5.2 0.07%	41 0.21%
Living tree wood	13097 88.3%	16757 88.8%	5787 77.6%	16600 87.0%
Living sapling & shrub wood	196 1.3%	330 1.7%	412 5.5%	55 0.29%
Total aboveground carbon mass(g/m²)	14840	18878	7460	19076
Soil organic carbon mass(g/m²) (0-100 cm)	13700	10900	10900	19300

Notes: Carbon mass calculated as one half of pool dry mass (Fahey et al., 2005). Soil organic carbon mass per unit area from Ricker and Lockaby (2015); are based on their values reported as means for Congaree soil series (10900 g/m²) and Chastain soil series (19300 g/m²) within Congaree National Park; community groups 2 and 3 are mapped as Congaree soil series, group 4 as Chastain soil series, and group 1 has 3 plots at the interface of the two soil series and 2 plots within the Congaree soil series; the average of 2 Congaree and 1 Chastain value soil organic carbon is assumed.

Figure 5.1. Location of the study area; inset shows plots by community groups and soil series map.



CHAPTER SIX

CONCLUSIONS

In this study, community groups were established post hoc based on numerous recorded community metrics and variables using ordination and Indicator Species Analyses to take all those parameters into consideration and define the most meaningful ecological groupings. Utilizing 20 plots, we characterized four distinct forest community groups on the floodplain in Congaree National Park (CONG): younger mixed bottomland hardwoods at higher elevations; old growth mixed bottomland hardwoods at both higher and intermediate elevations; and mature cypress backswamp at lowest elevations. Differences in elevation and the associated differences in the frequency, duration, and intensity of flooding in conjunction with tree species composition were the defining gradients separating communities with additional refinement of communities defined by tree size classes. Community groups 2 and 3 are mixed bottomland hardwood forests located at higher elevations on the active natural levee and on remnant levees separated from the active levee by intervening intermediate elevation flats. Flooding occurs during overbank flooding and is of relatively short duration and limited depth. Canopy species composition in these two communities consists of facultative species and is very similar with differences in the proportion of the canopy represented by a given species. These groups are separated in the analyses by the size class of trees with group 2 having 24.7% of trees > 50 cm DBH and group 3 with only 7.6% of trees this large. Community group 4 is a backwater swamp located in two adjoining sloughs representing abandoned channel meanders with a canopy of obligate species dominated by bald cypress at 91.7% of the tree layer. Flooding occurs via overbank and backwater flooding via “gut” channels with seasonal interaction with ground water. Duration of inundation is variable depending on amount and seasonality of rainfall, and the site may experience several periods of inundation and dry down in a single year, and has an extended inundation maximum depth of 0.6 to 0.9 m. However, watermarks on tree trunks indicate pulse inundation depths of 1.8 to 2.4 m do occur. The herbaceous layer in this community is more diverse and species rich compared to the other groups, containing mostly obligate species capable of enduring an extended period of inundation. Community group 1 occupies an intermediate elevation along intervening flats located between the active levee and relict levees. Species composition is a mix of facultative, facultative wet, and obligate species with a greater preponderance of facultative wet tree species compared to community groups 2 and 3. Due to the mix of species and a position intermediate in hydrologic regime, this community exhibits higher tree richness, evenness, and diversity compared to the other community groups. Flooding in this community is intermediate in frequency and duration, experiencing overbank flooding with occasional interaction with groundwater and receipt of water via backwater flooding. Extended inundation periods have a maximum depth of a 0.05 to 0.3 m, however, watermarks on tree trunks indicate pulse inundation depths of 0.9 to 1.5 m do occur.

The reason for the significant differences in tree size classes among community groups defined in this study cannot be answered with confidence. Stochastic variability exists in systems both disturbed, and undisturbed. Chance alone may be responsible, a portion of the reason, or in combination with an inadequate number of sample plots. Other contributing factors may be historical patterns created by natural disturbances such as

Hurricane Hugo or by historic and/or continuing patterns induced by anthropogenic disturbances such as water level controls, shifts in the fire regime, or selective logging.

Two rapidly expanding invasive species in alluvial floodplains, Japanese stilt-grass and Chinese privet, were recorded at higher elevations and appear likely to spread. Results of this study showed little relation between tree and sapling layer matrices, raising questions about successional patterns in this system and suggesting manipulations to hydrology and sedimentation may be responsible for an increase in exotic species density and may have changed successional patterns.

We found that the annual percentage of mass gain for tree wood is greater at higher and intermediate elevations on the Congaree floodplain compared to the backswamp. Additionally, our results suggest that the percentage of tree wood gained annually is greater at a given elevation for plots having the majority of tree biomass in younger trees. These observations are best illustrated by our calculated metric - productivity efficiency ratio. Even though the efficiency of tree mass gain is lower for areas having younger trees, the actual magnitude of mass gain and thus carbon sequestration is greater in areas having a larger proportion of very large trees. Sapling density and biomass is greatest at higher elevations on the floodplain and sapling wood should be considered in ANPP estimations, at least for areas that rarely flood. We also suggest that the contribution of cane to ANPP calculations may result in a considerable underestimation of productivity in floodplain forests. We conclude that topographic position, a surrogate for both hydrology and sedimentation, as well as stand age and size metrics result in differing productivity rates and thus carbon sequestration within forested floodplains of the southeast.

Studies have shown that the community composition and structure of the vegetation, and thus the productivity rate, in the Congaree Swamp is dependent upon the frequency, timing, and duration of saturated soil conditions and inundation, sedimentation dynamics, and microtopography. The hydrologic regime can be said to have become more homogenous within CONG due to operation of the Saluda Dam, and this has most likely affected productivity. The interrelated dynamics of hydrology and sedimentation both help shape and interact with small scale elevational differences on southeastern floodplain forests to yield communities composed of species best suited to the characteristics of a given habitat. Productivity varies among community types across forested floodplains, and this variation can be attributed to the magnitude of, and spatial and temporal characteristics of, inundation and dry down patterns coupled with heterogeneity in both the rate and composition of deposited material.

