Influence of microtopography and nutrient limitation on belowground productivity in an old-growth floodplain forest at Congaree National Park, SC, USA

by

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Abstract

This study was designed to improve our understanding of nutrient cycling, C storage and belowground net primary productivity (BNPP) in an old-growth floodplain forest. Four microsites were established parallel to the Congaree River on a floodplain in Congaree National Park, SC, decreasing in elevation from the river (natural levee > flat > transitional > backswamp). Response variables for each microsite included: BNPP (June 2011-March 2013) and results from two fertilized root in-growth core studies (summer 2012, fall 2012). BNPP decreased significantly in the following order: natural levee, flat, transitional, and backswamp. Combined N+P fertilization treatments significantly increased fine root productivity relative to the control, suggesting that N and P co-limit fine root productivity in this floodplain forest. Results indicate that significant differences in root growth patterns and nutrient dynamics occur along an elevational gradient, and water availability has a greater effect on fine root productivity than does a single nutrient.

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Chapter 1:

Thesis Introduction

Globally, floodplain forests are unique and diverse ecosystems that provide many ecosystem services such as flood control, stream flow maintenance, retention of sediments, stabilization of banks, fish and wildlife habitat, and maintenance of water quality (Penka et al., 1985; Craft and Casey, 2000; Copeland et al., 2010; Gregory et al., 1991). They also trap sediments and pollutants (Lowrance et al., 1986; Noe and Hupp, 2009; Montreuil et al., 2010) as well as sequester C (McCarty et al., 2009; Copeland et al., 2010).

Human impacts to wetlands are one of the most important ecological issues of current times. According to Copeland et al. (2010), over 89 million hectares of wetlands, including floodplain forests, are thought to have existed in the lower 48 United States in the 1600s. Now, over half the original wetland area has been drained and converted to other uses, the largest of which is agriculture. Climate change, disruption of upland to aquatic linkages, shoreline modification, altered sediment supply and transport, altered hydrology, land-use change, development on uplands, chemical and microbiological alterations, invasive species, introduction of non-native organisms, and disruption of fire regimes are a few examples of other anthropogenic alterations that occur in or otherwise impact wetlands (Euliss et al., 2008; Cox et al., 2006; Keddy, 2010). Floodplain forested ecosystems are at risk of being degraded or destroyed due to anthropogenic disturbances, such as urbanization or agriculture, and are especially susceptible to changes to patterns of sediment deposition (Vogt et al., 1995; Mahaney et al., 2004; Cavalcanti and Lockaby, 2005). Sediment deposition influences many functions of a floodplain forest such as nutrient enrichment and, in some cases, changes can indirectly cause increased tree mortality (Lowrance et al., 1986; Craft and Casey, 2000; Prior and Johnes, 2002; Mahaney et al., 2004; Jolley et al., 2009).

Flooding plays a dominant role in the function of a floodplain forest. The driving force behind the major interactions, productivity, and existence of a river-floodplain system is the concept of flood pulse (Junk et al., 1989). The flood pulse concept states that the pulsing of river discharge is the major force controlling biota in rivers and floodplains, meaning that the lateral exchange between the floodplain and river, and nutrient cycling in the floodplain, directly impacts the floodplain biota (Vannote et al., 1980; Junk et al., 1989). The magnitude, duration, and timing of flooding are important factors in controlling net primary production (NPP) in these forests (Megonigal and Day, 1992) because NPP affects the amount of oxygen that reaches the roots as well as control the life cycles and abundances of primary producers and decomposers: these, in turn affect the level of utilization and regeneration of nutrients (Junk et al., 1989). Fertility in floodplains relies on the nutrient status of the water and sediments suspended in the water (Junk et al., 1989). Timing of floods can have varying effects on productivity in forests. Huffman and Forsythe (1981) state that flooding typically impedes tree growth because the rhizosphere and soil become anaerobic; although in floodplain forests, Gosselink et al. (1981) found that winter or spring floods have a positive effect on productivity because nutrients and water are distributed to the soil before aboveground plant growth begins.

When flooding occurs, sediments and nutrients are deposited onto the floodplain. Although sedimentation can influence floodplain ecosystems positively by augmenting soil fertility (Naiman and Decamps, 1997; Hupp, 2000), high rates of sedimentation may act as a stress by reducing gas exchange (Lockaby et al., 2005). An increase in sedimentation may produce negative effects on NPP by altering both light availability to seedlings and soil temperature (Mahaney et al., 2004), by creating anoxic conditions in soils similar to flooding (Cavalcanti and Lockaby, 2005; Lockaby et al., 2005), by decreasing the growth rate of certain tree species such as red oak (*Acer rubrum*), green ash (*Fraxinus pennsylvanica*), and pin oak (*Quercus palustris*) (Walls et al., 2005), by reducing the establishment and germination of seedlings (Mahaney et al., 2004) and by causing declines in important features of biotic communities, such as decreased tree growth (Bazemore et al., 1991). Decreases in belowground productivity have been reported with sedimentation rates as low as 0.01 cm yr^{-1} (Jolley et al., 2009). Other comparable sites to the Congaree National Park floodplain have average sedimentation rates ranging from 0.02—0.64 cm yr^{-1} (Hupp and Morris, 1990; Hupp and Bazemore, 1993; Hupp et al., 1993; Heimann and Roell, 2000; Hupp et al., 2008).

Fine root dynamics are an important pathway by which water, energy, and nutrients can be transferred from the soil to the atmosphere in a forested ecosystem. Fine roots are defined as non-woody, small diameter roots with mycorrhizae (Nadelhoffer and Raich, 1992), with a range in diameter from 0 to less than or equal to 3 mm and can account for up to 75% of NPP in some forests (Nadelhoffer and Raich 1992; Jackson et al., 1997) and about half of the C being cycled each year in forests (Vogt et al., 1996). Forests play an important part in C sequestration not only by storing C in above ground biomass but also in fine roots. Litterfall and fine roots allow a pathway for C to be transferred from vegetation to soil and therefore sequester C underground. Although this portion of vegetation is important in many biogeochemical processes that maintain the forest production and structure, most productivity research in forested floodplains focuses only on estimations of litterfall and wood production since they are less difficult to study (Brinson et al., 1980; Conner, 1994; Megonigal et al., 1997).

Changes in belowground biomass can serve as an early indicator of stresses in an ecosystem since changes in aboveground ecosystem structure are not apparent until the system is sufficiently degraded to reflect visual changes (Vogt et al., 1993). Flooding initially affects plant roots; therefore, prolonged flooding may not show damage to the aboveground vegetation immediately (Broadfoot and Williston, 1973). When roots undergo prolonged flooding, damage may occur from lack of oxygen and from microbial communities breaking down root components. Many studies have found that fine root productivity was reduced in poorly drained sites along a wetness gradient (Megonigal and Day, 1988; Powell and Day, 1991; Baker et al., 2001; Clawson et al., 2001; Newman et al., 2006; Chacón et al., 2008).

General knowledge of belowground productivity in floodplain forested ecosystems is limited (Vogt et al., 1986; Megonigal et al., 1997; Lockaby and Walbridge, 1998). Since the fine root system is one of the least studied portions of floodplain forests, this research effort investigated the effects of an elevational gradient and nutrient augmentation on fine root dynamics in Congaree National Park, SC. The specific goals were to 1) assess the dynamics of fine roots and quantify how belowground net primary production changes along a topographical sequence and wetness gradient and 2) determine if N or P limits productivity.

> <u>Hypothesis 1</u>: Two peaks in fine root productivity will occur: spring and winter. The spring peak is associated with warming soil and air temperatures and also increasing daylight. The fall peak is associated with senescence of foliage, plants will be able to expend more energy on belowground growth than aboveground growth. Fine root production will decrease as microsite elevation decreases. Fine root biomass will decrease as distance from the natural levee increases due to an increasing wetness

gradient which reduces oxygen that is available to roots, impeding root respiration and development (Kozlowski et al., 1991).

Hypothesis 2: In a redwater alluvial floodplain such as the Congaree National Park, N will limit forest productivity more than P. Floodplain forests that are located adjacent to redwater rivers, which are characterized by high sediment and nutrient loads derived from Piedmont soils (Sharitz and Mitsch, 1993), are typically N deficient and consequently N will play a stronger role in limiting production (Lockaby et al., 1996; Lockaby and Conner, 1999; Schilling and Lockaby, 2005; Schilling and Lockaby, 2006).

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Chapter 2:

Fine root productivity across a topographical sequence in an old-growth floodplain forest at Congaree National Park, SC, USA

Abstract

The effects of an elevational gradient on fine root dynamics were examined in the Congaree National Park, SC. Live and dead fine roots (0.1-1.0, 1.1-2.0, 2.1-3.0 mm) were collected from 20 plots at four microsites (natural levee > flat > transitional > backswamp) from June 2011 to March 2013. Samples were dried, weighed and analyzed for C, N, and P. Belowground net primary productivity decreased in the following order: natural levee (684 g m^{-2}), flat (482 g m^{-2}), transitional (431 g m^{-2}), and backswamp (341 g m^{-2}). Fine root turnover rates (10.3, 10.1, 12.4, 13.4 yr^{-1}, respectively) increased as elevation decreased and wetness increased from the natural levee to the backswamp. Live fine root C, N and P contents followed the same trends as biomass, decreasing from natural levee, to flat, to transitional, and reaching least contents in the backswamp microsite. Live roots also had a larger C:N ratio than dead roots. Results indicated that significant differences in root growth patterns and nutrient dynamics occur along elevational gradients, providing key information for understanding C storage on forested floodplain systems.

Key words: fine roots, belowground net primary production, elevational gradient, floodplain forest

Research on the response of forested systems to drought, flooding, and climate change usually evaluates only aboveground biomass (Gutenspergen and Vairin, 1998; Conner et al., 2002; Conner et al., 2011). Data on drought effects on fine roots are generally minimal, but are even more scarce for floodplain forests, especially in the southeastern United States where drought impacts are predicted to become more intense and frequent. Forecasts from climate change models used by the Cornerstone Futures in the Southern Forest Futures Report indicate a warmer climate in the future with an average increase of 2.5 to 3.5°C in annual temperature by 2060 (McNulty et al., 2011). Hydrologic regime is one of the major controlling factors of forest structure and productivity (Conner and Day, 1982; Anderson and Mitsch, 2008). Since precipitation levels are predicted to decrease in the southeast (McNulty et al., 2011), it is beneficial to understand the effect that this shift may have on fine root production, turnover, and nutrient cycling, especially in forested wetland systems that serve as filters of excess nutrients for many major cities throughout the southeast. Changing climates will affect not only net primary production (NPP), but also C storage (Intergovernmental Panel on Climate Change, 2007). Fine roots can account for up to 75% of the C allocated underground (Nadelhoffer and Raich, 1992; Vogt et al., 1996; Jackson et al., 1997). Floodplain forests have the ability to store C within soils, which would reduce the amount in the atmosphere. Anthropogenic changes in floodplain forests can alter the ability of many of these forests and soils to sequester C and it has been suggested that C allocation belowground can be greater than aboveground (Nadelhoffer and Raich, 1992).

