NUTRIENT DYNAMICS IN AN OLD-GROWTH BOTTOMLAND FOREST: CONGAREE NATIONAL PARK, SOUTH CAROLINA

by

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Abstract

Floodplains are important landscapes that act as boundaries between terrestrial and aquatic ecosystems. Past research efforts have illustrated that floodplains perform many beneficial functions, such as sediment retention and nutrient transformations, but little is known about old-growth riparian forests due to historical wetland losses in the United States. Thus, the goal of this study was to examine the effect of floodplain landscape variability on nutrient storage and transformations within an old-growth floodplain forest at Congaree National Park (CONG), South Carolina. Our specific objectives were to quantify: (i) soil organic carbon (SOC) storage, (ii) key biogeochemical indices such as microbial biomass, net nitrogen (N) mineralization, and soil phosphorus (P) saturation, and (iii) woody debris decomposition rates and nutrient dynamics. We measured SOC pools in four distinct floodplain landscapes (natural levee, flats, hydric mineral soil wetlands, hydric organic soil wetlands) within CONG. Mean SOC stocks (0-200 cm) were significantly greater in hydric mineral and organic soils when compared to non-wetland soil landscapes because of deep carbon (C) stocks associated with buried surfaces. We also measured biogeochemical indices and woody debris decomposition over a 2 year period on a soil toposequence ranging from the well drained river levee to a poorly drained backswamp. Soil microbial biomass was relatively consistent throughout the study, unlike net N mineralization, which showed significant seasonal variations. Nitrate (NO_3-N) was the predominant product of net N mineralization and soil P saturation was low across all toposequence positions. Prolonged drought conditions during the study allowed red imported fire ants to infest and damage the outer bark of downed woody debris. Invertebrate activity and microbial mineralization contributed to extremely fast wood decay rates in all landscapes. Woody debris C content decreased throughout the study, while N and P displayed periods of net immobilization. Results from this research indicate that the soils in the old-growth floodplain forests of CONG function as a sink for C, N, and P. However, rapid woody debris turnover rates and net NO_3-N production suggest that the Park may mineralize nutrients quickly from forest litter and be relatively leaky with regard to ecosystem N retention.

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Table of Contents

List of Tables

Chapter 2

Chapter 3

Chapter 4

List of Figures

Chapter 2

Chapter 3

Chapter 4

Chapter 1:

Dissertation Introduction

Floodplains are important components of the landscape that act as interfaces between upland and aquatic systems. Floodplain forests provide numerous environmental functions including sediment and contaminant retention (Costa, 1975; Lowrance et al., 1986; Craft and Casey, 2000; Noe and Hupp, 2009), sites of high biodiversity (Gregory et al., 1991), and carbon (C) storage (Stallard, 1998; McCarty et al., 2009). Anthropogenic disturbances over the past two centuries in the southeastern USA have resulted in increased soil erosion from uplands and concomitant sedimentation in low lying depositional environments, such as floodplains (Liu et al., 2003). Land use change has the potential to affect riverine forest functions via increased runoff, sedimentation, and stream downcutting (Hupp and Bazemore, 1993; Wissmar et al., 2004; Lockaby et al., 2005; Jolley et al., 2009). To date, relatively little is known about how sedimentation impacts specific floodplain processes such as soil organic carbon (SOC) storage and nutrient circulation.

Historically, many studies have been conducted on nutrient dynamics in uplands with fewer comparable studies in floodplains. Floodplains are complex ecosystems where sedimentation patterns are typically controlled by microtopography and geomorphic characteristics (Hupp and Bazemore, 1993). Therefore, riverine forests exist in complex landscapes containing many fluvial landforms such as natural levees, meander scroll complexes, backswamps, and sloughs (Hupp, 2000; Hupp et al., 2005). In addition, these landforms typically have varying characteristics including hydroperiod, soil properties, and plant communities (Hupp et al., 2005; Schilling and Lockaby, 2005). Episodic alluvial additions on floodplains have long been reported to produce fertile soils and support high rates of annual net primary productivity

(NPP) (Zhang and Mitsch, 2007). However, more recent research efforts have indicated that increased sedimentation associated with watershed disturbances can alter soil properties, biogeochemical processes, nutrient cycling, and species composition, as well as increase tree mortality and decrease annual NPP (Cavalcanti and Lockaby, 2005; Lockaby et al., 2005; Cavalcanti and Lockaby, 2006; Jolley et al., 2009; McCarty et al., 2009; Jolley et al., 2010a).

In the United States >50% of total wetlands have been lost since European settlement (Dahl, 1990). The remaining wetlands that have not been filled or drained have typically been logged in the past (Lockaby, 2009). As a result of wetland losses, very few studies have been conducted in true old-growth bottomland forests. Upland old-growth forests have been shown to have greater aboveground biomass, yet less annual NPP and nutrient demands when compared to young aggrading forests (Harmon et al., 1986). Old-growth forests that receive nutrient additions from outside sources (atmospheric or alluvial deposition) are relatively “leaky” in terms of nutrient retention, because ecosystem biological demand is less than annual inputs leading to saturation or net export of mineral nutrients (Hedin et al., 1995). Thus, generalizations about biogeochemical cycles derived from young secondary growth floodplain forests may not accurately reflect the processes occurring in old-growth ecosystems. In addition, knowledge of nutrient cycling in old-growth riverine forests will become increasingly important in the USA as forested wetlands that have been federally protected since the 1970s begin to reach advanced levels of maturity (Dahl and Allord, 1996).

The Congaree River floodplain on the upper Coastal Plain of South Carolina supports one of the largest and most productive bottomland forests in the United States (Doyle, 2009). As a result, nearly 9,000 ha of old-growth forest were protected in what is now Congaree National Park, by federal mandate in 1976 to “…preserve and protect for the education, inspiration, and enjoyment of present and future generations an outstanding example of a near-virgin southern hardwood forest" (Public Law 94–545, 1976). Knowledge concerning the specific processes that contribute to soil fertility and high rates of NPP within old-growth systems such as Congaree National Park is sparse. This research will provide insights into specific soil and biogeochemical functions which support one of the most productive and unique old-growth bottomland forests in the USA. An assessment of landscape variation within the floodplain and associated impacts on forest nutrient cycling will also allow for better natural resources management to maintain adequate conditions for the growth and persistence of healthy old-growth trees in Congaree National Park.

To that end, the goals of this research were to examine the effect of floodplain landscape variability (i.e., differences in relative elevation, hydroperiod, sedimentation) on soil C storage and key biogeochemical indices such as net nitrogen (N) mineralization rates, microbial biomass, and phosphorus (P) saturation. In addition, we quantified ecosystem nutrient storage in downed woody debris, wood decomposition rates, and nutrient cycling across a range of varied floodplain landforms. These data will provide valuable baseline biogeochemical information on old-growth bottomlands for comparison with alternate regional ecosystems.

Floodplain Soil Carbon Storage

Soil is the largest terrestrial reservoir of C on Earth and an accurate assessment of the spatial extent of SOC storage is critical for global C budgets (Schlesinger, 1990; Lal, 2003). Current and historical human disturbance has resulted in accelerated erosion from uplands and deposition in low-lying landscapes (Costa, 1975; Lowrance et al., 1986; Hupp and Bazemore, 1993; Stallard, 1998; Liu et al., 2003; Berhe et al., 2007). It has also been estimated that >80% of eroded soil materials are retained at a catchment-scale (Stallard, 1998; Smith et al., 2005), and the majority of eroded materials are trapped in terrestrial sinks, such as reservoirs and floodplains (Stallard, 1998; Smith et al., 2005; Walter and Merritts, 2008). Thus, riverine forests associated with fluvial systems may represent a significant sink for atmospheric C.

Historically, anthropogenic soil erosion was thought to be a net source of atmospheric CO_2 due to increased C oxidation resulting from the destruction of stable soil aggregates (Lal, 2003; Liu et al., 2003). However, it has been suggested that a portion of eroded SOC is preserved in depositional landscapes (Stallard, 1998). Field studies using chronosequence and clay pad accumulation methods have indicated relatively high rates of C accumulation (0.40-5.57 Mg C ha^{-1} yr^{-1}) on forested floodplains of the southeastern United States (Wigginton et al., 2000; Noe and Hupp, 2005; Noe and Hupp, 2009). A large proportion (≥50%) of total floodplain C accumulation is likely derived from autochthonous sources (i.e., NPP) with the remainder deposited as allochthonous C from watershed sources (Noe and Hupp, 2009). These findings suggest a linkage between sedimentation and SOC sequestration, yet the mechanisms responsible for this relationship are poorly understood. Moreover, floodplain soils may represent large watershed-scale sinks for eroded C that have not yet been rigorously quantified.

Soil wetness is a confounding factor related to SOC sequestration and storage in riverine forests. The height of the seasonal high water table can limit oxygen diffusion rates and result in anaerobic soil conditions which slow the mineralization of SOC (Ponnamperuma, 1972; Stallard, 1998). SOC storage is typically greatest in poorly and very poorly drained wetland soils (Kern et al., 1998) with greater SOC stored in wetland riparian soils compared to adjacent uplands (Ritchie and McCarty, 2003; Ricker et al., 2013). Accreting floodplain soils form via episodic alluviation and have the potential for deep C storage beyond typical 1-2 m sampling depths. For example, Grossman et al. (1998) reported that floodplain soils in Nebraska contained 66% of total Holocene age SOC below 1.5 m depth. Therefore, deep SOC storage may also be an important function of floodplain soils which is often overlooked when constructing global-scale C budgets.

Global C budgets are essential to understand the interactions between atmospheric and terrestrial C pools. Most of the variability in terrestrial soil C estimates is within freshwater mineral soil wetlands (Bridgham et al., 2006). A portion of this variability is due to inherent issues pertaining to spatial scale. Most global-scale models utilize coarse input datasets such as the State Soil Geographic Database (STATSGO2) at a 1:250,000 scale. However, large riverine forests, including the Congaree River floodplain, typically contain multiple soil-landscapes ranging from very poorly drained back swamps to well drained natural levees. Alluvial landform differences (soil drainage, sedimentation patterns, plant cover) within floodplains likely contribute to variability associated with SOC storage estimates from freshwater mineral wetland soils aggregated at a coarse spatial scale. Soil survey approaches (mapping units 1:15,840 scale) to C accounting have been shown to significantly reduce the variability (coefficients of variation <50%) in mean estimates of SOC pools (Kern et al., 1998). However, a great deal of uncertainty still exists regarding the exact factors that control SOC storage in floodplain landscapes. Assessment of the spatial relationships among fluvial landforms, sedimentation rates, and SOC storage would provide valuable insights into the fundamental processes which govern SOC stocks in floodplain forests.

Net Nitrogen Mineralization and Microbial Biomass

Net N mineralization is the breakdown of organic N into inorganic, plant available forms. This process includes the sum of ammonification (formation of ammonium NH_4^+) and nitrification (formation of nitrate NO_3^-), which are the initial steps in ecosystem cycling of N.

Plant available N is typically a limiting nutrient for terrestrial plant growth (Vitousek, 1982), thus N mineralization rates can be an indicator of relative soil fertility. Net N mineralization rates are highly variable among landscapes and are typically dependent upon many factors including soil wetness, pH, bulk density, temperature, microbial activity, and humus or litter quality (Vepraskas and Faulkner, 2001; Jolley et al., 2010a).

Previous studies of headwater riparian zones in the southeastern United States have reported that long-term sedimentation rates as low as 0.2 cm yr^{-1} can decrease net N mineralization (Lockaby et al., 2005; Jolley et al., 2010a). Annual sedimentation rates exceeding this level are common for floodplains of the Southeast (Hupp et al., 2005; Noe and Hupp, 2009), and knowledge regarding the effects of sediment deposition is critical for understanding riverine forest nutrient cycling. Episodic sedimentation alters soil physical properties such as bulk density, porosity, temperature, and moisture content (Koning, 2004; Jolley et al., 2010a). In turn, abrupt changes to intrinsic soil properties can reduce soil microbial activity and result in decreased rates of N circulation (Insam and Domsch, 1988). N mineralization is also dependent upon soil humus and surface litter quality. Shifts in plant species composition, structure, and nutrient contents have been reported as a result of increased sedimentation in riverine forests of the Southeast (Lockaby et al., 2005; Cavalcanti and Lockaby, 2006; Jolley et al., 2009; Jolley et al., 2010b). Shifts in plant species composition and litter quality may be a key component in the observed reduction of net N mineralization in floodplains. An additional consideration with regard to N mineralization on floodplains is changes in stream discharge and floodplain hydrology. Land use and impervious surface cover tend to increase stream discharge, flooding frequency, and floodplain scouring (Wissmar et al., 2004). Thus, changes in floodplain hydrology may scour deposited organic litter resulting in a net export of organic materials downstream before nutrients can be recycled within the floodplain. Initial biogeochemistry data are necessary to further develop the functional relationships among floodplain sedimentation, soil properties, and nutrient circulation. However, there is no information regarding biogeochemical processes available for old-growth systems such as the Congaree River floodplain, and evaluation of N mineralization rates would be a logical “first step” in understanding the effects of sedimentation patterns on ecosystem nutrient circulation.

Another important indicator of soil quality is microbial biomass. Microbial biomass is composed of organic bound (non-plant available) nutrients associated with the cell structure of soil microbes. Microbial biomass C is an important portion of total SOC storage and microbes are important for nutrient (N, P) immobilization in soils (Schilling et al., 1999; Allen and Schlesinger, 2004). While microbial biomass is a relatively small percentage of total soil nutrients, it is often a critical constituent that controls nutrient availability in forest ecosystems (Holmes and Zak, 1994). Thus, microbial biomass can be compared among landscapes and used as an indicator of the biogeochemical status of a floodplain forest (Groffman et al., 1992). Microbial biomass typically fluctuates seasonally, with greater biomass accumulation during warmer months of the year. Studies have shown similar or in some cases greater amounts of microbial biomass in wetlands compared to uplands (Groffman et al., 1992; Groffman et al., 1996; Schilling and Lockaby, 2005). These observations are likely due to limitation on microbial growth associated with soil nutrient deficiencies (Groffman et al., 1996; Allen and Schlesinger, 2004).

Disturbances in forested ecosystems can result in alterations of soil properties and subsequent changes in microbial biomass (Insam and Domsch, 1988; Schilling et al., 1999). The exact effects of soil disturbance on microbial biomass are unclear, with some studies indicating increases in microbial biomass C and N following disturbance (Entry et al., 1986), while others have reported decreases (Insam and Domsch, 1988; Schilling et al., 1999). Changes in floodplain sedimentation can also act as a disturbance mechanism by altering soil bulk density, temperature, pH, and moisture content (Jolley et al., 2010a). Previous studies have indicated that deposition rates between 0.2 and 0.3 cm yr^{-1} of sandy alluvium can significantly decrease microbial biomass C and N in riparian forest soils (Lockaby et al., 2005; Jolley et al., 2010a). However, these thresholds were established for small headwater streams with high rates of predominantly sandy deposition. Intrinsic sediment characteristics such as particle size distribution and nutrient contents may also be a critical factor controlling the specific effects of sedimentation on biogeochemical indices. For example, biogeochemical processes on a floodplain receiving 0.25 cm yr^{-1} deposition of nutrient-poor sand may respond differently than those of a floodplain receiving similar amounts of silty nutrient-rich alluvium.

Soil Phosphorus Retention and Saturation

Fine-grained alluvial soils containing poorly crystalline Fe and Al have a high potential for P sorption (Darke and Walbridge, 2000). In floodplains, this soil property can be an important water quality improvement function (Brinson, 1993; Darke and Walbridge, 2000; Wright et al., 2001). P sorption is dependent on many site-specific factors including concentrations of soil Fe and Al, pH, redox potential, particle size distribution, preexisting P saturation, and current P loading rates (Darke and Walbridge, 2000; Kadlec and Wallace, 2009).

Floodplain and wetland soils contain greater quantities of poorly crystalline Fe than upland soils (Shaw et al., 2003). In the southeastern USA, there is typically >20% poorly crystalline Fe (of total extractable Fe) in alluvial soils compared to <10% in adjacent uplands (Shaw et al., 2003; Schoonover et al., 2007). Thus, alluvial soils should provide ideal sites for P retention. However, iron-phosphates can undergo redox in response to reducing soil conditions and release previously immobilized P (Moore and Reddy, 1994; Wright et al., 2001). In addition, wetland P adsorbing capacity is proportional to finite quantities of poorly crystalline Fe and Al and it is possible to saturate the soil system with regard to P (Maguire and Sims, 2002). Once the P sorbing capacity of a soil has been exceeded, it will cease to act as a sink and instead transmit P in solution (Vepraskas and Faulkner, 2001). An additional consideration is the effect of episodic sedimentation on P sorbtion capacity. Alluviation can add poorly crystalline Fe and Al materials to floodplain surfaces from surrounding upland sources (Schoonover et al., 2007), thus maintaining a viable sink for P. However, little information is available regarding sedimentation thresholds necessary to maintain P sorption and the specific effects of sedimentation on soil P saturation in riverine forests.

Downed Woody Debris in Floodplain Ecosystems

Woody debris is an important ecosystem component for accumulation and long-term storage of organic matter and nutrients (Currie et al., 2002; Muller, 2003). Ecosystem inputs and losses of woody debris are dependent upon species composition, landscape position, rates of disturbance, inherent physical and chemical properties of the wood, substrate quality, and climate (Harmon et al., 1986; Laiho and Prescott, 2004). The periodicity of inputs of woody debris to the soil surface has been described as bimodal in nature, with the greatest inputs following disturbance events, an eventual “equilibrium” state as the forest regenerates (inputs equal to losses), and increased wood input as the stand progresses towards old-growth (Harmon et al., 1986). It has been suggested that woody debris is a minor pool of nutrients during all stages of stand development when compared to soil and leaf litter (Laiho and Prescott, 2004). However, most woody debris studies in North America have been conducted in northern latitude upland landscapes of the United States and Canada (Harmon et al., 1986; Tyrrell and Crow, 1994; Laiho and Prescott, 2004) and very few studies of dead wood have been done in floodplains or wetlands of the Southeast (Day, 1982; Rice et al., 1997).

We are aware of no reports regarding woody debris decomposition dynamics in old-growth bottomland hardwood forests of the Southeast. Climatic factors such as humidity and annual temperatures may accelerate decay rates resulting in less nutrient storage in downed wood compared to northern forests (Currie et al., 2002). However, slower rates of C mineralization due to soil wetness and nutrient immobilization from floodwaters may contribute to larger woody debris nutrient pools than one would expect in an upland landscape. In addition, episodic hurricane damage and annual flooding within Congaree National Park may result in increased tree mortality (Putz and Sharitz, 1991; Rice et al., 1997; Jolley et al., 2009). Tree mortality could contribute to increased inputs of wood to the forest floor and result in greater nutrient storage. To date, woody debris nutrient pools within Congaree National Park have not been quantified. These data would be valuable to quantify the relative importance of woody debris to overall ecosystem nutrient pools.

Woody Debris Decomposition Rates and Nutrient Source-Sink Relationships

Measurement of *in situ* leaf litter decomposition is more common in wetlands than woody debris (Day, 1982). Decay of wood is typically slower than leaf litter (Day, 1982; Harmon et al., 1986; Rice et al., 1997; Schilling and Lockaby, 2005). Some studies have indicated more rapid litter decay rates in seasonally flooded areas (Lockaby et al., 1996; Rice et al., 1997) while others have found initial litter quality to be a controlling factor of decomposition (Day, 1982; Laiho and Prescott, 2004; Schilling and Lockaby, 2005). Bottomland forests often contain diverse forest communities existing across a heterogeneous continuum of alluvial landforms ranging from permanently flooded wetlands to well drained bottomland flats. To date, there have not been any comprehensive studies to address the combined effects of floodplain landform characteristics and sedimentation on species-specific woody debris decomposition.

Wood decay studies in wetlands are scarce compared to those completed in uplands (Harmon et al., 1986; Laiho and Prescott, 2004). Wetland woody debris decay rate constants (*k*) in the Southeast have been reported to range from 0.050 yr^{-1} for pumpkin ash (*Fraxinus profunda*) in Louisiana to 0.305 yr^{-1} for red maple (*Acer rubrum*) in Virginia (Rice et al., 1997; Day, 1982, respectively). Chueng and Brown (1995) also reported a mean *k* of 0.089 yr^{-1} for silver maple (*Acer saccharinum*) wood in a bottomland forest of Illinois. Wood decomposition rates are highly variable among species due to differences in initial litter quality (Harmon et al., 1986; Tyrrell and Crow, 1994). Decay rates are also dependent upon woody debris size, with larger diameter wood typically decaying slower and having longer turnover times (Abbott and Crossley, 1982; Laiho and Prescott, 2004). Moreover, the general lack of wood decomposition studies in floodplains coupled with the use of varying species, time intervals, and diameter size classes make direct comparisons among specific decomposition studies difficult.

Woody debris is important for long-term storage of organic matter and circulation of nutrients. Nutrient mineralization-immobilization trends in woody debris are controlled by microbial processes and seasonal leaching from throughfall organic matter (Day, 1983; Harmon et al., 1986). Downed wood nutrient source-sink behavior is largely dependent on initial nutrient content as well as the level of microbial activity within the woody debris and underlying soil (Harmon et al., 1986; Currie et al., 2002). Wood decay results in cumulative losses of mass and volume as C is mineralized and evolved as CO_2 (Pregitzer and Euskirchen, 2004). The slow rates of wood decay, compared to leaf litter, make it a relatively long-term sink for C (Currie et al., 2002). High sedimentation rates have also been reported to slow decomposition of leaf litter in riparian forests (Lockaby et al., 2005; Jolley et al., 2010a). If rates of woody debris decomposition are similarly reduced due to sedimentation and progressive burial, it may result in longer turnover times. Thus, sedimentation may increase the importance of woody debris with regard to C storage in riverine forests.

In contrast to C dynamics, N and P are typically immobilized during the initial stages of wood decomposition and are eventually mineralized during advanced stages of decay (Harmon et al., 1986; Harmon and Hua, 1991; Chueng and Brown, 1995; Rice et al., 1997; Laiho and Prescott, 2004). The literature also suggests that, because of minimal initial nutrient concentrations, downed woody debris is not a significant source of nutrients when compared to soil and leaf litter in most upland ecosystems (Laiho and Prescott, 2004). However, given the vast differences in hydrology, soil properties, and plant species between bottomland and upland forests, it would not be surprising if this commonly held assumption was not an accurate generalization for riverine forests. It is evident that more data regarding wood decomposition rates and nutrient circulation are needed for wetland and riverine forests in order to better evaluate the importance of woody debris in ecosystem nutrient budgets.

Study Objectives and Hypotheses

The primary objective of this research was to measure floodplain nutrient storage and cycling in Congaree National Park, South Carolina. The specific goals were to i) quantify and compare SOC storage among alluvial soil landscape units; ii) examine the effect of landscape variability on soil biogeochemistry through net nitrogen N mineralization, microbial biomass, and phosphorus P saturation; iii) quantify ecosystem nutrient storage in downed woody debris and; iv) assess woody debris decomposition and nutrient source-sink relationships using *in situ* methodologies.

Our research methods were designed to test the following specific hypotheses:

1: Alluvial soil C pools are dependent upon both extended hydroperiods and episodic burial of floodplain surface horizons; progressive burial of SOC will therefore result in significantly greater SOC storage in floodplains compared to other regional upland landscapes.

2: Increased sedimentation rates hinder floodplain biogeochemical functions. As a result, fluvial landscapes with higher rates of sedimentation will have decreased net N mineralization and microbial biomass (C and N).

3: Sedimentation will limit soil P saturation and increase P sorbtion capacity through annual additions of alluvial clays and amorphous Fe/Al.

4: Downed woody debris is a major nutrient pool in old-growth riverine forests. Therefore, long-term storage of nutrients (C, N, P) in dead wood will be a significant portion of overall ecosystem nutrient pools.

5: Woody debris decomposition is an important source of “slow release” nutrients to floodplain soils and vegetation. Thus, wood decay will result in slow net mineralization of C, N, and P, with initial short-term microbial immobilization of N and P.

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Chapter 2:

Soil organic carbon stocks in a large eutrophic floodplain forest of the southeastern Atlantic Coastal Plain, USA

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Abstract

Anthropogenic land use activities have significantly altered sediment and nutrient dynamics at watershed-scales, resulting in significant erosion from uplands and redeposition within large floodplain ecosystems. Some upland land uses have had documented negative effects on soil carbon (C) stocks, although the specific impacts of these catchment disturbances on soil organic carbon (SOC) dynamics in depositional environments are poorly understood. Assessment of SOC stocks in floodplain environments would allow for more precise estimates of watershed C distribution and enhance C models at regional and global scales. In this study, we measured SOC pools to depths of 100 and 200 cm in four distinct floodplain landscapes (natural levee, flats, mineral wetlands, organic wetlands) in a large bottomland forest in Congaree National Park, South Carolina, USA. These data were utilized to assess the spatial trends in SOC storage within the greater Congaree floodplain. Mean SOC stocks to a depth of 100 cm were 108-109 Mg C ha^{-1} in flats and levees, 193 Mg C ha^{-1} in mineral wetlands, and 533 Mg C ha^{-1} in organic wetlands. In addition, hydric soils contained significantly more SOC in deep horizons (100-200 cm depths) because of burial and preservation of previous soil surfaces. At a regional scale, similar alluvial soils within large floodplains were estimated to store approximately 0.l Pg of SOC. These results highlight the importance of inclusion of deep SOC storage in alluvial settings when estimating watershed C budgets and suggest that large floodplains may play a more important role as sinks for C than previously thought.

Keywords: Floodplain, soil carbon, fluvial processes, riparian forest

Introduction

Soils are the largest terrestrial reservoir of atmospheric carbon (C) which is estimated to be nearly three times greater than C stored in vegetation (Eswaran and others 1993; Schlesinger 1997; Lal 2003). Soil organic carbon (SOC), primarily derived from plant productivity, represents the majority (>65%) of the terrestrial soil C pool (Batjes 1996). Quantification of current SOC stocks has become increasingly important because many soils have the capacity to sequester significant amounts of atmospheric CO_2 via afforestation (Lal 2005). In addition, mineral soils that are rich in SOC tend to have greater water holding capacity, infiltration, and plant productivity (Karlen and others 1997; Lal 2005). SOC is also necessary for many beneficial biogeochemical functions in soils such as removal of excess nitrate (NO_3^-) from pore, ground, and surface waters via denitrification (Nelson and others 1995; Groffman and others 2009). Recognition of the many functions and values associated with SOC has led to an increase in the number of C accounting studies undertaken to quantify the spatial extent of SOC at watershed, regional, and global scales (Post and others 1985; Eswaran and others 1993; Dixon and others 1994; Batjes 1996; Davis and others 2004; Izaurralde and others 2007; Ricker and others 2013).

Alluvial landscapes are depositional environments that have the potential to accumulate and store large quantities of organic C (Stallard 1998; Smith and others 2005; Zehetner and others 2009). Floodplain soils contain both SOC derived from local vegetation productivity (autochthonous C) and allochthonous C deposited with mineral sediment during flood events (Noe and Hupp 2009). Floodplain ecosystems can be directly influenced by changes in watershed land uses and thus can act as sinks for C eroded from catchment uplands (Stallard 1998; Lal 2003). Increased agricultural or urban land use can result in significant losses of upland SOC stocks (Lal 2005), as well as increasing rates of riparian sedimentation or scour, overbank flooding, and nutrient inputs (Trimble 2008; McCarty and others 2009; Jolley and others 2010). Fundamental changes in watershed hydrology and sediment dynamics can increase allochthonous inputs to the floodplain surface, but may also limit autochthonous C production. For example, decreased aboveground net primary productivity (NPP), root productivity, and microbial biomass have been observed in riparian forests receiving high rates of sandy sediment deposition (Cavalcanti and Lockaby 2005; Jolley and others 2009; Jolley and others 2010). In addition, large spatially heterogeneous floodplains contain various alluvial landforms that can have significantly different potentials for sequestration of organic C due to variations in annual hydroperiod, plant species composition, soil characteristics, and microbial communities (Clawson and others 2001; Cierjacks and others 2011). Spatial heterogeneity in freshwater mineral wetland soils and floodplain forests likely contributes to the observed variability of landscape-scale SOC pools in these ecosystems (Kern 1994; Bridgham and others 2006; Ricker and others 2013). In addition, floodplains cover greater than 2.0×10^6 km^2 of the global land area (Tockner and Stanford 2002) and more comprehensive data regarding C dynamics in these ecosystems would be invaluable to global C models (Zehetner and others 2009). To date, relatively few C accounting efforts have been completed in floodplains, and detailed field studies are still needed to elucidate the major factors responsible for SOC accumulation and storage in floodplain landscapes.

Another important consideration for watershed-scale SOC analyses is the role of floodplains in regulating C losses during land use change. There are many reports of impacts on upland SOC resulting from conversion of native forest to agricultural land use (Schlesinger 1997; Lal 2003; Lal 2005). However, it is unclear what proportion of SOC is mineralized during land disturbance and how much is retained within depositional landscapes such as floodplains, wetlands, and freshwater reservoirs (Stallard 1998; Lal 2003; Smith and others 2005; Cole and others 2007). Agricultural “legacy sediments” are an example of drastic sediment and C redistribution in the eastern United States. Legacy sediments were deposited in riparian areas during periods of unsustainable upland agricultural activities in the 19th and early 20th centuries (Costa 1975; Jacobson and Coleman 1986). During this time period, stream sediment loads drastically increased and in many watersheds various dam structures increased sediment trapping efficiencies, resulting in entrainment of eroded materials within riparian areas and stream channels (Trimble 2008; Walter and Merritts 2008). These combined factors have resulted in large quantities of relatively young sediment (deposited over the past 400 yrs) on floodplains of the eastern USA and, in many cases, these deposits exceed 100 cm in depth (Costa 1975; Jacobson and Coleman 1986). In some large floodplains, legacy sediment depth can exceed 400 cm (Hupp and others 2009). Thus, to completely understand SOC dynamics at watershed-scales, both upland SOC losses due to land conversion and depositional SOC additions must be taken into account (Izaurralde and others 2007).

Many SOC studies are based on sampling depths of 100 cm, which is typically sufficient in uplands because inputs of autochthonous SOC are greatest at the soil surface resulting in a shallow distribution of C (Jobbágy and Jackson 2000; Harrison and others 2011). However, assessment of deep SOC storage (>100 cm) is much more important in floodplain ecosystems where soil formation is related to fluvial processes and soil surfaces undergo episodic burial leading to establishment of a new floodplain surface and rapid incorporation of additional autochthonous SOC (Carter and others 2009; Zehetner and others 2009). As a result of these processes, multiple buried surfaces (Ab horizons) can be found within the upper 100 cm (Blazejewski and others 2009), resulting in deeper SOC storage than is typical in uplands (Ricker and others 2013). In addition, large floodplains can contain deep buried C forms that are not accounted for in the upper 100 cm of soil (Grossman and others 1998; Blazejewski and others 2009). Thus, sampling of deep soil horizons in floodplains may be necessary to construct more precise ecosystem SOC budgets and evaluate the fate of eroded C at the watershed scale (Izaurralde and others 2007). Clearly, additional data regarding the spatial distribution of alluvial SOC are necessary to better understand terrestrial SOC distribution, floodplain soil genesis, and soil biogeochemical functions in riverine forest ecosystems. Therefore, the specific goals of this research were to i) quantify the vertical and spatial distribution of alluvial soil properties in relation to SOC stocks, ii) quantify SOC pools in common floodplain landscapes of the Atlantic Coastal Plain, and iii) utilize these data to estimate regional SOC storage in large alluvial floodplains of the southeastern USA.