Litter decomposition rates in this study tended to be higher than those reported in other regional forested floodplain sites. Observationally, this is reinforced by, for the most part, the absence of a duff layer, lack of a soil O horizon, and a thin, discontinuous litter layer (except for a short period following maximum leaf fall). Despite these observations being common to forested floodplains of the southeastern US, we found comparatively high litter decomposition rates suggesting an optimal decomposition environment for the study area. Although it took 80 to 100 weeks for all initial mass to be reduced to < 2% mass remaining, the contents of the litter bags at week 64 showed little to no structure and would be more accurately described as humus. We conclude that litter decomposition and the cycling of the nutrient contents of the litter are comparatively rapid processes under the prevailing climatic conditions on the area of the Congaree River floodplain studied. Warm, moist, and humid conditions coupled with nutrient import associated with flooding events and the prevalence of species producing high quality litter appear to create an ideal decomposition environment and likely supports a diverse and dense decomposer community. With the low quality oak litter showing only a slightly lower decomposition rate than the high quality site specific mixed litter, it is suggested that the rapid cycling of high quality litter has created edaphic nutrient content that buffers nutrient limitation regardless of litter quality. However, it is likely this would change over time if dominance shifted to species producing low quality litter. Relatively faster decay of single species litter in lower elevation areas compared to groups 2 and 3 suggests periodic inundation ameliorates moisture limitations and aids in the decomposition of recalcitrant lower quality litter such as white oak. It is probable that extended drought or extended inundation could result in litter accumulation, but unless these conditions become a long-term trend, the prevailing decomposition environment will prevent the formation of a continuous litter layer, duff layer, or organic soil horizon.

Three flood events occurred in our study area in the spring of 2011 (between collection weeks 4 and 12); one of which inundated all community groups. Import of nutrients associated with the flood events are likely the reason for the accumulation of P and N found in samples between weeks 4 and 16 across communities and litter types. The subsequent steady state in nutrient content that followed may be due, at least in part, to immobilization of nutrients by the decomposer community as decomposer populations enter a rapid period of growth and proliferation as temperatures warm requiring rapid nutrient assimilation. As the decomposer community population reaches a seasonal high, immobilization declines as nutrient needs are reduced and mineralization of nutrients ensues as C respiration outpaces the need for nutrient assimilation by the decomposer community.

Results indicate that the mass and sequestered C in both live and dead wood are at the high end of both measured and modeled ranges reported in the literature for US forests in general and within the range for regional floodplain forests specifically. For all pools of aboveground sequestered C, we found cumulative values of 14840, 18878, and 7460 (younger stands) grams C/m^2 for bottomland hardwood forest and 19076 grams C/m^2 for the bald cypress swamp. As such the forests on the floodplain of the Congaree River represent a substantial and important store of sequestered C. The data indicate differences in C stocks within a given pool are more strongly related to a stand's tree age/size distribution than to elevation. Spatial complexity of old growth remnants and old growth mortality associated with episodic disturbances such as hurricanes and strong thunderstorms/microbursts are likely determinant reasons for comparatively high mass as well as very high spatial variation in dead wood units in CONG. The importance of old growth characteristics to higher dead wood loads in CONG is made apparent by a relatively higher decay rate for the study area compared to the majority of studies referenced. Our results also reinforce the trend of increasing dead wood mass with increasing stand age and productivity observed by other researchers. Our comparison of species composition, wood mass and volume, and unit quantities between the dead and live wood fractions, in conjunction with decay class of dead wood used as a temporal proxy, suggests there are ongoing shifts in both the canopy and understory in the bottomland hardwood forest stands while the bald cypress swamp appears to be stable. It appears that sweetgum, box elder, and bald cypress are declining and sugarberry, green ash, and laurel oak are increasing as canopy components of bottomland hardwood forests and that Chinese privet is likely to increase and expand within the understory of higher elevation bottomland hardwood forests, particularly in canopy gaps left by senescence of sweetgum and box elder. Although our data suggests green ash is increasing, this species is susceptible to the invasive beetle emerald ash borer that was first detected in South Carolina in 2017.

The future of CWD as a significant carbon pool in the study area may be affected both directly and interactively by human induced factors such as spread of invasive species, hydrology manipulations, and climate change. As the mean temperature increases in association with climate change it is likely the decay rate of dead wood carbon pools will accelerate resulting in a decrease in importance of woody detritus as a C sequestration pool in this system. However; if the prediction of increasing frequency and intensity of severe weather events such as hurricanes is born out, there may be an appreciable shift of stored organic C from the live wood pool to the dead wood pool – a shift that would decrease C storage time. Human flow manipulations and/or climate change induced precipitation patterns may affect CWD decay rates via inundation patterns; increased duration of inundation may depress decomposition via anaerobic conditions or may increase the decay rate by removing moisture limitations when frequency increases but duration is not limiting. The rooting and foraging of feral pigs often fragments advanced decay class CWD which is likely to speed decomposition and shorten the residence time of C within this pool. Spread and infestation by emerald ash borer has the potential to eliminate green ash as a canopy component and cause a spike in dead wood volume within the study area, which in conjunction with the probable increase of decomposition rates associated with climate change will reduce the residence time of C stored within green ash.

APPENDICES

Appendix 1

List of all plant species recorded during data collection in this study.