Fine roots are essential in regulating biogeochemical cycles in all ecosystem types and are important to understanding how these systems respond to global climate change. Fine root production depends on the quality of an ecosystem; any stressor, especially drought, can cause shifts in fine root biomass (Vogt et al., 1993). With increasing drought and urbanization in the southeast, problems are likely to arise concerning forest production, especially involving fine roots. For example, increased water use due to larger cities and dam construction will lower river levels and consequently create drier microsites. Alterations to a microsite, like flow regulation through dam construction and stream channelization, could lead to changes in sediment supply conditions (Hupp et al., 2009). Floodplains are affected most by dam construction and downstream impacts to these microsites include severe reduction in the peak stages, frequency and duration of over bank flows, and sediment transport (Williams and Wolman, 1984). Vogt et al. (1993) examined the potential for fine roots to serve as early indicators of stress on forested ecosystems prior to any indications shown by aboveground counterparts. As precipitation decreases, there will be a greater need to monitor ecosystems with low water and/or nutrient levels that are located within this extreme stress gradient. Roots may serve as a potential early indicator of the changing stress regimes (Vogt et al., 1993).

Fine roots are a significant pathway for water, energy, and nutrient flow throughout a forested ecosystem. Since fine roots are important in the retranslocation of nutrients and turnover, they are also important in C sequestration (Gordon and Jackson, 2000). Belowground net primary production (BNPP) may account for up to 50% or more of total NPP (Vogt et al., 1986; Nadelhoffer and Raich, 1992; Baker et al., 2001; Jolley et al., 2009) and 30-50% of total C fixed by plants (Baker et al., 2001; Clawson et al. 2001). General knowledge of BNPP in floodplain forested ecosystems is lacking (Vogt et al., 1986; Megonigal et al., 1997; Lockaby and Walbridge, 1998).

Increased drought and more variable precipitation will influence C storage patterns in forests. Root turnover is a critical part of C cycling in ecosystems and likely will be influenced by climate change, which may recalibrate net primary production and the potential for systems to sequester C (Norby and Jackson, 2000). Root turnover rates vary greatly within and among species and within ecosystems (Majdi et al., 2005). Therefore, more knowledge on root turnover dynamics is critical when examining C fluxes in forests. Several models are used to calculate fine root turnover, and thus approaches used to define root turnover vary (Dahlman and Kucera, 1965; Aber et al., 1985; Hendrick and Pregitzer, 1993; Majdi et al., 2005).

Brassard et al. (2009) described three different scenarios of fine root turnover response to elevated temperatures. In the first scenario, root turnover increases and causes an overall input of C to the soil as root detritus increases; implying that soil C pools will remain relatively unchanged as an increase in microbial activity utilizes the new C sources. The second scenario predicts a decrease in root turnover and soil C pools decline due to an increased dependence of soil microbes on soil C sources. The third scenario predicts no change in root turnover while soil C pools remain largely unchanged since root detritus inputs, microbial activity, and C cycling will not be enhanced. The effect of changing temperatures, drought, and variable precipitation patterns on fine root turnover is unclear and therefore more research is required to predict climate change impacts. Our understanding of the different factors affecting fine root production is limited and is much less compared to those controlling aboveground production (Olesinski et al., 2012).

The specific goals of this research were to: 1) determine the dynamics of fine roots in a floodplain forest; and 2) assess the effects of microtopography on BNPP. Results from this study will clarify the effects of sedimentation on fine root productivity, and therefore BNPP, in the Congaree National Park, SC. The purpose of this study was to expand our knowledge and understanding on the effects of anthropogenic disturbances, specifically sedimentation, on the biogeochemistry of floodplain forests and give insight into the effects of climate change on forest productivity.

METHODS AND MATERIALS

Site Description and Fine Root Sampling

This study was conducted at Congaree National Park in Richland County near Columbia, SC (33°47’0” N, 80°47’0” W) (Fig. 2.1): the park extends over 11,000 ha. Congaree National Park contains the largest intact expanse of old-growth bottomland hardwood forest communities in the United States (Zhao et al., 2006). The Park centers on an 8991 ha portion near the east bank of the Congaree River and contains 4452 ha of old-growth forest with trees estimated to be older than 200 years (Wohl et al., 2011). Congaree National Park has two major forest types that are influenced primarily by hydrologic regime (Allen et al., 2005). The first forest type includes areas that are infrequently flooded or flooded for a short period of time consisting of sweetgum (*Liquidambar styraciflua*), American holly (*Ilex opaca*), oak species (*Quercus* spp.), sugarberry (*Celtis laevigata*), green ash (*Fraxinus pennsylvanica*), elm species (*Ulmus* spp.), red maple (*Acer rubrum*), and other hardwood species, as well as loblolly pine (*Pinus taeda*). The other forest type is associated with frequently flooded sloughs. Species composition in these areas is dominated by baldcypress (*Taxodium distichum*), black gum (*Nyssa sylvatica*), Chinese privet (*Ligustrum sinense*), loblolly pine, pawpaw (*Asimina triloba*), pond cypress (*Taxodium ascendens*), swamp tupelo (*Nyssa biflora*), sweetgum, water tupelo (*Nyssa aquatica*), and water oak (*Quercus nigra*), among others (Allen et al., 2005). The oldest loblolly pines are >247 years old and the oldest bald cypress are 700-1000 years old (Wohl et al., 2011).

The soil series on the study site include Chastain and Congaree soil series (Soil Survey Staff, 2012). Chastain soils are fine, mixed, semiactive, acid, thermic Fluvaquentic Endoaquepts that are typically poorly drained and have frequent or occasional periods of inundation. These soils occur farther from the natural levee in the backswamp microsite. Congaree soils are fine-loamy, mixed, active, nonacid, thermic Oxyaquic Udifluvents that are well to moderately drained soils and occur closer to the natural levee of the floodplain (Soil Survey Staff, 2012).

Twenty circular plots (4.0 m diameter) were established parallel to the Congaree River in a portion of the Park that has limited access to the public. The sites were grouped into four microsites according to distance from the river (and therefore elevation), with five plots in each microsite. The microsites were the natural levee, flat, transitional, and back swamp (Fig. 2.1). The natural levee was defined as the highest elevation sites with the best drained soils, while each subsequent microsite was at a lower elevation and had increased soil wetness. Relative elevation was measured according to plot 5 on the natural levee, the highest plot on the study site, and decreased in elevation 1.9 m to plot 20 on the backswamp, the lowest plot in the study site. Natural levee and flat microsites tended to have a more open canopy and more dense understory. Ricker (2013) reported soil characteristics of these sites. Soils on the natural levee had lower soil moisture content, lower clay, and higher base saturation and CEC (cmol kg^{-1}). Transitional and backswamp microsites had a more closed canopy, with larger older trees, and a less dense understory. Soils located within the backswamp tended to have a higher soil moisture content and clay percentage, and lower base saturation and CEC (cmol kg^{-1}) (Table 2.1).

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

Fine Root Productivity Analyses

Sequential coring, a widely used method (Pearcy et al., 1989; Caldwell and Virginia, 1991; Mackie-Dawson and Atkinson, 1991; Vogt and Persson, 1991; Fahey et al., 1999), was used to collect root samples. Two samples were taken from each plot at times spaced approximately 6 weeks apart from June 2011 to March 2013 to measure fine root biomass and BNPP. This timeframe made it possible to determine peaks in fine root production and mortality.

Samples were collected using an 8 cm diameter poly vinyl chloride (PVC) tube. The tube was inserted into the soil, with a hammer, to a depth of 11 cm. Previous studies have found that most fine roots are located within the top layer of the soil surface, or top soil (Baker et al., 2001; Clawson et al., 2001; Powell and Day, 1991; Cavalcanti and Lockaby, 2005). Any roots extending past the end of the tube were carefully cut away. After samples were collected, they were inserted into a plastic bag, stored on ice, and transported back to the Auburn laboratory and stored at 4˚C. Cores were washed with tapwater using a manual low pressure rinse, and fine roots were extracted from soil and sorted according to size and type classes. Fine roots in this study are defined as those ≤3.0 mm in diameter. Roots were separated between type classes of live and dead as well as size classes including 0-1.0 mm, 1.1-2.0 mm, and 2.1-3.0 mm. Live roots were flexible, normally contained many lateral branches, and were white in color, while dead roots were inflexible, fragmented, and usually dark in color showing signs of decay (Powell and Day, 1991). Samples were oven-dried at 70˚C for at least 72 hours and weighed. Weights were converted to g m^{-2} to an 11 cm depth.

Fine root NPP was calculated by subtracting biomass production between subsequent sample periods (i.e., Aug. 2011—June 2011, Sept. 2011—Aug. 2011, etc. until Mar. 2013—Feb. 2013) and then adding all positive differences (Persson, 1978; Vogt et al., 1998; Baker et al., 2001; Clawson et al., 2001; Cavalcanti and Lockaby, 2005; Jolley et al., 2009). Fine root turnover, or root longevity, was calculated as BNPP divided by mean standing crop (Aber et al., 1985; Aerts et al., 1992).

Fine Root Nutrient Analyses

Samples were ground to pass through a 0.40 mm sieve, and total C and N concentrations were quantified using thermal combustion (Perkin-Elmer 2400 series II CHNS/O analyzer; Perkin Elmer Corp., Norwalk, CT, USA). Concentrations of P were measured for live roots on a subset of all samples when enough sample (0.25 g) was left after C and N analyses. Total P samples were dry-ashed and P measured using the vanadomolybdate procedure (Jackson, 1958; Clawson et al., 2001). Total P values were read on a Spectronic 501 spectrophotometer (Milton Roy Co., Rochester, NY, USA). Total C, N, and P contents were calculated as a product of root dry weight and nutrient concentration.

Soil Analyses

Soil data were collected for each floodplain topographic position, including depth to shallow water table, bulk density, percent sand, percent clay, organic matter, pH, CEC and base saturation (Table 2.1). Soils on the study plots were described from auger cores to a depth of 100 cm (Schoeneberger et al., 2002). Four additional soil cores per plot were collected to a depth of 10 cm for laboratory analyses. Cores were oven-dried at 105°C to calculate bulk density using the core method (Soil Survey Staff, 2004). Soil pH was calculated from air dried subsamples using a 1:1 soil-deionized water slurry (Soil Survey Staff, 2004). Major extractable element concentrations (P, K, Fe, Ca, Mg, Mn, Na, Zn) were quantified using inductively coupled plasma atomic emission spectroscopy (ICP-AES) after double extraction (Mehlich-1; Mehlich, 1953) to calculate cation exchange capacity (CEC). The percent base saturation was determined as the ratio of extractable bases to CEC. Total soil C and N concentrations were quantified using thermal combustion (Perkin-Elmer 2400 series II CHNS/O analyzer; Perkin Elmer Corp., Norwalk, CT, USA). Soil particle distribution (texture) was quantified using the hydrometer method as described by Gee and Bauder (1986).

Statistical Analyses

Significant effects of microsite on fine root variables, including standing crop biomass, production, and nutrient concentrations and contents, between sample periods within each type and size class were identified using a one-way ANOVA (PROC GLM, SAS Institute, Inc. 9.2 2002-2008). Tukey's Range Test ($\alpha = 0.05$) was used to test for differences of fine root production among microsites. Differences were considered statistically significant at $\alpha = 0.05$. In addition, linear regression analyses (PROC REG, SAS Institute, Inc. 9.2 2002-2008) were performed to determine whether a relationship existed between relative elevation and BNPP.

RESULTS

Temperature and Precipitation Patterns

The winter, fall, and summer months had lower than average precipitation, and the spring months had higher than average precipitation during the study period. The Palmer drought index indicated that moderate drought conditions occurred from June 2011 to April 2012 (Fig. 2.2).