Study Site

Soil samples were taken from an old-growth bottomland hardwood forest within Congaree National Park (CONG). The Park is located in the Upper Coastal Plain physiographic region of central South Carolina, approximately 30 km downstream from the city (2010 population 129,272) of Columbia (Figure 1). The Congaree River is a large eutrophic (red water) river that drains a large portion (>21,000 km^2) of the Piedmont physiographic province of central and northern South Carolina. The basin has varied current land cover characteristics from mixed forested, agricultural, and rural residential land uses in the basin headwaters to highly urbanized regions, such as the greater Columbia metropolitan area. As of 2006, land area within the watershed was 67.7% forested or wetlands, 22.7% agricultural, and 9.6% developed or barren land, of which about 2.0% was impervious surface (2006 National Land Cover Dataset, Fry and others 2011). Historically, the entire Congaree basin underwent widespread deforestation for cotton agriculture during the late 19th and early 20th century (Trimble 2008).

The region has a humid subtropical climate that receives approximately 1220 mm of annual precipitation and has an average annual air temperature of 17.6 °C. The Congaree floodplain contains many fluvial landscapes including the natural river levee, hardwood flats, sloughs, backswamps, oxbow lakes, and depressional seep wetlands. Forest composition within CONG varies by alluvial landforms (Allen and others 2005) with mixed hardwoods such as, sugarberry (*Celtis laevigata* Willd.), sweetgum (*Liquidambar styraciflua* L.), American sycamore (*Platanus occidentalis* L.), and mixed bottomland oaks (e.g. *Quercus laurifolia* Michx., *Q. nigra* L., *Q. phellos* L.) associated with drier landscapes (levees, flats, ridges) of the floodplain. Bottomland wetlands (sloughs, backswamps, oxbows) are dominated by more flood tolerant overstory species such as baldcypress (*Taxodium distichum* (L.) Rich.), water tupelo (*Nyssa aquatica* L.), and swamp tupelo (*Nyssa biflora* Walter).

Materials and Methods

Soil coring locations representative of common floodplain landforms were selected using available geographical information system (GIS) soil survey geographic (SSURGO, 1:20,000 map scale) database spatial layers. Samples were taken within the four major soil mapping units (18 total polygons) of the Park (Table 2.1), which are mapped at a series level as Congaree (Fine-loamy, mixed, active, nonacid, thermic Oxyaquic Udifluvents), Tawcaw (Fine, kaolinitic, thermic Fluvaquentic Dystrudepts), Chastain (Fine, mixed, semiactive, acid, thermic Fluvaquentic Endoaquepts), and Dorovan (Dysic, thermic Typic Haplosaprists) (Soil Survey Staff 2013). Congaree and Tawcaw units are mineral soils mapped on the well drained (WD) natural river levee and somewhat poorly drained (SPD) hardwood flats of the floodplain, respectively. Chastain units denote poorly drained (PD) freshwater mineral wetlands and Dorovan units indicate the presence of very poorly drained (VPD) organic soils (Histosols) in depressional seep wetlands located at the upland margins of the active floodplain (Figure 2.1). A total of 15 cores (0-100 cm) were taken from each of the four major soil mapping units for a total of 60 soil cores within the floodplain. A subset of 20 core locations (n = 5 per mapping unit) were selected for additional deep (100-200 cm depths) sampling (Figure 2.1). All sample locations were recorded using hand-held GPS instruments and geo-referenced relative to the active river channel.

Field Sampling

Soil pedons were described in the field (Schoeneberger and others 2002) and sampled incrementally to compare soil properties by depth. Samples were collected from 0-10 cm and in 15 cm increments (10-25, 25-40, 40-55, 55-70, 70-85, 85-100 cm) downward to 100 cm. Deep soil samples were collected at 25 cm increments (100-125, 125-150, 150-175, 175-200 cm). Bulk soil samples were taken for each depth increment by hand using bucket or clay augers in mineral soils and a customized Macaulay peat auger in mucky mineral or organic soils. In mineral soils, a bulk density probe (5 cm length, 5 cm diameter) was used to collect soil cores of known volume from each sampling increment. Soil samples were sealed in plastic sample bags, placed on ice in coolers during transport, and stored at 4 °C until processed in the laboratory.

Laboratory Analyses

Soil bulk density samples were dried to a constant weight at 105 °C, passed through a 2 mm sieve to remove coarse fragments, and bulk density was quantified using the core method corrected for coarse fragment mass and volume (Blake and Hartge 1986; Soil Survey Laboratory Staff 2004). Soil texture was estimated for mineral soil materials using the hydrometer method

(Gee and Bauder 1986). Bulk soil samples were air dried and passed through a 2 mm sieve to remove coarse mineral and organic fragments. A homogenized subsample of approximately 5 g was ground with mortar and pestle and passed through a 0.25 mm mesh (number 60) sieve. Ground subsamples were used to quantify total soil C and N concentrations using thermal combustion on a Perkin Elmer 2400 Series II CHNS/O analyzer (Perkin Elmer, Waltham, MA). A representative subsample of soil materials (n = 15) were qualitatively analyzed for the presence of carbonates using dilute 1 N HCl, and further quantitative analysis (n = 5) was carried out using concentrated 3 N HCl (Jackson 2005). All samples contained minimal (<0.1% mass) carbonates, and total C was therefore assumed to be equivalent to SOC. Sample increment depths and bulk density values were used to convert soil C and N concentrations to a landscape-scale mass per unit area (Mg C ha^{-1}).

Spatial Analysis of Floodplain SOC Stocks at Regional Scales

Digital soil survey data were utilized to estimate total floodplain SOC storage at local and regional scales. The SSURGO data (1:20,000 map scale) used to define the sample units (Figure 2.1) were also used to scale-up estimates of SOC storage within CONG. The mean SOC pools (Mg C ha^{-1}) from each major floodplain map unit were multiplied by the area of each map unit to yield the total SOC storage (Mg C) within CONG to a depth of 200 cm. Digital General Soil Map of the United States (STATSGO2, 1:250,000 map scale) data were also used to calculate SOC storage in CONG and to scale-up estimates to the greater southeastern Coastal Plain. STATSGO2 data consist of soil survey data aggregated into broadly defined soil associations. Each association has defined proportions of expected soil landscape units, thus weighted averages that take into account the expected area of each soil mapping series were used to scale-up SOC storage estimates beyond CONG. In addition to the soil associations mapped within the

Congaree River floodplain, there are a number of similar STATSGO2 associations mapped along large rivers of the southeastern Coastal Plain (i.e., Riverview-Chewacla-Chastain and Toccoa-Congaree-Chewacla map units). These alluvial soils have similar climate, genesis, and natural drainage classes to those evaluated within CONG (Soil Survey Staff 2013). Thus, these soils were assigned mean SOC pools based on natural drainage class and weighted averages were calculated as described above. The SOC pools were then multiplied by the total area of these mapped associations within the Coastal Plain of the southeastern USA to obtain regional estimates of alluvial SOC storage.

Statistical Analysis

All descriptive and statistical analyses were performed in SAS 9.2. Mean comparisons between two groups were completed using Student's t-tests, such as hydric mineral soils containing buried surfaces vs. those without and the upper 100 cm SOC pool vs. 100-200 cm SOC pool. One-way analysis of variance (ANOVA) with Tukey's honest significant difference tests (PROC GLM) were used for mean comparisons among three or more groups, such as mean SOC stocks among soil mapping units. Associations between SOC pools and specific sample attributes such as distance to the river channel, clay content, bulk density, total nitrogen, and sample depth were assessed using Spearman's rank order correlations (PROC CORR). All statistical tests were performed using $\alpha = 0.05$.

Results

Depth Distributions of Alluvial Soil Properties

Depth distributions of soil C varied across the landscapes of the Congaree floodplain (Figure 2.2A). Mean soil C concentration displayed a regular decrease (constantly decreasing concentration) with depth for the mineral soils (Congaree, Tawcaw) from 2.2% near the surface to <0.4% C at 200 cm. Among the mineral soils, Congaree units along the natural river levee had higher C concentrations with depth compared to the Tawcaw units. By contrast the hydric mineral soils (Chastain) displayed an irregular decrease (variable decrease or increase in concentration with depth) in C concentration (range 5.5-1.5%). In addition, these data had larger standard errors because of the presence of buried surface horizons at various depths within the sampled units. The VPD organic soils (Dorovan) had significantly higher C concentrations (range 15-33% C) compared to mineral soils of the floodplain, but showed an irregular decrease in C concentration similar to the mineral hydric soils (Figure 2.2A). Soil bulk density increased with depth in all soil mapping units investigated (Figure 2.2B). The non-hydric floodplain soils had the highest bulk density values, ranging from 1.0 to 1.5 Mg m^{-3}. Dorovan organic soils had the lowest mean bulk density values, ranging from 0.23 to 0.59 Mg m^{-3}. Bulk density mean variability increased in samples >100 cm as a function of smaller sample sizes and increased sand content within certain floodplain landscapes (Figure 2.2B).

Depth distributions of soil C:N ratios were variable among the CONG mapping units (Figure 2.2C). The non-hydric soils generally displayed decreasing C:N ratios with depth, from mean values of 11-13 at the soil surface to 5-8 at depths >100 cm. The Chastain units had similar C:N ratios with depth and means only ranged from 11-15. The Dorovan organic soils showed a large increase in C:N ratios with depth from a mean value of 17 at the soil surface to >32 at 200 cm depths (Figure 2.2C). In contrast to the variable distribution of C:N ratios, clay content within the mineral soils of CONG showed a similar distribution with depth (Figure 2.3). Mineral soils contained an increase in clay from the soil surface with increases from 30-100 cm depths and decreasing clay content around 200 cm, as sand content increased in deep horizons. Overall, Chastain soils had the greatest amount of clay ranging from 34% at the surface to 45% between

30 and 75 cm. Congaree soils of the natural levee had the least amount of clay, ranging from 20% at the soil surface to 31% at 100 cm (Figure 2.3).

Landscape-Scale SOC Pools

Measurements of soil C concentration, bulk density, and depth were used to construct landscape-scale SOC pools for CONG (Figure 2.4). Within the upper 100 cm there was a clear gradient of significantly ($p < 0.01$) greater SOC storage from the non-hydric soils (108-109 Mg C ha^{-1}), to the PD Chastain mineral soils (193 Mg C ha^{-1}), and the VPD Dorovan units (533 Mg C ha^{-1}). In addition, approximately 47% of the PD Chastain soils contained buried floodplain surfaces (Ab horizons) within the upper 100 cm. Separation of the Chastain soils based on these horizons resulted in significantly ($p < 0.001$) greater SOC in the soils that contained buried surfaces (Figure 2.4). In addition, mean SOC pools of the PD Chastain units that lacked these horizons were similar to the non-hydric soils of CONG (108 Mg C ha^{-1}).

Similar landscape-scale SOC pools were calculated for the 100-200 cm depths. These data were more variable than the upper 100 cm due to fewer samples ($n = 5$ per soil unit). However, there was a numerical increase in deep SOC from < 100 Mg C ha^{-1} in the non-wetland units to 160 Mg C ha^{-1} in the PD Chastain units. There was significantly ($p < 0.05$) more SOC storage at depth in the organic Dorovan soils compared to that of the mineral soil units (Figure 2.4). Depth distributions, displayed as a percent of the total SOC pool to 200 cm, showed significantly ($p < 0.01$) more SOC in upper 100 cm for Congaree and Tawcaw soils (Figure 2.5). In contrast, there were no significant differences in SOC storage between the upper 100 and 100-200 cm depths for both Chastain (48% SOC below 100 cm) and Dorovan (56% SOC below 100 cm) series.

Relationships between Floodplain Soil Attributes and SOC Pools

Relationships among mineral soil attributes were examined in both vertical (sample depth) and lateral (distance from the active river channel) dimensions (Table 2.2). In the vertical dimension, the most significant positive correlation with depth was bulk density (Spearman rank correlation $r_s = 0.41$, $p < 0.001$) followed by clay content ($r_s = 0.22$, $p < 0.001$). There were also significant negative vertical associations with both SOC ($r_s = -0.42$, $p < 0.001$) and total soil N content ($r_s = -0.30$, $p < 0.001$). In the lateral dimension, both total soil N content ($r_s = 0.38$, $p < 0.001$) and clay content ($r_s = 0.31$, $p <0.001$) significantly increased as the distance from the active river channel increased. SOC content and bulk density values were not significantly correlated with distance to the active river channel (Table 2.2). Among the soil properties measured, the strongest positive correlation was between SOC content and total N content ($r_s = 0.68$, $p < 0.001$). In addition, SOC and total N content both significantly decreased as bulk density increased ($r_s = -0.58$ and -0.45, respectively, $p < 0.001$). There were no significant relationships between clay and nutrient (C, N) content in the mineral soils assessed (Table 2.2).

Total Alluvial SOC Stocks at Local and Regional Scales

Landscape-scale SOC pools to a depth of 200 cm and SSURGO data were utilized to estimate total floodplain SOC storage within CONG (Table 2.3). Spatial analyses indicated that the majority of the floodplain area within CONG was mapped as Tawcaw (4420 ha) or Congaree (2031 ha) units. The wetland landscapes mapped as Chastain (1013 ha) and Dorovan (244 ha) comprised the remainder of the floodplain area. The total SOC storage within CONG was estimated to be 1.64×10^6 Mg C, with approximately 62% of this SOC stored in the upper 100 cm (Table 2.3). Among the soil mapping units, Tawcaw contained the largest proportion (39.8%) of the total floodplain SOC storage. Congaree and Chastain units contained similar percentages (21.8 %) of the total SOC storage despite Congaree units representing nearly double the land area of the Chastain landscapes. Dorovan units had minimal extent within CONG (244 ha), yet contained 16.6 % of the total SOC within the Park.

Spatially averaged SOC pools were utilized in conjunction with coarse-scale soil survey data (1:250,000 map scale STATSGO2) to calculate CONG SOC storage and extrapolate to a regional-scale (Table 2.4). CONG is mapped at a 1:250,000 scale as a Chastain-Tawcaw soil association. These data indicated that total SOC storage, to a depth of 200 cm, in CONG was 1.75×10^6 Mg C (Table 2.3). Chastain-Tawcaw associations cover over 210,000 ha of major floodplains (4th order rivers and above) within six states (Alabama, Florida, Georgia, North Carolina, South Carolina, Virginia) encompassing the southeastern Coastal Plain. Total SOC storage in these alluvial landscapes was estimated to be 4.85×10^7 Mg C (Table 2.4). Similar floodplain soil associations are found throughout the region, primarily mapped as Riverview-Chewacla-Chastain or Toccoa-Congaree-Chewacla. SOC storage estimates, based on natural drainage class, were 5.33×10^7 Mg C in these associations. The total SOC storage to a depth of 200 cm in these three regional soil associations was 9.79×10^7 Mg C, approximately 0.1 Pg (Table 2.4).

Discussion

Depth Distribution and Relationships between Soil Properties

SOC concentrations decreased with depth in the Congaree and Tawcaw landscapes of CONG (Figure 2.2A). The regular decrease in SOC is similar to many upland soils, suggesting the total C pool is influenced mainly by modern autochthonous additions from NPP (Batjes 1996; Jobbágy and Jackson 2000). By contrast, the hydric soil landscapes (Chastain, Dorovan) had irregular decreases in SOC content with depth, indicating that episodic burial and preservation of SOC in previously stable soil surfaces has occurred. This was not surprising since alluvial hydric soils preserve buried SOC more efficiently than non-wetlands, where aerobic soil conditions allow mineralization of buried C. Although SOC content varied with depth, there were no apparent lateral controls on C storage as indicated by non-significant correlations with distance to the active river channel (Table 2.2). Clay content was positively correlated with distance to the river channel, indicating fine grained materials were preferentially deposited at further distances from the river. This positive correlation did not extend to soil C, which was not significantly correlated to clay content. Past research has indicated that fine particle content (silt + clay) is positively correlated with SOC concentration in floodplains, usually representing allochthonous C inputs (Pinay and others 1992; Cabezas and others 2010). However, in most alluvial landscapes, stabilization of floodplain surfaces following large depositional events occurs (Carter and others 2009) and incorporation of organic matter from floodplain NPP leads to accumulation of SOC at the surface, regardless of particle size (Wigginton and others 2000; McCarty and others 2009). For example, Ricker and others (2012) found contemporary and buried surfaces (A, Ab horizons) with similar SOC content had formed in alluvial deposits ranging from loamy sands (>77% sand content) to silts (<12% sand content). Similarly, our data suggest that CONG SOC pools are not strongly influenced by particle size and instead may simply reflect periods of autochthonous C incorporation. These trends may become more pronounced as future scenarios of reduced precipitation within the CONG basin (McNulty and others 2013) cause reduced frequency of flooding.

The variation in C:N ratios with depth among the CONG landscapes suggest that alluvial soils store and cycle C in relatively different ways (Figure 2.2C). The soil C:N ratios tended to decrease with depth in non-hydric floodplain soils, similar to the distribution of C:N observed in uplands. In many soils this relative decrease in C:N ratio results from oxidation of C exceeding losses of N in highly decomposed organic matter at depth (Rumpel and Kögel-Knabner 2011). In contrast, there was a relatively uniform vertical C:N profile for the hydric mineral soils mapped as Chastain. Burial of organic matter in anaerobic soils limits C mineralization in the subsoil horizons because of limited oxygen diffusion (Mausbach and Richardson 1994). Sedimentation processes in wetlands that result in rapid burial have been shown to preserve organic matter in a chemical state similar to that at the time of deposition on the surface (Gurwick and others 2008), which explains the relatively uniform C:N ratios with depth in the Chastain mapping units. In contrast, organic Dorovan soils displayed an increase in soil C:N ratios with depth. This trend is due to the occurrence of constantly saturated conditions, allowing for more efficient C mineralization at the soil surface and limiting microbial respiration at depth (Post and others 1985). Greater C:N ratios at depth within the CONG peat deposits could also indicate preferential loss of N from the subsurface relative to C (Kuhry and Vitt 1996). This process could be a result of long-term phytocycling involving plant uptake of inorganic N and subsequent deposition at the soil surface as litter-bound organic N. The varying trends in C:N ratios suggest aerobic floodplain soils may cycle C rapidly, similar to uplands, while anaerobic floodplain soils can store significant subsurface SOC due to combined effects of burial and limited C mineralization at depth.

Alluvial SOC Pools

CONG landscape SOC pools significantly increased from 109 to 533 Mg C ha^{-1} as a result of soil drainage class (Figure 2.4). Mean SOC pools from 0-100 cm in non-hydric soil landscapes of CONG (108-109 Mg C ha^{-1}) were similar to those reported for alluvial soils (Fluvisols) by Batjes (1996) of 93 Mg C ha^{-1}, but greater than estimates reported for the contiguous USA (Fluvents, 74 Mg C ha^{-1}, Kern 1994). Batjes (1996) also reported a mean content of 68 Mg C ha^{-1} from 100-200 cm in alluvial soils, which was greater than estimates for Tawcaw, but similar to those of the Congaree soils in our study. Mean estimates of SOC storage to 100 cm in hydric mineral soils of CONG (Chastain units) were greater than those reported for Aquepts (135 Mg C ha^{-1}) by Kern (1994), but less than those in hydric riparian soils of the northeastern USA (246 Mg C ha^{-1}, Ricker and others 2013). SOC pools in CONG wetlands were significantly greater (2.7-times) if buried surfaces were present within the upper 100 cm (Figure 2.4). These findings were similar to those reported by Ricker and others (2013), who indicated significantly (1.5-times) greater SOC storage in riparian landscapes containing buried surfaces. These trends suggest floodplain landscapes that undergo episodic sedimentation (C burial) combined with high water tables store the most SOC. However, not all soils evaluated contained buried surfaces and the total SOC pools in mineral wetlands that did not contain buried horizons were similar to those of the drier floodplain landscapes (Figure 2.4).

Very high spatial variability in SOC pools of freshwater mineral wetlands has been noted (Bridgham and others 2006). Aggregation based on ecosystem type (i.e., freshwater swamps, etc.) encompasses many soil types with varied natural drainage classes, plant species composition, and disturbance history (Kern 1994; Davis and others 2004; Trimble 2008). Separation of soil mapping units based on their capacity for burial and preservation of previously deposited SOC would be beneficial to model floodplain SOC storage, construct watershed-scale C budgets, and predict the location of biogeochemical “hot spots” within large riparian ecosystems (Stallard 1998; Groffman and others 2009). Currently, alluvial soil-landscapes are delineated similarly (i.e. all hydric mineral soils in CONG are mapped as Chastain, despite significant differences in morphology and SOC storage), but future incorporation of map phase criteria with spatial soil survey data could differentiate between units with high and low SOC storage (Ricker and others 2013).

Estimates of SOC storage in the upper 100 cm of organic soils in CONG were less than the average for conterminous USA peatlands (1500 Mg C ha^{-1}, Bridgham and others 2006). Total SOC storage to a depth of 200 cm in the Dorovan units was 1118 Mg C ha^{-1}, which was significantly greater than any of the mineral soils of CONG (Figure 2.4), but less than global estimates for Histosols (Batjes 1996; Bridgham and others 2006). Dorovan soils in CONG are located at the margins of an active floodplain within a humid subtropical climate (Figure 2.1), and were composed of highly decomposed organic matter (sapric material) mixed with thin alluvial mineral deposits. Therefore, SOC storage was highly variable in the Dorovan units, ranging from 380 to 687 Mg C ha^{-1} to 100 cm. The organic soils in CONG may be quite different from Histosols that form in cooler northern latitudes because most peatlands there contain organic inputs derived from bryophyte production (e.g., *Sphagnum* spp.), and form in closed depressions with little mineral input (Kuhry and Vitt 1996; Bridgham and others 2006). The Histosols of CONG are located within open ground water seep wetlands that are dominated by tree species (Table 2.1). As a result the peat deposits are composed almost entirely of highly decomposed (sapric) leaf and woody litter derived from overstory production. The depressional seep wetlands of CONG also receive some sediment influx from the Congaree River or adjacent upland slope erosion, as evident by thin stratified mineral layers preserved within the peat. Influx of mineral materials coupled with climatic conditions that favor rapid litter decomposition has likely limited the ability of these organic soils to store SOC relative to closed depressional systems located at more northern latitudes. Thus, a closer approximation to our mean SOC pool estimates was that reported for forested wetlands containing highly decomposed organic matter (Haplosaprists) in New England, USA (586 Mg C ha^{-1} to 100 cm depth, Davis and others 2004).

Total SOC Storage in Large Floodplains

Determination of the spatial extent of hydric soils on large floodplains is critical, because they store disproportionately high SOC relative to non-hydric alluvial soils. Similar results were reported for headwater (1st-2nd order stream) watersheds in the northeastern USA where the mean ratio of total watershed SOC storage to area (% watershed SOC / % watershed area) was 1.5 in alluvial wetlands (Ricker and others 2013). These data suggest that floodplain wetland landscapes are particularly important for SOC storage. Moreover, Dorovan units encompass small areas of southeastern USA floodplains and may be underrepresented in regional-scale soil survey data. For example, Dorovan units comprised 244 ha of the CONG floodplain and were found to store 16.6% of the total SOC within the Park boundaries, yet these units are not included in broader soil associations (STATSGO2 Chastain-Tawcaw units) of the same spatial area (Table 2.4).

Quantifying SOC pools from individual pedons that represent soil map units and multiplying these estimates by the spatial area of the units (measure-and-multiply) has been a common approach to scale-up SOC data (Post and others 1985; Eswaran 1993; Grossman and others 1998; Bridgham and others 2006). Although this method is widely used, it tends not to account for inherent spatial variability of soil-landscapes. Thus, recent modeling approaches that take into account both lateral and vertical variability in soil properties have been utilized to map SOC distributions in uplands (Mishra and others 2009). However, modeling approaches may not be as effective for large floodplain soils that are highly complex due to influences from both current sediment dynamics as well as past fluvial processes. Therefore, processes contributing to

SOC production, entrainment, and burial today may not reflect past conditions (Jacobson and Coleman 1986; Lockaby 2009; Hupp and others 2009). For these reasons, many contemporary watershed-scale factors (i.e., land use, slopes, soil erodibility) are poor predictors of total alluvial SOC pools because antecedent watershed conditions have in many cases drastically impacted the distribution of C within floodplains (Blazejewski and others 2009; Ricker and others 2012). Thus, more accurate approaches to floodplain SOC accounting must be used to develop models relating C dynamics to temporal trends in watershed-scale land use, climate, and geomorphic factors.

Extensive research in uplands has demonstrated significant losses of SOC stocks (20-50%) during conversion of forests to agricultural land use (Lal 2005). These estimates have been used to evaluate the impact of anthropogenic activities on the terrestrial SOC cycle. While a considerable amount of SOC is mineralized as a result of clearing of forested land, previous studies have also noted that some portion of SOC is likely eroded, transported, and retained in watershed sinks (Meybeck 1993; Stallard 1998; Lal 2003). Recent watershed-scale C budget analyses have shown that erosion associated with anthropogenic activities can result in net losses or in some cases gains of SOC within the watershed (Izaurralde and others 2007). Therefore, to properly assess net terrestrial SOC fluxes, both erosion and depositional processes must be accounted for. Our data suggest that typical soil sampling depths from 0 to 100 cm may not be adequate to construct complete watershed SOC budgets (encompassing the start of land use until present), because significant quantities of post-disturbance C are stored in deposits that are >100 cm in depth. On average, >27% SOC was stored from 100-200 cm in non-hydric alluvial landscapes and approximately 50% or greater total SOC was stored from 100-200 cm in hydric floodplain soils.

Although we did not obtain radiometric dates for alluvial deposits, distinctive morphological features indicative of legacy sediment boundaries, such as buried wetlands (Walter and Merritts 2008) and abrupt textural or color changes (Jacobson and Coleman 1986; Trimble 2008) were not observed in the mineral soils of CONG (Figure 2.3). Given trends of legacy sediment deposition within the region (Trimble 2008) it would not be surprising if the entire mineral SOC pool to 200 cm in CONG represented only alluvium deposited over the past 400 years. Thus, future efforts need to be undertaken to link total upland SOC losses with complete depositional gains (modern to pre-historic alluvial deposits of varying depths) to evaluate anthropogenic impacts on modern SOC dynamics at watershed-scales.

Although our data indicate that the alluvial landscapes of CONG store significant quantities of SOC, changes to these buried pools are possible due to predicted climate change in the region. Several global climate models suggest that the southeastern USA will not only become warmer, but also drier as a result of decreased annual precipitation and increased evapotranspiration rates through the next century (McNulty and others 2013). These changes, coupled with increased urbanization of the landscape could result in water supply stress and further water utilization for municipal purposes. Most rivers have dam controlled flows, both world-wide and regionally, which has decreased frequency and duration of floodplain inundation since the early 20th century (Tockner and Stanford 2002; Hupp and others 2009). Loss of hydrologic connectivity between large river systems and their floodplains, as a result of further river flow regulation, could result in net mineralization of stored alluvial SOC. These changes would be especially evident in hydric soil landscapes, which are currently inundated with floodwaters and undergo anaerobic soil conditions for multiple months of the year (Doyle 2009). Fluxes of both mineral sediment and allochthonous C associated with flooding may also decrease if hydrologic connectivity is not maintained, altering total SOC sequestration within large floodplain forests. Although the impacts that future climate and land use changes may have on large riparian forests are uncertain, our research indicates that these ecosystems store up to 0.1 Pg of SOC and future alterations to floodplain hydrologic connectivity may have profound effects on the ability of these landscapes to continue to sequester and store C.

Conclusions

Results from this study indicate that alluvial hydric soils contain significantly greater amounts of SOC to depths of 100 and 200 cm compared to non-hydric floodplain landscapes. C depth distributions suggest that deep (>100 cm) SOC storage is particularly important in hydric floodplain soils, with no significant difference in the amount of SOC stored from 0-100 and 100-200 cm. These trends reflect episodic burial and preservation of former floodplain surfaces in mineral wetlands versus progressive thickening of peat deposits in organic soils. Spatial analysis of SOC storage within CONG and the greater regional Coastal Plain indicate that approximately 0.1 Pg of SOC is stored in large floodplains of the southeastern USA This estimate is significant considering the spatial extent of major floodplains used for the regional SOC analysis represents <0.06% of the total contiguous USA land area. These data suggest that large floodplains may serve as watershed sinks for terrestrial C derived from anthropogenic land disturbance and atmospheric sources. In addition, the largest quantities of alluvial SOC were stored in hydric relative to non-hydric soil landscapes, but coarse-scale soil associations tended to omit small spatial components, such as organic Histosols. These analyses suggest that determination of the spatial extent of floodplain wetlands is critical for obtaining accurate estimates of SOC stocks and regional estimates may underestimate the true extent of SOC storage in alluvial settings if deep (>100 cm) or Histosol SOC pools are not properly accounted for.

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Table 2.1. Summary of soil mapping unit characteristics used to define the sampling units within Congaree National Park.

Soil Series†	Soil Order†	Drainage Class	Flooding Frequency‡	Fluvial Landforms	Dominant Tree Species
Congaree	Entisols	Well/Moderately Well	Occasional	Natural Levees, Ridges	*Celtis laevigata*, *Liquidambar styraciflua*, *Quercus* spp.
Tawcaw	Inceptisols	Somewhat Poorly	Occasional	Flats, Ridges	*Quercus* spp., *L. styraciflua*, *C. laevigata*
Chastain	Inceptisols	Poorly	Frequent	Sloughs, Meander Scars, Backswamps, Oxbows	*Taxodium distichum*, *Nyssa aquatica*
Dorovan	Histosols	Very Poorly	Frequent	Depressional Groundwater Seep Wetlands	*Nyssa biflora*, *Ilex opaca*

† Soil mapping series and Order based on soil survey data and U.S. Soil Taxonomy (Soil Survey Staff 2013).

‡ Flooding frequency for soil map units as defined by (Soil Survey Staff 2013): occasional, 5 to 50% chance; frequent, >50% chance of flooding on an annual basis.

Table 2.2. Spearman correlation coefficients (r_s) for the Congaree mineral soils dataset ($N = 315$, $\alpha = 0.05$). Statistically significant correlations are indicated in bold.

	Sample Depth (cm)	Distance to River (m)	Clay Content (%)	Bulk Density (Mg m^{-3})	Soil Carbon (Mg ha^{-1})	Soil Nitrogen (Mg ha^{-1})
Sample Depth	-					
Distance to River	0.00	-				
Clay Content	**0.22*** **	**0.31*** **	-			
Bulk Density	**0.41*** **	-0.09	**-0.13* **	-		
Soil Carbon	**-0.42*** **	0.01	-0.02	**-0.58*** **	-	
Soil Nitrogen	**-0.30*** **	**0.38*** **	0.09	**-0.45*** **	**0.68*** **	-

$* p < 0.05$, $** p < 0.01$, $*** p < 0.001$

Table 2.3. Estimated soil organic carbon (SOC) storage within the Congaree National Park floodplain forests using the Soil Survey Geographic (SSURGO, 1:20,000 map scale) database. Means ± standard error.