CODE	Scientific Name	Common Name	Authority	Family	Duration	Form	Native
ACNE	*Acer negundo*	box elder	L	Aceraceae	perennial	tree	Yes
ACRU	*Acer rubrum*	red maple	L	Aceraceae	perennial	tree	Yes
AMAR	*Ampelopsis arborea*	pepper vine	(L) Koehne	Vitaceae	perennial	vine	Yes
ANCA	*Anisostichus capreolata*	cross vine	(L) Bureau	Bignoniaceae	perennial	vine	Yes
ARDR	*Arisaema dracontium*	green dragon	(L.) Schott	Araceae	perennial	forb	Yes
ARGI	*Arundinaria gigantea*	Cane	(Walter) Muhl.	Poaceae	perennial	grass	Yes
ARTR	*Arisaema triphyllum*	jack in the pulpit	(L.) Schott	Araceae	perennial	forb	Yes
ASPE	*Asclepias perennis*	aquatic milkweed	Walter	Ascleiadaceae	perennial	forb	Yes
ASPL	*Asplenium platyneuron*	ebony spleenwort	(L.) Oakes	Aspleniaceae	perennial	fern	Yes
ASTR	*Asimina triloba*	pawpaw	L (Dunal)	Annonaceae	perennial	tree	Yes
BOCY	*Boehmeria cylindrica*	false nettle	Swartz	Urticaceae	perennial	forb	Yes
BOVI	*Botrychium virginianum*	rattlesnake fern	(L.) Swartz	Ophioglossaceae	perennial	fern	Yes
CAAQ	*Carya aquatica*	water hickory	(Michaux f.) Nuttall, Walter H.	Juglandaceae	perennial	tree	Yes
CACA	*Carpinus caroliniana*	ironwood	Walter	Betulaceae	perennial	tree	Yes
CACO	*Carex comosa*	bottlebrush sedge	Boott	Cyperaceae	perennial	grass like	Yes
CAFR	*Carex frankii*	Frank’s sedge	Kunth	Cyperaceae	perennial	grass like	Yes
CAGR	*Carex grayi*	Gray’s sedge	Carey	Cyperaceae	perennial	grass like	Yes
CALE	*Carex leptalea*	bristly-stalked sedge	Wahlenb.	Cyperaceae	perennial	grass like	Yes
CAOL	*Carex oligocarpa*	richwoods sedge	Schkuhr	Cyperaceae	perennial	grass like	Yes
CAPE	*Cardamine pensylvanica*	bitter cress	MUHL	Brassicaceae	bienniel	forb	Yes
CARA	*Campsis radicans*	trumpet vine	(L) Seemann	Bignoniaceae	perennial	vine	Yes
CASQ	*Carex squarrosa*	squarrose sedge	L	Cyperaceae	perennial	grass like	Yes
CELA	*Celtis laevigata*	sugarberry	Willd.	Ulmaceae	perennial	tree	Yes
CEOC	*Cephalanthus occidentalis*	buttonbush	L.	Rubiaceae	perennial	shrub	Yes
CHPR	*Chaerophyllum procumbens*	wild chervil	L. (Crantz)	Apiaceae	annual	forb	Yes
CIAR	*Cinna arundinacea*	swamp wood reed	L	Poaceae	perennial	grass	Yes
COFL	*Corydalis flavula*	Yellow fumewort	(Raf.) DC.	Fumariaceae	annual	forb	Yes
CRMA	*Crataegus marshallii*	parsley hawthorne	Eggl.	Rosaceae	perennial	shrub	Yes
CRVI	*Crataegus viridis*	green haw	L.	Rosaceae	perennial	tree	Yes

CODE	Scientific Name	Common Name	Authority	Family	Duration	Form	Native
DEBA	*Decumaria barbara*	wood vamp	L.	Saxifragiaceae	perennial	vine	Yes
ELVI	*Elymus virginicus*	wild rye	L	Poaceae	perennial	grass	Yes
FRPE	*Fraxinus pennsylvanica*	green ash	Marshall	Oleaceae	perennial	tree	Yes
GAAP	*Galium aparine*	bedstraw	L.	Rubiaceae	annual	forb	Yes
GATI	*Galium tinctorium*	marsh bedstraw	L.	Rubiaceae	perennial	forb	Yes
ILDE	*Ilex decidua*	possumhaw	Walter	Aquifoliaceae	perennial	tree/sapling	Yes
ILOP	*Ilex opaca*	American Holly	Aiton	Aquifoliaceae	perennial	tree	Yes
JUOV	*Justicia ovata*	water willow	(Walter) Lindau.	Acanthaceae	perennial	forb	Yes
LEOR	*Leersia oryzoides*	rice cutgrass	(L.) Swartz	Poaceae	perennial	grass	Yes
LEVI	*Leersia virginica*	white grass	Willd.	Poaceae	perennial	grass	Yes
LIBE	*Lindera benzoin*	spicebush	(L.) Blume	Lauraceae	perennial	shrub	Yes
LISI	*Ligustrum sinense*	Chinese privet	Lour	Oleaceae	perennial	shrub	No
LIST	*Liquidambar styraciflua*	sweetgum	L	Hamamelidaceae	perennial	tree	Yes
LUMU	*Luzula multiflora*	wood rush	Retzius (Lej.)	Juncaceae	perennial	grass like	Yes
MIVI	*Microstegium vimineum*	Japanese grass	(Trinius) A. Camus.	Poaceae	annual	grass	No
MORU	*Morus rubra*	red mulberry	L.	Moraceae	perennial	tree	Yes
MYVE	*Myosotis verna*	forget-me-not	Nuttall	Boraginaceae	annual	forb	Yes
NEMI	*Nemophila microcalyx*	baby blue eyes	(Nuttall) F.&M.	Hydrophyllaceae	annual	forb	Yes
PAAG	*Panicum agrostoides*	tall panic grass	Nash	Poaceae	perennial	grass	Yes
PAGY	*Panicum gymnocarpon*	Savannah panic grass	Ell.	Poaceae	annual	grass	Yes
PAQU	*Parthenocissus quinquefolia*	Virginia creeper	L. (Planchon)	Vitaceae	perennial	vine	Yes
PLAQ	*Planera aquatica*	water elm	Walter ex JF Gmelin	Ulmaceae	perennial	tree	Yes
PLOC	*Platanus occidentalis*	sycamore	L	Platanaceae	perennial	tree	Yes
POAU	*Poa autumnalis*	autumn bluegrass	Muhl. Ex Ell.	Poaceae	perennial	grass	Yes
POHE	*Populous heterophylla*	swamp cottonwood	L	Salicaceae	perennial	tree	Yes
POHY	*Polygonum hydropiperoides*	knotweed	Michaux	Polygonaceae	perennial	forb	Yes
QULA	*Quercus laurifolia*	laurel oak	Michaux	Fagaceae	perennial	tree	Yes
QULY	*Quercus lyrata*	overcup oak	Walter	Fagaceae	perennial	tree	Yes
RAAB	*Ranunculus abortivus*	kidney leaf buttercup	L.	Ranunculaceae	annual	forb	Yes
SACE	*Saururus cernuus*	lizard’s tail	L	Saururaceae	perennial	forb	Yes
SEGL	*Senecio glabellus*	Butterweed	Poiret	Asteraceae	annual	forb	Yes
SMRO	*Smilax rotundifolia*	roundleaf greenbrier	L.	Lilliaceae	perennial	vine	Yes