Standing Crop Biomass, Belowground Net Primary Production, and Root Turnover

Standing crop biomass of live roots was much greater at plots with higher elevation, such as those on the natural levee and flat microsites, and decreased with decreasing elevation for the 0.1-1.0 mm and 1.1-2.0 mm diameter size classes as well as for all diameter size classes combined (Figs. 2.3, 2.4, 2.6). The 2.1-3.0 diameter size class did not show any prominent trend among the different microsites (Fig. 2.5). Significant differences ($p < 0.05$) were observed in all months across microsites for total live roots and, in all cases, the natural levee was significantly higher than the backswamp in total standing crop biomass. As expected, seasonal fluctuations were observed in standing crop biomass for live roots. Total standing crop biomass peaked in December 2011 and November 2012 on the natural levee. The flat microsite had peaks in total standing crop biomass in September 2011 and July 2012. The transitional microsite had peaks of standing crop biomass in August 2011 and May 2012. Backswamp root standing crop biomass fluctuated little over the sampling period, apart from a large peak in April 2012 (Fig. 2.6). Total live root biomass for the natural levee ranged from 34.4 g m^{-2} to 58.4 g m^{-2} and ranged from 27.7 g m^{-2} to 42.2 g m^{-2} for the flat microsite. For the lower elevation microsites, total live root biomass ranged from 23.1 g m^{-2} for the transitional microsite and 15.1 g m^{-2} to 32.5 g m^{-2} for the backswamp microsite.

Total dead fine roots varied little over the sampling period in all plots, with the most fluctuations on the natural levee (Fig. 2.6). All microsites had peaks of dead fine roots in August 2011, as well as in December 2012 for the natural levee, in May 2012 for the flat and transitional microsites, and in April 2012 for the backswamp microsite (Fig. 2.6). Dead fine roots varied from 12.6 g m^{-2} to 27.9 g m^{-2} on the natural levee, from 10.2 g m^{-2} to 18.0 g m^{-2} on the flat, from 6.0 g m^{-2} to 17.0 g m^{-2} on the transitional microsite, and from 4.1 g m^{-2} to 10.5 g m^{-2} on the backswamp. Peaks in total dead fine roots occurred in August 2011 and December 2012 (Fig. 2.6). Significant differences ($p < 0.05$) were observed in 11 out of the 16 collections for total dead root biomass.

Belowground net primary productivity decreased from the natural levee to the backswamp and, for fine roots, was significantly different for the natural levee versus the transitional microsite and backswamp (Fig. 2.7). The natural levee had the greatest BNPP (684.9

g m^{-2}), followed by the flat (482.1 g m^{-2}) and the transitional microsite (431.1 g m^{-3}). The backswamp had the lowest BNPP (341.2 g m^{-2}). There was a positive relationship between BNPP and increasing elevation ($r^2 = 0.30$, $p < 0.0003$) (Fig. 2.8).

Turnover was calculated as annual BNPP divided by mean standing crop (Aber et al., 1985). Fine root turnover rates were 3.5, 3.5, 4.7, and 4.8 (yr^{-1}) for the natural levee, flat, transitional, and backswamp microsites, respectively, but showed not significant differences between microsites.

Fine Root Nutrients—C, N, and P

Fine root C content reflected live and dead biomass trends (since nutrient content is a combination of nutrient concentration and dry weight), with the natural levee having the greatest C content and the backswamp the lowest (Tables 2.2, 2.3). Live fine root C content was significantly different among microsites for all collections throughout the sampling period. Average live fine root C content declined in the order: natural levee (73.2 g m^{-2}), flat (53.0 g m^{-2}), transitional microsite (40.0 g m^{-2}) and backswamp (28.1 g m^{-2}) (Table 2.2). Average dead fine root C content was less than that of live fine roots and followed the same microsite trend: natural levee (12.0 g m^{-2}), flat (9.2 g m^{-2}), transitional (6.3 g m^{-2}), and backswamp (3.7 g m^{-2}) (Table 2.3, Fig. 2.9). C concentrations were also compared to determine if any differences existed among microsites. Live and dead fine root C concentrations fluctuated little during the study period (Tables 2.4, 2.5), although live fine root C concentrations were higher than those of dead fine roots (Fig. 2.9). For live fine root C concentration, only one significant difference existed throughout the sampling period among microsites (Table 2.4), while dead fine root C concentrations showed significant differences among microsites for less than half of the collections (Table 2.5). Seasonal C concentrations for live roots for all microsites were greatest in the fall and winter of both years and lowest in the summer. Dead fine roots had the greatest C concentration in fall 2011 (Table 2.5).

N content in fine roots also tracked live and dead root biomass, decreasing as elevation increased. Over half of the sampling collections showed significant differences for live fine N content among microsites, i.e. natural levee (2.2 g m^{-2}), flat (1.8 g m^{-2}), transitional microsite (1.3 g m^{-2}), and backswamp (1.0 g m^{-2}) (Table 2.6). Dead fine root N contents also decreased from the natural levee to the backswamp (0.5, 0.4, 0.3, and 0.2 g m^{-2}) and showed significant differences for over half the sample collection dates (Table 2.7). Significant differences did exist on a few sampling periods between the natural levee and transitional microsite for concentrations in both live and dead roots, but no definite pattern emerged (Tables 2.8, 2.9). Seasonally, live fine root N concentration peaked in the winter of 2011 and 2012 for all microsites (Table 2.8). Fine root N concentration was higher in dead roots than live roots on average (Fig. 2.10). Dead fine root standing crop biomass showed peaks for the natural levee in fall 2011/spring 2013, flat in fall 2011/winter 2013, transitional microsite in winter 2011/winter 2012, and backswamp in spring 2012 and then decreased to its lowest value and remained low for the remainder of the study (Table 2.9).

P concentrations were only calculated for live fine roots due to lack of samples for dead roots. Some samples were also combined for each microsite depending on amount of sample collected. P concentrations decreased from the natural levee to the backswamp (Table 2.10). The natural levee exhibited the greatest P concentration of 3.50 g kg^{-1}, decreasing to 3.07 g kg^{-1} on the flat, then 2.25 g kg^{-1} on the transitional microsite, and finally to 2.20 g kg^{-1} on the backswamp. Significant differences were observed among all the microsites except the transitional microsite and backswamp (Table 2.10). P content was not calculated due to lack of samples.

Soil Nutrients

Total soil N, the combination of NH_4-N and NO_3-N, peaked in the falls of 2010, 2011 and 2012 (9.98, 13.37, 9.54 mg L^{-1}) and then dropped as time progressed into winter 2011, 2012, and 2013 (5.34, 8.73, 5.59 mg L^{-1}). N concentrations in live roots showed peaks in the winter of 2011 and 2012, corresponding to the drops in soil N (Table 2.8).

DISCUSSION

Standing Crop Biomass

Seasonal variations have been well documented for standing crop biomass of both live and dead roots in floodplain forests (Schilling et al., 1999; Baker et al., 2001; Clawson et al., 2001; Cavalcanti and Lockaby, 2005; Jolley et al., 2009). Powell and Day (1991) observed peaks in the summer and winter of fine root production in a mixed hardwood stand. Clawson et al. (2001) found different peaks in root biomass along the Flint River with the wettest site having peaks in April, September, and January; intermediate sites having peaks in September; and poorly drained sites remaining relatively constant throughout the study period. Spring and fall peaks were reported in fine root biomass along the Pearl River, MS (Schilling et al., 1999), and at Ft. Benning, GA (Jolley et al., 2009). Trees and understory plants are thought to produce extensive fine root networks in the spring to meet nutrient and water needs during leaf production and subsequent photosynthesis (Brassard et al., 2009).

Drought may have contributed to the lack of variation in dead fine roots. Water stress throughout the study period may have caused root mortality to remain constant indirectly by increasing root temperature and maintenance respiration and by inhibiting photosynthate transport to root systems (Marshall, 1986). Other studies have reported annual dead fine root biomass to peak in the late summer or fall (Hendrick and Pregitzer, 1993; Cavalcanti and Lockaby, 2005; Jolley et al., 2009). Joslin and Henderson (1987) reported peaks in the late spring/early summer and also late summer and autumn in an oak stand. Generally, fine root mortality is more evenly distributed throughout the year (Hendrick and Pregitzer, 1996; Burton et al., 2000; Brassard et al., 2009).

Precipitation data showed a period of drought for the majority of the study (Fig. 2.2), which probably affected root production. The drought preceded the first collection date by about four months, and lasted over half of the study period. Peaks in biomass are speculated to correspond with peaks in rainfall and temperature. For example, a peak in mean precipitation occurred in April 2012, and all microsites exhibited an increase in production after April 2012, suggesting that increased rainfall events had a positive effect on root growth. Data suggested that fine root biomass was controlled by drought. In upland temperate forests, fine root production is generally influenced by temperature and moisture (Burke and Raynal, 1994), while in southern floodplain forests fine root production and mortality is controlled by both temperature (if moisture is not limiting) and hydrologic regime (Baker et al., 2001; Mitsch and Gosselink, 2007). Fine root production also coincides with leaf growth in the canopy, as well as an increase in available nutrients with rainfall (Yavitt and Wright, 2001; Lima et al., 2012).

A number of climate change models predict less precipitation in the southeast from 2010-2050, as well as more variable weather patterns and increased temperatures (McNulty et al., 2011). Forested ecosystems may become stressed in the future due to these climatic events, especially when they are combined with an increased demand for water supply from a growing population in parts of the southeastern United States (Lockaby et al., 2011). Altered climate regimes could potentially lead to significant shifts in forest fine root production due to compositional changes in dominant tree species and increased decomposition, and these patterns and changes are important in understanding belowground C allocation (McCormack et al., 2013; Savage et al., 2013). For example, fine root production could increase under drought conditions in order to foster water uptake by increasing root surface area and by exploitation of wetter soils (Gaul et al., 2008). However, limited availability of nutrients and carbohydrates, or soil that is difficult for roots to penetrate, could restrict root growth (Joslin et al., 2000; Metcalfe et al., 2008).

There is a general lack of information describing the effects of climate change on fine root production in the southeastern United States. Many studies have been conducted in boreal forests and these have shown a positive relationship between fine root production and annual temperature due to longer growing seasons (Steele et al., 1997; Yuan and Chen, 2010; Olesinski et al., 2012). Olesinski et al. (2011) found that NPP was enhanced in the year following a drought in a balsam fir forest. Similarly, Zang et al. (2013) reported an increase in fine root growth under moderate soil drought but a decrease under severe drought in planted beech saplings. Fine root biomass increases with mean annual precipitation in temperate and tropical forests and there is a positive relationship between fine root biomass and precipitation because soils are generally wet (Yuan and Chen, 2010).

Belowground Net Primary Production

Belowground net primary production decreased with elevation and increasing soil wetness (Fig. 2.8). The natural levee, located on the driest microsite, had the greatest fine root production, and the backswamp, the wettest microsite, had the lowest fine root production. Live root biomass fluctuated more where elevation was lower and soil was wetter. Clawson et al.

(2001) found that fine root production along the Flint River in GA decreased as wetness increased, and that the driest plots had the largest allocation of BNPP, while intermediately wet and wet areas had smaller amounts of fine root production (211, 131, and 56 g m^{-2}, respectively). Similarly, a study conducted along the Coosawhatchie River in SC reported that BNPP decreased from 181 g m^{-2} on well drained sites to 90 g m^{-2} on poorly drained sites (Baker et al., 2001). Another study in the Great Dismal Swamp of VA reported BNPP estimates of 490, 354, 139, and 135 g m^{-2} for communities that became progressively wetter (Powell and Day, 1991). Likewise, Megonigal and Day (1988) reported that sites that were wetter or partially flooded had less fine root productivity. Chacón et al. (2008) determined that total fine root mass declined along a flooding gradient along the Mapire River in southeastern Venezuela. Newman et al. (2006) found a negative correlation between BNPP and soil water content, with xeric sites having higher production rates than mesic, on the Cumberland Plateau, KY.