Congaree National Park		Mg C ha^{-1}			Total SOC Pool (Mg C)‡			
SSURGO Soil Mapping Unit(s)	Drainage Class†	Mean SOC Pool (0-100 cm)	Mean SOC Pool (100-200 cm)	Area (ha)	0-100 (cm)	100-200 (cm)	0-200 (cm)	% Total SOC
Congaree	WD/MWD	109 ± 4.2	68 ± 12	2031	2.21×10^5	1.38×10^5	3.59×10^5	21.8
Tawcaw	SPD	108 ± 6.9	40 ± 10	4420	4.77×10^5	1.77×10^5	6.54×10^5	39.8
Chastain	PD	193 ± 27	160 ± 60	1013	1.96×10^5	1.62×10^5	3.58×10^5	21.8
Dorovan	VPD	533 ± 25	585 ± 83	244	1.30×10^5	1.43×10^5	2.73×10^5	16.6
Total				7708	1.02×10^6	6.20×10^5	1.64×10^6	100

† WD = well drained, MWD = moderately well drained, SPD = somewhat poorly drained, PD = poorly drained, VPD = very poorly drained

‡ Rounded to 3 significant figures

Table 2.4. Estimated soil organic carbon (SOC) storage within the Congaree National Park floodplain forests and the Atlantic Coastal Plain using U.S. General Soil Map (STATSGO2, 1:250,000 map scale) data. Means ± 1 standard error.

		Mg C ha^{-1}			Total SOC (Mg C)‡		
STATSGO2 Soil Mapping Unit(s)†	Drainage Classes†	Mean SOC Pool (0-100 cm)	Mean SOC Pool (100-200 cm)	Area (ha)	0-100 (cm)	100-200 (cm)	0-200 (cm)
Congaree National Park							
Chastain-Tawcaw	PD-SPD	137 ± 11	90 ± 23	7708	1.06×10^6	6.94×10^5	1.75×10^6
Southeastern USA Coastal Plain							
Chastain-Tawcaw	PD-SPD	137 ± 11	90 ± 23	213786	2.93×10^7	1.92×10^7	4.85×10^7
		Similarly Mapped Alluvial Soils§					
Riverview-Chewacla-Chastain	WD-SPD-PD	122 ± 8	82 ± 19	218884	2.67×10^7	1.79×10^7	4.46×10^7
Toccoa-Congaree-Chewacla	WD-MWD-SPD	109 ± 6	54 ± 11	29326	3.20×10^6	1.58×10^6	4.78×10^6
Total				461996	6.36×10^7	4.12×10^7	9.79×10^7

† WD = well drained, MWD = moderately well drained, SPD = somewhat poorly drained, PD = poorly drained

‡ Rounded to 3 significant digits

§ Spatially averaged SOC pools based on natural drainage class

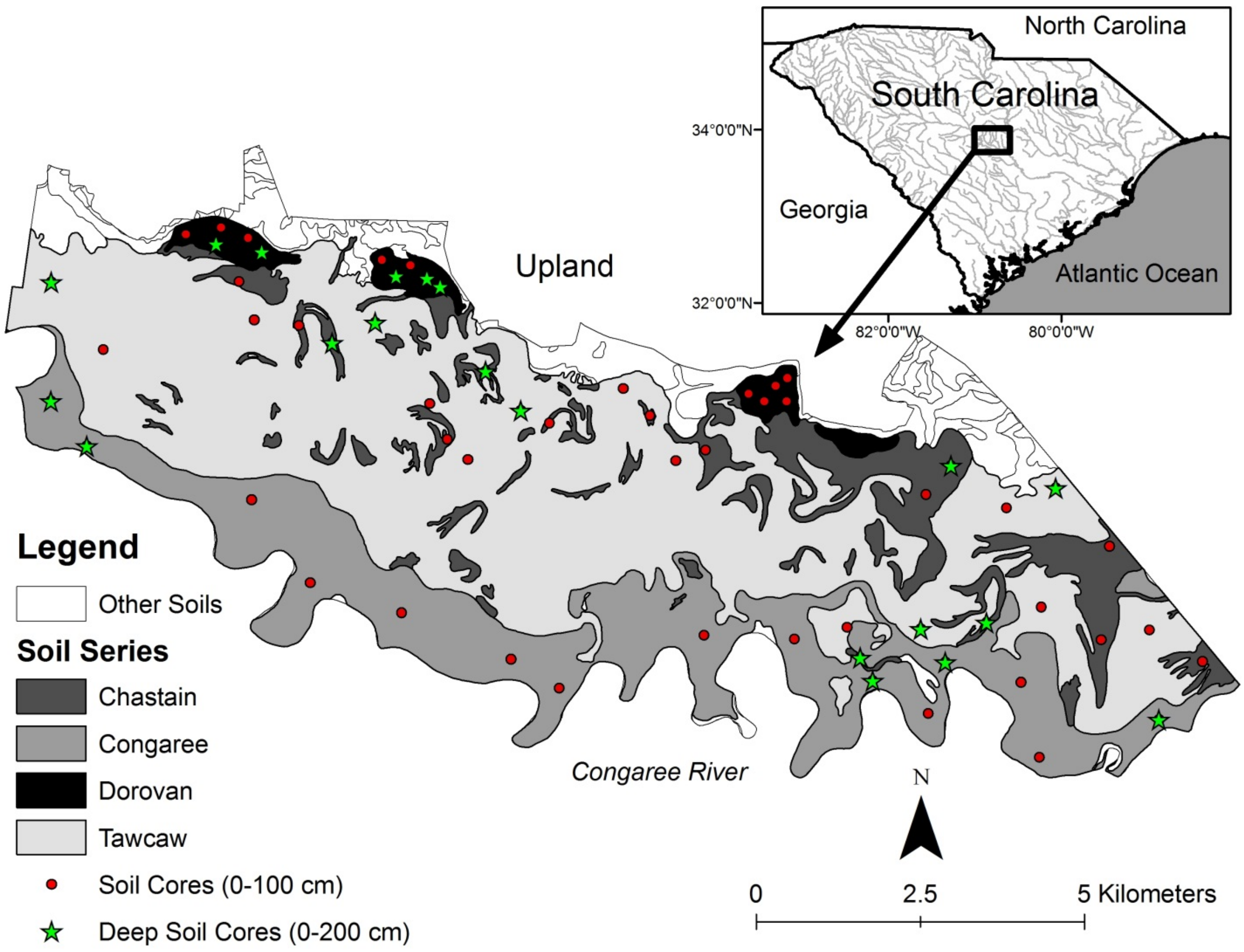

Figure 2.1. General location map of Congaree National Park, South Carolina. Soil coring locations from 0-100 cm and from 0-200 cm are indicated by circle and star symbols, respectively. A total of 15 cores were taken from each of the four major soil mapping units (Congaree, Tawcaw, Chastain, Dorovan series) within the Park.

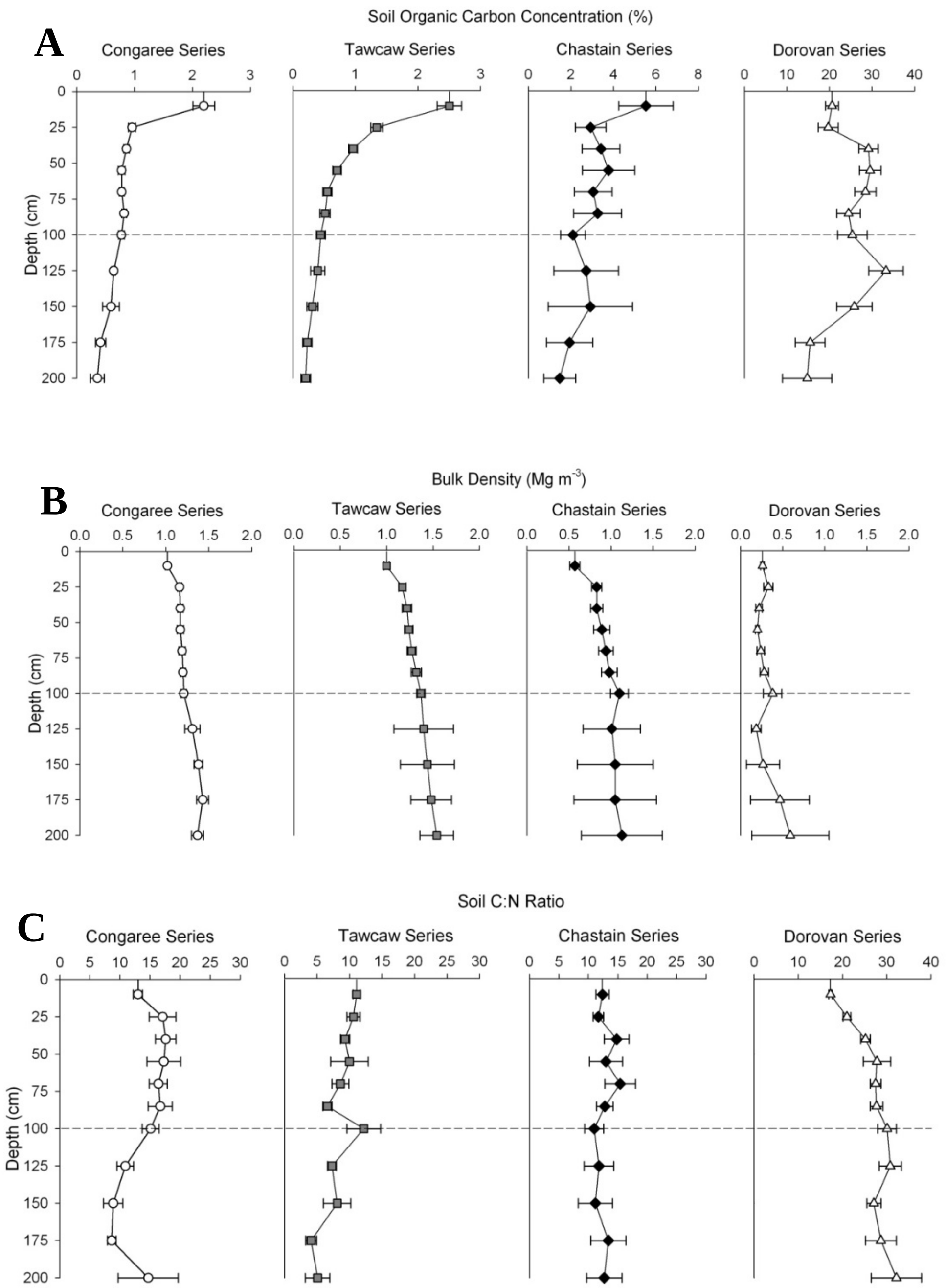

Figure 2.2. Mean depth profiles for A: soil organic carbon concentration (note different x-axis scales for Chastain and Dorovan series), B: bulk density and, C: soil C:N ratios (note the different x-axis scale for Dorovan series). Means by depth ± 1 SE, n = 15 for 0-100 cm samples, n = 5 for >100-200 cm samples. Soil mapping units represent a drainage sequence from well

drained (Congaree series) to poorly drained mineral soils (Chastain series) and very poorly drained organic soils (Dorovan series).

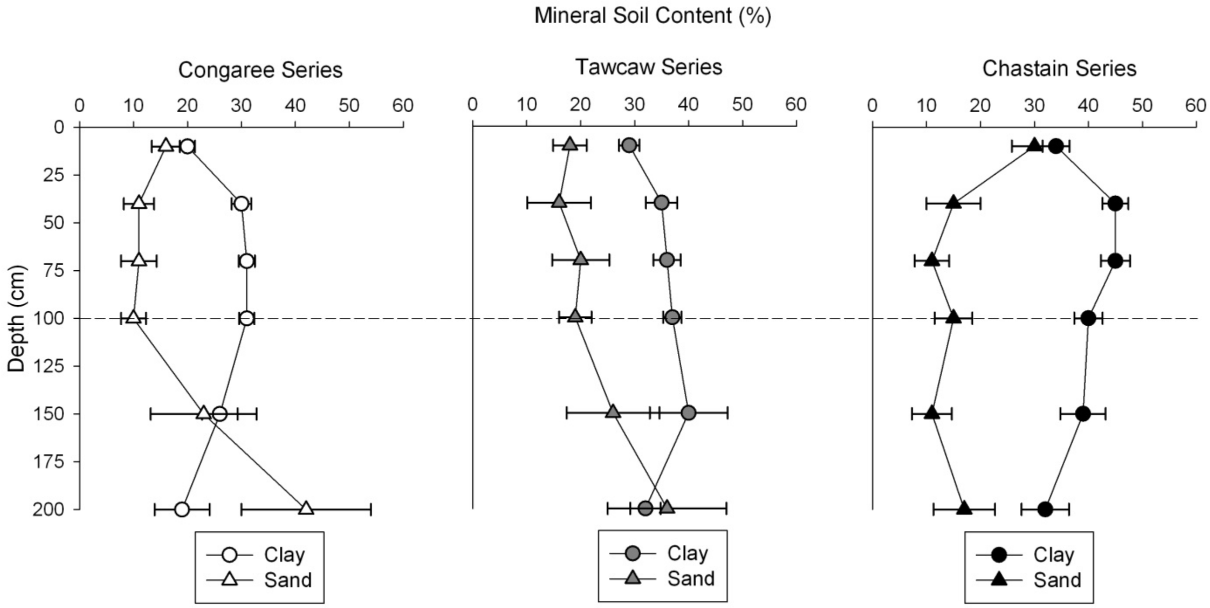

Figure 2.3. Mean sand and clay content with depth for the alluvial mineral soils of the Congaree floodplain. Means ± 1 SE, n = 15 for 0-100 cm samples, n = 5 for >100-200 cm samples.

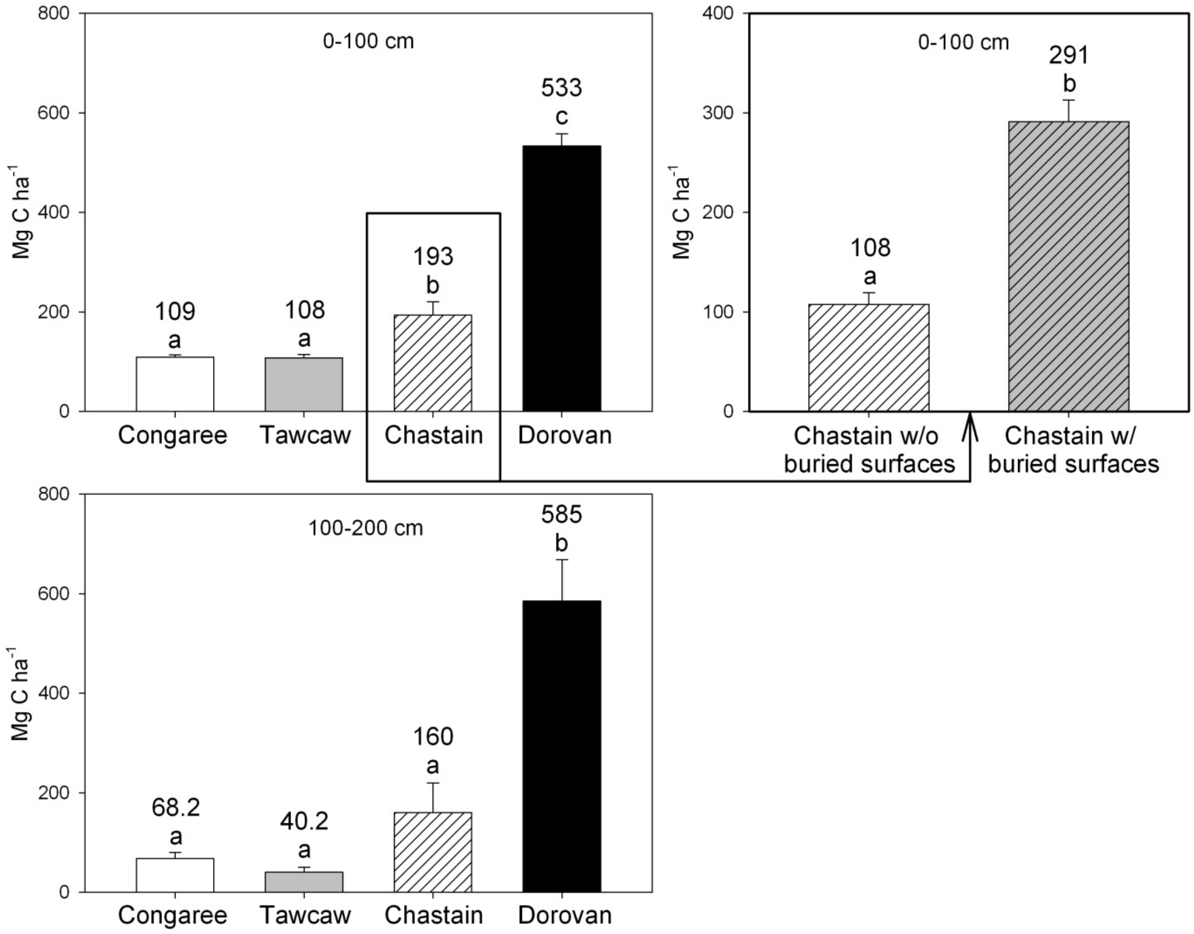

Figure 2.4. Mean soil organic carbon (SOC) pools for 0-100 cm (n = 15 per series) and 100-200 cm (n = 5 per series) depths. Means with different letters are significantly different according to one-way ANOVA (α = 0.05) and Tukey's HSD tests. Chastain mineral wetland soils separated by soil morphology (without buried surfaces (n = 8) vs. contained buried surfaces (n = 7)) were significantly different according to Student's t-tests (α = 0.05).

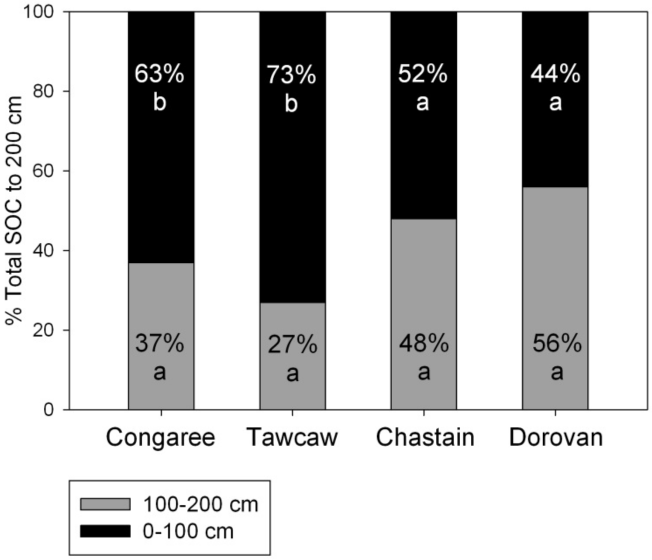

Figure 2.5. Distribution of total soil organic carbon (SOC) to 200 cm stored in the upper 100 cm vs. 100-200 cm depths. Mean percentages with different letters are significantly different according to Student’s t-tests (n = 10, α = 0.05).

Chapter 3:

Soil biogeochemical processes across a lateral toposequence in an old-growth floodplain forest

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Title: Soil biogeochemical processes across a lateral toposequence in an old-growth floodplain forest

Abstract

Floodplain forests are important landscapes that retain and transform nutrients derived from watershed sources. Although significant research has been conducted regarding biogeochemical processes in floodplains, very few studies have been conducted in old-growth bottomland forests. Therefore, the goal of this study was to quantify how landscape variability and environmental factors influence floodplain biogeochemistry in old-growth ecosystems. The study was conducted in a unique old-growth bottomland forest at Congaree National Park (CONG), South Carolina. Over a 2-yr period we measured a suite of biogeochemical indices along an alluvial soil toposequence that included seasonal variation in microbial biomass, net N mineralization, and soil P saturation. Soil microbial biomass was relatively consistent throughout the study and displayed few relationships to environmental variables. Net N mineralization showed distinct seasonal variations, with greatest mineralization occurring in summer months. NO_3-N was the predominant product of net N mineralization in all seasons, which may have been a result of regional drought producing aerobic soil conditions at all study sites. Only the hydric soils in low-lying topographic positions had appreciable NH_4-N production, which generally occurred after spring flood pulsing. Soils were not saturated with P across the study toposequence, due to abundant poorly crystalline Fe and Al, indicating that the soils are viable sites for P sorption. These results suggest that the intrinsic biogeochemical processes within the old-growth bottomland forests at CONG differ from those of aggrading stands of the southeastern United States, especially with regard to N cycling and production of excess NO_3-N.

List of abbreviations: CONG, Congaree National Park; MBC, microbial biomass carbon; MBN microbial biomass nitrogen; PD, poorly drained; PDSI, Palmer drought severity index; SHWT, seasonal high water table; WD, well drained; WFPS, water filled pore space

Introduction

Floodplain forests provide numerous environmental functions including sediment retention (Craft and Casey, 2000; Lockaby et al., 2005; Trimble, 2008) and acting as sites for nutrient (specifically C, N, and P) storage and transformations (Pinay et al., 1995; Noe et al., 2013). Floodplains can store large amounts of organic nutrients in aboveground vegetation, roots, forest floor litter, and soil horizons (Pinay et al., 1992; Schilling et al., 1999; Craft and Casey, 2000; Jolley et al., 2009). Microbial biomass C and N are also important components of total ecosystem nutrient stocks because these pools immobilize inorganic nutrients and are indicators of additional processes such as nutrient mineralization rates (Groffman et al., 1996; Jolley et al., 2010). Inorganic forms of N are typically limiting nutrients for terrestrial plant growth (Vitousek et al., 1982), thus N mineralization rates can be an indicator of relative soil fertility among floodplains. P is also an important nutrient that can be stored and cycled within riparian forests (Noe et al., 2013). Fine-grained soils containing poorly crystalline Fe and Al have a high potential for P sorption (Maguire and Sims, 2002; Nair et al., 2004), which can be an important water quality improvement function in floodplains (Darke and Walbridge, 2000; D’Angelo, 2005). Nutrient dynamics within large floodplains are complex and depend on specific landscape characteristics such as hydroperiod, soil redox conditions, temperature, sedimentation rates, vegetation type, forest age, and intrinsic soil properties (Groffman et al., 1992; Pinay et al., 1995; Schilling and Lockaby, 2005; Jolley et al., 2010; Shrestha et al., 2012).

Thus, alluvial landscapes will store and cycle nutrients in various ways depending on site-specific conditions. Although numerous studies have documented biogeochemical processes in forested floodplains, much of our current understanding is derived from research in anthropogenically altered riparian systems consisting of young secondary-growth forests.

In the United States >50% of total wetlands have been lost since European settlement, which includes extensive tracts of bottomland forest (Dahl, 1990). The remaining wetlands that have not been filled or drained have typically been logged in the past (Lockaby, 2009). As a result of wetland losses, very few studies have been conducted in true old-growth floodplain forests. Nutrient cycles in old-growth ecosystems can be fundamentally different than aggrading stands because they tend to have greater aboveground biomass, yet less annual net primary productivity and nutrient demands (Vitousek and Reiners, 1975; Harmon et al., 1986). Old-growth forests that receive nutrient additions from external sources (atmospheric or alluvial deposition) are relatively “leaky” in terms of nutrient retention, because biological demands are less than annual inputs leading to saturation or net export of mineral nutrients (Aber et al., 1991; Hedin et al., 1995). Thus, generalizations about floodplain biogeochemical cycles derived from young secondary-growth forests may not accurately reflect the processes occurring in old-growth ecosystems.

In addition, many changes to the intrinsic properties of regional watersheds are expected in the future as global climate change and urbanization occur. In the southern USA, climate models predict warmer ambient air temperatures, slightly decreased annual precipitation, and greater water supply stress associated with increasing populations (McNulty et al., 2013; Lockaby et al., 2013). Riparian forests tend to be resilient to environmental stressors associated with periodic annual flooding and it is therefore possible that these landscapes are better suited to adapt to climate change than contiguous uplands (Capon et al., 2013). However, the specialized adaptations of many floodplain species are suited to annual flooding and anaerobic soil conditions, but not to prolonged periods of drought or water stress (McKevlin et al., 1998). Many rivers in the southern USA are dam controlled, and as a result, the magnitude, frequency, and duration of flood events have decreased across the region since the early to mid 20th century (Doyle, 2009; Hupp et al., 2009). Climate change and increased municipal water demand associated with urbanization are likely to result in further decreased river flows, which may have drastic impacts on riverine forests due to stresses associated with progressive drying of these ecosystems. Therefore, information regarding current biogeochemical indices within mature and old-growth floodplain forests will allow for better management of these unique ecosystems into the future.

As mentioned previously, very few old-growth bottomland forests remain in the USA and an assessment of biogeochemical processes in these ecosystems would be beneficial to understand how floodplain nutrient retention and cycling vary across a range of successional ages. Thus, our study was completed within one of the largest remaining old-growth bottomland hardwood forest tracts in the southern USA, located within Congaree National Park (CONG) in central South Carolina. CONG is a large floodplain that contains many heterogeneous fluvial landscapes and therefore we chose to study nutrient dynamics along a lateral toposequence that includes well to poorly drained mineral soils and associated forest communities. The goal of our study was to quantify a number of biogeochemical indices to understand how environmental variables, such as landscape variability, impact nutrient cycling in old-growth floodplain forests. The specific objectives of this study were to: (i) quantify seasonal variations in microbial biomass (C and N) and net N mineralization, (ii) assess the degree of soil P saturation within

CONG, and (iii) compare our results with past studies to understand how biogeochemical processes may differ between old-growth and aggrading floodplain forests.

Study Site

CONG is located along the Congaree River in central South Carolina, approximately 30 km downstream from the state capital city of Columbia. CONG is within the Upper Atlantic Coastal Plain and contains approximately 11,000 ha of bottomland hardwood forest. The Congaree River is a large eutrophic (i.e., red water) waterway that drains a large portion (>21,000 km^2) of the Piedmont physiographic province of northern South Carolina. The region has a humid subtropical climate that receives approximately 1220 mm of annual precipitation and has an average annual air temperature of 17.6 °C. River flows are regulated by a series of large dams, the closest being Saluda Dam that forms Lake Murray located approximately 78 km upstream of CONG. Dam flow regulation in the Congaree River watershed has resulted in reduced frequency and duration of large flood events in the Park since the 1930s (Doyle, 2009).

Our study was conducted in an old-growth bottomland forest tract near Butterfly Pond (33° 46’ 19.33” N, 80° 43’ 36.55” W). Five transects were established perpendicular to the active Congaree River channel to assess biogeochemical indices along an alluvial soil toposequence (Figure 3.1). Four permanent circular research plots were established along each study transect (20 total plots, 5 m radius, 78.5 m^2) during the summer of 2010. Plots were selected based on relative elevation as well as soil and vegetation characteristics. The transects covered four general fluvial landscapes including the natural river levee, hardwood flat, transitional swamp, and backswamp plots. The study site contained a range of soil types from well drained (WD) mineral soils of the natural river levee (south end of the transects) to the poorly drained (PD) mineral wetland soils within a backswamp slough (north end of the transects). Soils in this section of the floodplain are mapped as Congaree (Fine-loamy, mixed, active, nonacid, thermic Oxyaquic Udifluvents) and Chastain (Fine, mixed, semiactive, acid, thermic Fluvaquentic Endoaquepts) (Soil Survey Staff, 2013). Dominant overstory tree species were mixed hardwoods such as sweetgum (*Liquidambar styraciflua* L.), sugarberry (*Celtis laevigata* Willd.), sycamore (*Platanus occidentalis* L.), and bottomland oaks (*Quercus* spp.) on the river levee and flats (plots 1-10) and baldcypress (*Taxodium distichum* (L.) Rich.) in the transitional and backswamp landscapes (11-20).

Materials and Methods

Soil Characterization

Plot soil morphologies were described to a depth of 100 cm using standard methods (Schoeneberger et al., 2002). Multiple soil cores (n = 4 per plot, 0-10 cm) were collected from each study plot for further laboratory analyses. Samples of known volume were oven dried at 105 °C to calculate soil bulk density using the core method (Soil Survey Laboratory Staff, 2004). Soil pH was quantified from air dried subsamples using an 1:1 soil-deionized water slurry (Soil Survey Laboratory Staff, 2004). Concentrations of major extractable elements (P, K, Fe, Ca, Mg, Mn, Na, Zn) were determined using inductively coupled plasma atomic emission spectroscopy (ICP-AES) after double-acid extraction (Mehlich-1; Mehlich, 1953). Mehlich-1 extractable elements were used to estimate cation exchange capacity (CEC_{sum}) by summing the milliequivalents of bases (Ca, Mg, K, and Na) and exchangeable hydrogen as determined by direct titration with 0.023M $Ca(OH)_2$. The percent base saturation was calculated as the ratio of extractable bases to that of CEC_{sum}. Total soil C and N content was quantified using thermal combustion on a Perkin Elmer 2400 Series II CHNS/O analyzer (Perkin Elmer, Waltham, MA).

Soil particle size distribution (texture) was quantified using the hydrometer method (Gee and Bauder, 1986).

Net Nitrogen Mineralization and Microbial Biomass

Net N mineralization was estimated using the *in situ* buried-bag method (Hart et al., 1994). N mineralization samples were collected seasonally at 3 month intervals (January, April, July, October) from autumn 2010 until winter 2013. Two soil cores were extracted to a depth of approximately 10 cm within each study plot (total 40 samples per collection). Soil materials from each core were homogenized in the field and packed into two 532-ml polyethylene (0.064 mm thickness) whirl-pak bags (Nasco, Fort Atkinson, WI). Polyethylene sample bags were used because they allow for gas diffusion, but prevent liquids from entering the sample during the incubation period (Gordon et al., 1987; Hart et al., 1994). One bag was buried to a depth of 10 cm and incubated for approximately 28 d, the other pre-incubation sample was returned to the laboratory. Wire exclosures (1 m^2) were also installed around sample locations to protect the polyethylene bags from damage by feral hogs (*Sus scrofa*) and pin flags were placed in sample locations to prevent resampling of soils during the study.

Field samples were placed on ice during transport to the laboratory and stored at 4 °C until processed. Samples were homogenized in the laboratory and passed through a 2-mm (number 10) sieve to remove coarse fragments. Soil processing for net N mineralization consisted of extracting a 10-g subsample in 100 mL of 2M KCl. The soil–KCl suspension was shaken for 1 hour, gravity filtered (Whatman #42 filters), and frozen. Soil extracts were analyzed for NH_4–N and NO_3–N concentration using microscale batch methods (modified indophenol blue technique) outlined by Sims et al. (1995) on a Bio-Rad Model 450 microplate reader (Bio-Rad Laboratories, Hercules, CA). Rates of net N mineralization were estimated as the difference in total N (sum of NH_4–N and NO_3–N) between pre- and post-incubation samples and dividing by the duration of the incubation. Values were converted to a per-hectare basis using soil bulk density values for each study plot. Percent nitrification and ammonification were calculated as the total NO_3-N and NH_4-N production divided by net N mineralization, respectively.

Microbial biomass was quantified using the chloroform-fumigation extraction technique (Vance et al., 1987; Horwath and Paul, 1994). Soil subsamples were taken from the pre-incubated samples collected for N mineralization (upper 10 cm of soil). For fumigated samples, 18.5 g of moist soil was exposed to alcohol-free $CHCl_3$ in vacuum desiccators for 24 hours and then extracted with 125 mL of 0.5M K_2SO_4. The soil–K_2SO_4 suspension was shaken for 30 minutes, vacuum filtered through Whatman #5 filters, and frozen prior to further analyses. Unfumigated samples were extracted in the same manner. Samples were thawed and analyzed for total organic C and N using a Shimadzu TOC-V and total N combustion analyzer (Shimadzu Scientific Instruments, Columbia, MD). The difference in extracted organic C and N between fumigated and unfumigated samples was used to calculate microbial C and N.

Hydrologic and Climatic Data Collection

River stage data were collected from a United States Geological Survey station (USGS 02169625: Congaree River near Gadsden, South Carolina) located approximately 14 km upstream from the Butterfly Pond study transects. Soil surface heights were measured at each study plot by United States Geological Survey personnel using a TopCon GTS-240NW total station (Topcon Positioning Systems Inc., Livermore, CA, USA) **wi**th ± 2 mm vertical accuracy (Edward Schenk, personal communications). River stage heights were compared with average floodplain surface heights at the study transects to estimate periods of flooding. These estimates were confirmed via field observations of inundation within the study site at various river stages.