CODE	Scientific Name	Common Name	Authority	Family	Duration	Form	Native
SPCE	*Spiranthes cernua*	Nodding lady tresses	(L.) Richard	Orchidaceae	perennial	forb	Yes
STME	*Stellaria media*	chickweed	(L.) Cyrillo	Caryophyllaceae	annual	forb	Yes
TADI	*Taxodium distichum*	bald cypress	(L) Richard	Taxodiaceae	perennial	tree	Yes
THTH	*Thalictrum thalictroides*	rue anemone	Boivin	Ranunculaceae	perennial	forb	Yes
TORA	*Toxicodendron radicans*	poison ivy	L	Anacardiaceae	perennial	vine	Yes
ULAM	*Ulmus americana*	American elm	L	Ulmaceae	perennial	tree	Yes
URCH	*Urtica chamaedryoides*	dwarf stinging nettle	Pursh.	Urticaceae	annual	forb	Yes
VIRO	*Vitis rotundifolia*	muscadine grape	Michaux	Vitaceae	perennial	vine	Yes
VISO	*Viola sororia*	common blue violet	Willd.	Violaceae	perennial	forb	Yes
WOAR	*Woodwardia areolata*	netted chain fern	(L.) Moore	Blechnaceae	perennial	fern	Yes
WOVI	*Woodwardia virginica*	Virginia chain fern	Smith	Blechnaceae	perennial	fern	Yes

Appendix 2

Indicator Species Analysis for woody species recorded using point intercept method (0-2 meters).

Species Code – Woody Vegetation 0-2 meters	**Community Group with maximum IV**	**Observed Indicator Value (IV)**	**IV from randomized groups**		***p****
			Mean	**SD**	
ACNE	3	0.378	0.248	0.126	0.4847
ACRU	4	0.290	0.261	0.136	0.7587
AMAR	1	0.081	0.274	0.180	1.0000
ANCA	3	0.424	0.260	0.113	0.3247
ARGI	2	0.522	0.262	0.135	0.1169
ASTR	3	0.471	0.265	0.121	0.2020
CARA	1	0.061	0.271	0.149	1.0000
CELA	1	0.174	0.271	0.129	1.0000
CRMA	1	0.397	0.397	0.003	1.0000
FRPE	*4*	*0.733*	*0.285*	*0.136*	*0.0220*
ILDE	1	0.174	0.272	0.129	1.0000
LISI	*3*	*0.638*	*0.269*	*0.129*	*0.0344*
LIST	2	0.577	0.290	0.150	0.1285
PAQU	3	0.471	0.266	0.122	0.2069
PLAQ	*4*	*1.000*	*0.283*	*0.135*	*0.0003*
POHE	*4*	*0.866*	*0.290*	*0.149*	*0.0042*
QULA	2	0.577	0.272	0.156	0.2076
SMRO	1	0.182	0.260	0.113	1.0000
TADI	*4*	*0.882*	*0.269*	*0.152*	*0.0012*
TORA	1	0.126	0.247	0.126	1.0000
ULAM	1	0.303	0.271	0.149	0.7425
VIRO	3	0.378	0.270	0.154	0.5117
Column Averages	N/A	0.441	0.280	0.130	0.4885

Notes: Indicator Species Analysis – Monte Carlo test of significance of observed maximum indicator value for cumulative % hits of woody species between 0-2 meters using the point intercept method (tabulated in four zones (0.0-0.5, 0.5-1.0. 1.0-1.5, and 1.5-2.0 meters) readings taken during 2011 growing season; 125 points along a 25 meter transect for each plot; matrix is 20 plots by 22 species). * Proportion of randomized trials with indicator value (IV) equal to or exceeding the observed IV. Significant IV shaded and in italics at $p \leq 0.10$. p = (1 + number of runs ≥ observed)/(1 + number of randomized runs). Randomization test for sum of IV_{max} – 9.706 = observed sum of IV_{max} across all columns; 7 = number of randomization runs with sum of $IV_{max} \geq$ observed value; 15000 = number of randomization runs; p = 0.00053.

Appendix 3

Indicator Species Analysis for herbaceous species recorded using quadrat sampling method.