Our data support conclusions from previous studies and show a negative relationship between BNPP and elevation ($r^2 = 0.30$, $p < 0.0003$) (Fig. 2.8). Elevational and topographic differences over relatively short distances affect local hydroperiod and sedimentation and strong relationships may occur between increased sedimentation and decreased BNPP (Hupp and Bazemore, 1993; Cavalcanti and Lockaby, 2005; Jolley et al., 2009). Sediment deposition can produce the same effects as flooding by creating anoxic conditions in the soil and reducing oxygen that is available to roots, impeding root respiration and development (Kozlowski et al., 1991), unless species are adapted to flooded conditions. Since fine root biomass and production are greatest in moist, aerated soils and least in anaerobic soils, flooding stress may cause a shift from belowground production to aboveground production (Lugo et al., 1990).

Fine root production in this study falls within the ranges found elsewhere. Powell and Day (1991) found that BNPP for a mixed hardwood forest that is rarely flooded ranged from 354-989 g m^{-2} and for a cypress community that experienced some flooding the range was between 68-308 g m^{-2}. In other areas of the southeast, BNPP was found to be lower along the Flint River, GA (Clawson et al., 2001), along the Coosawhatchie River, SC (Baker et al., 2001), and at Ft. Benning, GA (Jolley et al., 2009). These three studies only included roots that were <2 mm in diameter, so this could account for the smaller BNPP values. Cavalcanti and Lockaby (2005) found that sites which were lower in elevation and the catchment area, consequently receiving more sedimentation, produced lower BNPP than those that were higher in elevation across a disturbance regime.

The influence of different species' root traits is important for understanding standing crop biomass and seasonal trends. Fine root production in a boreal forest was higher for those stands dominated by early-successional species than by late-successional species (Yuan and Chen, 2010). Since the Congaree National Park is predominantly old-growth forest and late-successional species dominate stands, fine root production could be less than that for other floodplain forests in the southeast due to the age of the Congaree trees.

Fine Root Turnover

Fine root lifespan is vital for plant growth, maintenance, productivity, plant interactions, and belowground C storage and nutrient cycling (Anderson et al., 2003). The lifespan of fine roots is affected by many different factors. A plant that has lower turnover, or keeps its roots longer, allocates less C to the production of more roots; however, the plant expends more energy in the form of root respiration in maintaining those older roots that may be less efficient at nutrient and water uptake compared to newer roots (Norby and Jackson, 2000). After roots die and decompose, C is released to the atmosphere, and some remains in the soil as organic matter, therefore root turnover is a major portion of ecosystem C fluxes and sequestration (Norby and Jackson, 2000).

McCormack et al. (2013) described a model in which fine root lifespan was calculated for the eastern portion of the United States in relation to CO_2 emissions and climate scenarios. For some portions of the southeast, including western FL, central SC and south central NC, slower root turnover rates were predicted; whereas for other parts of the southeast, parts of LA, AR, and TX, a predicted potential increase in root turnover rate was observed (McCormack et al., 2013). These predicted increases and decreases in root turnover were related to changes in dominant species; for example, when a slower predicted turnover rate was observed this corresponded to a shift from sweetgum, which has faster turnover rates, to turkey oak (*Quercus laevis*), which has a slower root turnover rate (McCormack et al., 2013). Conversely, when a faster turnover rate was observed, it was more difficult to attribute the rate to specific increases and decreases of certain species and likely resulted from more subtle changes across many species (McCormack et al., 2013).

Considerable variation exists among approaches for calculating turnover rates for fine roots, e.g., BNPP/max. standing crop (Dahlman and Kucera, 1965), BNPP/min. standing crop (Hendrick and Pregitzer, 1993), BNPP/mean standing crop (Aber et al., 1985), and from minirhizotron data using median root longevity (Madji et al., 2005). Currently there is no standard approach to calculating or defining root turnover. Consequently, a clear understanding of fine root turnover contribution to total ecosystem C and nutrient pools remains elusive because of variation in calculation forms (Trumbore and Gaudinski, 2003; Madji et al., 2005).

Fine Root Nutrients—C, N, P

Fine root nutrient contents for C, N, and P are a product of both root dry weight and nutrient concentration, although data suggest biomass drives nutrient contents for both live and dead roots (Schilling et al., 1999; Cavalcanti and Lockaby, 2005; Jolley et al., 2009). Significant differences existed among microsites for both C and N contents of live and dead fine roots and these were due to changes in fine root biomass. C and N content decreased significantly as fine root biomass decreased (Tables 2.2, 2.3, 2.6, 2.7). Fine root C and N contents were higher in live roots than dead roots and similar trends have been noted for C and N content in other fine root nutrient studies (Clawson et al., 2001; Cavalcanti and Lockaby, 2005; Jolley et al., 2009; Jolley et al., 2010). No significant differences were discovered in C and N concentrations for either live or dead fine roots. Fine root C and N concentrations did not vary much within each microsite type. Gordon and Jackson (2000) reported that N concentrations in dead roots were slightly higher than in live roots, suggesting a trend towards increasing N concentrations which is also common in the initial stages of leaf litter decomposition (Barnes et al., 1998).

Significant differences were documented among microsites for P concentration, with the natural levee having the greatest P concentrations and these decreased towards the backswamp (Table 2.9). In a study comparing boreal forest fine roots, Yuan and Chen (2010) found that species differences affect nutrients in fine roots. Stands dominated by broad-leaved species contain more N but have similar P to those dominated by conifers and early-successional stands had higher N contents than late-successional species. McClaugherty et al. (1982) found that N concentration was greater in roots associated with greater N in the forest floor, while Jolley et al. (2010) found higher N concentration in roots associated with a greater density of N-fixing shrubs. Fine root N and P contents were also affected by precipitation, decreasing with increasing mean annual precipitation (Yuan and Chen, 2010).

Effects of Future Climate Change

General circulation models (GCMs) used in the Southern Forest Futures Project predict warmer temperatures, ranging from 19.3-20.2°C, and more variable precipitation, ranging from 912-1106 mm, by 2060 in the southeastern United States (McNulty et al., 2011). Coupled with predicted increases in evapotranspiration, increases in agriculture and urbanization (Simmons et al., 2007), deforestation (Osterkamp and Hupp, 2010), and reservoir construction (Hupp et al., 2009), these increases have the potential to damage floodplain forested systems and may greatly decrease productivity and nutrient and sediment storage. Alterations to the landscape, like flow regulation through dam construction and stream channelization, could lead to changes in sediment supply conditions (Hupp et al., 2009). Floodplains are also affected by dam construction and the downstream impacts to these landscapes include severe reduction in flood frequency, flood duration, peak flows, and peak discharge, and sediment transport, as well as altered timing of floods and more frequent periods of low flows (Williams and Wolman, 1984). Hupp et al. (2009) suggest that in future years, floodplain surfaces may become flatter because sediment trapping may occur primarily in the backswamp leading to a higher floodplain with little to no topographical relief, which in turn decreases connectivity. This in turn will affect hydroperiod and ultimately nutrient loading and cycling with negative impacts on plant diversity and productivity (Hupp et al., 2009).

Hydrology is a controlling factor in many ecological communities (Dixon and Turner, 2006), consequently flood regime changes are most often associated with the decline of bottomland hardwood forests (Alldredge and Moore, 2012). It is well known that slight changes in elevation can alter species composition, richness, and diversity of these communities (Sharitz and Mitsch, 1993; Naiman et al., 2005; Kupfer et al., 2010). Floodplain plants are selective to where they establish because they are sensitive to alterations in flooding frequency and duration, as well as soil types (Battaglia and Sharitz, 2006). Since bottomland hardwood tree species differ in their tolerance to flooding (Wharton et al., 1982; Kozlowski, 2002), changes in flood regime could create shifts in plant communities. Altered hydrologic regimes could cause a decline in obligate wetland species, and wetland species could eventually be replaced by non-wetland species once the older, larger plants die off, consequently changing forest composition and structure (Kupfer et al., 2010). This is especially susceptible in areas lower on the landscape that are susceptible to drier conditions; although, this process may take between 100-200 years to take place (Hughes, 1997). The lowest areas on the landscape, in this study the backswamp, are the only areas on the floodplain that receive enough flooding disturbance to limit non-wetland species, while higher elevation sites like the natural levee receive less frequent disturbance and can support non-wetland species (Streng et al., 1989; Dewey et al., 2006).

With reduced water availability, trees may adjust by changing the size and positioning of their roots and also by modifying root morphology and physiology to increase water uptake efficiency (Eissenstat et al., 2000). Root plasticity is one strategy of trees to respond to climate change, especially in response to decreased water availability (Eissenstat, 1992). Plants produce thinner fine roots with a larger surface area in order to optimize the cost-benefit ratio of fine root operation (Eissenstat and Yanai, 1997; Eissenstat et al., 2000; Pregitzer et al., 2002). West et al. (2004) showed a decreasing mean fine root diameter with decreasing water availability in a longleaf pine (*Pinus palustris*) savanna. Likewise, Meier and Leuschner (2008) found that specific root length and root area increased while average root diameter decreased with decreasing precipitation. Fine root adaptations, including increased root biomass and decreased diameter, could cause changes in C cycling and sequestration. Changes in the production and turnover of roots in forests in response to climate change, including increasing temperatures and more variable precipitation, rising CO_2 concentrations, and N deposition could be an important link between forest responses and changes in soil organic matter and C cycling (Norby and Jackson, 2000).

CONCLUSION

Results from this study suggest that small decreases in elevation in floodplain forests are associated with significant declines in belowground forest productivity. Prior to this study, the natural levee was hypothesized to have the most BNPP, decreasing towards the backswamp as elevation decreased and wetness increased. This proved to be correct (natural levee 685 > flat 482 > transitional 431 > backswamp 341 g m^{-2}). The results support conclusions of other researchers, who found that biomass is influenced by hydroperiod (Megonigal and Day, 1988; Clawson et al., 2001; Powell and Day, 1991; Baker et al., 2001; Cavalcanti and Lockaby, 2005; Jolley et al., 2009). My data suggest that fine root biomass in Congaree National Park was controlled by drought stress. Many studies predict an increase in root growth and mortality as long as soil moisture and nutrient availability are adequate (Pregitzer et al., 2000). Warming may cause a change in seasonality of root dynamics with perennial plants rooting earlier in the spring (Pregitzer et al., 2000). Results of this study also suggest that future drought may have a significant impact on forest productivity and C storage in the southeastern United States. In order to determine how future changes in precipitation and temperature may impact floodplain forest productivity, it is critical that studies be conducted that encompass longer periods of time, especially regarding the belowground portion of these ecosystems.