Monthly climate data including precipitation (mm), mean daily air temperature (°C), and Palmer drought severity index (PDSI) values were collected from the nearest continuous monitoring station located approximately 32 km northeast of the study plots at the Columbia Metropolitan Airport, South Carolina (National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, NC, USA).

Water filled pore space (WFPS) has also been linked to nitrification rates in floodplain soils (Noe et al., 2013) and thus was used for comparison with nitrate production. WFPS was calculated following the equation outlined by Linn and Doran (1984):

$$\%\ WFPS = (\theta_v/TP) \times (100)$$

where θ_v = percent volumetric water content = (calculated as % θ_m × BD), where BD = soil bulk density ($g\ cm^{-3}$), and θ_m = gravimetric water content ($g\ g^{-1}$), and TP = percent total soil porosity (calculated as (1 - BD/PD) × 100), where PD = average soil particle density assumed to be 2.65 $g\ cm^{-3}$.

Phosphorus Saturation

Soil P saturation was estimated using composite soil samples (three 10 cm cores) collected from each study plot during summer 2011. Samples were air dried, homogenized, and passed through a 2 mm sieve (number 10) to remove coarse fragments. Oxalate extractable P was determined from composite samples using standard acid ammonium oxalate methods (Soil Survey Investigation Staff, 2004). Duplicate subsamples (0.5 g) were treated with 0.2M ammonium oxalate solution buffered at pH 3.0 and extracted with a mechanical vacuum extractor in the dark. Elemental concentrations (specifically Fe, Al, P) were measured by ICP-AES. Water soluble P was quantified using a 1:20 soil to deionized H_2O slurry that was mechanically shaken for 1 hour, centrifuged for 5 min at 500 RPM, and gravity filtered through

Whatman #40 filters. Soil extracts were immediately analyzed for P content using the molybdenum blue method of phosphate determination on a spectrophotometer at 700 nm (Murphy and Riley, 1962).

Ammonium oxalate degree of P saturation (DPS_{ox}) was calculated as:

$$DPS_{ox} = [(Ox\text{-}P)/\alpha(Ox\text{-}Fe + Ox\text{-}Al)] \times 100$$

Where Ox-P, Ox-Fe, and Ox-Al are oxalate extractable P, Fe, and Al in mmol kg^{-1} and α is an empirical factor that compares soil P saturation, set to 0.50 for this study (Maguire and Sims, 2002; Nair et al., 2004).

Auxiliary Forest Cover and Potential Nitrification Experiments

Nitrification rates are typically low or absent in acid soils (De Boer and Kowalchuk, 2001), such as those located in the humid southeastern USA. However, during the first year of *in situ* incubations at CONG, nitrate was the major product of net N mineralization. Given the unusual nature of these initial findings, two possible factors were identified and tested: i) forest cover within the study plots was unique for the region, consisting of old-growth hardwood forest that may have limited plant N uptake leading to increased nitrification, and ii) prolonged drought conditions within the region (Figure 3.2) may have limited microbial N immobilization and allowed for aerobic soil conditions necessary for nitrification across the study toposequence, which in turn increased soil nitrate production.

Field experiments to test the effects of forest cover were carried out in October, 2011. In contrast to the old-growth hardwood forest at the Butterfly Pond transects, additional *in situ* buried bag incubations were completed under young secondary growth hardwood and conifer forest cover. Three additional sites located approximately 5 km downstream from the primary study transects were used to assess forest cover effects on soil nitrate production (Figure 3.1, inset map). The study sites were situated along the Congaree River channel and contained a similar alluvial soil toposequence (natural river levee transitioning to backswamp wetlands) to the Butterfly Pond study site. Two plots were located in a tract of land that had been clear cut in the 1980s and contained secondary growth forest (clear cut levee site mapped as Congaree series, clear cut swamp site mapped as Chastain series). A third plot was located on the river levee and contained row-planted loblolly pine (*Pinus taeda* L.). Five nested *in situ* N mineralization samples were taken from each of the three plots (total n = 15) to compare total N mineralization and NO_3-N production among the old-growth study plots and those of varying forest cover. Field and laboratory methods were carried out in a similar manner to those previously described for *in situ* net N mineralization (Hart et al., 1994).

Laboratory incubations were used to evaluate the impacts of regional drought on soil nitrification rates. Potential net N mineralization and nitrification were assessed at constant temperature and soil moisture content using similar methods to those described by Vitousek et al. (1982). Duplicate soil samples were collected from the primary study plots in October, 2012 (n = 40) and returned to the laboratory for analysis. Prior to incubation, samples were passed through a 2 mm mesh sieve to remove coarse fragments and roots. One subsample was used to quantify initial extractable NO_3-N and NH_4-N content using 2M KCl as described previously for field incubation samples (Hart et al., 1994). Approximately 50-g of field-moist soil was placed in 250 ml glass Erlenmeyer flasks for a 28-d laboratory incubation. Mass soil water content was calculated prior to incubation and average organic matter content and particle size distribution were used to calculate water holding capacity for each sample (Saxton and Rawls, 2006). Ambient soil moisture was adjusted to 80% water holding capacity using deionized water and incubation flasks were sealed with perforated parafilm to prevent significant evaporation, yet allow for oxygen diffusion. Samples were incubated for 28 d in the dark at a constant temperature of 23.9 °C. In order to ensure aerobic conditions throughout the incubation the flasks were unsealed at 7 d intervals and flushed with laboratory air for approximately 5 min. After the incubation period, NO_3-N and NH_4-N content was quantified and net N mineralization was calculated in a similar manner to *in situ* samples described above (Hart et al., 1994).

Statistical Analysis

Statistical analyses were performed in SAS 9.2 (SAS Institute, Cary, NC). Mean comparisons between two groups were completed using Student's t-tests ($\alpha = 0.05$), such as net nitrate vs. ammonium production. One-way analysis of variance (ANOVA) with Tukey's honest significant difference tests (PROC GLM, $\alpha = 0.05$) were used for mean comparisons among three or more groups, such as soil characteristics and biogeochemical indices (net N mineralization, MBC, MBN) among the four transect landscapes (levee, flat, transitional, backswamp). Linear regression analysis (PROC REG, $\alpha = 0.05$) was used to evaluate the relationship between water soluble P content and degree of soil P saturation within CONG. Associations between biogeochemical indices (MBC, MBC, net N mineralization, nitrite and ammonium production) and specific environmental attributes such as PDSI, precipitation, air temperature, river stage, and WFPS were assessed by fluvial landscape using Spearman's rank order correlations (PROC CORR, $\alpha = 0.01$).

Results

Toposequence and Climate Characteristics

There was a significant gradient in both relative elevation and soil characteristics along the study toposequence (Table 3.1). Mean relative elevation change was significant ($p < 0.05$) across the study site and ranged from -0.07 m at the natural levee to -1.62 m in the backswamp.

Mean depth to the seasonal high water table also decreased significantly from 0.85 m on the levee to 0.13 m in the backswamp. Soil C:N ratios, organic matter, and sand content were statistically similar for all landscapes; however clay content (0-10 cm) did increase significantly from 26% on the levee to 45% in the backswamp. Mean soil pH, CEC_{sum}, and base saturation also decreased significantly from the levee and flat to the transitional and backswamp landforms (Table 3.1).

Climatic conditions reflected regional drought from 2010-2012 (Fig. 3.2). Mean air temperatures were generally above average, especially from the summer of 2011 until the winter of 2013. Only during winter 2011 were temperatures well below the 30-yr average for the region. Monthly precipitation data were below average, especially from October, 2010 until April, 2012. Above average temperatures and lack of precipitation resulted in moderate to severe drought conditions throughout the central South Carolina region (Fig. 3.2). Above average precipitation from May-August 2012 ended the drought conditions.

Drought conditions during the study period also resulted in lower than average flows in the Congaree River (Fig. 3.3). Low flow river conditions (<1.0 m stage height) were common and there were also few flood events from 2010-2012. Over the course of the study, the lowest elevation backswamp plots (16-20) were only flooded 4 times (April 2011, May 2012, December 2012, January 2013) to depths < 2.0 m and for short durations (< 7 d). Only one flood event in January 2013 was large enough to top the natural levee and completely inundated the transitional and backswamp plots (11-20) and covered most of the levee and hardwood flat plots (1-10) in intermittent northward flow paths <15 cm in depth (Fig. 3.1).

Microbial Biomass

Soil MBC was statistically similar across the toposequence during most seasonal collections (Fig. 3.4). Statistically significant separation only occurred among the landscapes in spring 2011, summer 2012, and winter 2013. Mean MBC values typically ranged from 416 ± 44 to 1013 ± 270 μg g^{-1} dry soil except during fall 2012 when values ranged from 1413 ± 164 to 2116 ± 329 μg g^{-1} dry soil. MBN was more variable and had multiple significant differences by landscape units (Fig. 3.5). In general, the drier levee and flat landscapes had significantly more MBN content when compared to the seasonally flooded transitional and backswamp positions. Mean MBN values ranged from 67 ± 8 to 212 ± 41 μg g^{-1} dry soil during all seasons and there was a pronounced increase in MBN during the fall 2012 collection, similar to MBC.

MBC and MBN content had a highly significant positive correlation ($p < 0.0001$) at all landscape positions along the study toposequence (Table 3.2). In addition, a number of environmental variables were also correlated with MBC and MBN. MBC had a significant positive correlation with PDSI on the levee ($r_s = 0.24$, $p = 0.02$) and transitional ($r_s = 0.23$, $p = 0.02$) landscapes. Total precipitation showed a significant ($p < 0.05$) positive correlation with MBC in the wetter transitional and backswamp landscapes and MBN was significantly correlated to precipitation in the levee ($r_s = 0.31$, $p < 0.01$) and backswamp ($r_s = 0.21$, $p = 0.04$) positions. MBC and MBN were positively correlated with soil WFPS, although the only significant correlations occurred on the flat (MBC $r_s = 0.26$, $p = 0.01$, MBN $r_s = 0.28$, $p < 0.01$) and transitional swamp (MBC $r_s = 0.20$, $p = 0.05$, MBN $r_s = 0.23$, $p = 0.03$) toposequence positions.

In Situ Net N Mineralization

Net N mineralization was statistically similar across the toposequence landscapes, but showed distinct seasonal trends (Fig. 3.6). Mean net N mineralization rates ranged from 186 ± 22 to 412 ± 73 g N ha^{-1} d^{-1} in summer and 37 ± 9 to 124 ± 24 g N ha^{-1} d^{-1} in winter. Only during winter 2013 was there significantly ($p < 0.05$) greater N mineralization on the levee compared to the backswamp. In contrast, potential N mineralization showed significant ($p < 0.05$) stratification based on landscape, with the levee having higher potential rates than the backswamp (Fig. 3.6). Potential net N mineralization ranged from 259 ± 31 g N ha^{-1} d^{-1} in the backswamp to 439 ± 38 g N ha^{-1} d^{-1} for the levee soils. Summer *in situ* net N mineralization was similar to laboratory potential rates during 2011, but less than potential on the drier toposequence positions (levee, flat) in 2012.

Net N mineralization was most significantly correlated ($p < 0.0001$) to NO_3-N production in all landscape positions (Table 3.2). The only significant correlation ($r_s = 0.20$, $p = 0.05$) between net N mineralization and NH_4-N production was in the backswamp landscape. NH_4-N and NO_3-N production also showed a significant negative correlation ($r_s = -0.29$, $p < 0.01$) in the backswamp. In addition, the backswamp was the only landscape with significantly positive ($p < 0.01$) correlations among MBC, MBN, and both net N mineralization and NO_3-N production. Across all landscapes, net N mineralization and NO_3-N production were most correlated with total precipitation, mean air temperature, and maximum river height (Table 3.2). In addition, PDSI showed significant positive correlations ($p \leq 0.01$) with net N mineralization and NO_3-N production in the backswamp and NH_4-N production in the transitional swamp. Soil WFPS only displayed significant negative correlations with NH_4-N production in the levee ($r_s = -0.54$, $p < 0.0001$) and transitional swamp ($r_s = -0.29$, $p < 0.01$).

Nitrate and Ammonium Production

Net N mineralization rates were primarily related to nitrification regardless of toposequence position (Table 3.2). When expressed as a percent of total N mineralization, NO_3-N production was significantly greater ($p < 0.05$) than NH_4-N in all seasons (Fig. 3.7). NO_3-N production was greatest in summer and fall seasons, making up >93% of the total N mineralized. During the cooler winter and spring months, NO_3-N still made up >80% of the total N produced. In addition, there were no significant differences in percent NO_3-N production between seasons.

Auxiliary *in situ* and laboratory incubations yielded similar results to those of the CONG toposequence, with significantly greater NO_3-N production compared to NH_4-N (Fig. 3.8). The *in situ* incubations showed significantly higher nitrate-N production regardless of stand age (clear-cut secondary growth 91-99% vs. old-growth 94% NO_3-N) in fall 2011. Sites with hardwood overstory trees produced significantly more NO_3-N (>91% total) than NH_4-N. The plantation pine overstory site also had numerically greater nitrification (73% total N mineralization), but it was not significantly greater than NH_4-N production.

Laboratory incubations of soils collected from the primary study toposequence also indicated significantly greater potential nitrate-N production (Fig. 3.8). NO_3-N production made up 97-98% of total mineralized N in the higher elevation levee/flat soils and >99% in the transitional/backswamp landscapes. Laboratory potential net N mineralization was nearly twice that of *in situ* incubations during fall 2012 (Fig. 3.6), yet the major product of both analyses was NO3-N.

Phosphorus Saturation

DPS_{ox} and water soluble P were quantified to assess current P saturation status and potential P leaching from the alluvial soils within CONG. Soil DPS_{ox} showed a weak linear relationship ($R^2 = 0.02$, $p = 0.586$) with water soluble P for all study plots (Fig. 3.9). DPS_{ox} values ranged from 6 to 11%, with a mean value of approximately 8%. Water soluble P concentrations were low regardless of landscape position and all measurements were less than

1.0 mg kg^{-1}, with a mean of 0.53 mg kg^{-1}. All samples tested were well below the suggested change points (20-25% DPS$_{ox}$) where water soluble P leaches from soil.

Discussion

Microbial Biomass

Mean MBC and MBN concentrations at CONG were greater than those reported for headwater riparian forests with sandy soils in the region (Jolley et al., 2010), but similar to those of eutrophic floodplains in the southern USA (Schilling et al., 1999; Schilling and Lockaby, 2005). Both microbial biomass C and N showed little seasonal variation, as evidenced by non-significant correlations between microbial biomass and ambient air temperatures. There was a significant increase in microbial biomass during fall 2012, which came after a wet period that ended drought conditions in the region (Fig. 3.2). Microbial biomass displayed positive correlations to precipitation and WFPS (Table 3.2) suggesting that regional drought may have impacted the microbial community at CONG by suppressing growth. Severe drought can lead to direct mortality of soil microorganisms through dehydration or result in a prolonged period of dormancy (Schimel et al., 2007). Droughts also restrict the movement of dissolved organic matter and other essential soil solutes, hence limiting the growth of microorganisms due to a lack of substrate availability (Zak et al., 1999; Curtin et al., 2012). Drought conditions were persistent until the summer of 2012; however, soil microbial biomass did not peak until the autumn of that year. This apparent lag in response to soil rewetting may be due in part to high ambient temperatures (>25 °C) during the summer which can limit soil microbial biomass production (Curtin et al., 2012). In addition, microbial biomass may also have been limited by C availability, because forest floor biomass and associated nutrients are typically at an annual minimum during late summer (Berg and McClaugherty, 2008). Given the timing of the large autumn increase in microbial biomass, a combination of adequate precipitation and litter input likely drove immobilization of available C and N.

Nitrogen Mineralization

Net N mineralization was statistically similar across the study toposequence, but showed distinct seasonal trends reflecting ambient air temperatures. These results are similar to those reported by Jolley et al. (2010) which indicated higher rates of N mineralization during warmer months in headwater riparian zones. These field results confirm laboratory studies that suggest temperature is a primary controlling factor with regard to total net N mineralization rates in soils (Zak et al., 1999; Curtin et al., 2012). Potential aerobic net N mineralization measured in the laboratory was similar to summer 2011 *in situ* rates, but greater than summer rates in 2012 after prolonged drought, especially in the topographically high landscapes (Fig. 3.6). These data suggest that insufficient soil moisture may have limited the amount of net N mineralization on the levee and flats. However, the low-lying lateral positions were equal to potential N mineralization during both summers, which is probably a result of more available soil moisture because of higher water tables in the hydric soils of the backswamp landscapes. In addition, since total net N mineralization showed a highly significant positive correlation with nitrification rates, regional drought could have increased the potential for the transitional and backswamp landscapes to produce NO_3-N by allowing for aerobic soil conditions (Ward, 2008). Thus, net N mineralization was likely limited on the high topographic landscapes of CONG due to prolonged drought stress, yet enhanced in the low-lying toposequence positions because lowered water tables resulted in adequate soil moisture and aerobic conditions that favor NO_3-N production.

Nitrate production was high across all toposequence landscapes, but during winter and spring collections, minor flood pulsing in the transitional and backswamp positions limited nitrification and stimulated NH_4-N production (Table 3.2). Limited soil O_2 available during periods of prolonged flooding is a stress on NO_3-N production because most microorganisms responsible for nitrification are obligate aerobes (Ward, 2008). Therefore, riparian soils with shallow water tables tend to produce NH_4-N and nitrification is greatest in non-hydric alluvial landscapes (Groffman et al., 2003; Hefting et al., 2004). In addition to flooding inhibition, nitrate can also be lost from the soil as a result of denitrification during periods of flooding (Groffman et al., 1992; Hefting et al., 2004). The *in situ* buried bag approach to net N mineralization allows for diffusion of gases but not liquids (Hart et al., 1994), hence limited O_2 diffusion can result in denitrification of NO_3^- during periods of inundation. Thus, denitrification may create a soil N deficiency that stimulates ammonium production from organic N sources following periods of flooding. Our data indicate that seasonal flood pulsing in the low-lying toposequence landscapes of CONG corresponds to shifts from net NO_3-N to NH_4-N production.

NO_3-N production was greatest in summer and autumn months which correspond to annual minimums of the soil water table, further suggesting that drought may have played a role in nitrate production within the floodplain forests of CONG. Recent research has indicated that plant uptake of inorganic N is severely limited during dry seasons and lowered uptake of NH_4-N can promote nitrification (Sullivan et al., 2012). Drought conditions are also thought to alter soil microbial communities and stress specialized gram negative bacteria, such as nitrifiers, more than gram positive bacteria or fungi (Schimel et al., 2007). However, field-based research has indicated that microbial processes, such as nitrification, occur at equal or greater rates during dry seasons (Parker and Schimel, 2011; Sullivan et al., 2012). Soil WFPS (an indicator of soil moisture) has been identified as one of the most negatively correlated environmental factors to nitrification in floodplains of the Piedmont physiographic province of the southeastern USA

(Noe et al., 2013; Wolf et al., 2013). However, our data from CONG showed non-significant correlations with WFPS and net NO_3-N production occurred from <35 to 100% WFPS. Auxiliary laboratory analyses of potential N mineralization with optimum soil moisture also showed mostly (>97%) nitrate production under aerobic incubations. These data suggest that prolonged drought may have limited the total net N mineralized, but other intrinsic factors contribute to nitrate production within CONG.

The effects of prolonged drought on floodplain microbial communities have not been thoroughly studied. However many of the biological communities associated with floodplains are adapted to tolerate annual flooding and drying cycles (Capon et al., 2013). The large quantities of nitrate production and relatively stable temporal trends in microbial biomass (Fig. 3.4) suggest that nitrifying microorganisms are metabolically active during both wet and dry seasons. In addition, narrow microbial biomass C:N ratios (5.5 ± 0.5 on the levee to 7.1 ± 0.7 in the backswamp) suggest a bacteria dominated biomass (Reichardt et al., 2000), hence the proportion of nitrifying bacteria may be high at the study toposequence. However, additional analyses of the microbial community are needed to better understand the observed trends in N mineralization at CONG.

Additional factors that could contribute to soil nitrate production include the age and species composition of forest stands. In general, late successional mature and old-growth forests have less nutrient demands for biomass production when compared to early successional forests (Vitousek and Reiners, 1975). Thus, mature old-growth forests tend to be “leaky” in terms of N retention, often exhibiting increased nitrate export within streams draining these ecosystems (Hedin et al., 1995). These effects are particularly evident in forests receiving elevated N inputs from anthropogenic activities. Therefore, the forests of CONG should be expected to export N due to low biological demands, because the floodplain receives N inputs from both the atmosphere and floodwaters. As a test we evaluated net N mineralization in two previously clear cut sites downstream of the CONG toposequence and results from these areas showed similar nitrate production (>91% total N mineralization) to the old-growth stands. This observation suggests that NO_3-N production is high under deciduous forests of the CONG floodplain, regardless of stand age. Overstory species composition can also be correlated with nitrification and leaching losses of nitrate, with deciduous forests producing more nitrate relative to coniferous ones (Lovett et al., 2002; Evans et al., 2011). Results from our study confirm these general observations, with relatively greater NH_4-N production (27% total N mineralized) under loblolly pine relative to deciduous (<9%) forests (Fig. 3.8). Therefore, overstory composition and associated litter quality may influence nitrate production on the CONG floodplain. However, loblolly pine stands are restricted to small patches on topographically high ridges within floodplains of the region and thus are not a major overstory component of the alluvial landscapes in CONG (Doyle, 2009).

Our results suggest that NO_3-N production is high among all of the alluvial landscapes we studied in CONG; therefore, additional environmental or edaphic factors must be influencing forest N cycling. The bottomland forests of CONG are low within the watershed, >200 km from the headwaters of the system in northwest South Carolina. Within the framework of the river continuum concept, lower river reaches are expected to receive greater inputs of nutrients from upstream ecosystems (Vannote et al., 1980). In addition, N inputs from anthropogenic activities such as agriculture and urban runoff can result in greater soil nitrate concentrations and production in riparian forests (Groffman et al., 1992). Increased N inputs to large floodplains situated along the lower reaches of a watershed may increase the potential for N mineralization and nitrification (Evans et al., 2011). Thus, increased anthropogenic N loading from upstream sources may have resulted in excess ecosystem N that is contributing to high nitrification levels observed within the floodplains of CONG.

Intrinsic soil properties may also have influenced rates of NO_3-N production at CONG. One of the most important factors related to nitrification in forest soils is pH. Soils with pH <5.0 tend to have minimal rates of nitrification, although a number of studies have reported nitrate production in acid soils (Vitousek et al., 1982; De Boer and Kowalchuk, 2001). Nitrification is dependent upon ammonia (NH_3) concentrations, which decrease with lower pH, but some acid tolerant autotrophic nitrifying microorganisms have been identified in forest soils (De Boer and Kowalchuk, 2001). The soils along the study toposequence at CONG have relatively buffered pH values, with average values ranging from 5.91 ± 0.08 to 5.01 ± 0.05 (Table 3.1). Relatively high pH on the levee and flat landscapes may have facilitated high rates of nitrification, although additional factors are likely involved. Forests with narrow soil and litter C:N ratios also have greater tendencies to produce excess nitrate compared to those with wide ratios (Finizi et al., 1998). Soils with narrow C:N ratios have greater available N for heterotrophic microorganisms and thus mineralization of organic N to nitrate is more likely to occur (Lovett et al., 2002). The soils within our study toposequence had relatively low C:N ratios (mean values <12.6 ± 0.5) which may have been a contributing factor to the high rates of nitrification we observed. An additional soil property that has been identified as being positively correlated with nitrate concentrations in floodplains is silt and clay content (Pinay et al., 1992). Alluvial soils containing more fine particles tend to have greater net N mineralization and nitrate production because the physical environment allows for greater water holding capacity which supports microbial communities responsible for N cycling (Pinay et al., 1995; Jolley et al., 2010). The topsoils at CONG are silt loams, silty clay loams, or silty clays with <8% total sand content (Table 3.1), which suggests they are ideally suited to support diverse microbial communities, including nitrifying microorganisms.

Although our data indicate that the conditions at CONG support high rates of NO_3-N production, further quantitative analyses are needed to understand the ultimate fate of nitrate within the ecosystem. Excess NO_3-N production can be recycled or lost from the floodplain in multiple ways such as plant uptake, denitrification, and physical leaching or erosion to ground or surface waters (Aber et al., 1991; Bechtold et al., 2003). Due to the limitations of the scope of our study, we are only able to report that nitrate production is high in CONG, but the same soil properties (fine texture, available soil organic matter) that promote nitrification also have been shown to support greater rates of *in situ* denitrification and minimize physical leaching (Groffman et al., 1992; Pinay et al., 1995). Thus, nitrate fluxes from the old-growth forests of CONG to local water bodies may be low, but additional analyses are needed to confirm this hypothesis.

Phosphorus Saturation

Our data suggest that the soils at CONG are not saturated with P (Fig. 3.9). All values of DPS_{ox} were well below the empirically established change points (approximately 20-25%) where water soluble P increases in Coastal Plain soils (Maguire and Sims, 2002; Nair et al., 2004). In addition, water soluble P concentrations were very low in all samples (<1.0 mg kg^{-1}) further suggesting the soils of CONG are not an active source of P. The floodplain soils of CONG are relatively young and have formed from post-colonial alluvium derived from wide-spread agricultural activities in the Piedmont over the past 300 years (Trimble, 2008). Young soils on active floodplains contain significant quantities of poorly crystalline Fe (Shaw et al., 2003), which makes them viable sinks for P. However, this function is finite and potential sorption sites can be filled if P loading rates are high. Floodplain forests are unique in that they receive episodic influx of sediment, nutrients, and other essential elements with floodwaters. Since P has no gaseous phase (Vitousek et al., 2010) and the forests of CONG are not fertilized, the primary inputs to the ecosystem are from floodwaters. Annual P loading in the system is probably not great enough to saturate available soil sorption sites because Piedmont river loads contain large quantities of poorly crystalline Fe and Al (Schoonover et al., 2007), which are deposited at the soil surface during floods. Annual additions of fresh sediment that contain both Fe and Al may buffer the ability of red water floodplains to bind P.

Implications for the Future

The results of our study illustrate that the old-growth riverine forests of CONG produce excess NO_3-N and are viable sinks for P sorption. Floodplain biogeochemical cycles are closely tied with regional climate, flood pulsing, and floodplain hydrologic connectivity (Junk et al., 1989; Groffman et al., 2003; Noe et al., 2013), hence future alterations to these processes may alter N and P cycling within CONG. Recent climate model projections for the southeastern USA predict that the region will undergo a rise in annual air temperature of approximately 3 °C by the year 2100 (McNulty et al., 2013). Temperature increases may contribute to greater evapotranspiration rates resulting in lowered water tables and water stress in riverine forests. The Piedmont region is also predicted to undergo continued urbanization which may increase water supply stress throughout the southern USA (McNulty et al., 2013; Lockaby et al., 2013). As mentioned previously, the Congaree River is a dam regulated waterway and future stresses may result in greater quantities of water being retained within large reservoirs (Doyle, 2009). Increased water demand upstream and associated dam regulated flows may further decrease the frequency, magnitude, and duration of flood events within large Coastal Plain floodplain forests of the region (Hupp et al., 2009). The predicted changes in temperature, evapotranspiration, precipitation, and water resource allocation over the next century may have long-lasting impacts on the biogeochemistry of CONG.

Drier climatic and floodplain conditions would promote NO_3-N production at CONG (Groffman et al., 2003), as reflected by our data collected during drought. Topographically high landscapes such as the natural river levee, flats, and ridges may undergo greater drought stress, leading to decreases in total net N mineralization (Curtin et al., 2012). Reduced flood pulsing could also impact hydric soil landscapes, such as sloughs and backswamps, because reductions in the height of the water table promote aerobic soil conditions that are necessary for nitrification (Hefting et al., 2004; Ward, 2008). If abnormally dry conditions persist for long periods, there is the added potential for shifts in plant species and microbial community composition, which could further alter trends in N mineralization (Schimel et al., 2007). Reductions in flooding at CONG would also limit the river-floodplain interactions necessary for soil P sorption (D’Angelo, 2005). Although the exact impacts of future climate and river flow conditions on floodplain biogeochemical processes are unknown, it is clear that any changes in hydrologic connectivity will likely alter both N and P dynamics within the old-growth forests of CONG.

Conclusions

We found that the dominant product of net N mineralization in CONG was NO_3-N, which is unusual among acid forest soils of the southeastern USA. Only intermittent spring flood pulsing resulted in significant NH_4-N production within low-lying topographical landscapes, suggesting annual flood pulsing is necessary to inhibit nitrification and stimulate ammonium production. Nitrate production was ubiquitous among the floodplain hardwood forests we studied regardless of stand age and soil moisture content, which suggests that inherent soil properties (including the microbial community structure) drive nitrification rates. CONG soils have buffered pH values, low C:N ratios, and high silt and clay content. These factors are all associated with high nitrification rates. However, the ultimate fate of excess NO_3-N is unknown because key fluxes such as *in situ* denitrification and plant uptake remain unquantified.

The biogeochemical indices outlined here are important for future planning efforts regarding large floodplains of the Atlantic Coastal Plain. River flows will continue to decrease as a result of warming air temperatures and increased evapotranspiration associated with climate change in the southeastern USA. Additional water stress to meet the demands of an urbanizing landscape may also contribute to a progressive drying of large floodplains in the region. Limited river-floodplain hydrologic connectivity may reduce the ability of these landscapes to act as a sink for P and reductions in river high flows may also increase the duration of aerobic soil conditions that favor nitrification. Excess production of soil NO_3-N during dry periods may ultimately leach to surrounding waterways. Therefore, careful evaluation of future river flow scenarios are needed to understand the possible alterations to current biogeochemical functions associated with mature old-growth riverine forests of the Atlantic Coastal Plain.

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Table 3.1: Mean soil characteristics for each floodplain landscape, standard error is shown in parentheses (n = 5, per landscape). Means by column with different letters are significantly different according to Tukey's HSD tests ($\alpha = 0.05$).

			Toposequence Soil Characteristics (0-10 cm)							
Landscape	Plots	Relative Elevation (m)†	Depth to SHWT (m)‡	Organic Matter (%)	C:N Ratio	Sand (%)	Clay (%)	Soil pH	CEC_{sum} (cmol kg^{-1})§	Base Saturation (%)§
Levee	1-5	-0.07 (0.03)a	0.85 (0.07)a	6.8 (0.4)a	12.6 (0.3)a	5 (0.4)a	26 (2.0)a	5.91 (0.08)a	16.6 (1.1)a	88.5 (1.4)a
Flat	6-10	-0.15 (0.05)a	0.82 (0.12)a	8.2 (0.4)a	11.6 (0.4)a	8 (0.9)a	27 (0.5)a	5.72 (0.17)a	17.0 (1.4)a	84.7 (2.7)a
Transitional	11-15	-1.02 (0.15)b	0.44 (0.04)b	7.5 (0.8)a	11.9 (0.4)a	7 (0.8)a	39 (1.0)b	5.01 (0.05)b	12.2 (0.7)b	62.4 (2.4)b
Backswamp	16-20	-1.62 (0.11)c	0.13 (0.02)c	6.9 (0.9)a	12.6 (0.5)a	6 (0.9)a	45 (1.4)c	5.11 (0.08)b	12.1 (0.5)b	64.7 (2.9)b

† Elevation relative to the highest point along the transects (natural river levee, plot 5)

‡ Seasonal high water table (SHWT), interpreted as depth to common (>2%) redox depletions

§ Calculated from Mehlich-1 (double acid) extracts

Table 3.2: Spearman correlations of biogeochemical indices and environmental variables across the Congaree toposequence landscapes. Spearman correlation coefficients (r_s) and associated p values below in parentheses, highly significant correlations are indicated in bold (α = 0.01), significant correlations are underlined (α = 0.05).