Species Code – Herbaceous Layer	**Community Group with maximum IV**	**Observed Indicator Value (IV)**	**IV from randomized groups**		***p****
			Mean	**SD**	
ARDR	*2*	*0.630*	*0.271*	*0.154*	*0.0615*
ARTR	4	0.397	0.397	0.003	1.000
ASPE	4	0.577	0.276	0.158	0.2163
ASPL	2	0.397	0.397	0.003	1.000
BOCY	*4*	*0.577*	*0.261*	*0.140*	*0.0658*
BOVI	3	0.397	0.397	0.003	1.000
CAFR	*4*	*1.000*	*0.285*	*0.136*	*0.0002*
CACO	*4*	*0.882*	*0.272*	*0.152*	*0.0018*
CALE	4	0.289	0.289	0.149	0.8729
CAOL	1	0.333	0.249	0.124	0.6853
CASQ	4	0.406	0.271	0.129	0.3873
CAPE	1	0.289	0.290	0.149	0.8725
CHPR	1	0.404	0.274	0.181	0.5612
CIAR	*4*	*1.000*	*0.285*	*0.136*	*0.0002*
COFL	*2*	*0.577*	*0.262*	*0.140*	*0.0671*
ELVI	3	0.467	0.282	0.135	0.2886
GAAP	*2*	*0.303*	*0.271*	*0.129*	*0.0327*
GATI	4	0.397	0.397	0.003	1.0000
JUOV	*4*	*0.882*	*0.271*	*0.153*	*0.0013*
LEOR	*4*	*0.638*	*0.271*	*0.129*	*0.0327*
LEVI	1	0.467	0.282	0.135	0.2876
LUMU	3	0.243	0.243	0.002	1.0000
MIVI	1	0.192	0.273	0.157	1.0000
MYVE	3	0.577	0.275	0.158	0.2146
NEMI	1	0.289	0.291	0.152	0.8707
PAAG	1	0.397	0.397	0.003	1.0000
PAGY	*4*	*1.000*	*0.285*	*0.136*	*0.0002*
POAU	3	0.467	0.285	0.136	0.2953
POHY	4	0.397	0.397	0.003	1.0000
RAAB	1	0.397	0.397	0.003	1.0000
SACE	4	0.397	0.397	0.003	1.0000
SEGL	*3*	*0.522*	*0.261*	*0.133*	*0.0998*
SPCE	3	0.192	0.275	0.158	1.0000
STME	3	0.397	0.397	0.003	1.0000
THTH	3	0.303	0.273	0.149	0.7485
URCH	1	0.404	0.272	0.180	0.5587
VISO	1	0.126	0.269	0.152	1.0000
WOAR	2	0.192	0.272	0.156	1.0000
WOVI	4	0.577	0.277	0.159	0.2186
Column Averages	N/A	0.4596	0.290	0.110	0.5539

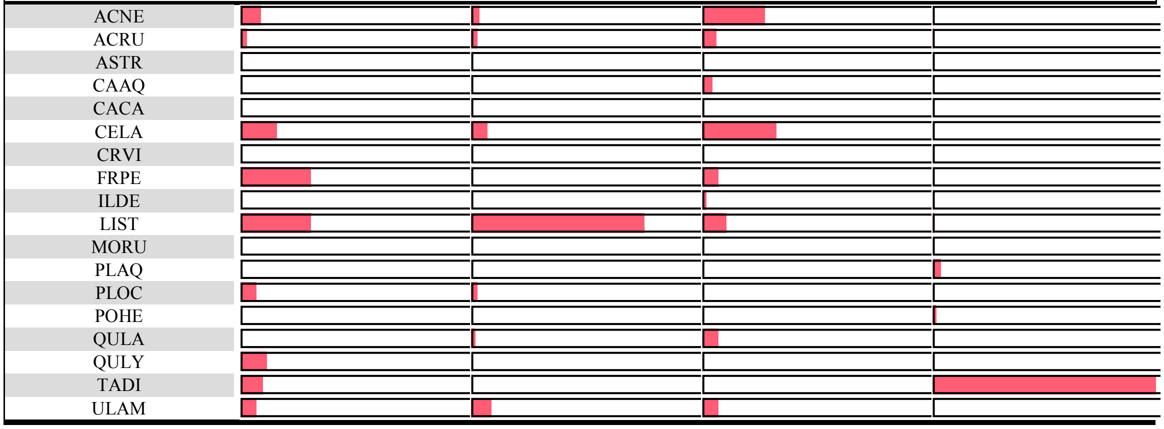
Notes: Monte Carlo test of significance of observed maximum indicator value for mean % cover of herbaceous species (maximum % cover plot mean for each species –3 readings in 2011 growing season; matrix 20 plots by 39 species). * Proportion of randomized trials with indicator value (IV) equal to or exceeding the observed IV. Significant IV shaded and in italics at $p \leq 0.10$. p = (1 + number of runs ≥ observed)/(1 + number of randomized runs). Randomization test for sum of IV_{max} – 18.382 = observed sum of IV_{max} across all columns; 0 = number of randomization runs with sum of IV_{max} ≥ observed value; 15000 = number of randomization runs; p = 0.00007.

Appendix 4

Percent of total basal area by tree and sapling species within community groups.

Community Group 2010 percent Basal Area (m^2) by tree species

Tree Species	**1 – FRPE/LIST/CELA**	**2 – LIST**	**3 – CELA/ACNE**	**4 – TADI**
ACNE	6.72%	3.77%	25.49%	0.00%
ACRU	2.60%	2.76%	5.87%	1.07%
ASTR	0.23%	0.35%	0.75%	0.00%
CAAQ	1.12%	0.00%	4.24%	0.00%
CACA	0.00%	0.78%	0.00%	0.00%
CELA	12.57%	7.33%	30.89%	0.00%
CRVI	0.62%	0.00%	0.00%	0.00%
FRPE	23.19%	0.00%	6.77%	0.42%
ILDE	0.41%	0.00%	1.90%	0.00%
LIST	23.73%	71.21%	10.21%	1.16%
MORU	0.00%	0.39%	0.00%	0.00%
PLAQ	0.57%	0.00%	0.00%	3.61%
PLOC	5.49%	2.93%	0.00%	0.09%
POHE	0.00%	0.00%	0.00%	1.67%
QULA	0.13%	2.29%	6.91%	0.20%
QULY	9.15%	0.00%	0.00%	0.05%
TADI	7.66%	0.00%	0.00%	91.73%
ULAM	5.82%	8.20%	6.97%	0.00%