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TABLES AND FIGURES

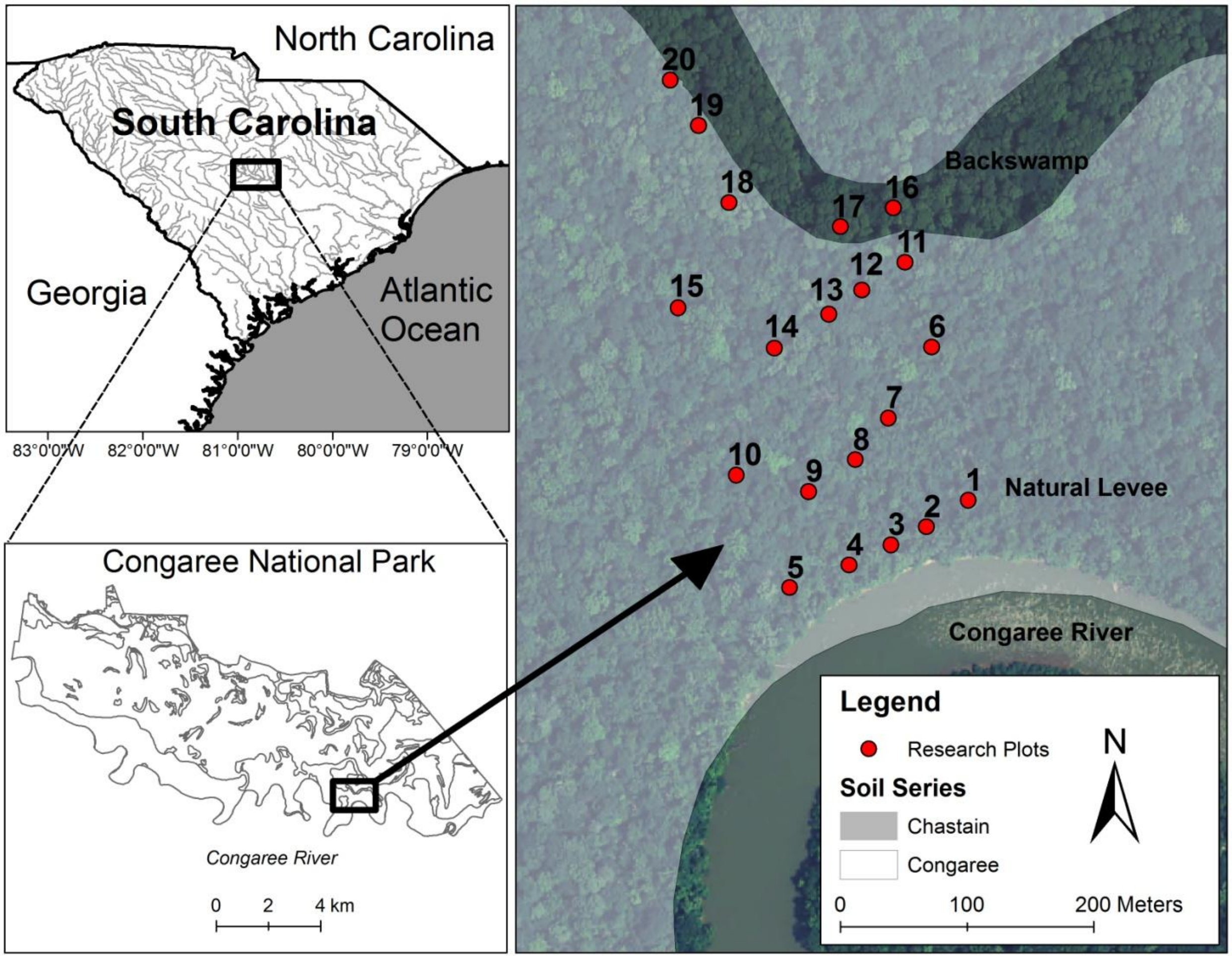

Figure 2.1. Location of Congaree National Park and research plots.

Table 2.1. Mean values of soil characteristics for each floodplain microsite type, standard error is shown in parentheses (n = 5, per microsite type). ***Mean values by column with different letters are significantly different (Tukey's HSD, α = 0.05). Source: Ricker, 2013.***

			Toposequence Soil Characteristics (0-10 cm)							
Microsite	**Plots**	**Depth to SHWT (m)†**	**Bulk Density (Mg m-^{3})**	**Sand (%)**	**Clay (%)**	**Organic Matter (%)**	**Soil pH**	**CEC (cmol kg^{-1}) ‡**	**Base Saturation (%)‡**	**C:N Ratio**
Levee	1-5	0.85 (0.07) a	1.02 (0.02) a	5 (0.4) a	26 (2.0) a	6.8 (0.40) a	5.91 (0.08) a	16.6 (1.1) a	88.5 (1.4) a	12.6 (0.3) a
Flat	6-10	0.82 (0.12) a	0.92 (0.05) a	8 (0.9) a	27 (0.5) a	8.2 (0.37) a	5.72 (0.17) a	17.0 (1.4) a	84.7 (2.7) a	11.6(0.4) a
Transitional	11-15	0.44 (0.04) b	1.03 (0.03) a	7 (0.8) b	39 (1.0) b	7.5 (0.78) a	5.01 (0.05) b	12.2 (0.7) b	62.4 (2.4) b	11.9 (0.4) a
Backswamp	16-20	0.13 (0.02) c	0.96 (0.04) a	6 (0.9) c	45 (1.4) c	6.9 (0.89) a	5.11 (0.08) b	12.1 (0.5) b	64.7 (2.9) b	12.6 (0.5) a

†Depth to seasonal high water table (SHWT), interpreted as depth to common (>2%) redox depletions

‡Calculated from Mehlich-1 (double acid) extracts

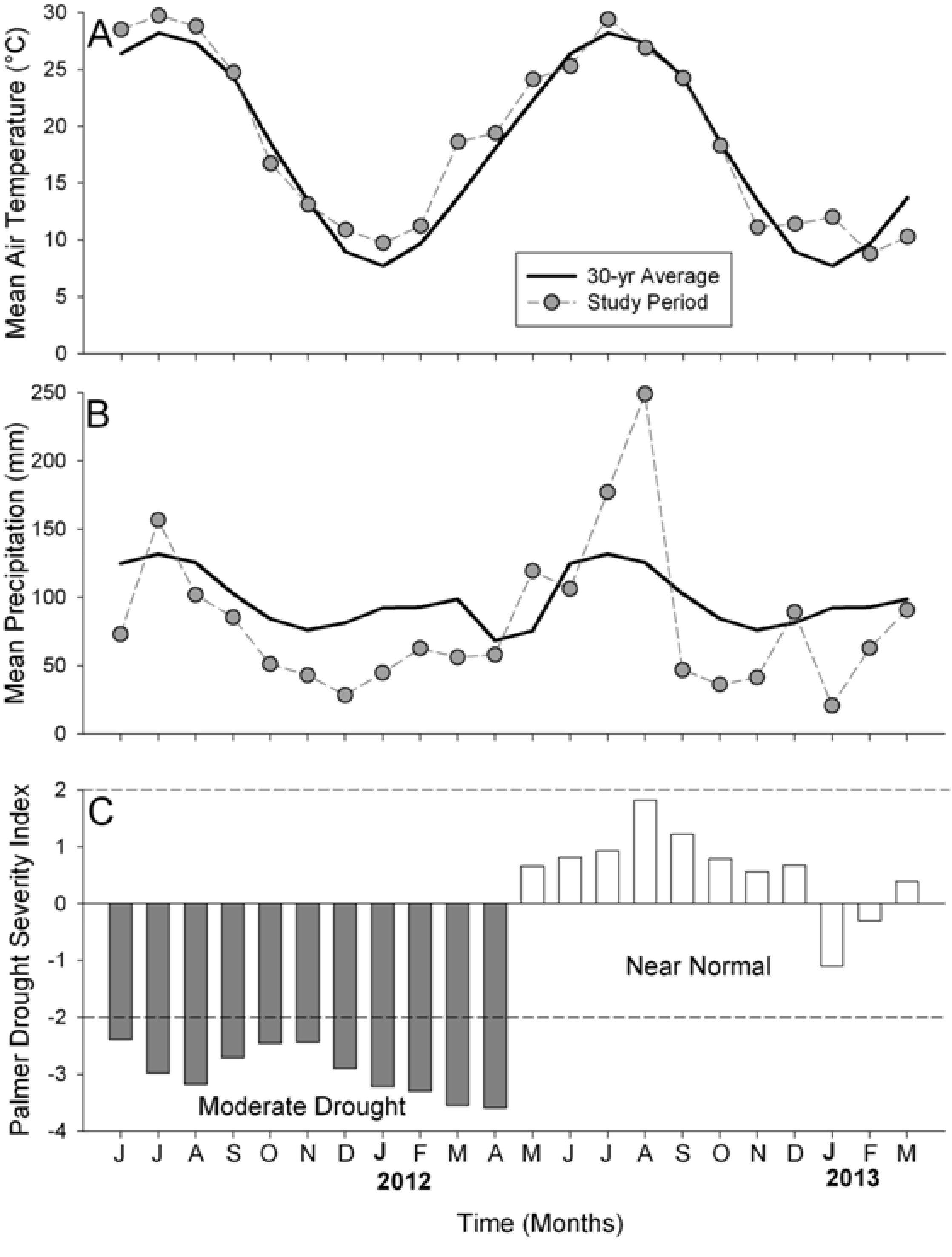

Figure 2.2. Monthly air temperature, precipitation, and Palmer drought severity index during the study period for the Columbia Metropolitan Airport, SC. *Source: U.S. Department of Commerce-National Oceanic & Atmospheric Administration*.

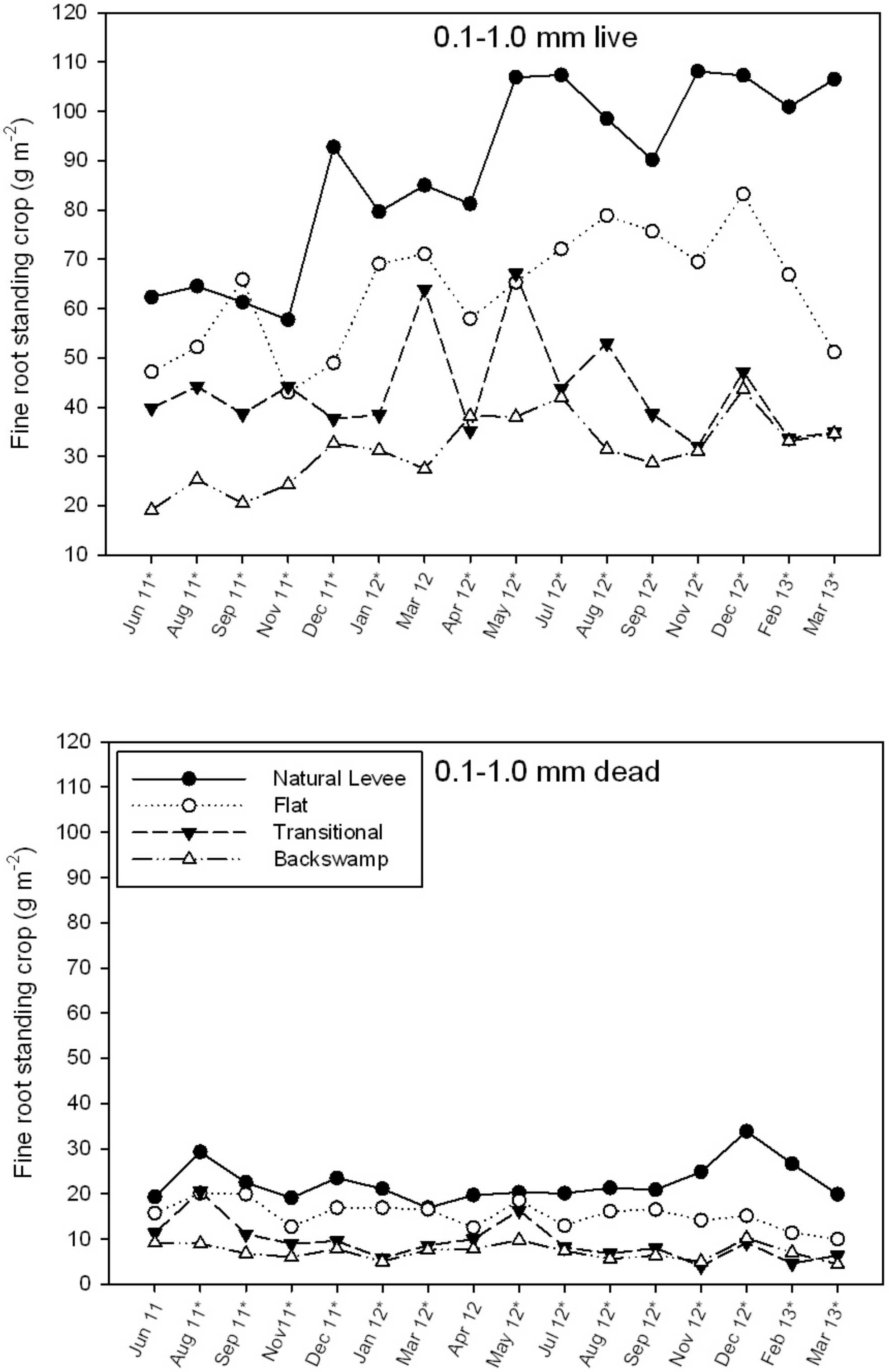

Figure 2.3. Fine root standing crop biomass for size class 0.1-1.0 mm on each microsite to a depth of 11 cm.