	Biogeochemical Indices					Environmental Variables				
	Microbial Biomass C µg g^{-1}	Microbial Biomass N µg g^{-1}	Net N Mineralization g N ha^{-1} d^{-1}	Net NO_3-N g N ha^{-1} d^{-1}	Net NH_4-N g N ha^{-1} d^{-1}	PDSI †	Total Precipitation mm	Mean Air Temperature °C	Maximum Gage Height m	Water Filled Pore Space %
	Natural River Levee (N = 89)									
Microbial Biomass C	1.00	**0.64**	-0.20	-0.20	-0.01	0.24	0.10	-0.10	-0.02	0.19
	-	**(<.0001)**	(0.06)	(0.06)	(0.94)	(0.02)	(0.35)	(0.40)	(0.84)	(0.07)
Microbial Biomass N		1.00	0.08	0.09	-0.01	0.16	**0.31**	0.23	-0.01	0.11
		-	(0.47)	(0.41)	(0.99)	(0.14)	**(<0.01)**	(0.29)	(0.92)	(0.29)
Net N Mineralization			1.00	**0.98**	0.21	0.15	**0.57**	**0.68**	**-0.31**	-0.04
			-	**(<.0001)**	(0.05)	(0.15)	**(<.0001)**	**(<.0001)**	**(<0.01)**	(0.71)
Net NO_3-N				1.00	0.08	0.16	**0.56**	**0.66**	**-0.30**	0.02
				-	(0.46)	(0.13)	**(<.0001)**	**(<.0001)**	**(<0.01)**	(0.86)
Net NH_4-N					1.00	0.10	0.17	0.13	-0.03	**-0.54**
					-	(0.34)	(0.11)	(0.24)	(0.79)	**(<.0001)**
	Hardwood Flat (N = 92)									
Microbial Biomass C	1.00	**0.70**	-0.14	-0.12	-0.06	0.16	-0.04	-0.20	0.19	**0.26**
	-	**(<.0001)**	(0.19)	(0.26)	(0.56)	(0.12)	(0.67)	(0.06)	(0.07)	**(0.01)**
Microbial Biomass N		1.00	0.19	0.20	-0.06	0.05	0.15	0.13	0.16	**0.28**
		-	(0.06)	(0.06)	(0.57)	(0.61)	(0.16)	(0.20)	(0.12)	**(<0.01)**
Net N Mineralization			1.00	**0.99**	0.14	0.12	**0.49**	**0.57**	**-0.40**	0.07
			-	**(<.0001)**	(0.20)	(0.27)	**(<.0001)**	**(<.0001)**	**(<.0001)**	(0.48)
Net NO_3-N				1.00	0.03	0.10	**0.52**	**0.59**	**-0.44**	0.08
				-	(0.75)	(0.34)	**(<.0001)**	**(<.0001)**	**(<.0001)**	(0.43)
Net NH_4-N					1.00	0.19	-0.11	-0.11	0.22	-0.10
					-	(0.07)	(0.31)	(0.28)	(0.04)	(0.37)

Table 3.2: Continued

	Biogeochemical Indices					Environmental Variables				
	Microbial Biomass C µg g^{-1}	Microbial Biomass N µg g^{-1}	Net N Mineralization g N ha^{-1} d^{-1}	Net NO_3-N g N ha^{-1} d^{-1}	Net NH_4-N g N ha^{-1} d^{-1}	PDSI †	Total Precipitation mm	Mean Air Temperature °C	Maximum Gage Height m	Water Filled Pore Space %
	Transitional Swamp (N = 94)									
Microbial	1.00	**0.72**	0.12	0.15	-0.07	0.23	0.22	0.03	-0.05	0.20
Biomass C	-	**(<.0001)**	(0.25)	(0.16)	(0.51)	(0.02)	(0.03)	(0.74)	(0.66)	(0.05)
Microbial		1.00	0.10	0.14	-0.19	-0.01	0.19	0.14	0.00	0.23
Biomass N		-	(0.35)	(0.19)	(0.06)	(0.94)	(0.07)	(0.18)	(0.98)	(0.03)
Net N			1.00	**0.97**	0.10	0.20	**0.63**	**0.56**	**-0.53**	0.08
Mineralization			-	**(<.0001)**	(0.33)	(0.05)	**(<.0001)**	**(<.0001)**	**(<.0001)**	(0.46)
Net NO_3-N				1.00	-0.05	0.18	**0.66**	**0.59**	**-0.58**	0.14
				-	(0.65)	(0.09)	**(<.0001)**	**(<.0001)**	**(<.0001)**	(0.19)
Net NH_4-N					1.00	**0.25**	0.10	0.14	0.15	**-0.29**
					-	**(0.01)**	(0.35)	(0.19)	(0.16)	**(<0.01)**
	Backswamp (N = 95)									
Microbial	1.00	**0.77**	**0.37**	**0.32**	-0.10	0.12	0.24	0.06	-0.19	0.15
Biomass C	-	**(<.0001)**	**(<0.01)**	**(<0.01)**	(0.35)	(0.23)	(0.02)	(0.54)	(0.07)	(0.15)
Microbial		1.00	**0.32**	**0.36**	-0.21	-0.05	0.21	0.17	-0.20	0.04
Biomass N		-	**(<0.01)**	**(<0.001)**	(0.04)	(0.61)	(0.04)	(0.10)	(0.06)	(0.72)
Net N			1.00	**0.79**	0.20	**0.33**	**0.54**	**0.40**	**-0.45**	0.01
Mineralization			-	**(<.0001)**	(0.05)	**(<0.01)**	**(<.0001)**	**(<.0001)**	**(<.0001)**	(0.93)
Net NO_3-N				1.00	**-0.29**	**0.35**	**0.52**	**0.30**	**-0.61**	-0.16
				-	**(<0.01)**	**(<0.01)**	**(<.0001)**	**(<0.01)**	**(<.0001)**	(0.13)
Net NH_4-N					1.00	0.12	0.09	0.21	**0.31**	0.12
					-	(0.26)	(0.37)	(0.04)	**(<0.01)**	(0.23)

† Palmer drought severity index (PDSI) values are relative to 0 and can range from positive (wet conditions) to negative (dry conditions). Negative values <-2 indicate drought conditions.

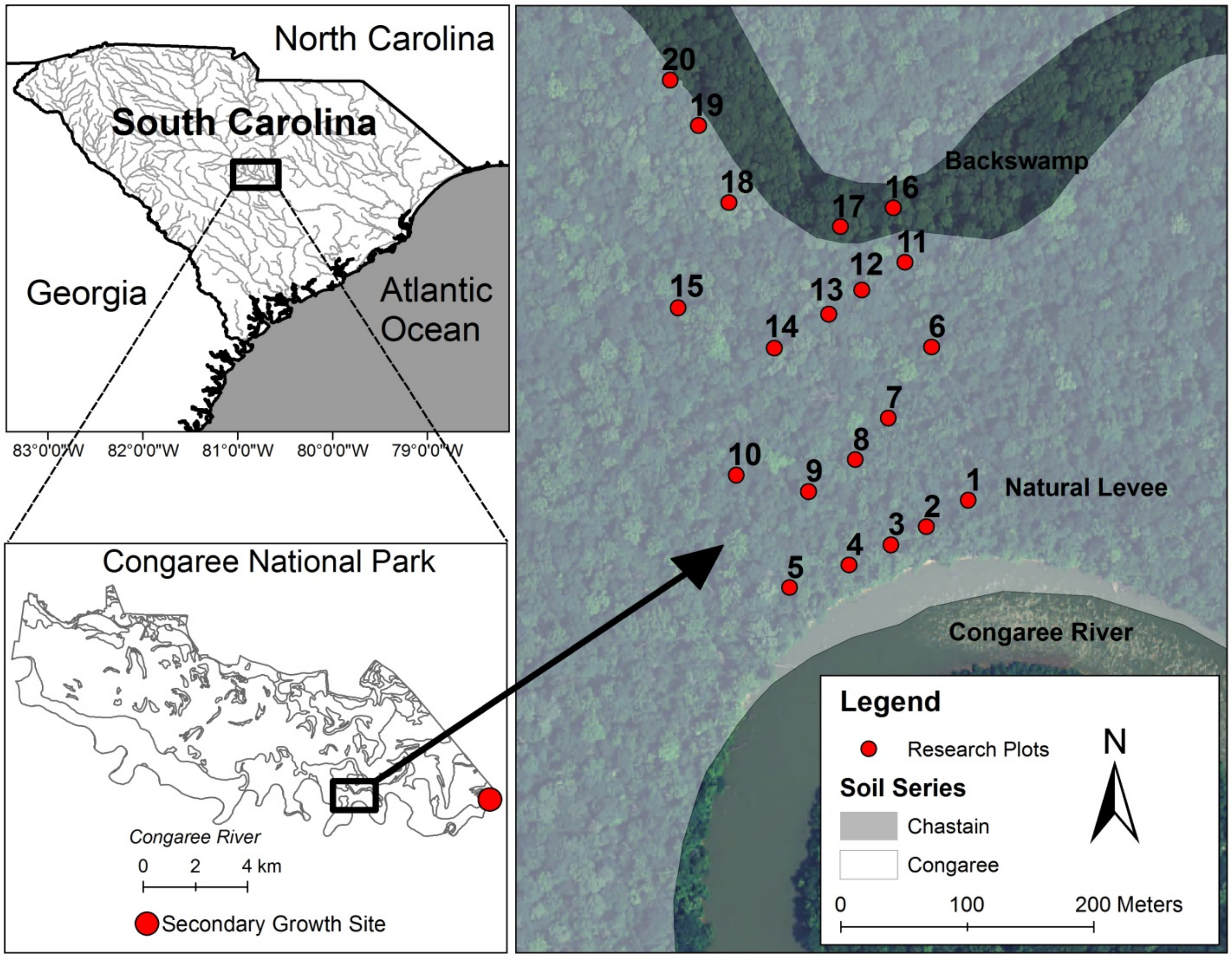

Fig. 3.1: Overview map of study transect locations and research plots. The secondary growth site was a previously clear-cut section of the Park where additional *in situ* nitrification studies were carried out to compare with the old-growth forest of the study transects.

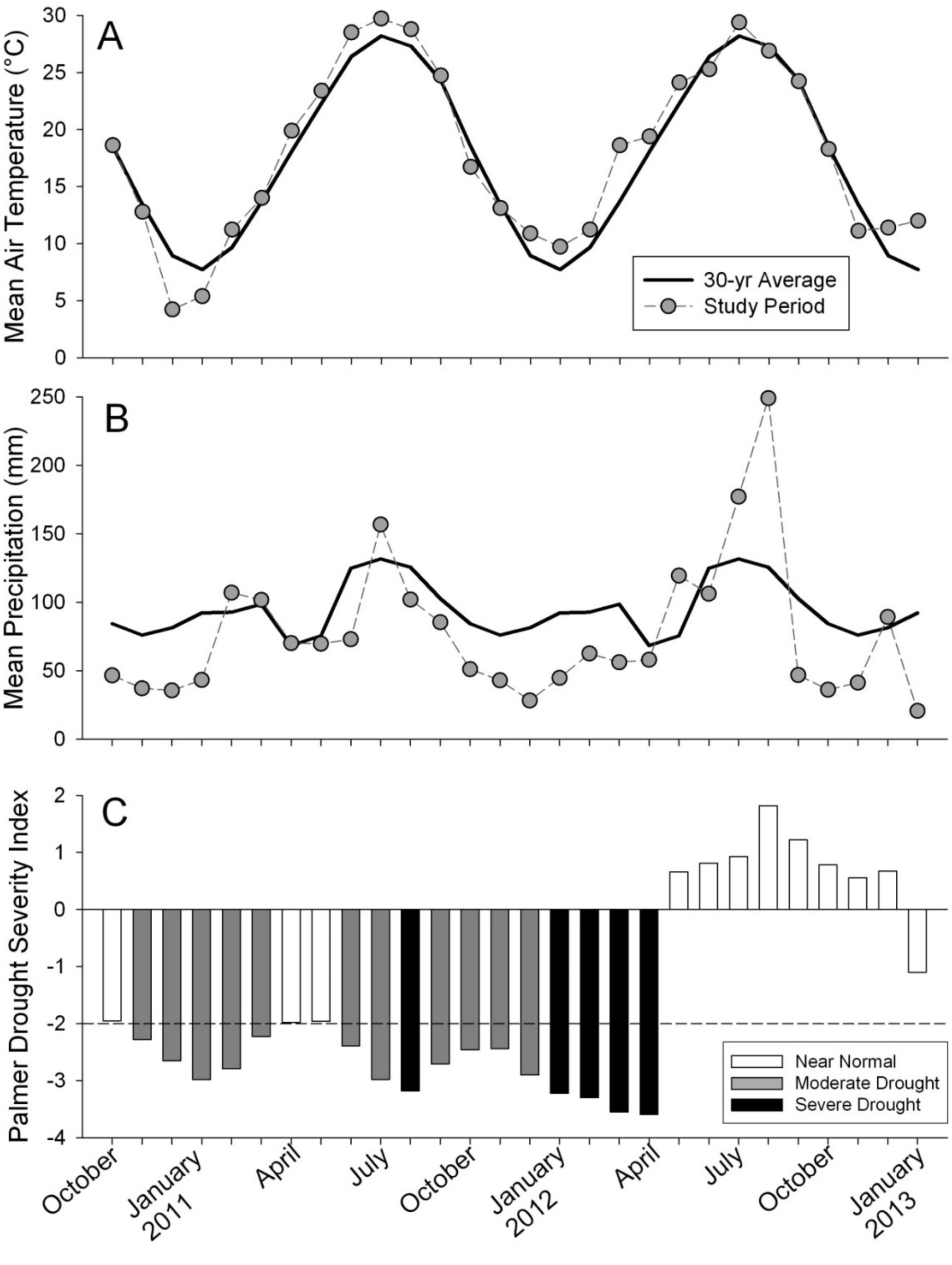

Fig. 3.2: Climatological data from the Columbia Metropolitan Airport monitoring station and corresponding Palmer Drought Severity Index (PDSI) for the central region (Division 6) of South Carolina (data source: National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, NC, USA). PDSI values <-2 are considered drought conditions.

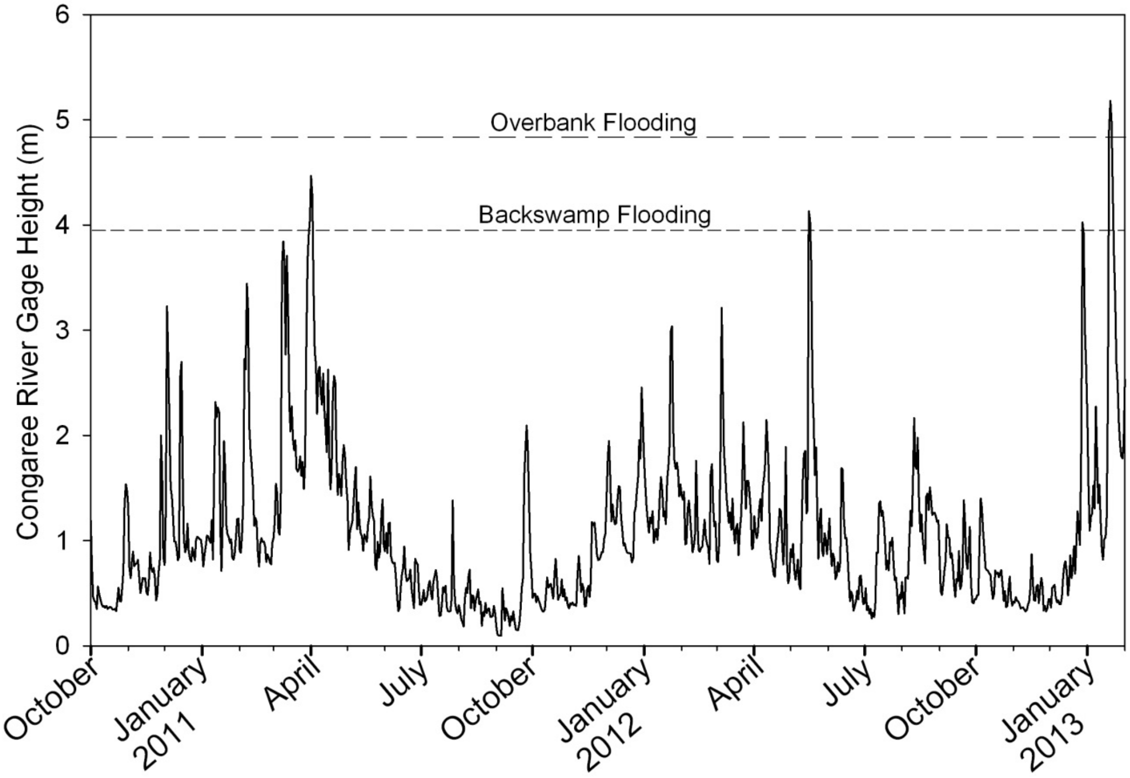

Fig. 3.3: Congaree River gage height during the study period. River stage above 3.96 m is sufficient to flood low-lying backswamp (plots 16-20) and stage levels >4.88 m top the natural river levee, resulting in complete inundation at the study transects.

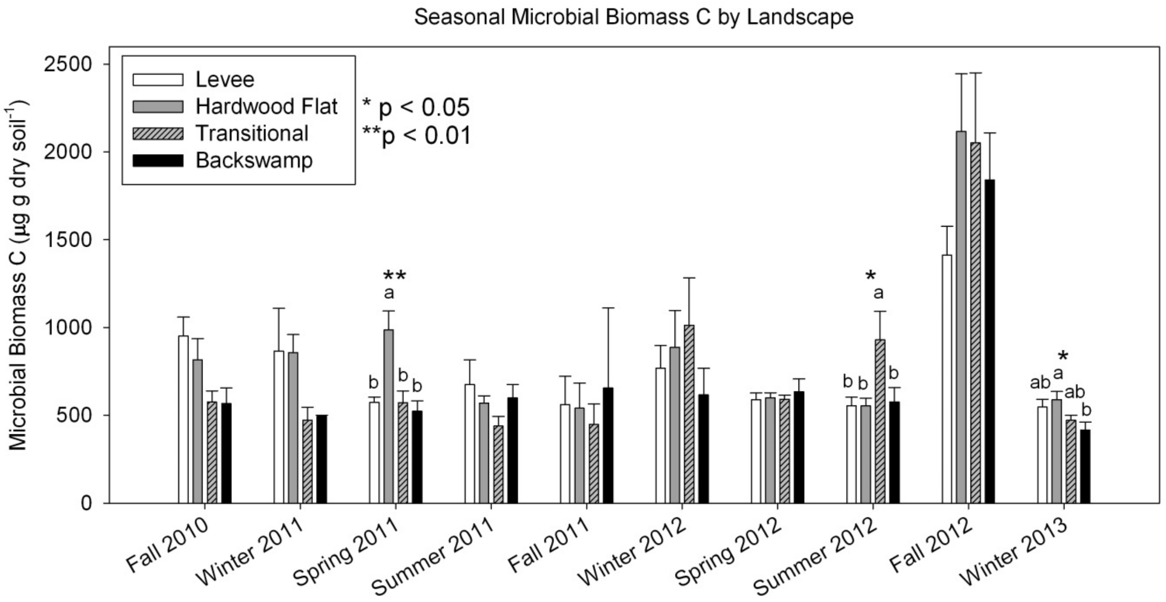

Fig 3.4: Seasonal dynamics of mean microbial biomass C by landscape (n = 10). Means (± 1 SE) with different letters within each season are significantly different (α = 0.05) according to Tukey's HSD tests.

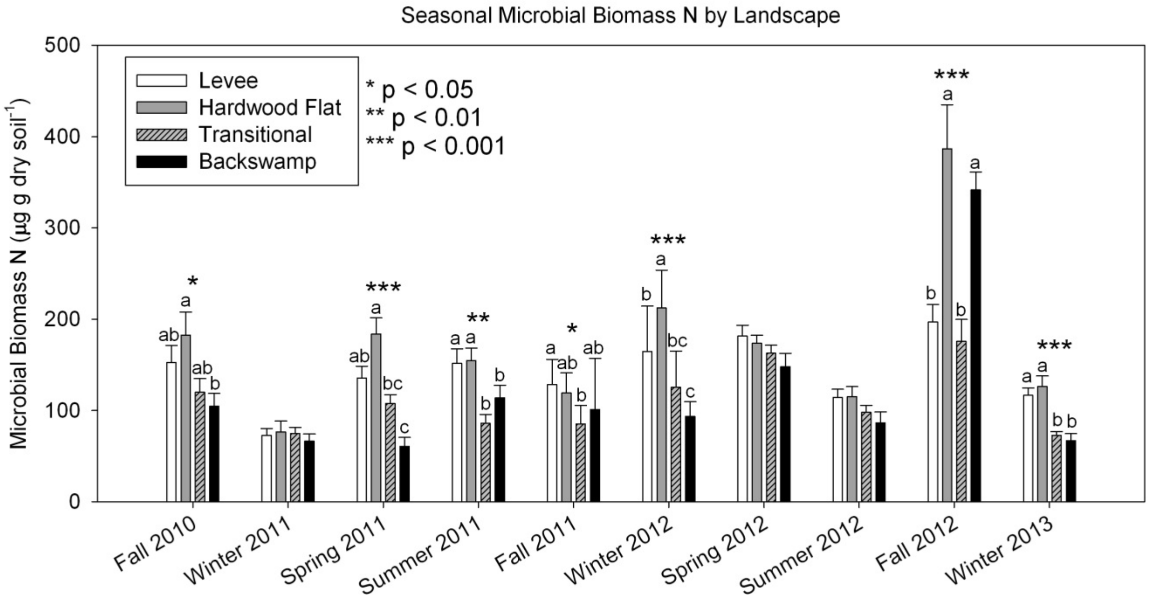

Fig 3.5: Seasonal dynamics of mean microbial biomass N by landscape (n = 10). Means (± 1 SE) with different letters within each season are significantly different (α = 0.05) according to Tukey's HSD tests.

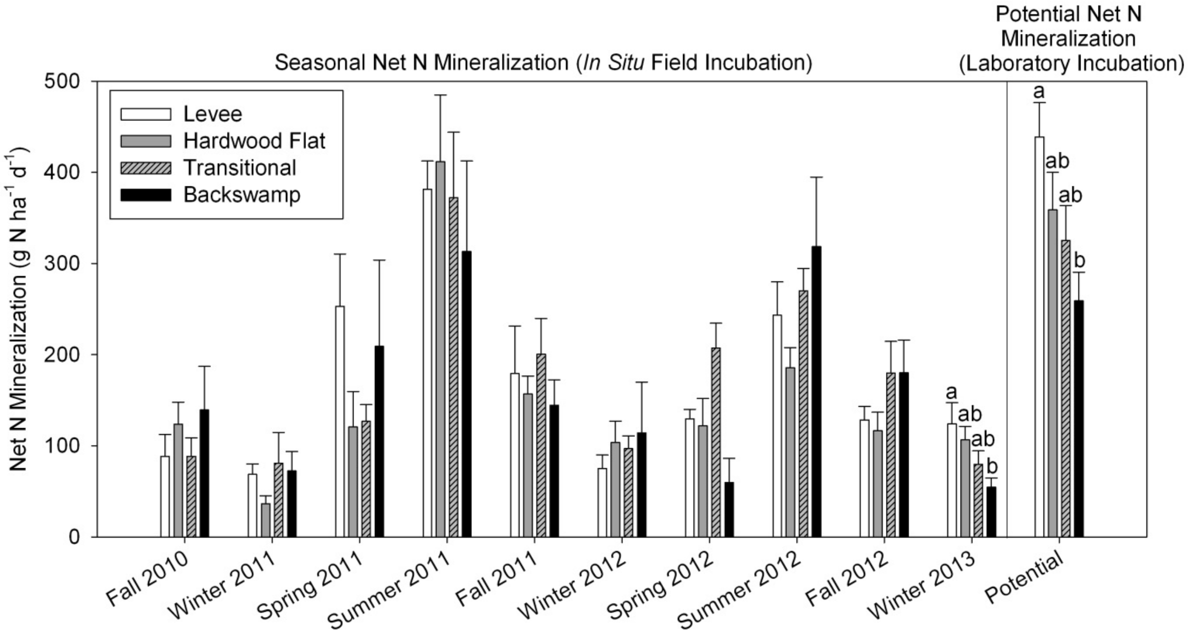

Fig. 3.6: Mean net N mineralization rates (± 1 SE) separated by landscape (n = 10) from both *in situ* field incubations and laboratory analysis of potential net N mineralization. Means with different letters within each season are significantly different (α = 0.05) according to Tukey's HSD tests.

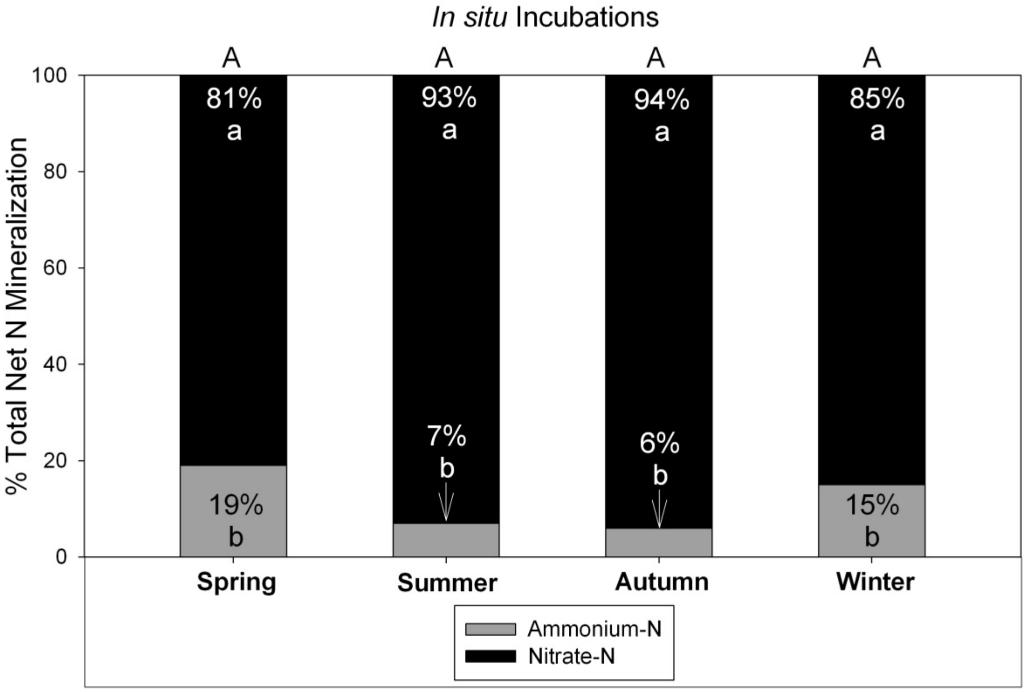

Fig. 3.7: Percentage of total net N mineralization in the form of ammonium and nitrate across seasons (spring, summer (n = 80), fall, winter (n = 120)). Means within each season with different lowercase letters are significantly different according to Student's t-test ($\alpha = 0.05$). There was no significant difference in nitrate production among seasons according to one-way ANOVA and Tukey's HSD tests (capital letters).

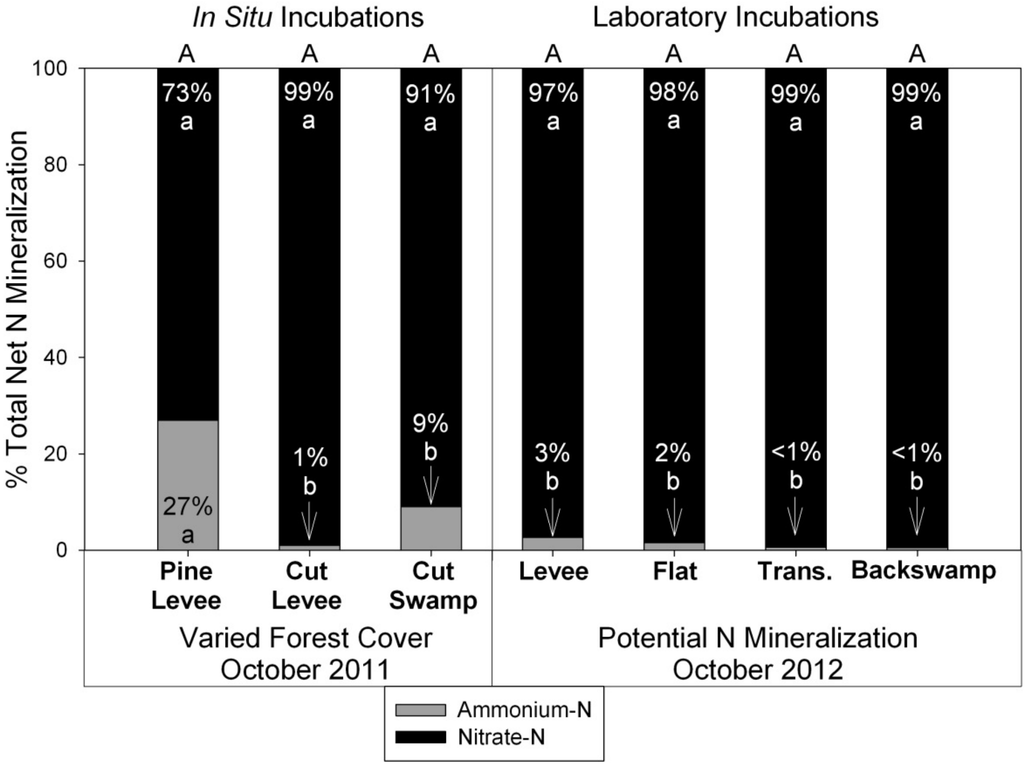

Fig. 3.8: Summary of auxiliary net N mineralization experiments to test the source of soil nitrate production in Congaree National Park. Mean percent inorganic N within each treatment with different letters are significantly different according to Student's t-test ($\alpha = 0.05$). There was no significant difference in nitrate production within the experiments (*in situ* incubations and laboratory incubations) according to one-way ANOVA and Tukey's HSD tests (capital letters).