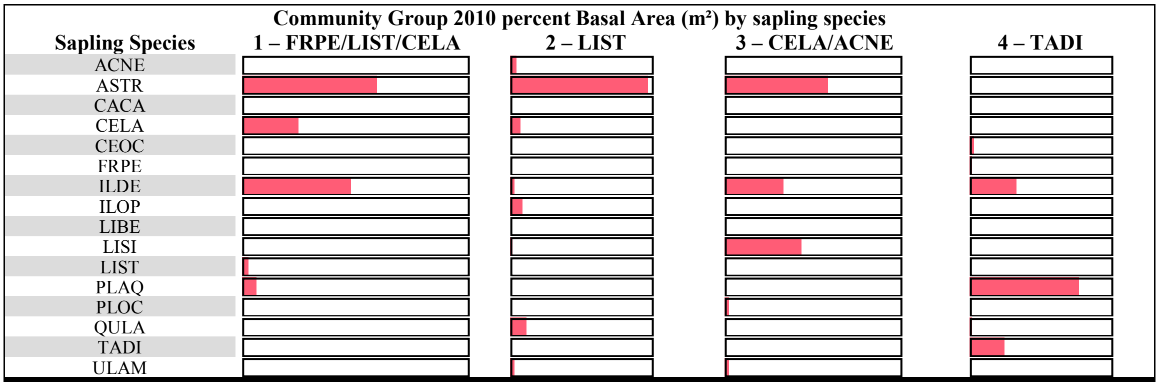


Number of trees within DBH size classes by community group.

Community Group	< 25 cm		25 – 50 cm		50 – 75 cm		> 75 cm	
	N	% of total	N	% of total	N	% of total	N	% of total
1 – FRPE/LIST/CELA	57	60.64%	25	26.60%	6	6.38%	6	6.38%
2 – LIST	47	58.02%	14	17.28%	14	17.28%	2	7.41%
3 – CELA/ACNE	46	58.23%	27	34.18%	6	7.59%	0	0.00%
4 – TADI	47	37.30%	44	34.92%	33	26.19%	2	1.59%

Community Group 2010 percent Basal Area (m^2) by sapling species

Sapling Species	**1 – FRPE/LIST/CELA**	**2 – LIST**	**3 – CELA/ACNE**	**4 – TADI**
ACNE	0.00%	3.56%	0.00%	0.00%
ASTR	41.71%	67.46%	41.14%	0.00%
CACA	0.05%	0.00%	0.00%	0.00%
CELA	17.66%	5.64%	0.00%	0.00%
CEOC	0.00%	0.00%	0.00%	2.75%
FRPE	0.00%	0.00%	0.00%	1.06%
ILDE	33.72%	2.95%	23.76%	23.19%
ILOP	0.00%	6.71%	0.00%	0.00%
LIBE	0.00%	0.66%	0.00%	0.00%
LISI	0.00%	1.60%	30.99%	0.00%
LIST	2.42%	0.00%	0.00%	0.88%
PLAQ	4.44%	0.00%	0.00%	53.80%
PLOC	0.00%	0.00%	1.85%	0.00%
QULA	0.00%	8.57%	0.00%	1.21%
TADI	0.00%	0.00%	0.00%	17.10%
ULAM	0.00%	2.85%	2.27%	0.00%

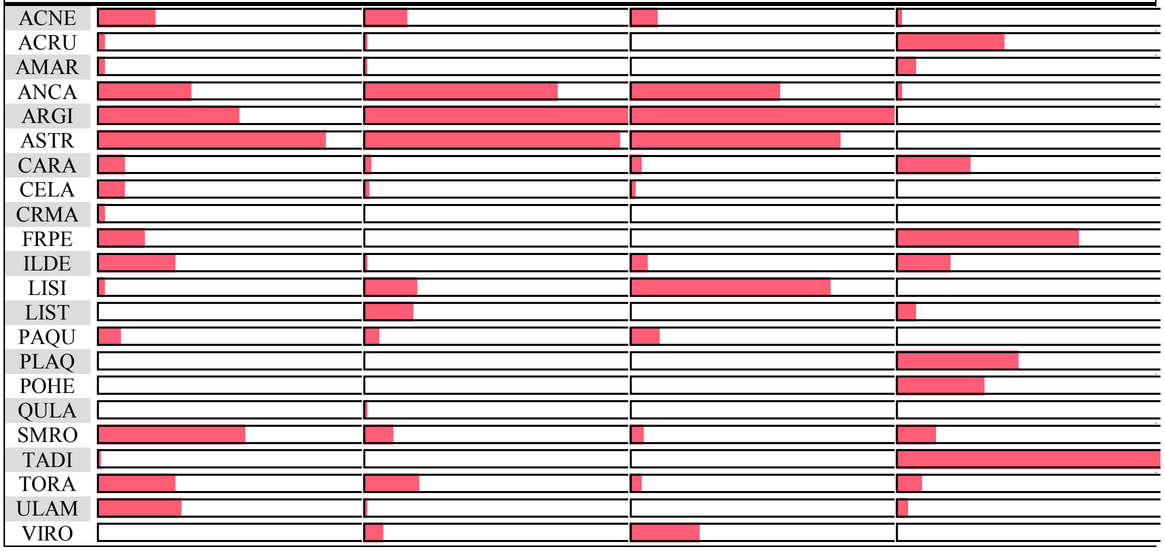


Community Group 2010 percent Basal Area (m²) by sapling species

Appendix 5

Percent of total point intercept hits by woody species within community groups (0-2 meters).