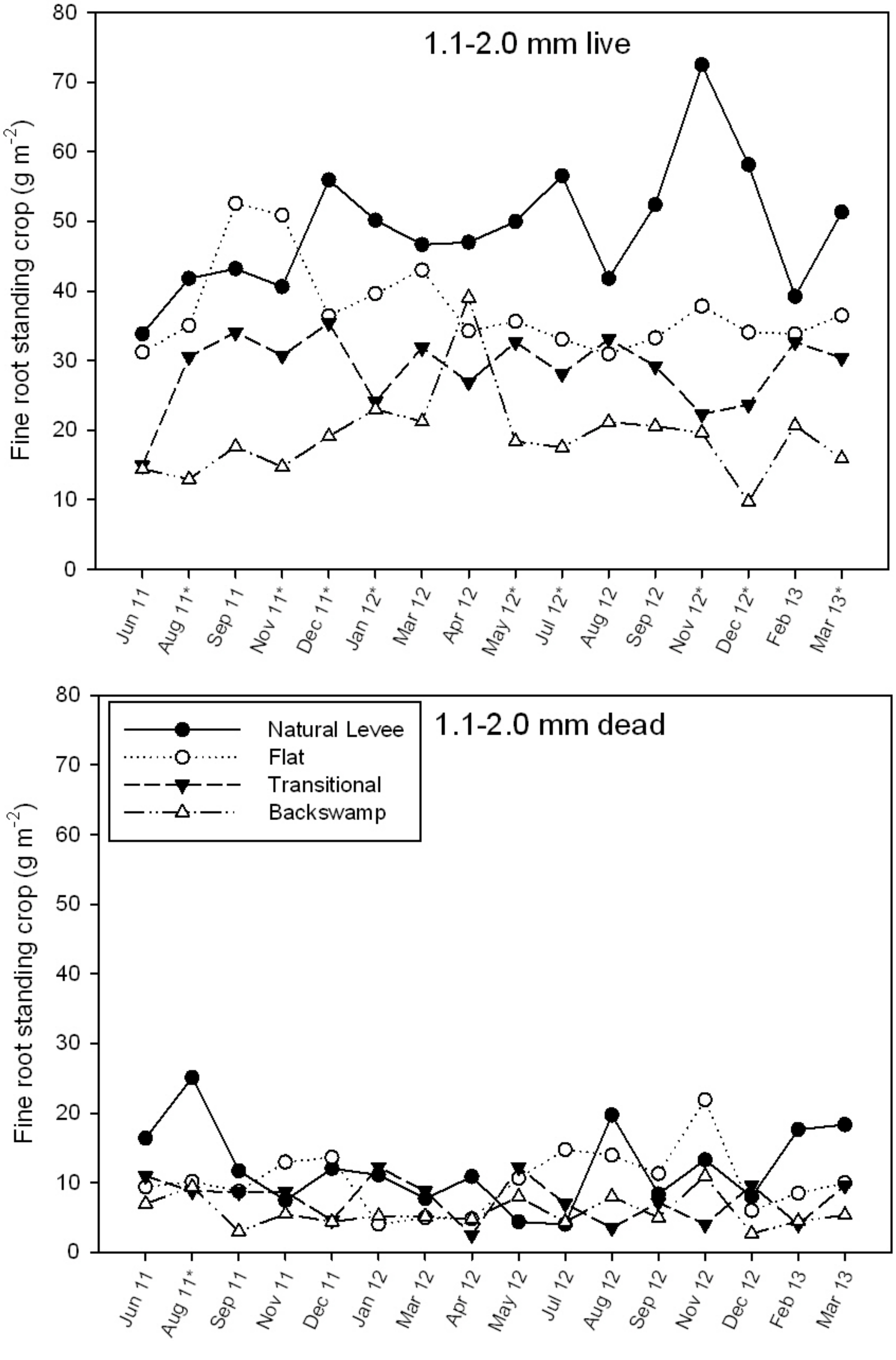

Figure 2.4. Fine root standing crop biomass for size class 1.1-2.0 mm on each microsite to a depth of 11 cm.

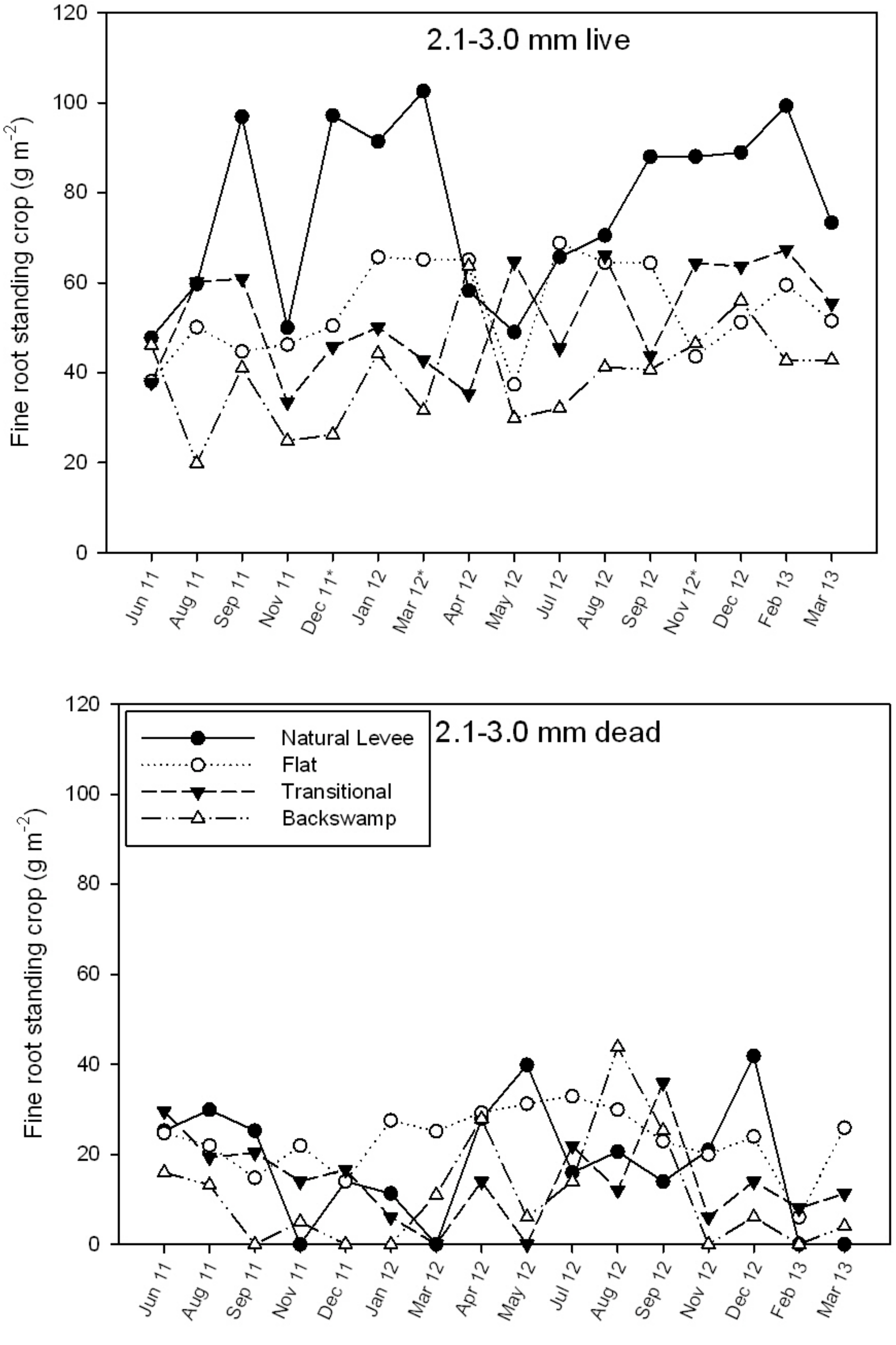

Figure 2.5. Fine root standing crop biomass for size class 2.1-3.0 mm on each microsite to a depth of 11 cm.