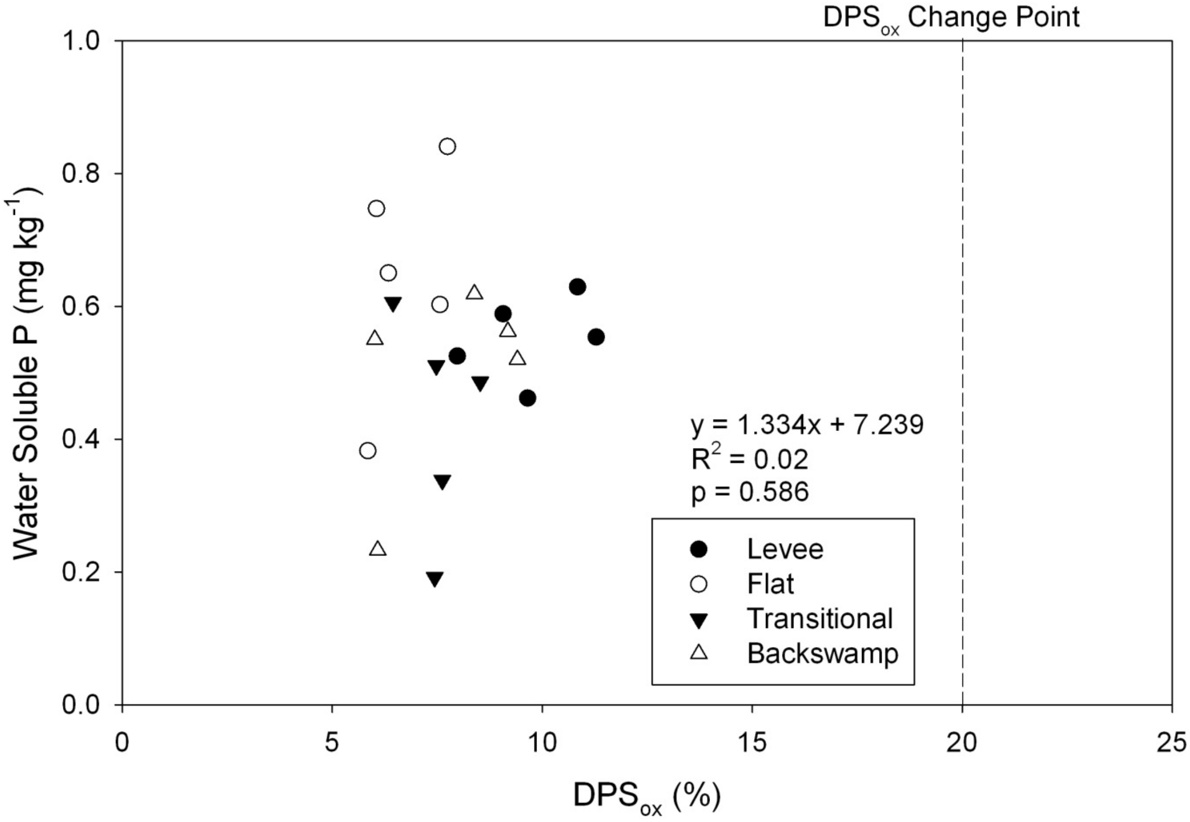

Fig. 3.9: Summary of oxalate extract degree of P saturation (DPS$_{ox}$) and water soluble P content of soils from the four transect landscapes. The linear relationship between the measures was not significant, however all values of DPS$_{ox}$ fell below the suggested critical P sink-source change point of 20%.

Chapter 4:

Effects of landscape variability and red imported fire ants (*Solenopsis invicta* Buren) on woody debris decomposition in an old-growth bottomland forest

Style manual or journal used:

Ecology

Computer software used:

Microsoft Word® 2010

Microsoft Excel® 2010

SAS® Version 9.2

Sigmaplot® 11.2

ESRI® ArcMap™ Version 9.3.1

Abstract

Downed woody debris is an important component of the forest floor, responsible for long-term storage of nutrients in many ecosystems. In large floodplain forests of the southeastern United States, wood loads are relatively low, suggesting these landscapes may promote rapid decomposition and nutrient turnover rates. The goals of this study were to identify the major factors responsible for wood decomposition and associated nutrient dynamics in an old-growth floodplain forest at Congaree National Park (CONG), South Carolina (USA). Twenty permanent research plots were installed along a lateral soil toposequence that contained four major landforms: the well drained natural river levee, moderately well drained hardwood flat, somewhat poorly drained transitional flat, and poorly drained backswamp. *In situ* decomposition and nutrient dynamics were quantified for 700 d (April 2011-March 2013) using wood from a common overstory species, red maple (*Acer rubrum* L.). During the study period, regional drought conditions allowed for red imported fire ant (RIFA, *Solenopsis invicta* Buren) colonization and infestation of the study wood after 183 d in the field. RIFA damage to the outer bark resulted in significantly less mass remaining as a result of direct wood fragmentation. Carbon (C) content decreased throughout the study, indicating net mineralization was occurring year-round. Invertebrate activity and microbial mineralization contributed to extremely fast decomposition rates (mean k range 0.639 ± 0.03 to 0.676 ± 0.06/yr) and wood turnover times (range 4.70 ± 0.37 to 4.97 ± 0.41 yrs) across all landscapes. In contrast to C dynamics, wood nitrogen (N) and phosphorus (P) content increased following RIFA infestation, displaying significant net nutrient immobilization in all landscapes. N continued to display periods of immobilization, while P generally mineralized, indicating that the decomposer community at CONG responds more to seasonal N availability. Data from this study suggest that disturbance by invertebrates can stimulate wood decomposition through direct fragmentation of wood and also enhance microbial mineralization. The rapid turnover rates measured at CONG indicate that the C storage function of woody debris may be diminished, but availability of mineralized N and P may also have increased the importance of wood stocks to support forest net primary productivity.

Key words: wood decomposition, nutrient cycling, old-growth forest

Introduction

Woody debris is an important ecosystem component for accumulation and long-term storage of organic matter and nutrients (Currie et al. 2002, Muller 2003). Inputs and losses of woody debris in forested ecosystems are dependent upon species composition, landscape position, rates of tree disturbance, substrate quality, and localized climate (Harmon et al. 1986, Laiho and Prescott 2004). It has been suggested that woody debris is a minor pool of nutrients during all stages of forest succession when compared to soil and leaf litter (Laiho and Prescott 2004). However, most woody debris studies in North America have been conducted in northern latitude upland landscapes of the United States and Canada (Harmon et al. 1986, Tyrrell and Crow 1994, Laiho and Prescott 2004) and relatively few studies of dead wood have been completed in unconfined, low gradient floodplains or wetlands (Day 1982, Rice et al. 1997, Wohl et al. 2011). Thus, current standing woody debris stocks and the processes contributing to decomposition and nutrient release from these pools remain unquantified in many large temperate and subtropical zone floodplain forests (Wohl 2013).

Measurement of *in situ* decomposition is more common for leaf litter than woody debris (Day 1982). Some studies have indicated more rapid litter decay rates in seasonally flooded areas, such as floodplains (Rice et al. 1997), while others have found initial litter quality to be a controlling factor of decomposition (Day 1982, Laiho and Prescott 2004, Schilling and Lockaby 2005). Wood decomposition rates are highly variable between species due to differences in initial litter quality (Harmon et al. 1986, Tyrrell and Crow 1994), but in most cases wood decay is much slower than leaf litter (Day 1982, Rice et al. 1997, Schilling and Lockaby 2005). Wood decay rates are also dependent upon volume, with larger diameter logs typically decaying slower and having longer turnover times than small diameter twigs or sticks (Abbott and Crossley 1982, Laiho and Prescott 2004). Floodplain woody debris is also a critical resource for many macroinvertebrates, acting as a source of food and shelter for many species of springtails, flies, spiders, millipedes, mites, beetles, termites, and ants (Harmon et al. 1986, Lockaby et al. 2002, Braccia and Batzer 2008). Macroinvertebrates are important components of the litter decomposition process, typically accounting for small portions (<30%) of total nutrient mineralization, but physical fragmentation associated with decomposer invertebrates may significantly increase total mineralization rates by stimulating microbial activity (Hättenschwiler et al. 2005, Bastow et al. 2008). For example, Genet et al. (2001) reported that average rates of mass loss were significantly greater (approximately 50-200 g/yr) when major invertebrate decomposers, such as termites and beetles, were present within downed wood of a subtropical forest in Puerto Rico. Although the importance of macroinvertebrates have been noted with regard to wood decay, separating their effects from physical and microbial mineralization processes is often difficult in field studies.

Woody debris is also important for mineralization of organic nutrients, usually referred to as a slow release sink for carbon (C), nitrogen (N), and phosphorus (P). Nutrient mineralization-immobilization trends in woody debris are largely controlled by microbial processes and local climate conditions that promote seasonal leaching from throughfall organic matter (Day 1983, Harmon et al. 1986). Downed wood nutrient source-sink behavior is largely dependent on initial nutrient content as well as the level of microbial activity within the woody debris and underlying soil (Harmon et al. 1986, Currie et al. 2002). Wood decay results in cumulative losses of mass and volume as organic C is mineralized and evolved as CO_2 (Pregitzer and Euskirchen 2004). The slow rates of wood decay, compared to leaf litter, make it a relatively long-term sink for C (Currie et al. 2002). High sedimentation rates have also been reported to slow decomposition of leaf litter in riparian forests (Jolley et al. 2010). If rates of woody debris decomposition are similarly reduced due to sedimentation and progressive burial, longer turnover times may result. In contrast to C, N and P are typically immobilized during the initial stages of wood decomposition and are eventually mineralized during advanced stages of decay (Harmon et al. 1986, Harmon and Hua 1991, Chueng and Brown 1995, Rice et al. 1997, Laiho and Prescott 2004). In most upland ecosystems downed woody debris is not a significant source of inorganic nutrients when compared to soil and foliar litter due to minimal initial nutrient concentrations (Laiho and Prescott 2004). However, given the vast differences in hydrology, soil properties, and vegetation types between floodplain and upland forests, it would not be surprising if this commonly held assumption was inaccurate for riparian ecosystems. It is evident that clarification regarding woody debris stocks, decomposition rates, and nutrient circulation are needed for wetland and riverine forests in order to better assess the importance of downed wood at an ecosystem scale.

In this study, we chose to investigate wood decomposition and nutrient dynamics in an old-growth bottomland hardwood forest located in Congaree National Park (CONG) in central South Carolina, USA. To date, relatively few decomposition studies have been completed in large old-growth floodplain forests, although there has been a previous study of woody debris volume and loads within CONG. This study indicated that the small tributaries within the floodplain had below average wood loads and relatively few logjams when compared to other old-growth floodplains in temperate climates (Wohl et al. 2011). The authors concluded that the relative scarcity of wood in the floodplain was likely a result of the combined effects of high wood transport capacity and fast rates of decay. Although there is hydrological evidence that frequent winter and spring floods facilitate wood transport at CONG, there have not been any substantial studies regarding wood decomposition rates within the floodplain forests of the Congaree River (Wohl et al. 2011). Knowledge of floodplain wood decay rates and associated nutrient dynamics would help elucidate the importance of woody debris in total ecosystem nutrient storage and circulation. To that end, the specific goals of this study were: (1) to quantify total downed woody debris mass and nutrient (C, N, P) pools; and (2) assess temporal trends of *in situ* woody debris decomposition and nutrient dynamics (mineralization and immobilization of C, N, P) over an approximate 2 yr period. We hypothesized that wood decay rates would be greater than those reported for other temperate old-growth forests because of the effects of wetting-drying cycles associated with annual flooding at CONG and the humid subtropical climate of the region, which allows for year-round C mineralization from downed wood.

Study Site

Congaree National Park (CONG) is located in central South Carolina, approximately 30 km southeast from the capital city of Columbia. CONG is located within the upper Atlantic Coastal Plain and contains approximately 11,000 ha of bottomland hardwood forest associated with the Congaree River. The Congaree River drains a large portion (>21,000 km^2) of the Piedmont physiographic province of central and northern South Carolina and the floodplain is classified as eutrophic (i.e., red water) because it receives nearly annual additions of silty, nutrient-rich sediment. The region has a humid subtropical climate that typically receives 1220 mm of annual precipitation and has an average annual air temperature of 17.6 °C. Our study was conducted in an old-growth bottomland forest tract near Butterfly Pond (33°46’19.33”N, 80°43’36.55”W). Five study transects (255-380 m in length) were established adjacent to the active Congaree River channel representing an alluvial soil toposequence (Fig. 4.1). The lateral toposequence (from south to north) included four major fluvial landscape units defined as the natural river levee, hardwood flat, transitional flat, and backswamp. Representative research plot sites were selected based on relative elevation with regard to the river channel and plant species characteristics. Four circular research plots were established along each transect (20 total plots, 5 m radius, 78.5 m^2) to represent the major fluvial landscape units. Soils in this section of the floodplain are mapped at a series level as well drained Congaree (Fine-loamy, mixed, active, nonacid, thermic Oxyaquic Udifluvents) and poorly drained Chastain (Fine, mixed, semiactive, acid, thermic Fluvaquentic Endoaquepts) units (Soil Survey Staff, 2013). Dominant overstory tree species in the study area ranged from mixed hardwoods such as sweetgum (*Liquidambar styraciflua* L.), sugarberry (*Celtis laevigata* Willd.), sycamore (*Platanus occidentalis* L.), and various bottomland oaks (*Quercus* spp.) on the river levee to baldcypress (*Taxodium distichum* (L.) Rich.) in the backswamp wetlands (see Appendix A for representative photographs and study plot descriptions).

Materials and Methods

Woody Debris Decomposition

Woody debris decomposition rates were assessed along the study toposequence using an *in situ* method similar to that described by Rice et al. (1997). Wood decomposition is dependent on initial litter quality, which can vary by tree species (Koch 1985, Berg and McClaugherty 2008). Therefore, a common species was selected to limit variability in initial wood quality. Red maple (*Acer rubrum* L.) wood was chosen, because this is one of the only overstory species that grows in both well drained natural river levees and poorly drained backwater sloughs of the region. Live red maple saplings were harvested in March 2011 from a common site located approximately 5.5 km downstream of the study transects (Figure 4.1). The harvest site was selected because it has similar soil characteristics to those of the study transects (a gradient from Congaree to Chastain soil mapping units).

Saplings were cut into approximately equal segments of 30 cm length and 3.0-4.5 cm diameter. Green wood segments were then air dried to a constant weight in the laboratory (approximately 2 weeks). Initial wood volume was calculated (to the nearest mm^3) from total length and mean diameter, measured at the edges and center of each segment using a hand-held caliper. Initial sample mass was assessed to the nearest 0.01 g and each segment was individually tagged for later identification. Control wood dowels (eastern white pine, *Pinus strobus* L.) were also cut into 30 cm lengths and initial mass was quantified in a similar manner to the red maple wood. Control wood dowels were used to evaluate the relative importance of landscape variability on decomposition of a substrate with homogeneous litter quality.

Red maple and control samples were placed in the field in April 2011. Tagged wood samples were placed in contact with the soil surface and tethered to trees on common strings to prevent sample loss during spring floods at CONG. Each string consisted of 10 wood segments, with duplicate red maple strings paired with a control wood string in each study plot (N = 400 maple, N = 200 control samples). Time zero maple and control wood samples were taken from each string and returned to the laboratory to estimate initial handling mass loss, nutrient contents, and litter quality. The remaining samples were left in the field and collected at intervals of approximately 1, 2, 3, 6, 12, 15, 18, 24 months to estimate decomposition and nutrient dynamics over time.

Initial wood samples were returned to the laboratory and oven dried to a constant weight (approximately 7 d) at 65 °C. Initial air dried weights were corrected to oven dried weights and wood sample volume and mass were also remeasured to calculate losses due to handling and transport. Ash weight (subsamples heated at 500 °C for 8 hr) was subtracted from total wood mass to correct for any mineral additions. Corrections for mean differences in moisture, handling loss, and ash weight were applied to all sample collections. Mass and volume were remeasured in a similar manner for all subsequent field collections to calculate wood decomposition rates over time.

Litter Quality and Nutrient Dynamics

Following mass and volume measurements, nutrient concentrations were quantified to assess litter quality and nutrient dynamics during wood decomposition. Three 2-cm disks (including bark, sapwood, and heartwood) were cut from each wood sample and ground to pass a 20-mesh (0.1 cm) screen with a laboratory Wiley mill. Composite samples from each stick were analyzed for total C and N concentration using thermal combustion on a Perkin Elmer 2400 Series II CHNS/O analyzer (Perkin Elmer, Waltham, Massachusetts, USA). Total plant tissue P was analyzed using the vanadomolybdate procedure on an HCl extract following sample-ashing at 500 °C (Jackson 1958). Lignin concentration was quantified using the acid detergent fiber method (Van Soest and Wine 1968). Nutrient concentrations were used to calculate molar C:N, C:P, N:P ratios and estimate total nutrient contents by multiplying the concentration by the wood dry mass (Rice et al. 1997). Wood nutrient content was quantified after each collection and changes in nutrient dynamics (mineralization and immobilization) were assessed relative to mean time zero content.

Study Site Characterization and Climate Data

Soil surface heights were measured at each study plot by United States Geological Survey personnel using a TopCon GTS-240NW total station (Topcon Positioning Systems Inc., Livermore, CA, USA) **wi**th ± 2 mm vertical accuracy (Edward Schenk, personal communications). Multiple soil cores (n = 3, 0-10 cm) were collected from each study plot for further laboratory analyses. Soil pH was quantified from air dried subsamples using an 1:1 soil-deionized water slurry (Soil Survey Laboratory Staff 2004). Soil particle size distribution (texture) was quantified using the hydrometer method (Gee and Bauder 1986). Soil organic matter content was estimated using loss on ignition (Soil Survey Laboratory Staff 2004). Total downed wood mass and volume were estimated from study plots using field methods outlined by Woodall and Williams (2005). Composite downed wood samples were collected from each study plot (n = 14 per plot) to calculate mean nutrient contents. Total woody debris C, N, and P were quantified in a similar manner to decomposition samples as indicated above. Monthly climate data including precipitation (mm), mean daily air temperature (°C), and Palmer drought severity index (PDSI) values were collected from the nearest continuous monitoring station located approximately 32 km northeast of the study plots at the Columbia Metropolitan Airport, South Carolina (National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, NC, USA).

Impacts of Red Imported Fire Ants

During the October 2011 field collection, we qualitatively observed significant damage to the bark and outermost sapwood of the majority of red maple sticks retrieved from the field (control wood was not affected). During laboratory processing approximately 65 live ants were collected from inside the red maple sample bags and later identified as red imported fire ants (RIFA, *Solenopsis invicta*) (Wayne Clark, personal communications). No other ant species were present at the time of sampling and wood damage was attributed to RIFA activity. Surface damage to the red maple wood was variable both within plots and across the study toposequnce. To assess the impact of RIFA damage on wood decomposition, percent damage was estimated using point count methods for each collection after infestation (October 2011 to March 2013). Photographs of the upper and lower (soil side down) sides of each individual red maple segment were taken at a fixed vertical distance from the sample (26 cm). Digital photographs (314 dpi) were downloaded and fixed at dimensions of 27×18 cm. Photographs were then overlain with a counting grid (2.25 cm^2 cells) and an equidistant dot grid (2.2 points per cm^2 density). Points falling within the photographed area of the sample stick were quantified into two categories; damaged or undamaged. Tallies were completed manually for both photographs of each sample and surface damage was quantified as a percent of total points tallied for each sample. Another important measure of invertebrate activity is the amount of wood fragmentation occurring during the decay process. Assuming faunal activity results in wood volume loss whereas microbial mineralization is a relatively isovolumetric process (Harmon et al. 1986), estimates of wood fragmentation can be calculated as the difference between density and total mass loss over time (Grier 1978, Yin 1999). Therefore, we calculated fragmentation rates, as a percentage of total mass loss, in this way to compare pre and post-RIFA infestation decomposition processes.

Statistical Analysis

Statistical analyses were performed in SAS 9.2 (SAS Institute 2009). Mean comparisons between initial (time 0) and final (after 700 d) litter quality metrics including lignin content, lignin:N, and molar nutrient ratios (C:N, C:P, N:P) were completed using Student’s t-tests. Mean soil characteristics, wood decomposition rates (mass remaining, *k* constants), and C, N, P content remaining were compared among the four transect landscapes (levee, flat, transitional, backswamp) using one-way analysis of variance (ANOVA) with Tukey’s honest significant difference tests (PROC GLM). Wood decomposition rates were quantified by fitting a negative exponential decay equation outlined by Olson (1963): $y = e^{-kt}$, where *k* is the decay constant, t the time (yrs), y is the fraction (mass at time t / initial mass) of original dry mass remaining at time t. Plot-specific *k* constants were used to calculate wood half-life (0.693/*k*) and 95% decomposition (3/*k*) rates (Olson 1963). To evaluate the relationship between RIFA damage and wood decomposition a logarithmic regression was fitted between surficial damage counts (% surface area) and mass remaining (% original mass). Nonlinear regressions were fitted in SAS (PROC NLIN) using multiple iterations and initial parameter estimates (β0, β1) derived from simple linear regressions (PROC REG). All statistical tests were evaluated using $\alpha = 0.05$.

Results

Toposequence and Climate Characteristics

The study toposequence had an overall elevation gradient of 1.62 m from the river levee to backswamp positions (Table 4.1). Mean surface soil pH was significantly ($F_{3,16} = 19.16$, $P < 0.001$) greater on the levee (5.91) and flat (5.72) landscapes compared to the lower transitional (5.01) and backswamp (5.11) positions. Clay content (0-10 cm depth) was significantly greater ($F_{3,16} = 43.32$, $P < 0.001$) in the backswamp (45%) and transitional (39%) areas compared to the higher elevation levee and flats (26-27%). Mean organic matter content in the upper 10 cm of soil ranged from 6.8 to 8.2% and was statistically similar ($F_{3,16} = 1.03$, $P = 0.41$) across the toposequence positions. Mean standing stocks of downed woody debris were variable for all landscapes, ranging from a minimum of 9.47 ± 2.63 Mg/ha for the flat to 23.67 ± 7.50 Mg/ha in the transitional landscape. There were no significant differences in total downed woody debris mass ($F_{3,36} = 1.05$, $P = 0.38$) or nutrient pools (C, N, P) by landscape (Table 4.1).

Climatic conditions during the study period generally reflected regional drought from 2011-2012 (Fig. 4.2). Mean air temperatures were generally above average, especially from the summer of 2011 until the winter of 2013. Monthly precipitation data were below average from

August 2011 until April 2012. The combination of above average temperatures and lack of precipitation resulted in moderate to severe drought conditions throughout the central South Carolina region in 2011 and early 2012 (Fig. 4.2). Above average precipitation from May-August 2012 ended the drought conditions.

Woody Debris Decomposition

Wood decomposition rates, expressed as a percent original mass remaining, were similar across the toposequence landscapes (Fig. 4.3). Control wood (milled *P. strobus*) was low in initial nutrients and decayed much slower than red maple samples. After 700 d in the field, average control wood mass remaining was still 90.0%. By contrast, the red maple samples decomposed much faster, with an average mass remaining of 28.6% after 700 d in the field. Mass remaining data were similar to wood C content and there were no statistical differences in mean C content by landscape during the study (Fig. 4.4). Carbon dynamics showed net mineralization during all collections and mean C remaining was only 29.4% after 700 d in the field.

Maple wood decomposition was approximately 3-times faster than control wood, suggesting litter quality was an important regulator of wood decay (Table 4.2). Initial lignin concentrations ranged from 12.5 ± 0.3 to 13.4 ± 0.4% and significantly increased over the decomposition study to >24% in all toposequence landscapes. Initial lignin:N ratios ranged from 50.7 ± 3.7 to 69.7 ± 8.7 and decreased in all landscapes as the wood decayed. Mean initial C:N ratios were wide, ranging from 194 ± 14 in the transitional position to 252 ± 25 in the backswamp. Over the course of the study C:N ratios decreased significantly to ≤125 in all landscapes. C:P ratios were variable, both initially and in the final wood collection (Table 4.2). The drier toposequence positions (levee, flat) showed net decreases in C:P with decomposition, while the wetter landscapes (transitional, backswamp) displayed increasing C:P ratios. These opposite trends are reflective of P dynamics, because C mineralization was similar among the landscapes (Figure 4.4). Wood N:P ratios were initially narrow (range 6.3 ± 0.5 to 6.9 ± 0.5) due to relatively less N content compared to P. However, after 700 d in the field N:P ratios widened to >10 in all landscapes.

Wood Nutrient Dynamics during Decomposition

Wood N content displayed both mineralization periods and immobilization peaks (Fig. 4.5). In general, N trends were similar in magnitude among the study landscapes. The largest immobilization phase was observed in the 183 d collection that followed RIFA disturbance in autumn 2011. There was numerically more relative N content in the wetter toposequence landscapes (>125%) compared to the higher elevation flat (111 ± 12.5%) and river levee (98.8 ± 7.6%). Following RIFA infestation and net immobilization phases, N gradually decreased below 100% original content. Only during the 459 d collection (July 2012) was there significantly ($F_{3,36} = 3.19$, $P = 0.035$) more relative N content in the transitional (92.6 ± 9.2%) position relative to the backswamp (58.5 ± 5.4%) landscape (Fig. 4.5). The levee and flat landscapes had similar N remaining (mean 75%), which was not significantly different from the other positions. Another immobilization peak occurred at 548 d (October 2012) followed by net mineralization of N. Mean wood N content after 700 d ranged from 50.8 ± 4.4 to 68.9 ± 6.0%, with a mean of 60.6% original N remaining.

Wood P content showed less immobilization compared to N (Fig. 4.6). From 0 to 59 d in the field, wood P mineralized. There was a significant difference ($F_{3,36} = 3.53$, $P = 0.024$) in P content at 59 d (June 2011), with greater P in the transitional (92.0 ± 5.0%) compared to the levee (70.9 ± 3.4%) positions. The following collection at 95 d indicated net P mineralization in all landscapes except the natural levee, which increased to 94.4 ± 6.4% P remaining. Wood P immobilization in the levee resulted in highly significant ($F_{3,36} = 13.82$, $P < 0.001$) differences among landscapes with the general relationship; levee > transitional ≥ flat ≥ backswamp. RIFA infested the wood in autumn 2011 and the 183 d collection (October 2011) displayed large immobilization peaks in the flat, transitional, and backswamp landscapes (Fig. 4.6). There was significantly ($F_{3,36} = 34.25$, $P < 0.001$) more P immobilization in the backswamp (262 ± 19%) and transitional (220 ± 12%) landscapes compared to the flat (148 ± 10%) and levee (94.8 ± 5.4%). Following the RIFA damage, wood P content displayed a general trend of mineralization and there were no significant differences among the toposequence landscapes. During the final 700 d collection, wood P remaining ranged from 28.9 ± 2.4 to 38.3 ± 3.7% of original content. P remaining after 700 d was numerically greater in the drier landscapes (levee, flat), leading to narrower final C:P and N:P ratios than those of the transitional and backswamp positions (Table 4.2).

Red Imported Fire Ant Impacts on Wood Decomposition

RIFA were noted in the maple wood during the October 2011 collection. Point count estimates of surficial damage were completed to assess the impact of ant infestation on decomposition. There were significant negative, logarithmic relationships between surface damage and mass remaining in all collections (Fig. 4.7). Immediately after infestation (October 2011), most wood had <20% surface damage, but there was still significantly ($R^2 = 0.22$, $F_{1,38} = 11.01$, $P < 0.01$) less mass remaining in samples with greater damage. The same general negative relationship occurred with subsequent samples. For all collections, samples displaying the most bark and outer sapwood damage decomposed faster relative to undamaged wood. As time progressed, samples displayed greater amounts of decay, although the relationship with surface damage remained significant. The effects of RIFA damage were most notable when calculating wood fragmentation over time (Fig. 4.8). There were no significant differences in fragmentation among toposequence landscapes, but fragmentation was minimal prior to ant infestation (mean 1.8 ± 0.4% after 95 d) and increased to 9.3 ± 0.8% at 183 d after RIFA infestation. Fragmentation continued to increase through time, eventually reaching 25.1 ± 1.0% at 700 d.

Following the final 700 d collection, decay constants (*k*) were calculated for each study plot and landscape. The combination of relatively low initial lignin concentration (Table 4.2) and invertebrate damage resulted in fast wood decomposition and high *k* values (Table 4.3). Mean exponential decay constants (*k*) were statistically similar ($F_{3,36} = 0.36$, $P = 0.78$) among the toposequence landscapes, with a mean *k* value (yrs) of 0.650 ± 0.02. Despite differences in RIFA damage, mean exponential decay model coefficient of determination (R^2) values ranged from 0.87 ± 0.03 to 0.92 ± 0.01, indicating the models fit the data fairly well. The average wood half-life and time until 95% decay was 1.11 ± 0.03 and 4.79 ± 0.15 yrs, respectively.

Discussion

Woody Debris Pools and Decomposition

Downed woody debris mass was highly variable (range 9.47-23.67 Mg/ha) along the study toposequence. Downed woody debris pools in CONG were within the range of those typically reported for temperate deciduous forests 11-38 Mg/ha (Harmon et al. 1986). Estimates of downed woody debris in CONG were also greater than those reported by Polit and Brown (1996) of 6.6 Mg/ha for a floodplain forest in Illinois (USA), but similar to values reported by Muller (2003) of 21.8 Mg/ha for an old-growth deciduous forest in Kentucky (USA). Woody debris nutrient pools (specifically N and P) were also variable across the study toposequence in CONG (Table 4.1). Average downed wood pools of N and P were greater in CONG than those reported by Polit and Brown (1996) of 26.5 kg N/ha and 1.67 kg P/ha in a secondary-growth floodplain forest. Our greater estimates of wood biomass and nutrient storage are a reflection of greater dead wood inputs associated with the old-growth forests at CONG (Harmon et al. 1986) and frequent landscape disturbances, such as hurricanes, in the region (Putz and Sharitz 1991, Allen et al. 2005). However, when compared to other old-growth forests downed woody debris stocks were relatively low at CONG, probably due to fast wood turnover times (Wohl et al. 2011).

Decay rates for red maple sticks in this study were very fast, as evident by a *k* rate constant of 0.650 ± 0.2/yr (Table 4.3). Wood decay rates at CONG were much higher than those reported for temperate forests, ranging from 0.004-0.520/yr, but typically <0.100/yr (Harmon et al. 1986, Mattson et al. 1987). A similar decomposition study conducted in an upland landscape of Massachusetts (USA) reported slower rates of decay for red maple sticks <5 cm diameter which had 25.4% mass remaining after 5 yrs (*k* = ~0.274/yr, Berg and McClaugherty 2008). In comparison to data from floodplains and wetlands, red maple wood decomposition at CONG was faster than whole silver maple (*Acer saccharinum* Marsh.) logs in Illinois (*k* = 0.089/yr, Chueng and Brown 1995) and red maple wood in the Great Dismal Swamp of North Carolina (*k* range 0.179-0.305/yr, Day 1982). Rice et al. (1997) also reported average mass remaining of pumpkin ash (*Fraxinus profunda* Bush) fine woody debris to be 42.4-48.1% after 2.5 yrs in the Atchafalaya basin of Louisiana (USA). These decomposition rates were all less than those at CONG, where 26.8-31.4% original wood mass remained after only 1.92 yrs (Fig. 4.3).

These data indicate that wood decay rates at CONG are much faster than those in other temperate zone forests, and approach values reported in tropical ecosystems (Clark et al. 2002). In tropical climates, whole bole *k* rates have been reported up to 0.67/yr (Chambers et al. 2000) and wood turnover times are typically fast, ranging from 5.9 to >20 yrs at the ecosystem level (Buxton 1981, Delaney et al. 1998, Chambers et al. 2000, Clark et al.2002). The average time required for 95% wood decomposition at CONG was 4.79 yrs, which is similar to rates reported in tropical climates. In our study, we utilized fine woody debris (3.0-4.5 cm diameter) from a single overstory species and it is important to note that the high rates of decomposition for these samples may not reflect all downed wood within the riverine forests of CONG. In fact, the majority (>90% total mass) of downed wood along the study toposequence was >7.5 cm in diameter and larger diameter wood from mixed hardwood species may decay at slower rates than those reported in this study (Harmon et al. 1986, Chambers et al. 2000). Although data from our study and past observations (Wohl et al. 2011) suggest extremely fast wood turnover within CONG, further analyses of wood from mixed-species and varied diameter classes are necessary to quantify ecosystem level wood decomposition dynamics.