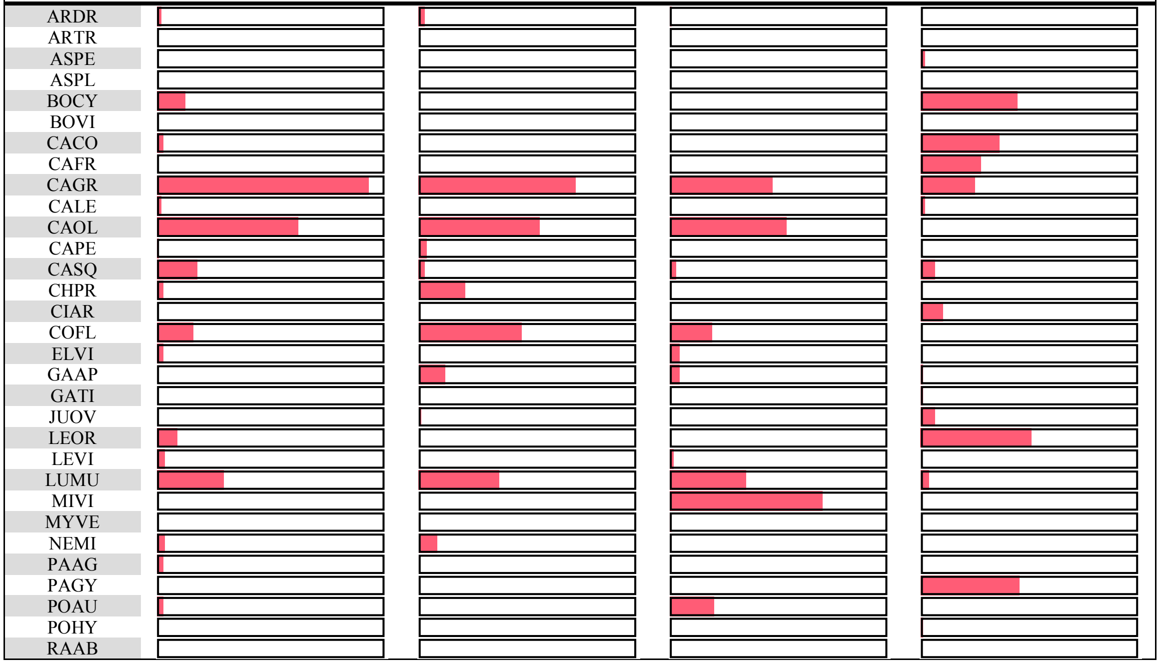
	Community Group Community Group - % of point intercept hits 0-2 meters by woody species			
Species	**1 – FRPE/LIST/CELA**	**2 – LIST**	**3 – CELA/ACNE**	**4 – TADI**
ACNE	5.43%	4.04%	2.71%	0.62%
ACRU	0.90%	0.39%	0.32%	9.94%
AMAR	0.90%	0.39%	0.00%	1.86%
ANCA	8.60%	17.73%	13.72%	0.62%
ARGI	13.12%	30.12%	29.98%	0.00%
ASTR	20.81%	23.34%	19.30%	0.00%
CARA	2.71%	0.78%	1.28%	6.83%
CELA	2.71%	0.65%	0.64%	0.00%
CRMA	0.90%	0.00%	0.00%	0.00%
FRPE	4.52%	0.00%	0.00%	16.77%
ILDE	7.24%	0.52%	1.75%	4.97%
LISI	0.90%	4.95%	18.34%	0.00%
LIST	0.00%	4.69%	0.00%	1.86%
PAQU	2.26%	1.56%	2.87%	0.00%
PLAQ	0.00%	0.00%	0.00%	11.18%
POHE	0.00%	0.00%	0.00%	8.07%
QULA	0.00%	0.39%	0.00%	0.00%
SMRO	13.57%	2.87%	1.44%	3.73%
TADI	0.45%	0.00%	0.00%	29.81%
TORA	7.24%	5.22%	1.12%	2.48%
ULAM	7.69%	0.39%	0.00%	1.24%
VIRO	0.00%	1.96%	6.54%	0.00%

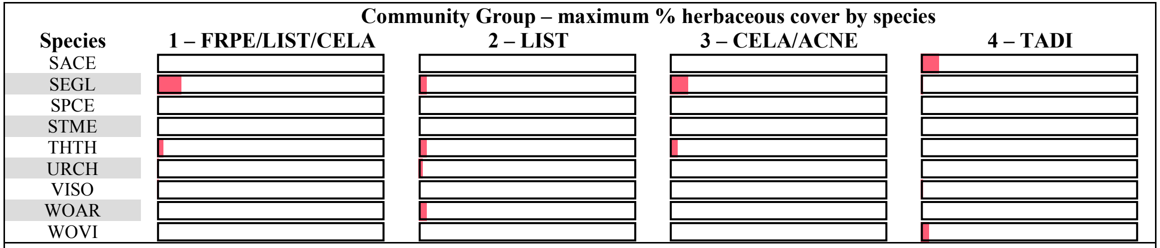


Appendix 6

Maximum percent cover by herbaceous species within community groups.