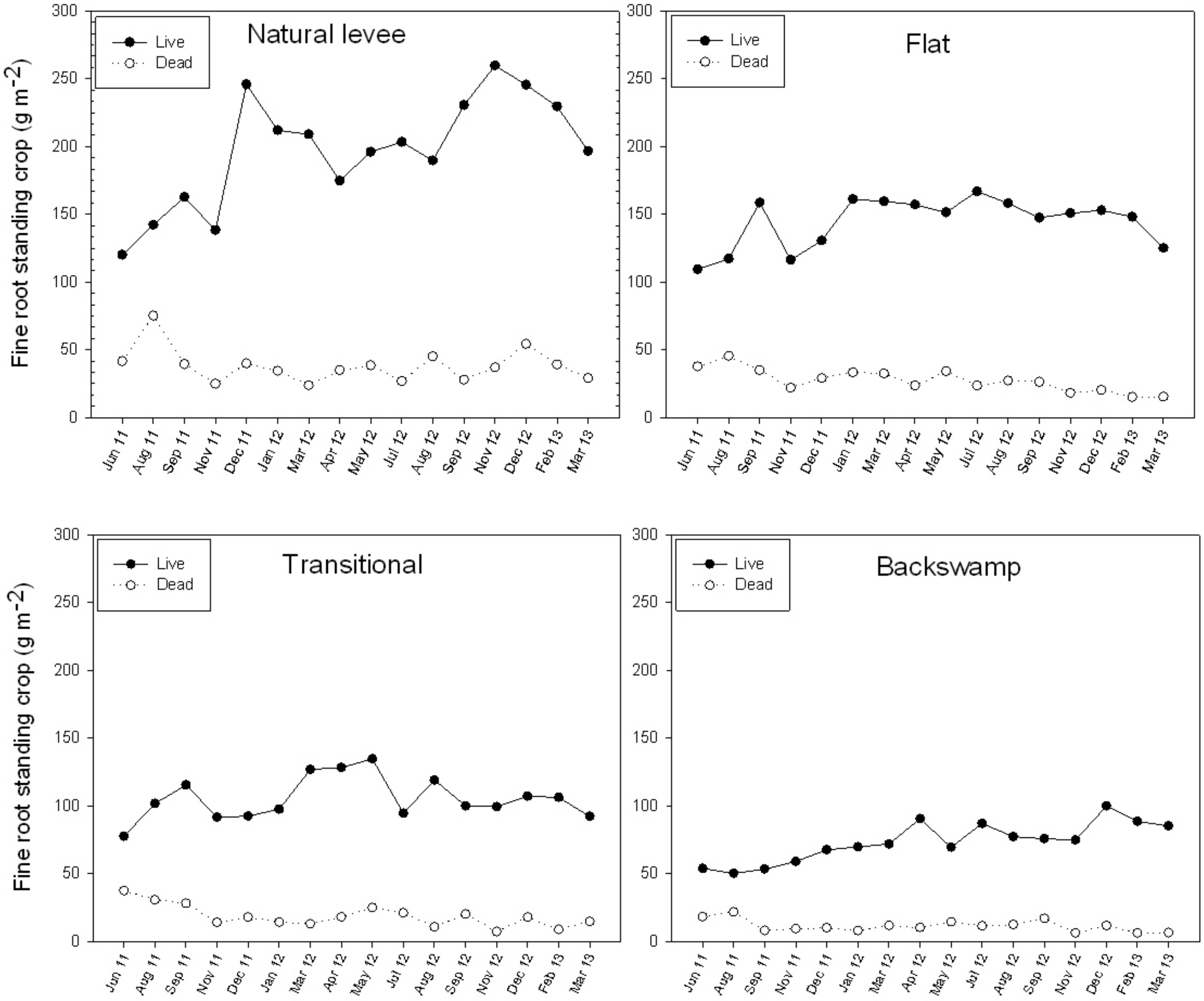

Figure 2.6. Total live and dead fine root standing crop biomass by microsite to a depth of 11 cm.

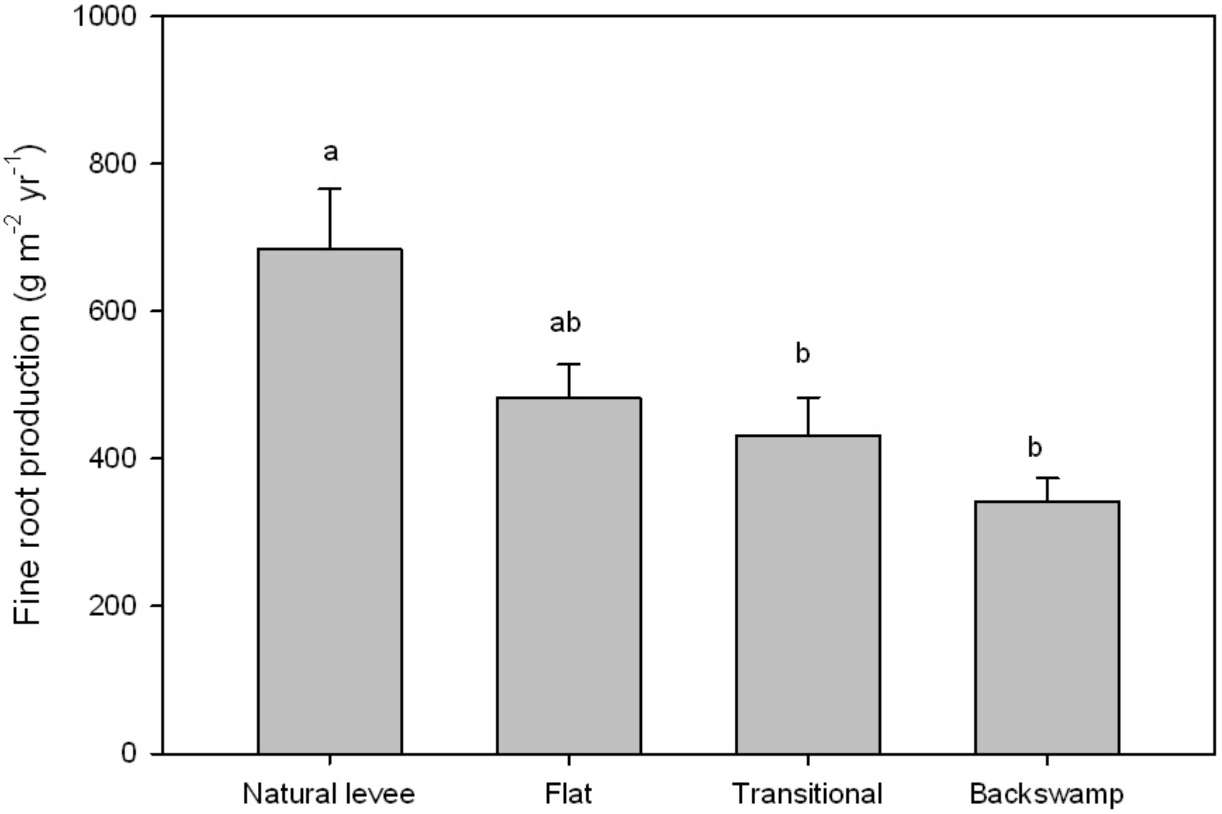

Figure 2.7. Comparison of fine root production estimates to a depth of 11 cm among microsites. Different letters above bars denote significant differences among microsites (Tukey's HSD, α = 0.05).

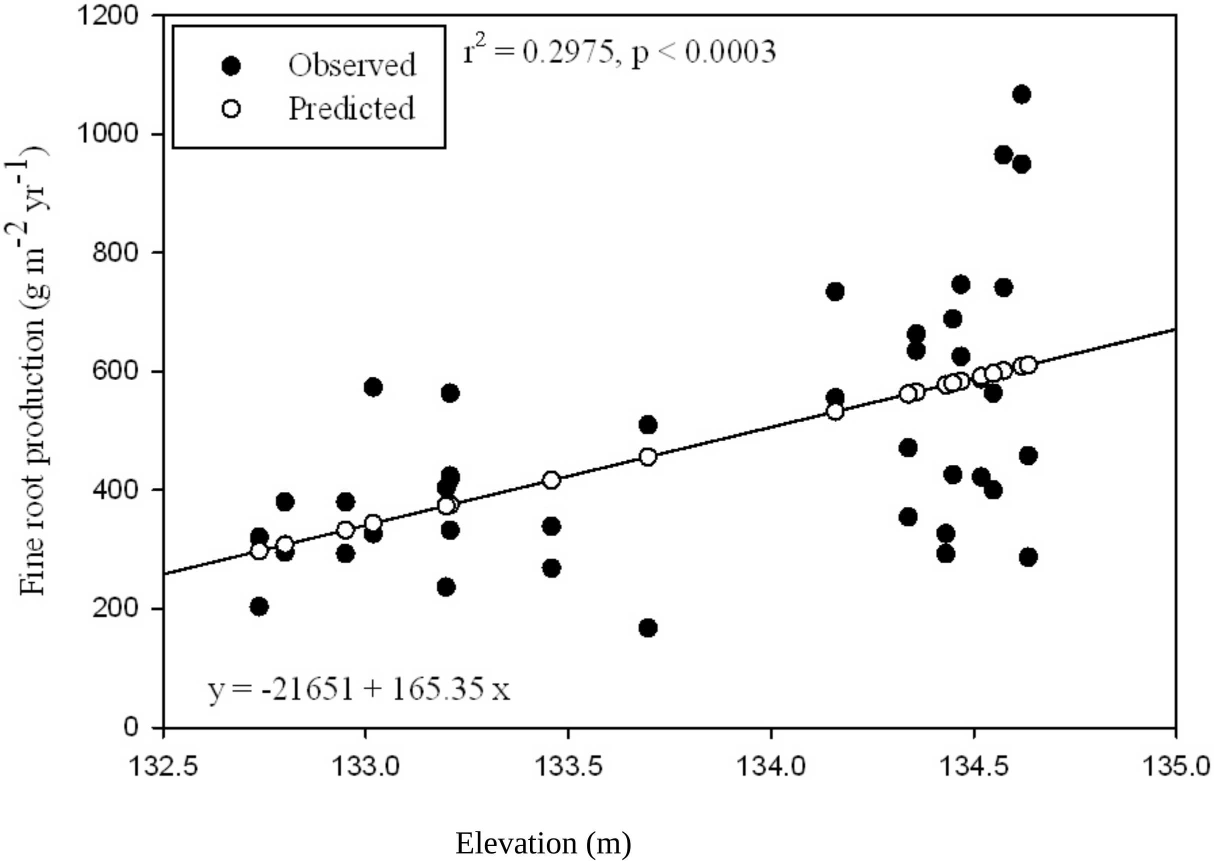

Figure 2.8. Linear relationship between fine root net primary productivity and relative elevation, relative to the highest point along the transects (natural river levee, plot 5).

Table 2.2. Monthly comparisons of live fine root C content (g m^{-2}) among different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11*	48.1	a	41.8	a	29.4	ab	19.3	b	0.0066
Aug-11*	49.7	a	41.2	ab	38.9	ab	17.9	b	0.0368
Sep-11*	62.9	a	60.1	a	47.5	ab	22.1	a	0.0662
Nov-11*	55.0	a	46.6	a	37.2	ab	24.8	a	0.0666
Dec-11*	96.6	a	52.2	b	36.8	b	26.3	b	0.0002
Jan-12*	82.8	a	58.8	ab	39.7	b	24.9	b	0.0054
Mar-12*	78.1	a	57.0	ab	47.1	ab	26.7	b	0.0227
Apr-12*	66.8	a	57.9	a	34.1	ab	47.2	a	0.0646
May-12*	68.4	a	51.0	ab	58.1	ab	24.7	b	0.0048
Jun-12*	75.7	a	60.6	ab	35.9	b	32.1	b	0.0024
Aug-12*	66.4	a	58.8	a	47.0	ab	27.7	a	0.0716
Sep-12*	87.2	a	53.3	ab	39.5	b	28.3	b	0.0070
Nov-12*	96.7	a	56.5	b	39.4	b	29.1	b	<0.0001
Dec-12*	87.2	a	52.1	ab	41.8	b	35.1	b	0.0025
Feb-13*	82.5	a	55.1	ab	41.2	ab	32.5	b	0.0195
Mar-13*	67.6	a	45.4	ab	32.1	b	30.8	b	0.0258
Average*	73.2	a	53.0	b	40.0	c	28.1	d	<0.0001

*Row means followed by different lowercase letters indicate significant differences among microsite types (Tukey’s HSD, α = 0.05).

Table 2.3. Monthly comparisons of dead fine root C content (g m^{-2}) among different microsites.

Date	Natural levee	Flat	Transitional	Backswamp	p-value
Jun-11*	14.9 a	14.0 a	14.3 ab	5.9 b	0.1016
Aug-11*	27.7 a	16.0 b	10.9 b	6.8 b	0.0002
Sep-11*	15.0 a	12.6 a	11.1 ab	2.8 b	0.0060
Nov-11*	8.6 a	8.8 a	5.1 ab	3.1 b	0.0417
Dec-11*	13.7 a	9.2 ab	5.7 b	3.1 b	0.0004
Jan-12*	11.5 a	11.4 a	5.4 ab	2.7 b	0.0091
Mar-12*	6.7 ab	11.0 a	4.6 ab	3.8 b	0.0303
Apr-12*	9.7 a	7.5 a	3.3 ab	5.5 b	0.2156
May-12*	11.5 a	10.8 a	8.5 ab	4.3 b	0.2030
Jun-12*	6.4 a	8.5 a	7.8 ab	2.4 b	0.1785
Aug-12*	14.7 a	7.9 ab	3.5 b	3.9 b	0.0007
Sep-12*	7.0 a	8.5 b	5.5 ab	5.0 a	0.5399
Nov-12*	11.0 a	5.0 b	2.2 b	2.1 b	0.0005
Dec-12*	13.8 a	6.4 ab	6.5 ab	2.9 b	0.0114
Feb-13*	9.8 a	4.8 b	3.4 b	2.0 b	0.0002
Mar-13	8.0 a	4.8 a	4.5 a	2.0 a	0.1671
Average*	12.0 a	9.2 b	6.3 c	3.7 d	<0.0001

*Row means followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, α = 0.05).