Fast rates of red maple wood decomposition observed at CONG are likely a result of multiple factors such as high initial litter quality, regional humid subtropical climate, and invertebrate activity. Initial litter quality is extremely important to the decomposition process (Melillo et al. 1982), and litter low in lignin and high in N content typically decays faster than materials with high lignin and low N content (Taylor et al. 1989). The lignin content of wood from CONG (Table 4.2) was nearly half the reported average values for red maple wood ranging from 20.6-24.0% (Koch 1985, Harmon et al. 1986). Although lignin content in CONG wood was low, implying favorable litter quality for decomposition, mean lignin:N ratios were wide (>50) because of low N concentrations. The lignin:N ratio at CONG was very high considering the low initial lignin content of the wood. For example, Melillo et al. (1982) reported a lignin concentration of 10.1% in red maple leaf litter, but a lignin:N ratio of 14.4. Our estimates of initial lignin content were similar to these values, however the lignin:N ratios of the wood were 4 times greater because of low N concentration. Initial wood C:N ratios at CONG were also at the upper limits of those typically reported for fresh (green) wood ranging from 80-250 (Koch 1985, Rice et al. 1997), further suggesting low N content. Initial nutrient contents are more important for short-term decay, while lignin controls later stages of decomposition (Taylor et al. 1989, Berg and McClaugherty 2008). Our data suggest that wood decay should have been initially slow due to low N content, but more rapid during later stages of decay when lignin controls conversion of organic matter to soil humus. However, initial decomposition rates (within the initial 95 d) were rapid across all toposequence landscapes at CONG (Figure 4.3) which suggests that additional landscape factors may have been of greater importance during the early stages of wood decay.

Climatic factors can be as important as initial litter quality for litter decomposition dynamics. Globally, litter decay rates are generally faster in warm and wet climates, compared to cool and dry regions (Harmon et al. 1986, Zhang et al. 2008). However, temperatures exceeding 40 °C or below 5 °C have been shown to inhibit mesophilic microbial processes, such as C mineralization (Harmon et al. 1986, Rabenhorst 2005). CONG is within a humid subtropical climate which rarely has average air temperatures <5 °C (Fig. 4.2), suggesting microbial mineralization can occur year-round at CONG. Carbon mineralization data from our study support this idea because trends in total C mineralization were directly proportional to mass remaining (Figs. 4.3, 4.4) and showed a linear trend throughout the study. These trends suggest that even during cooler months microbial mineralization of C was occurring and represented a major component of total mass loss. In addition, mean air temperatures during summer months (June, July, August, Fig 4.2) were within the optimum range for microbial mineralization of wood. Although temperature conditions were ideal during our study, the region also underwent a wide-spread drought which could have slowed microbial processes by limiting moisture availability within the red maple wood (Berg and McClaugherty 2008). Climatological data indicate that while CONG did undergo moderate to severe drought conditions in 2011-2012, there was approximately 50 mm or greater precipitation during these months (Fig. 4.2). This rainfall likely produced enough moisture to continue microbial decay of wood because net C mineralization occurred during and after drought conditions at the study toposequence (Fig. 4.4). While microbial decay and mineralization of C are recognized as major drivers of wood decomposition (Harmon et al. 1986, Currie et al. 2002), substantial losses of wood mass can also occur via faunal activity and physical fragmentation.

Effects of Surficial Invertebrate Damage on Wood Decay

Regional drought conditions within the study period (Fig 4.2) lowered ground water tables, prevented substantial overbank flooding, and allowed for the establishment of RIFA colonies under canopy openings throughout the CONG study site. The RIFA is a non-native invasive species that was introduced into the southern USA during the early 20th century (Allen et al. 2004). Since their introduction, RIFAs have had many documented impacts on native ecosystems. For example, Morrison (2002) reported that fire ant colonization impacted native ant populations, lowering abundance and species richness, especially in the early stages of landscape invasion. Many terrestrial vertebrates are also impacted by fire ants, specifically ground nesting bird species, reptiles, and certain burrowing mammals have all seen negative population impacts due to RIFA introduction (Allen et al. 2004). RIFAs can also alter soil properties and ecosystem biogeochemistry. Many researchers have reported significant increases in soil organic matter, clay, P, K, Ca, and Mg content within RIFA mounds (Lockaby and Adams 1985, Davis-Carter and Sheppard 1993, Green et al. 1998, Lafleur et al. 2005). RIFA colonies have also been associated with increased growth rates of seedlings in longleaf pine (*Pinus palustris* Mill.) plantations of Louisiana, presumably because ammonium (NH_4^+) concentrations were greater in and around RIFA mounds (Lafleur et al. 2005). RIFA tunnels and mounds also decrease soil bulk density (Lockaby and Adams 1985, Lafleur et al. 2005) which can allow for greater water infiltration and leaching of nutrients to the subsoil (Green et al. 1999). Inherent changes in soil properties can also increase heterotrophic respiration and greenhouse gas emissions (N_2O, CH_4, CO_2) from RIFA mounds (Bender and Wood 2003). Although many changes to soil properties are highly localized (i.e. at a mound scale), entire landscapes can be impacted within a matter of decades because RIFA colonies tend to construct and abandon mound sites frequently in the southern United States (Green et al. 1999).

In contrast to the research of RIFA impacts on native fauna and soils, there have been relatively few studies of their effects on litter decomposition. Invertebrates, such as ants, typically speed up litter decay through direct consumption or fragmentation of wood. However, recent studies in the southern USA have indicated that the presence of ant colonies in woody debris can slow decomposition, because ants prey on wood-consuming termites and limit saprophytic fungi growth through anti-microbial metapleural secretions (Warren II and Bradford 2012). These processes are not directly applicable in CONG because significant RIFA infestation was a one-time event and there was no evidence that the study wood was used as permanent nesting habitat after the autumn of 2011. The data from CONG suggest that RIFA damage increased surface area and allowed for increased decomposition via microbial colonization of the wood impacted by burrowing. Similar invertebrate impacts on wood decomposition have been reported, for example borings from ghost moths (*Hepialus californicus*) in fresh woody debris has been shown to significantly increase decay rates by increasing surface area and stimulating microbial decomposer colonization (Bastow et al. 2008).

RIFA presence in and utilization of wood as a food source is not unprecedented in the southern USA. RIFA nests have been observed in large downed wood and tree stumps following clear-cut operations in the region (Lockaby and Adams 1985). Moreover, RIFAs are omnivorous feeders and multiple reports of RIFA consuming tree sap, floral/extrafloral nectar, and bark have been made in the southern United States (Adams 1986, Banks et al. 1991; Wilder et al. 2011). Furthermore, damage to wood from RIFA activity typically occurs only from early fall through the winter months, corresponding to periods of high demand for carbohydrates (Adams 1986, Banks et al. 1991). CONG wood was infested and damaged by RIFAs in September and October, similar to previously reported time periods of RIFA wood infestation in the region (see Appendix A).

These results show that the surficial damage caused by invertebrate activity impacted the decomposition process and allowed for microbial colonization of freshly exposed wood surfaces. Over time, we noted that the total percent surficial damage was increasing as wood decomposed (see Fig. 4.7 x-axis). Mean wood surface damage immediately following RIFA infestation was only 11.4 ± 2.6% in October 2011, but increased significantly ($F_{4,198} = 12.87$, $p < 0.001$) during subsequent collections to 44.6 ± 3.9% after 700 d in the field. As surface damage increased, there was also a noticeable increase in wood fragmentation (Fig. 4.8). Invertebrate damage was limited to the outer bark and sapwood when RIFAs were found in the samples, but after 459 d in the field (July 2012), extensive invertebrate activity had stripped much of the bark down to the sapwood and wood-borings were also observed penetrating to the inner heartwood of many sticks (Fig. 4.9). Following the initial discovery of RIFAs, there were no more instances of RIFA presence in the study wood. Therefore, the significant increase in wood-borings, surface damage, volume loss, and wood fragmentation observed in collections from 459-700 d are probably not a direct result of RIFAs, but rather foraging invertebrates, such as termites or beetles. These trends highlight the importance of RIFA as facilitators of advanced wood decomposition by opening the outermost bark and sapwood for further invertebrate and microbial utilization over time.

Downed Woody Debris Nutrient Dynamics

In CONG, N content displayed multiple periods of immobilization, especially after RIFA infestation (Fig. 4.5). Invertebrate activity can increase N content in forest litter as a direct result of insect frass (fecal matter) which has high nutrient contents relative to woody material (Bocock 1964, Day 1982, Harmon et al. 1986). Sink activity of N has been noted in the early stages of wood decay in floodplain wetlands (Chueng and Brown 1995, Rice et al. 1997) which has been attributed to overstory throughfall additions, senesced litter leachates, and microbial immobilization of N (Day 1982, Harmon et al. 1986). The largest N immobilization peaks were at 183 and 550 d corresponding to autumn 2011 and 2012, time periods where the potential availability of N from throughfall and senesced litter is greatest. Increased N content during these periods suggests that decomposer microorganism communities within the wood are utilizing seasonal nutrient additions and hence may be N limited. Wood P dynamics at CONG differed from those observed for N and generally showed source activity (net mineralization) except for the 183 d collection immediately after RIFA infestation (Fig 4.6). The large peaks in both N and P after RIFA infestation suggest both nutrients were increased as a result of initial ant activity. Invertebrate activity can increase litter nutrient contents directly through deposition of frass materials (excrement and pellets) in the wood (Bocock 1964) and also through indirect inoculation of the substrate with microorganisms which can further immobilize nutrients

(Harmon et al. 1986, Berg and McClaugherty 2008). N and P dynamics in the study wood suggest more pronounced N limitation, because P generally mineralized after RIFA infestation and N showed more sink behavior indicating the microbial community was likely N deficient. In addition, the initial wood N:P ratios were narrow (<7.0, Table 4.2) further suggesting N limitation to vegetation growth within CONG (Bedford et al. 1999). These data fit the framework of terrestrial nutrient limitation, because CONG is a eutrophic floodplain forest associated with an alluvial red water river that receives mineral additions from watershed sources. Alluviation in red water floodplains deposits mineral and organic P at the soil surface which can exacerbate N limitation over time (Vitousek et al. 2010). Although these data support the idea that the ecosystem is N limited, further studies utilizing fertilization experiments are needed to determine the exact nature of nutrient deficiency within the floodplain forests of CONG.

Unlike N and P dynamics, C immobilization is rare in wood and net mineralization occurred at all stages of decomposition in CONG (Fig. 4.4). A major effect of C mineralization is relative increases in wood N and lignin content during advanced stages of decay (Harmon et al. 1986, Rice et al. 1997, Berg and McClaugherty 2008). Wood C:N ratios narrowed and lignin concentration increased at CONG, but lignin:N ratios also narrowed due to rates of lignin degradation exceeding those of N after 700 d in the field (Table 4.2). Increases in N content and narrowing lignin:N suggest litter quality improvement for further decomposition, but lignin concentration also increased. Average lignin concentrations after 700 d ranged from 24.6 ± 1.8 to 26.9 ± 2.7, which are close to those reported for fresh red maple wood (20.6-24.0%, Koch 1985, Harmon et al. 1986). Greater quantities of N coupled with low lignin concentrations during advanced stages of wood decay suggest that downed wood will continue to rapidly decompose beyond the 700 d period of our study. The activity of invertebrates and high wood litter quality likely contributed to the observed fast turnover times and validates earlier assumptions that rapid decay is partially responsible for the relatively small downed woody debris pools within the old-growth floodplain forests of CONG (Wohl et al. 2011).

Conclusions

In this study, we quantified wood debris pools and turnover times within an old-growth floodplain forest. Our results suggest that the relatively low standing stocks of woody debris are a function of extremely fast turnover times at CONG. The rapid decomposition we observed was a function of invertebrate activity leading to additional surface area, microbial inoculation, and wood fragmentation during the initial stages of decay. These processes facilitated additional mineralization of organic C because the humid subtropical climate of the region is rarely cold enough to limit microbial decomposition. In addition, the red maple wood utilized in our study was found to have high initial litter quality, characterized by low lignin concentration. During advanced stages of decomposition this low lignin content likely allows for more efficient mineralization of wood materials by saprophytic fungi. The fast turnover of wood within the floodplain forests of CONG has obvious consequences for the long term C storage function of woody debris. Although increased annual losses of C via mineralization may imply a net negative ecosystem function, associated rapid cycling of stored N and P may subsidize plant growth leading to increases in net primary productivity and a complete or partial offset of total ecosystem C losses associated with woody debris stocks. Our analysis indicates that woody debris pools are capable of cycling nutrients rapidly, especially in regions where climatic factors allow for nearly continuous year-round faunal disturbance and microbial mineralization. Further research is needed, however, to complete nutrient budgets and understand the importance of downed woody debris as a source and sink of nutrients in subtropical lowland floodplain forests.

In addition, these data have implications when considering the possible future impacts of regional climate change. Climate change is predicted to increase temperatures, decrease precipitation, and result in increased municipal water stress within the Congaree River basin (see McNulty et al. 2013). Warmer average air temperatures and lower frequency of overbank flooding within the region could further accelerate wood decay by providing more favorable conditions for terrestrial fauna (such as fire ants) and microbial mineralization. Many invertebrates responsible for wood decay require dry conditions and if overbank flood pulsing were to decrease due to climatic shifts, greater quantities of invertebrates could colonize the floodplain surface. Larger terrestrial fauna may also increase in numbers as flood pulses decrease. Invasive feral hogs (*Sus scrofa*) populations have been on the rise within CONG and this species is known to fragment large woody debris while foraging for invertebrate food sources. Increases in faunal populations could drastically increase wood turnover within floodplains of the region. Warmer winter temperatures associated with climate change would also allow for faster mineralization of downed wood in subtropical climate zones, further reducing the amount of C storage within short-term reservoirs such as forest floor woody and foliar litter (see Berbeco et al. 2012). Faster turnover of stored wood nutrient pools will further increase CO_2 flux from these once relatively long-term sinks and increase the importance of these components of the forest floor as sources of plant available nutrients. Thus, future nutrient budgets and ecosystem models should take into account woody debris as a changing and dynamic nutrient pool to better understand the impact of potentially rapid nutrient cycling on the functions and values associated with large riparian forests.

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Table 4.1. Summary of study toposequence characteristics, mean values with standard error in parentheses (n = 5, per landform). Different letters within columns are significantly different according to Tukey's HSD tests (α = 0.05).

		Toposequence Characteristics				Downed Woody Debris Mass and Nutrient Pools§			
Landform	Plots	Relative Elevation (m)†	Soil pH‡	Clay (%)‡	Soil Organic Matter (%)‡	Total mass (Mg/ha)	C (Mg/ha)	N (kg/ha)	P (kg/ha)
Levee	1-5	-0.07 (0.03)a	5.91 (0.08)a	26 (2.0)a	6.8 (0.4)a	10.36 (2.96)a	4.77 (1.36)a	25 (7.1)a	9 (3.7)a
Flat	6-10	-0.15 (0.05)a	5.72 (0.17)a	27 (0.5)a	8.2 (0.4)a	9.47 (2.63)a	4.36 (1.21)a	29 (8.3)a	9 (3.5)a
Transitional	11-15	-1.02 (0.15)b	5.01 (0.05)b	39 (1.0)b	7.5 (0.8)a	18.22 (10.1)a	8.40 (4.65)a	79 (52)a	23 (15)a
Backswamp	16-20	-1.62 (0.11)c	5.11 (0.08)b	45 (1.4)c	6.9 (0.9)a	23.67 (7.50)a	11.01 (3.51)a	113 (38)a	28 (10)a

† Elevation relative to the highest point along the study transects (natural river levee, plot 5)

‡ Quantified from topsoil samples (0-10 cm depth)

§ Estimated from sample transects following the methods outlined by Woodall and Williams (2005)

Table 4.2. Summary of mean litter quality at study initiation (time zero) and after the final collection (700 d in the field), standard error in parentheses. Column means within each landscape with different letters are significantly different according to Student's t-tests.

				Molar Ratios		
Landscape	n	Lignin (%)	Lignin:N	C:N	C:P	N:P
Levee						
Initial	10	13.4 (0.4)b	62.1 (3.8)a	218 (16)a	1543 (129)a	6.3 (0.5)a
Final	10	26.2 (3.2)a	56.4 (3.1)a	125 (14)b	1397 (142)a	11.5 (1.9)a
Flat						
Initial	10	12.8 (0.3)b	62.2 (6.0)a	228 (26)a	1632 (121)a	6.6 (0.9)b
Final	10	24.6 (1.8)a	41.6 (3.3)b	97 (11)b	1120 (105)b	10.5 (0.6)a
Transitional						
Initial	10	12.5 (0.3)b	50.7 (3.7)a	194 (14)a	1524 (110)a	6.9 (0.5)b
Final	10	26.9 (2.7)a	48.6 (9.9)a	94 (7)b	1605 (130)a	15.2 (1.2)a
Backswamp						
Initial	10	13.1 (0.4)b	69.7 (8.7)a	252 (25)a	1864 (215)a	6.8 (0.9)b
Final	10	24.8 (1.2)a	48.8 (2.5)b	104 (9)b	2266 (525)a	19.2 (4.1)a

Table 4.3. Summary of mean decay constants (*k*), exponential regression model coefficient of determination (R^2), and predicted mass loss data by landscape, standard error in parentheses.

Landscape	Plots	n	*k*	R^2	Half-Life (yrs)	95% Mass Loss (yrs)
Levee	1-5	10	0.676 (0.06)	0.90 (0.01)	1.09 (0.08)	4.70 (0.37)
Flat	6-10	10	0.637 (0.05)	0.87 (0.02)	1.15 (0.09)	4.97 (0.41)
Transitional	11-15	10	0.639 (0.03)	0.92 (0.01)	1.10 (0.05)	4.78 (0.20)
Backswamp	16-20	10	0.649 (0.03)	0.87 (0.03)	1.09 (0.05)	4.72 (0.22)
Grand Mean	1-20	40	0.650 (0.02)	0.89 (0.01)	1.11 (0.03)	4.79 (0.15)

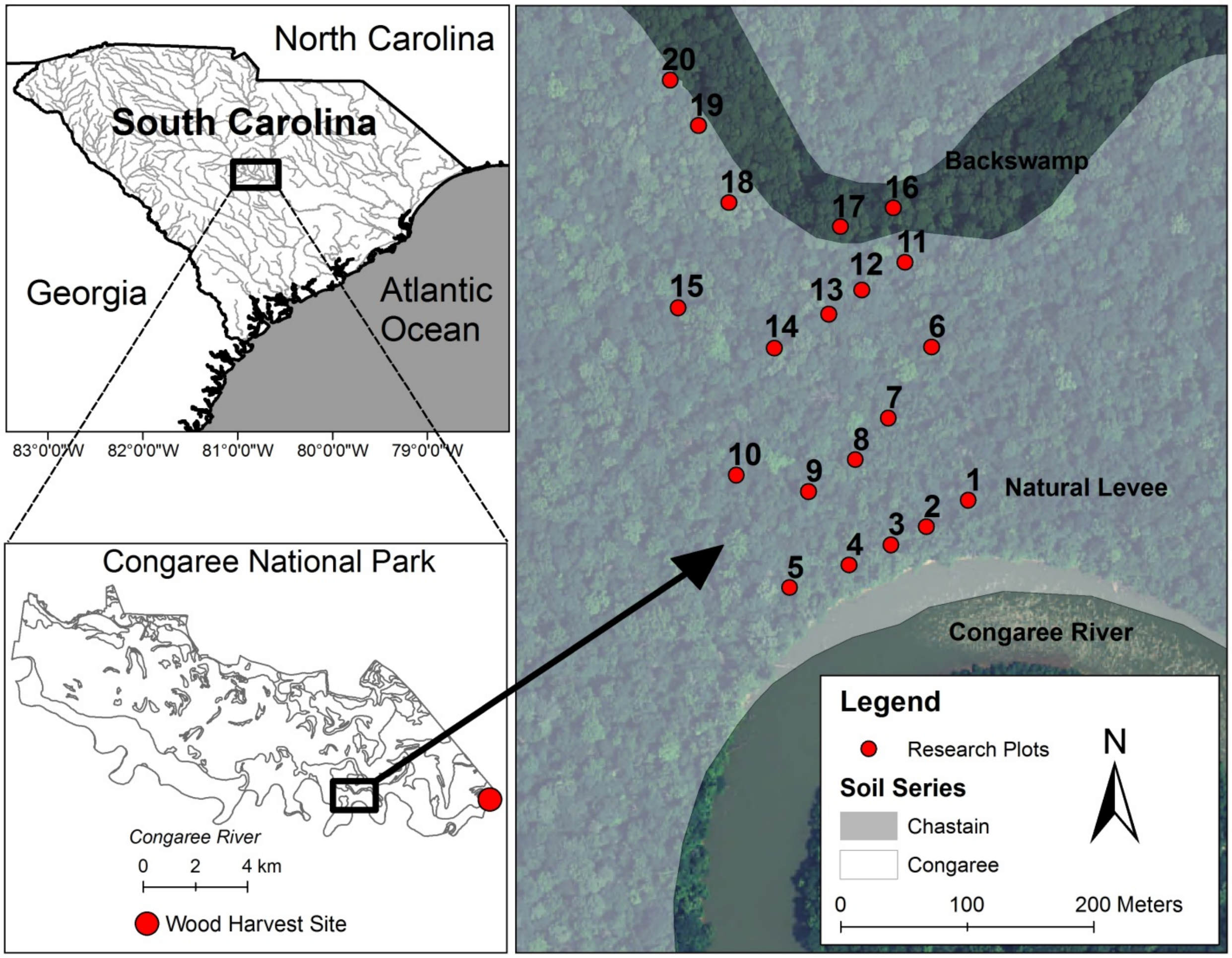


Fig. 4.1. Overview map of study transects and sample plots. The wood harvest site depicted in the inset map was where live red maple (*A. rubrum*) saplings were harvested for the decomposition study.

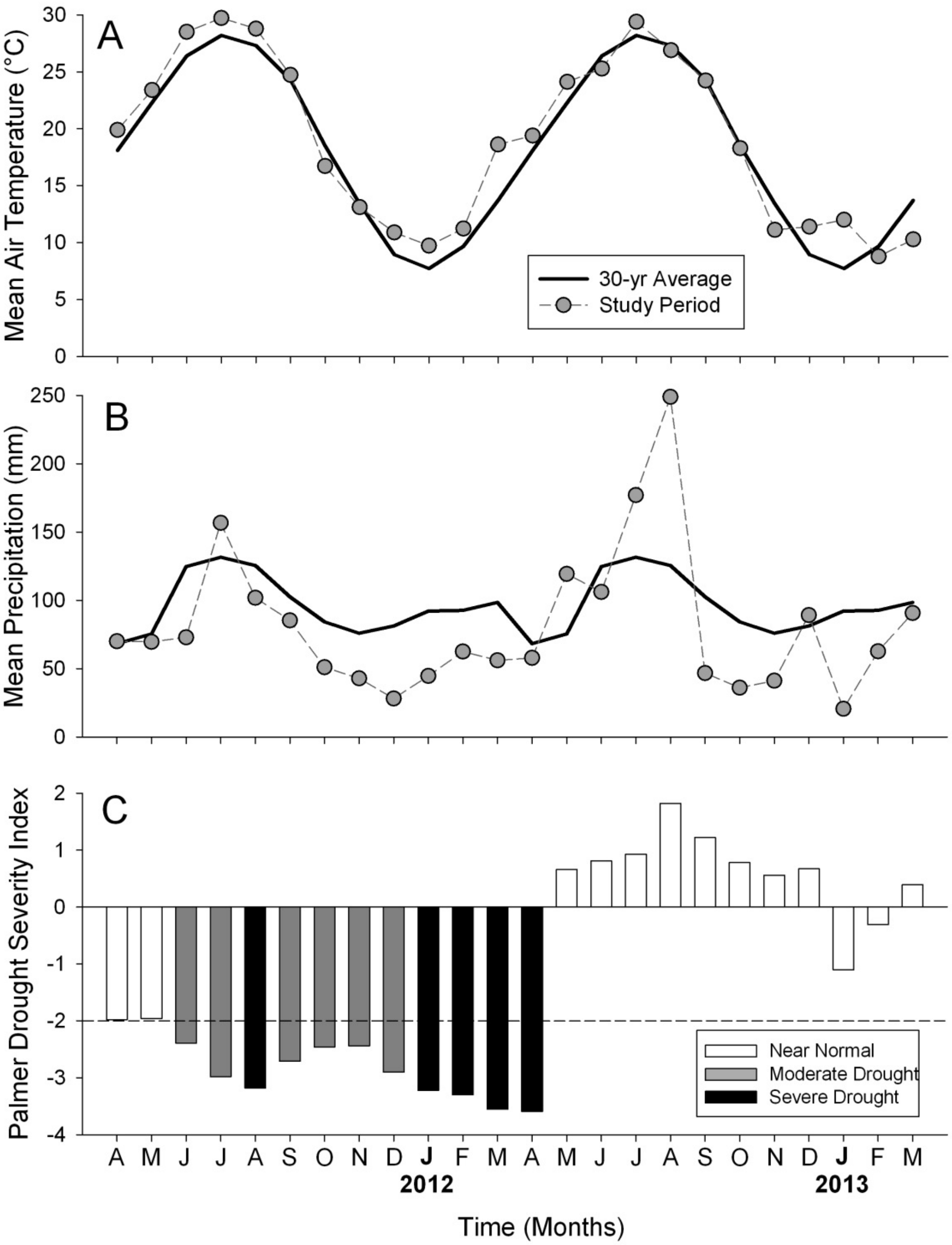


Fig. 4.2. Climatological data over the study period (April 2011-March 2013) from the Columbia South Carolina Metropolitan Airport monitoring station and corresponding Palmer Drought Severity Index (PDSI) for the central region (Division 6) of South Carolina (data source: National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, North Carolina, USA). PDSI values <-2 indicate drought conditions.

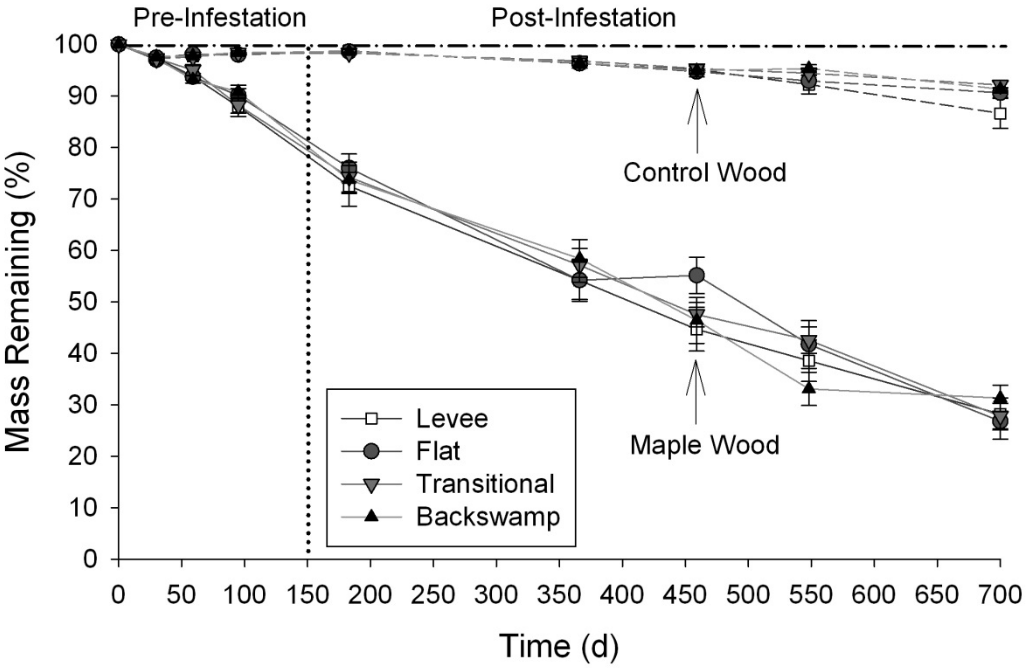


Fig. 4.3. Mean (± 1 standard error) red maple (*A. rubrum*) and control (*P. strobus* dowels) woody debris mass loss (ash free) by landscape from April 2011 to March 2013. Red imported fire ants (*Solenopsis invicta*) infested the red maple wood in September 2011, approximately 150 days into the decomposition study.

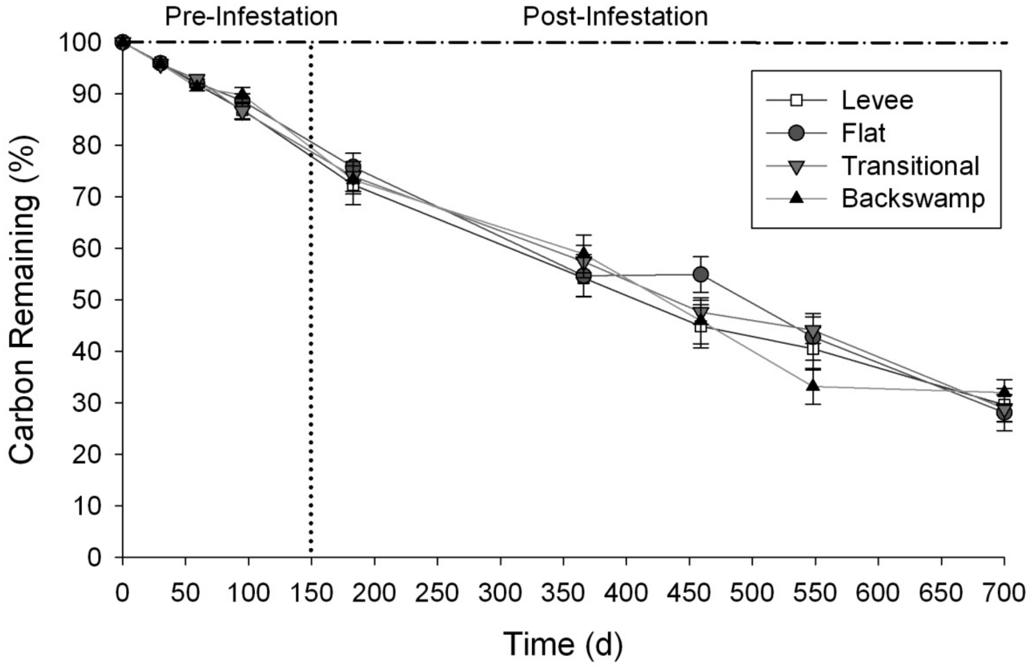


Fig. 4.4. Mean (± 1 standard error) carbon remaining in red maple woody debris by landscape from April 2011 to March 2013.

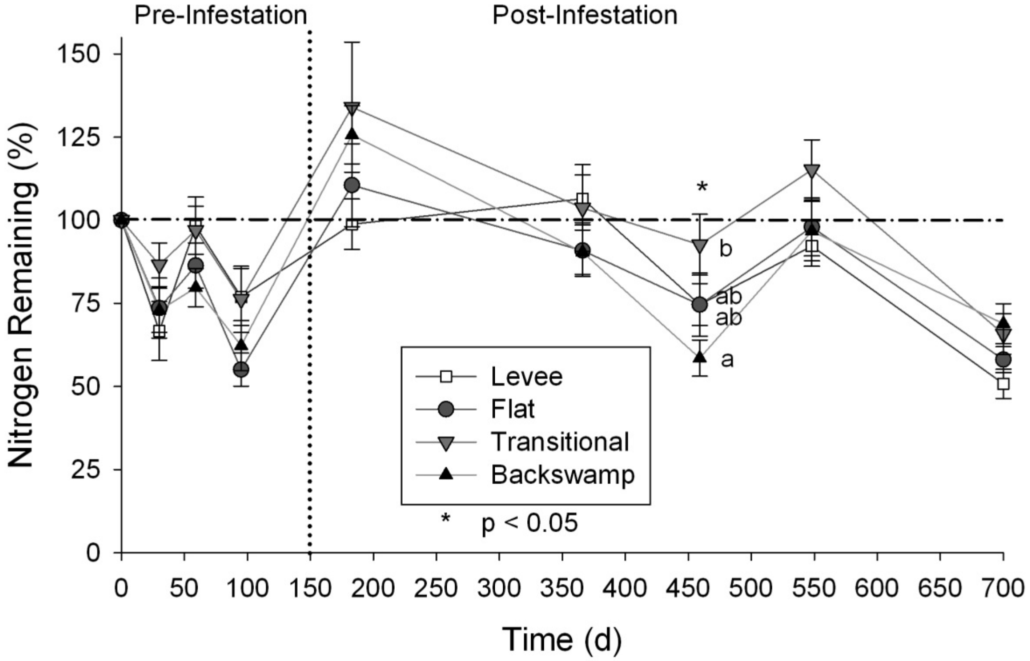


Fig. 4.5. Mean nitrogen remaining (± 1 standard error) in red maple woody debris by landscape from April 2011 to March 2013. Means with different letters are significantly different according to Tukey's HSD tests.