	Community Group – maximum % herbaceous cover by species			
Species	**1 – FRPE/LIST/CELA**	**2 – LIST**	**3 – CELA/ACNE**	**4 – TADI**
ARDR	0.74%	1.20%	0.64%	0.00%
ARTR	0.00%	0.00%	0.00%	0.13%
ASPE	0.00%	0.00%	0.00%	0.79%
ASPL	0.00%	0.24%	0.00%	0.00%
BOCY	4.47%	0.00%	0.32%	15.75%
BOVI	0.00%	0.00%	0.16%	0.00%
CACO	0.93%	0.00%	0.00%	12.71%
CAFR	0.00%	0.00%	0.00%	9.86%
CAGR	32.59%	25.30%	16.56%	8.87%
CALE	0.74%	0.00%	0.16%	0.66%
CAOL	21.79%	19.76%	18.97%	0.00%
CAPE	0.37%	1.45%	0.00%	0.00%
CASQ	6.33%	1.20%	1.13%	2.51%
CHPR	0.93%	7.71%	0.00%	0.00%
CIAR	0.00%	0.00%	0.00%	3.71%
COFL	5.59%	16.63%	6.91%	0.00%
ELVI	0.93%	0.00%	1.77%	0.26%
GAAP	0.19%	4.34%	1.93%	0.40%
GATI	0.00%	0.00%	0.00%	0.40%
JUOV	0.00%	0.48%	0.00%	2.38%
LEOR	3.35%	0.00%	0.32%	17.87%
LEVI	1.30%	0.00%	0.80%	0.13%
LUMU	10.24%	13.25%	12.38%	1.46%
MIVI	0.19%	0.00%	24.76%	0.00%
MYVE	0.00%	0.00%	0.48%	0.00%
NEMI	1.49%	3.13%	0.00%	0.00%
PAAG	0.93%	0.00%	0.00%	0.00%
PAGY	0.00%	0.00%	0.00%	16.15%
POAU	0.93%	0.00%	7.23%	0.00%
POHY	0.00%	0.00%	0.00%	0.40%
RAAB	0.19%	0.00%	0.00%	0.00%
SACE	0.00%	0.00%	0.00%	3.18%
SEGL	3.72%	1.45%	3.05%	0.40%
SPCE	0.00%	0.24%	0.16%	0.00%
STME	0.00%	0.00%	0.48%	0.00%
THTH	1.12%	1.45%	1.45%	0.00%
URCH	0.56%	0.72%	0.00%	0.00%
VISO	0.37%	0.00%	0.32%	0.40%
WOAR	0.00%	1.45%	0.00%	0.13%
WOVI	0.00%	0.00%	0.00%	1.46%





Notes: Data is the maximum % for each species; values are column %; column totals are 100% (*N*=5 plots per each group).

Appendix 7

List of all woody species included in aboveground net primary productivity and carbon pool calculations.

CODE	Scientific Name	Common Name	Authority	Family	Duration	Form	Native
ACNE	*Acer negundo*	box elder	L	Aceraceae	perennial	tree	Yes
ACRU	*Acer rubrum*	red maple	L	Aceraceae	perennial	tree	Yes
AMAR	*Ampelopsis arborea*	pepper vine	(L) Koehne	Vitaceae	perennial	vine	Yes
ANCA	*Anisostichus capreolata*	cross vine	(L) Bureau	Bignoniaceae	perennial	vine	Yes
ARGI	*Arundinaria gigantea*	Cane	(Walter) Muhl.	Poaceae	perennial	woody grass	Yes
ASTR	*Asimina triloba*	pawpaw	L (Dunal)	Annonaceae	perennial	tree	Yes
CAAQ	*Carya aquatica*	water hickory	(Michaux f.) Nuttall, Walter H.	Juglandaceae	perennial	tree	Yes
CACA	*Carpinus caroliniana*	ironwood	Walter	Betulaceae	perennial	tree	Yes
CARA	*Campsis radicans*	trumpet vine	(L) Seemann	Bigonoiaceae	perennial	vine	Yes
CELA	*Celtis laevigata*	sugarberry	Willd.	Ulmaceae	perennial	tree	Yes
CEOC	*Cephalanthus occidentalis*	buttonbush	L.	Rubiaceae	perennial	shrub	Yes
CRMA	*Crataegus marshallii*	parsley hawthorne	Eggl.	Rosaceae	perennial	shrub	Yes
CRVI	*Crataegus viridis*	green haw	L.	Rosaceae	perennial	tree	Yes
DEBA	*Decumaria barbara*	wood vamp	L.	Saxifragiaceae	perennial	vine	Yes
FRPE	*Fraxinus pennsylvanica*	green ash	Marshall	Oleaceae	perennial	tree	Yes
ILDE	*Ilex decidua*	possumhaw	Walter	Aquifoliaceae	perennial	tree/sapling	Yes
ILOP	*Ilex opaca*	American Holly	Aiton	Aquifoliaceae	perennial	tree	Yes
LIBE	*Lindera benzoin*	spicebush	(L.) Blume	Lauraceae	perennial	shrub	Yes
LISI	*Ligustrum sinense*	Chinese privet	Lour	Oleaceae	perennial	shrub	No
LIST	*Liquidambar styraciflua*	sweetgum	L	Hamamelidaceae	perennial	tree	Yes
MORU	*Morus rubra*	red mulberry	L.	Moraceae	perennial	tree	Yes
PAQU	*Parthenocissus quinquefolia*	Virginia creeper	L. (Planchon)	Vitaceae	perennial	vine	Yes
PLAQ	*Planera aquatica*	water elm	Walter ex JF Gmelin	Ulmaceae	perennial	tree	Yes
PLOC	*Platanus occidentalis*	sycamore	L	Platanaceae	perennial	tree	Yes
POHE	*Populous heterophylla*	swamp cottonwood	L	Salicaceae	perennial	tree	Yes
QULA	*Quercus laurifolia*	laurel oak	Michaux	Fagaceae	perennial	tree	Yes
QULY	*Quercus lyrata*	overcup oak	Walter	Fagaceae	perennial	tree	Yes
SMRO	*Smilax rotundifolia*	roundleaf greenbrier	L.	Lilliaceae	perennial	vine	Yes
TADI	*Taxodium distichum*	bald cypress	(L) Richard	Taxodiaceae	perennial	tree	Yes
TORA	*Toxicodendron radicans*	poison ivy	L	Anacardiaceae	perennial	vine	Yes
ULAM	*Ulmus americana*	American elm	L	Ulmaceae	perennial	tree	Yes
VIRO	*Vitis rotundifolia*	muscadine grape	Michaux	Vitaceae	perennial	vine	Yes

Notes: Nomenclature is that used in Radford et al. (1968). Only litter box data is included in ANPP for vines as stems were not measured; cane material was removed from litter box collections prior to weighing but is discussed in Chapters 3 and 5 as potential overlooked source of annual productivity and stored carbon.