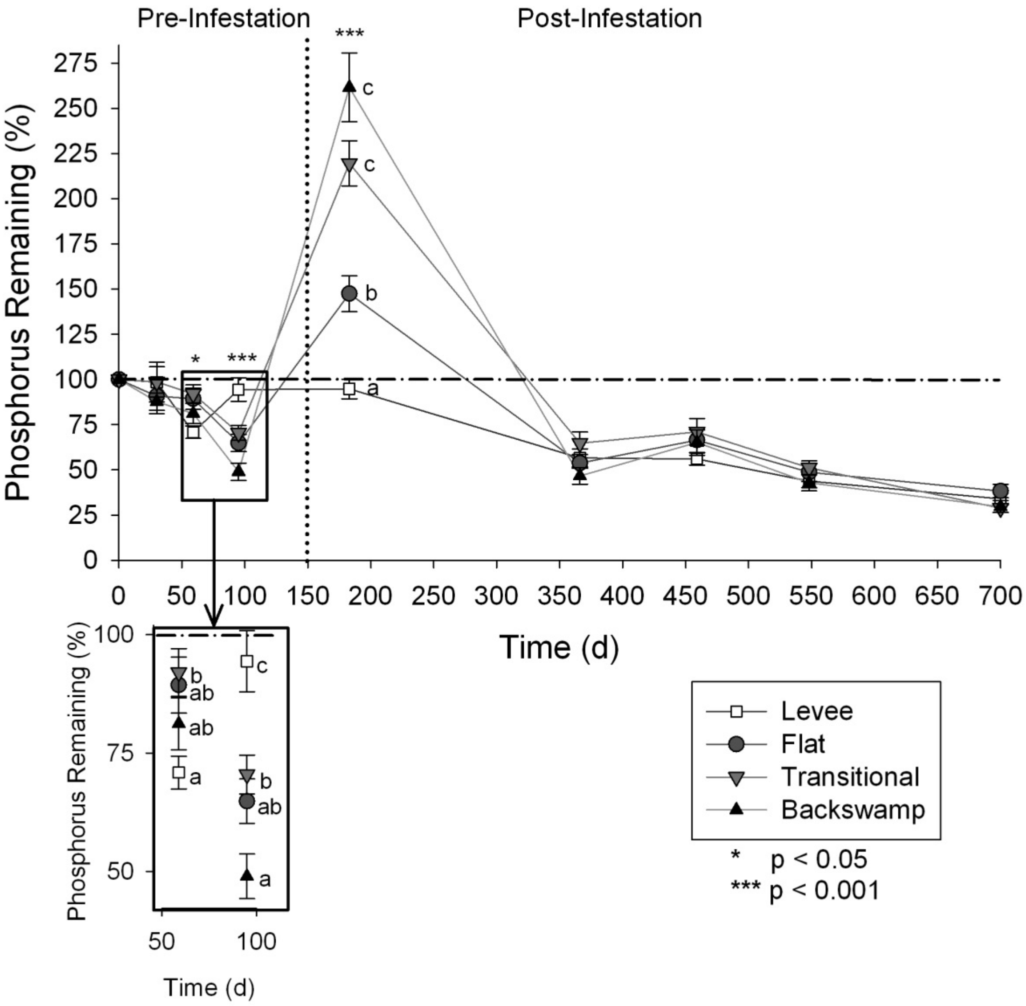
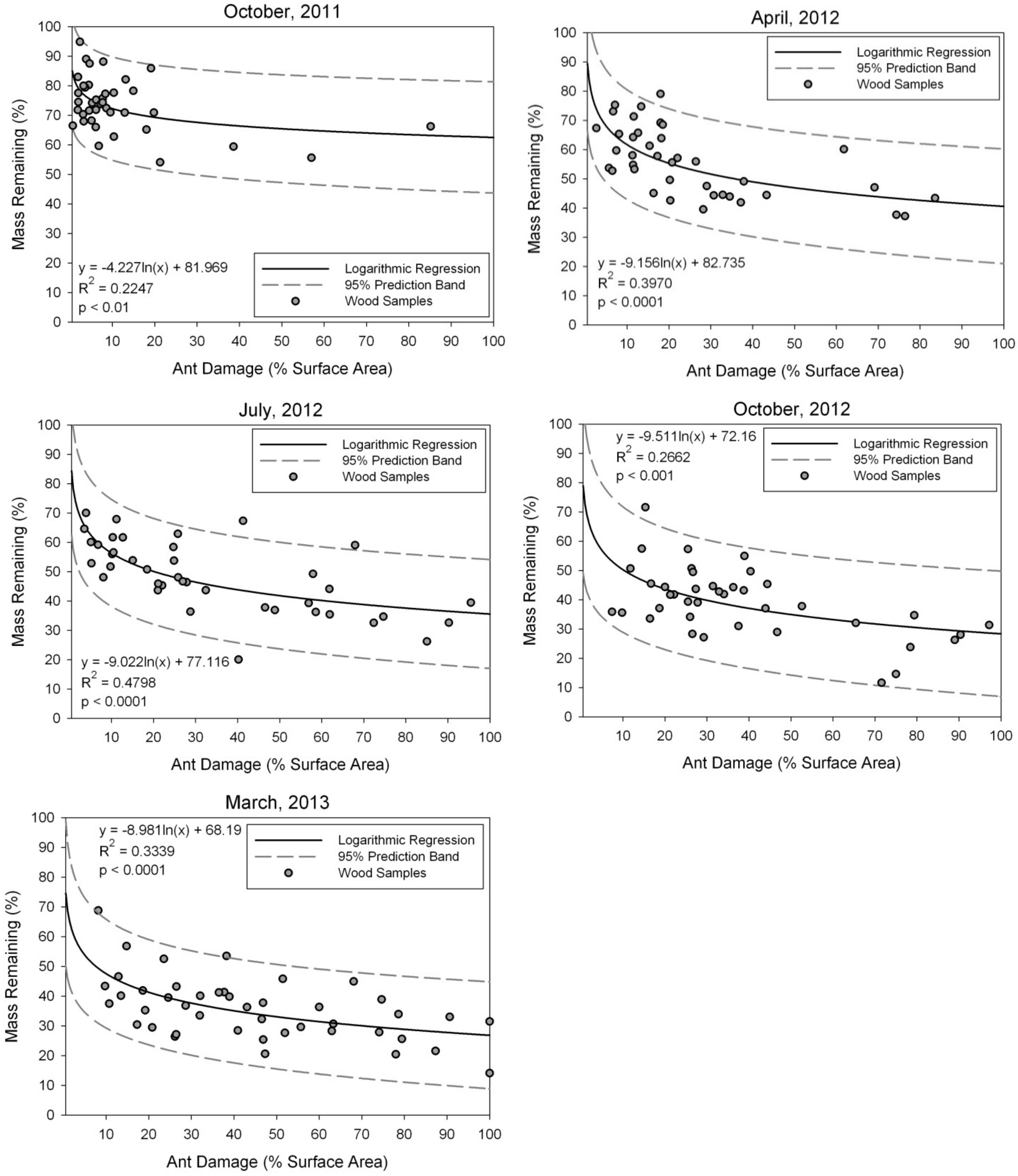


Fig. 4.6. Mean phosphorus remaining (± 1 standard error) in red maple woody debris by landscape from April 2011 to March 2013. Means with different letters are significantly different according to Tukey's HSD tests, note the graph inset of significant differences prior to ant infestation.


October, 2011

April, 2012

July, 2012

October, 2012

March, 2013

Fig. 4.7. Summary of significant logarithmic relationships between surface area damaged on red maple (*A. rubrum*) woody debris by red imported fire ants (*Solenopsis invicta*) and mass remaining through time averaged over all toposequence plots.

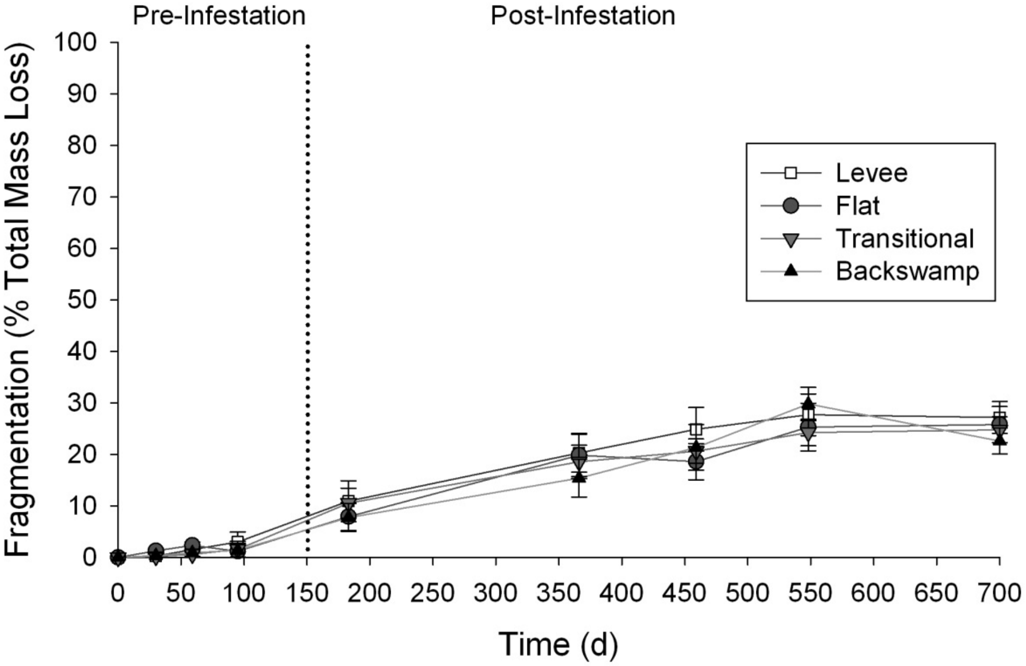


Fig. 4.8. Mean red maple wood fragmentation (± 1 standard error) by landscape from April 2011 to March 2013.

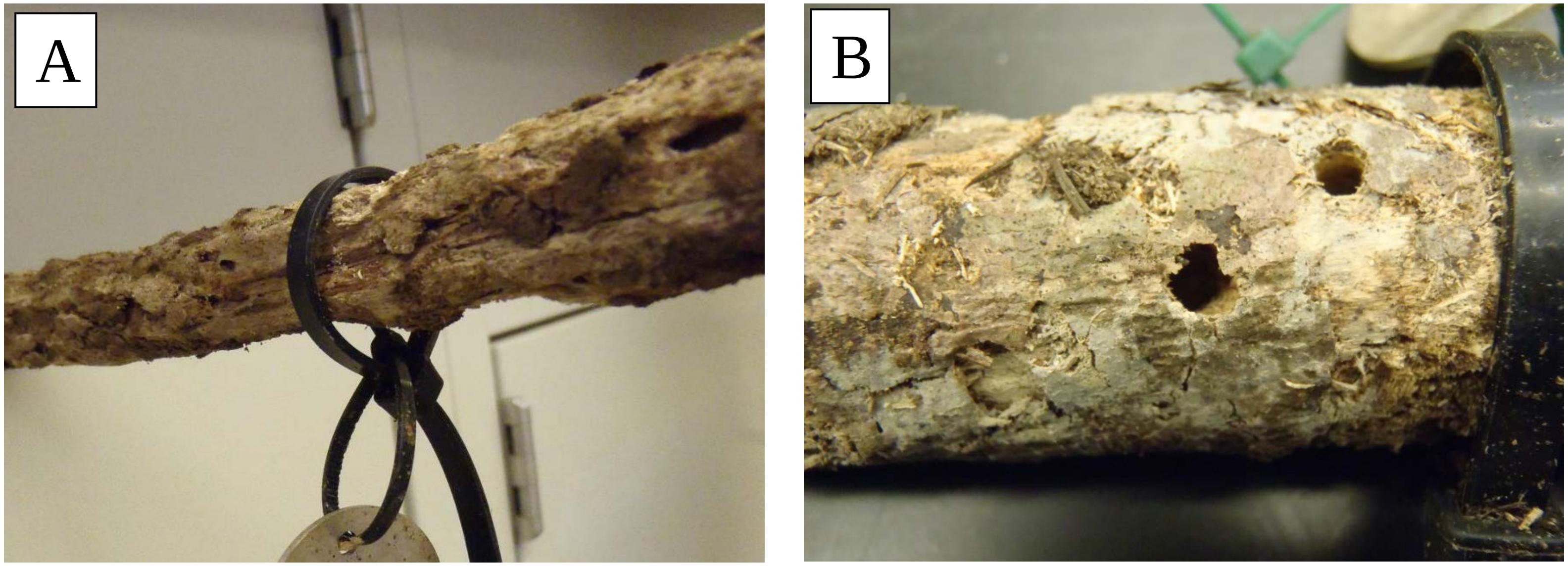


Fig. 4.9. Photographs of red maple (*A. rubrum*) wood in advanced stages of decay from July 2012 (after 459 d in the field). A: Photograph of significant invertebrate damage to outer bark and sapwood of a wood sample, resulting in significant original volume loss. B: Evidence of substantial wood-boring invertebrate activity, borings typically penetrated to the inner-most heartwood.

Chapter 5:

Summary and Conclusions

The primary objective of this research was to measure floodplain nutrient storage and cycling in Congaree National Park (CONG), South Carolina. The specific goals were to i) quantify and compare soil organic carbon (SOC) storage among alluvial soil landscape units; ii) examine the effect of landscape variability on soil biogeochemistry through net nitrogen (N) mineralization, microbial biomass, and phosphorus (P) saturation; iii) quantify ecosystem nutrient storage in downed woody debris and; iv) assess woody debris decomposition and nutrient source-sink relationships using *in situ* methodologies.

Results from this study indicated that alluvial hydric soil mapping units contain significantly greater amounts of SOC to depths of 100 and 200 cm compared to alluvial landforms mapped as non-hydric. Carbon (C) depth distributions showed that deep (>100 cm) SOC storage is particularly important in hydric floodplain soils, which reflect episodic burial and preservation of former floodplain surfaces. Spatial analysis of SOC storage within CONG and the greater Coastal Plain region indicated that approximately 0.1 Pg of SOC is stored in large floodplains. In addition, the largest quantities of alluvial SOC were stored in hydric soil landscapes, but coarse-scale soil associations tended to omit these small spatial components, such as organic Histosols. These analyses suggest that determination of the spatial extent of floodplain wetlands is critical for obtaining accurate estimates of SOC stocks and regional estimates may underestimate the true extent of C storage in alluvial settings if deep (>100 cm) soil horizons are not considered.

Results from our analyses of key biogeochemical indices showed that microbial biomass was relatively stable seasonally, displaying few significant correlations with environmental variables. In addition, the soils of CONG were not currently saturated with P, due to abundant poorly crystalline Fe and Al concentrations. Net N mineralization showed seasonal trends and the dominant product was NO_3-N, which is uncommon in acid forest soils of the southeastern United States. Only intermittent spring flooding resulted in significant NH_4-N production within low-lying topographical landscapes, suggesting annual flood pulsing is necessary to inhibit nitrification and stimulate ammonium production. Nitrate production was ubiquitous among the floodplain hardwood forests we studied regardless of stand age and soil moisture content, which suggests that inherent soil properties (including the microbial community structure) drive nitrification rates.

Our results regarding woody debris pools and turnover suggest that the relatively low standing stocks of woody debris at CONG are a function of extremely fast turnover times. The rapid decomposition observed within CONG was a function of invertebrate activity leading to microbial inoculation and wood fragmentation during the initial stages of decay. These processes facilitated additional mineralization of organic C because the humid subtropical climate of the region is rarely cold enough to limit microbial decomposition. In addition, the red maple wood utilized in our decay study was found to have high initial litter quality, characterized by low lignin concentration. Our analysis indicates that woody debris pools are capable of cycling nutrients rapidly; however, further research is needed to complete nutrient budgets and understand the importance of downed woody debris as a source and sink of nutrients in subtropical lowland floodplain forests.

Synthesis and Future Directions

To our knowledge, very little research has been completed in old-growth bottomlands and the biogeochemical indices quantified here represent baseline data upon which further studies can be undertaken. In the future, river flows will likely continue to decrease as the southeastern United States experiences water stress to meet the demands of a progressively urbanizing landscape. Drying of the alluvial landscapes at CONG may reduce the ability of the floodplain to act as a sink for C and P by limiting river-floodplain hydrologic connectivity. Reductions in river high flows may also increase the duration of aerobic soil conditions that favor net mineralization of stored SOC. High rates of nitrification were observed during drought within CONG and drier climate conditions in the future could also result in excess production of soil NO_3-N, which may ultimately leach to surrounding waterways. Warmer average air temperatures and lower frequency of overbank flooding within the region could also accelerate wood decay by providing more favorable conditions for terrestrial fauna (such as fire ants) and microbial mineralization, further reducing the amount of C storage within forest woody litter. Faster turnover of stored wood nutrient pools could increase CO_2 flux from these once relatively long-term sinks and increase the importance of these components of the forest floor as sources of plant available nutrients (N, P, base cations). Therefore, careful assessment of future climate and river flow scenarios is needed to predict changes in nutrient sink/source dynamics within the old-growth forests of CONG.

Appendix A: Representative photographs of study plots in Congaree National Park, South Carolina, USA (33°46’19.33”N, 80°43’36.55”W).

FIG. A1. Photograph of study plot #2 representative of the well drained natural river levee (painted marker represents the center of a 10 m diameter circular plot). Dominant overstory species include sweet gum (*Liquidambar styraciflua*), American sycamore (*Platanus occidentalis*), sugarberry (*Celtis laevigata*), and pawpaw (*Asimina triloba*). Photo credits: M.C. Ricker

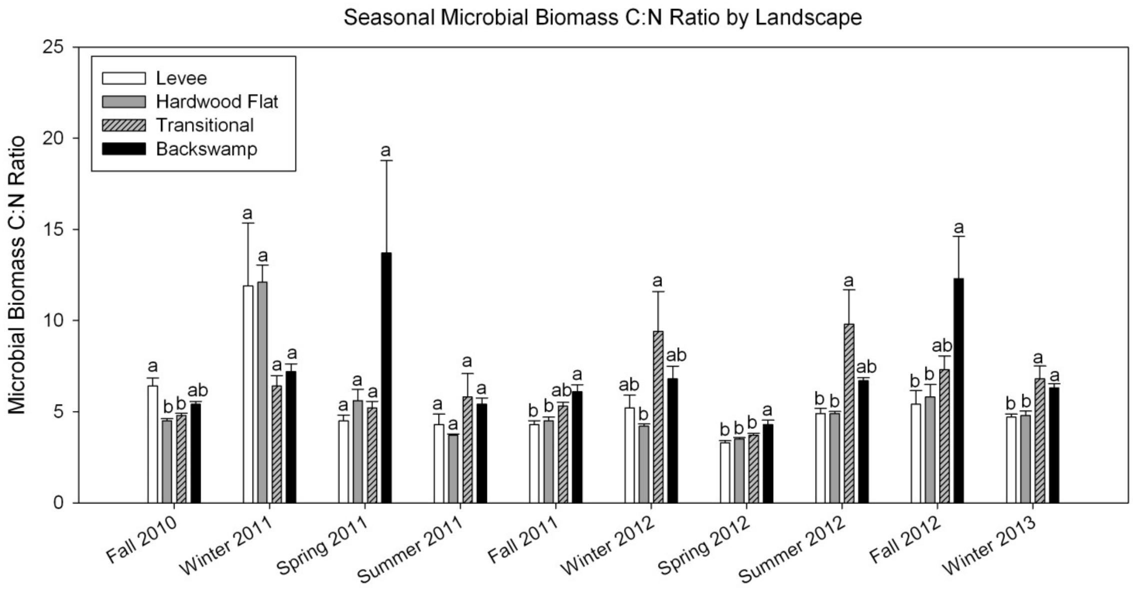
FIG. A2. Photograph of study plot #6 representative of the moderately well drained hardwood flat landscape (painted marker represents the center of a 10 m diameter circular plot). Dominant overstory species include sweet gum (*Liquidambar styraciflua*), sugarberry (*Celtis laevigata*), and various bottomland oaks (*Quercus* spp.). The flat understory contained many switchcane (*Arundinaria gigantea* (Walter) Muhl. ssp. *tecta* (Walter) McClure) breaks. Photo credits: M.C. Ricker

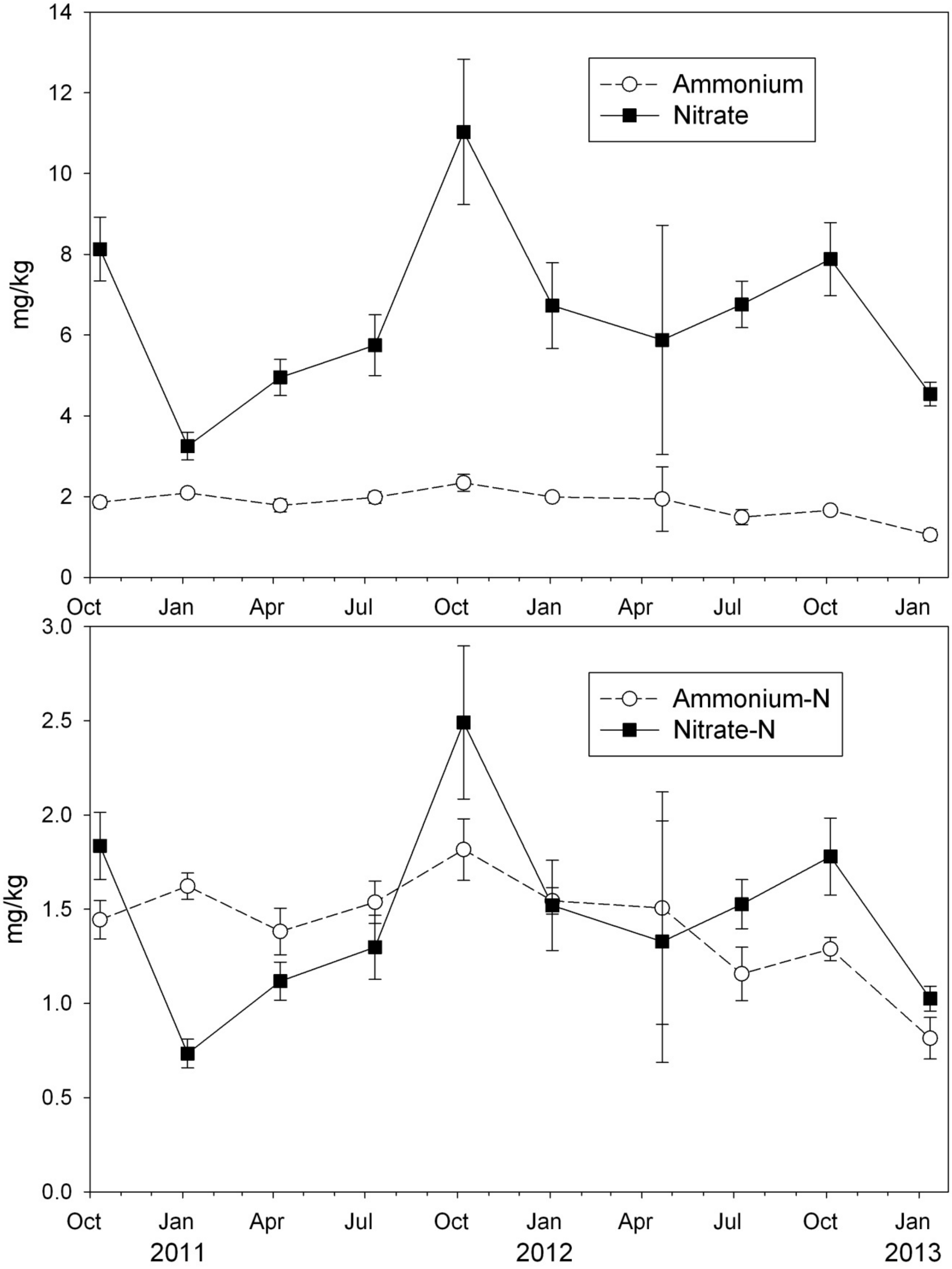
FIG. A3. Photograph of study plot #12 representative of the somewhat poorly drained transitional landscape (painted marker represents the center of a 10 m diameter circular plot). Dominant overstory species include various bottomland oaks (*Quercus* spp.), baldcypress (*Taxodium distichum*), and American sycamore (*Platanus occidentalis*). The transitional landscape understory was generally open and high water marks to 1.5 m were present on the tree trunks. Photo credits: M.C. Ricker

FIG. A4. Photograph of study plot #19 representative of the poorly drained backswamp landscape (painted marker represents the center of a 10 m diameter circular plot). The overstory was dominated by baldcypress (*Taxodium distichum*). The backswamp landscape understory was generally open and high water marks to >2.0 m were present on the tree trunks. Photo credits: M.C. Ricker

FIG. A5. Photograph of red imported fire ant (RIFA, *Solenopsis invicta*) workers actively stripping the outer bark and sapwood from freshly fallen woody debris at the edge of an urban forest patch in Auburn, Alabama, USA. Photo was taken 09/22/2013, corresponding to the general time period (early autumn) that RIFAs infested red maple (*Acer rubrum*) wood at Congaree National Park, South Carolina. Photo credits: M.C. Ricker

Appendix B: Chapter 3 Supplemental Data

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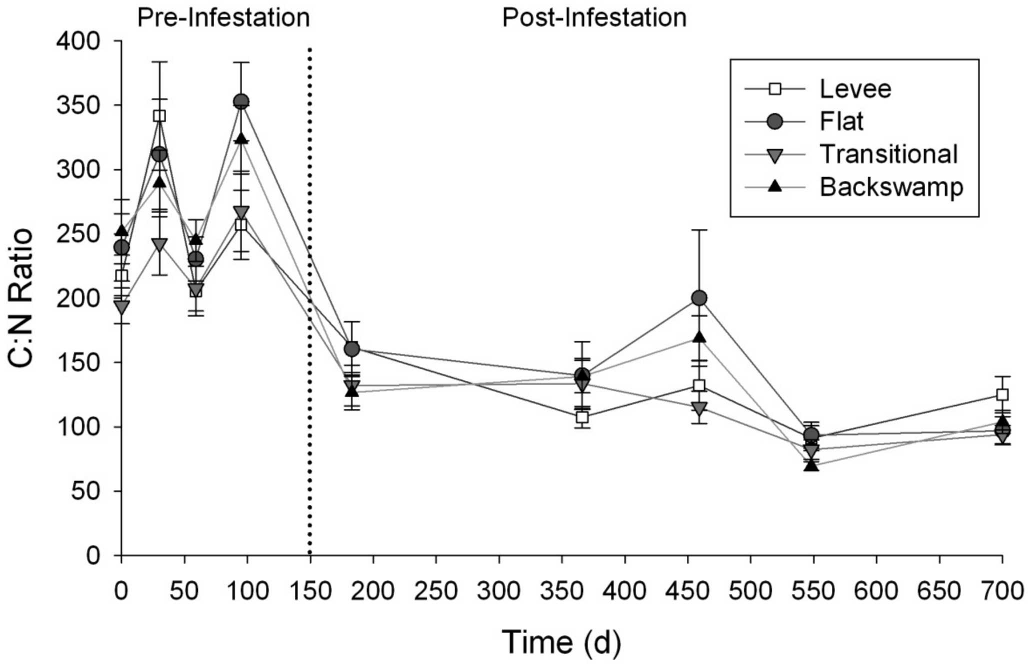
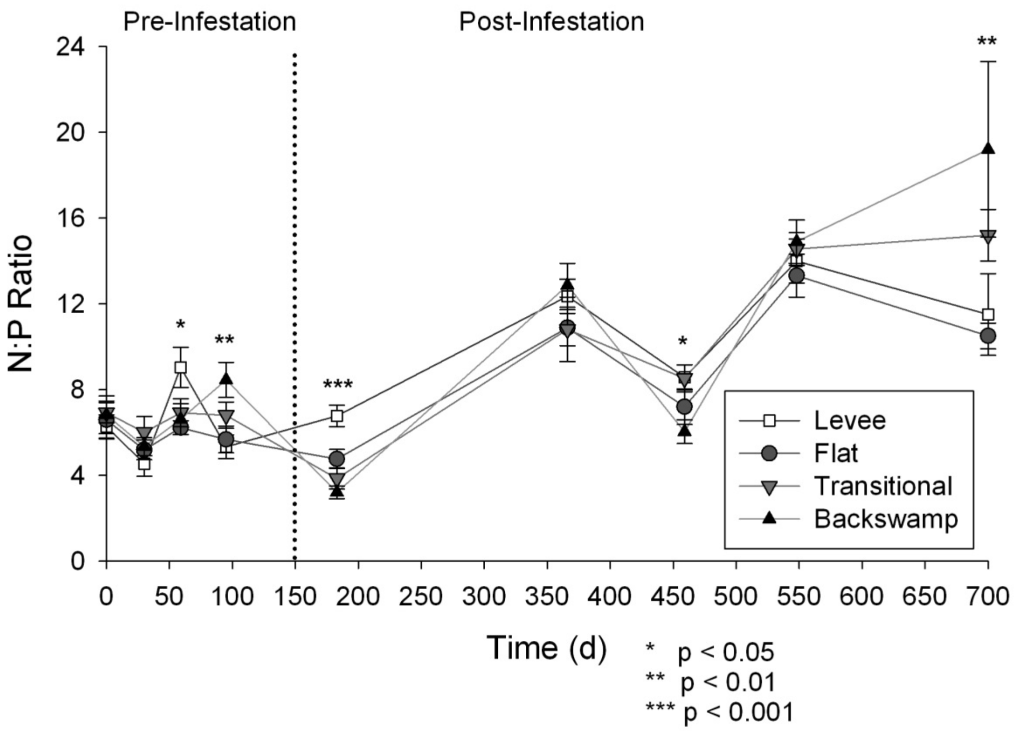
12
10
8
6
4
2
0
mg/kg
Ammonium
Nitrate
Oct
Jan
Apr
Jul
Oct
Jan
Apr
Jul
Oct
Jan
3.0
2.5
2.0
1.5
1.0
0.5
0.0
mg/kg
Ammonium-N
Nitrate-N
Oct
Jan
Apr
Jul
Oct
Jan
Apr
Jul
Oct
Jan
2011
2012
2013

Appendix C: Chapter 4 Supplemental Data





Pre-Infestation
Post-Infestation
N:P Ratio
24
20
16
12
8
4
0
0
50
100
150
200
250
300
350
400
450
500
550
600
650
700
Time (d)
*
**
***
*
**
Levee
Flat
Transitional
Backswamp
* p < 0.05
** p < 0.01
*** p < 0.001