Table 2.4. Monthly comparisons of live fine root C concentration (g kg^{-1}) among different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11	399	a	373	a	370	a	360	a	0.1236
Aug-11	349	a	350	a	365	a	352	a	0.8100
Sep-11	390	a	379	a	408	a	399	a	0.0763
Nov-11	395	a	398	a	403	a	416	a	0.1026
Dec-11	399	a	394	a	390	a	382	a	0.5489
Jan-12	388	a	366	a	382	a	354	a	0.2174
Mar-12	365	a	349	a	384	a	382	a	0.0785
Apr-12	377	a	368	a	369	a	380	a	0.8504
May-12*	349	ab	375	ab	384	a	345	b	0.0160
Jun-12	376	a	357	a	378	a	357	a	0.5219
Aug-12	340	a	363	a	368	a	346	a	0.4084
Sep-12	363	a	341	a	382	a	365	a	0.3894
Nov-12	375	a	370	a	384	a	382	a	0.8245
Dec-12	357	a	339	a	391	a	338	a	0.0818
Feb-13	366	a	365	a	386	a	353	a	0.2865
Mar-13	348	a	360	a	321	a	363	a	0.2128
Average*	371	ab	365	a	379	b	367	a	0.0159

*Row means followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, α = 0.05).

Table 2.5. Monthly comparisons of dead fine root C concentration (g kg^{-1}) among different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11*	374	a	378	a	386	a	335	b	0.0074
Aug-11*	372	a	348	a	343	a	298	b	0.0002
Sep-11	378	a	348	a	384	a	351	a	0.0608
Nov-11*	387	a	352	ab	366	ab	342	b	0.0182
Dec-11	334	a	312	a	335	a	317	a	0.5546
Jan-12	322	a	326	a	371	a	339	a	0.1635
Mar-12	297	a	329	a	354	a	332	a	0.1021
Apr-12	286	a	310	a	334	a	318	a	0.2834
May-12	298	a	314	a	339	a	299	a	0.0784
Jun-12*	285	ab	306	ab	342	a	241	b	0.0027
Aug-12	315	a	294	a	337	a	290	a	0.2436
Sep-12	283	a	273	a	277	a	294	a	0.9373
Nov-12*	282	b	248	b	355	a	292	ab	0.0029
Dec-12	265	a	299	a	347	a	270	a	0.1022
Feb-13*	302	b	315	b	226	a	382	c	<0.0001
Mar-13	278	a	315	a	305	a	315	a	0.5441
Average*	316	a	317	a	347	b	304	a	<0.0001

*Row means followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, $\alpha = 0.05$).

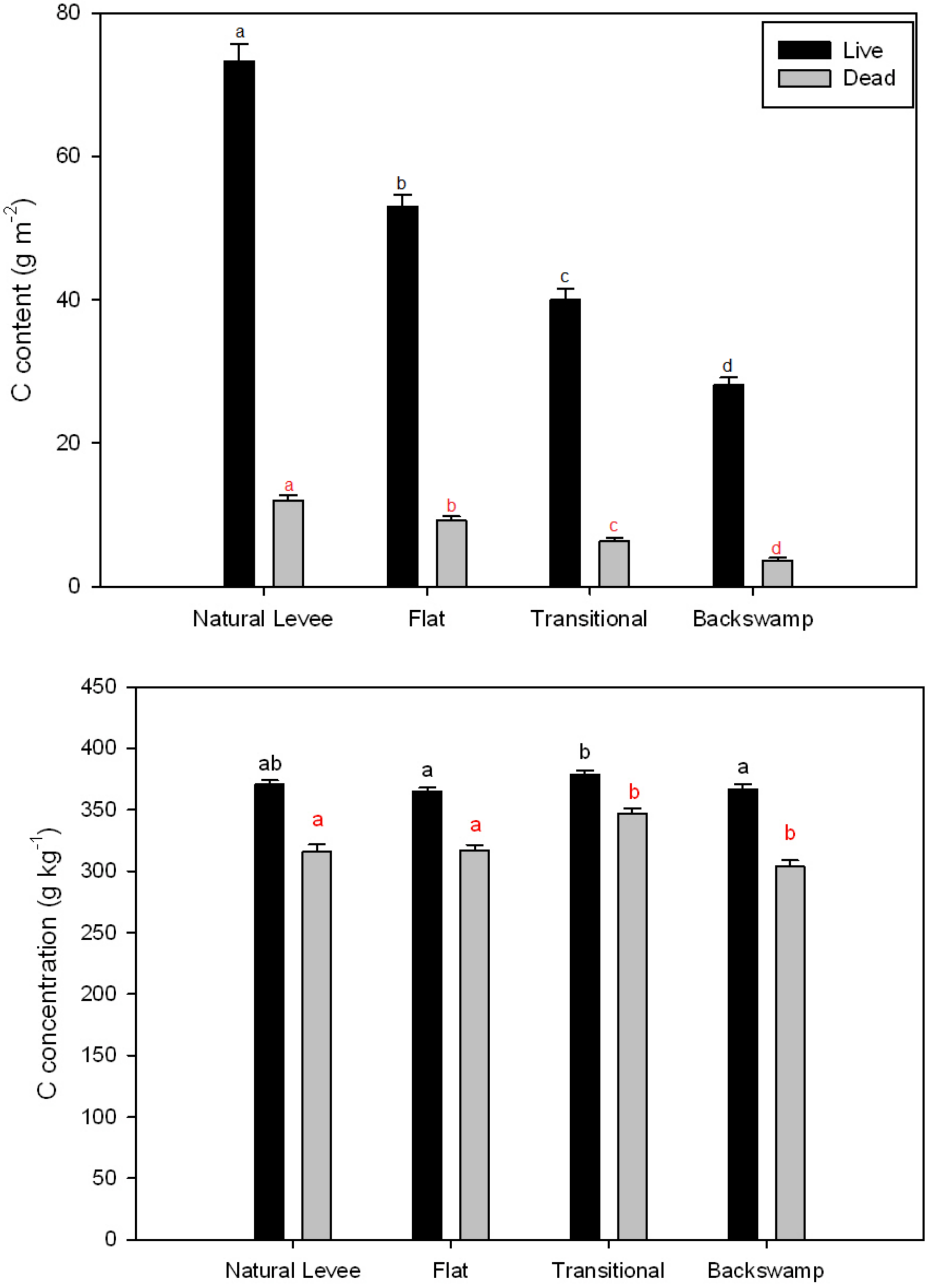

Figure 2.9. Live and dead fine root C content and C concentration by microsite. Different letters denote significant differences among microsites of either live or dead roots (Tukey's HSD, α = 0.05).

Table 2.6. Monthly comparisons of live fine root N content (g m^{-2}) among different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11*	1.31	ab	1.44	a	0.95	ab	0.69	b	0.0182
Aug-11*	1.44	a	1.57	a	1.17	ab	0.69	b	0.0136
Sep-11*	1.94	a	2.23	a	1.37	ab	0.68	b	0.0096
Nov-11	1.56	a	1.48	a	1.17	a	0.79	a	0.0689
Dec-11*	2.50	a	1.78	ab	1.18	b	0.85	b	0.0003
Jan-12*	2.57	a	2.28	ab	1.34	bc	0.87	c	0.0005
Mar-12	2.36	a	2.08	a	2.04	a	1.01	a	0.0773
Apr-12	2.12	a	1.96	a	1.11	a	1.57	a	0.0702
May-12*	2.17	a	1.76	ab	1.83	a	0.93	b	0.0028
Jun-12*	2.13	a	1.96	ab	1.09	bc	0.94	c	0.0029
Aug-12*	2.05	a	1.72	ab	1.35	ab	0.95	b	0.0470
Sep-12*	2.09	a	1.54	ab	1.12	b	0.86	b	0.0071
Nov-12*	2.63	a	1.79	ab	0.94	b	0.82	b	<0.0001
Dec-12	2.86	a	2.07	a	1.40	a	1.92	a	0.1984
Feb-13*	2.63	a	1.66	ab	1.36	b	1.03	b	0.0074
Mar-13*	2.39	a	1.61	ab	1.13	b	0.96	b	0.0164
Average*	2.17	a	1.81	b	1.28	c	0.97	d	<0.0001

*Row means followed by different lowercase letters indicate significant differences among microsite types (Tukey’s HSD, α = 0.05).

Table 2.7. Monthly comparisons of dead fine root N content (g m^{-2}) among different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11	0.48	a	0.54	a	0.50	a	0.22	a	0.1316
Aug-11*	0.84	a	0.55	ab	0.41	b	0.29	b	0.0015
Sep-11*	0.61	a	0.56	a	0.44	ab	0.12	b	0.0019
Nov-11*	0.35	a	0.34	ab	0.21	ab	0.13	b	0.0246
Dec-11*	0.49	a	0.41	ab	0.25	bc	0.15	c	0.0003
Jan-12*	0.50	a	0.47	a	0.21	b	0.11	b	0.0002
Mar-12	0.28	a	0.39	a	0.21	a	0.20	a	0.0962
Apr-12	0.40	a	0.32	a	0.16	a	0.21	a	0.1640
May-12	0.45	a	0.43	a	0.39	a	0.19	a	0.2395
Jun-12*	0.28	ab	0.33	a	0.25	ab	0.11	b	0.0588
Aug-12*	0.51	a	0.32	ab	0.16	b	0.15	b	0.0014
Sep-12	0.29	a	0.30	a	0.21	a	0.18	a	0.3964
Nov-12*	0.43	a	0.19	b	0.08	b	0.08	b	<0.0001
Dec-12*	0.56	a	0.28	ab	0.22	b	0.14	b	0.0066
Feb-13*	0.49	a	0.22	b	0.09	b	0.08	b	<0.0001
Mar-13	0.35	a	0.17	ab	0.19	ab	0.08	b	0.0635
Average*	0.45	a	0.36	a	0.25	b	0.15	c	<0.0001

*Row means followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, α = 0.05).

Table 2.8. Monthly comparisons of live fine root N concentration (g kg^{-1}) among different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11	11.3	a	13.5	a	12.5	a	14.2	a	0.0930
Aug-11	10.6	a	13.9	a	13.2	a	13.6	a	0.0609
Sep-11	12.8	a	14.2	a	13.4	a	13.5	a	0.6839
Nov-11	11.9	a	13.3	a	13.7	a	13.5	a	0.3219
Dec-11*	10.8	a	13.8	ab	15.0	b	12.8	ab	0.0268
Jan-12*	13.0	a	15.0	ab	16.8	b	12.8	a	0.0226
Mar-12*	12.2	a	13.7	a	18.6	b	14.5	ab	0.0028
Apr-12	12.3	a	12.8	a	13.8	a	12.3	a	0.5406
May-12	11.2	a	13.7	a	13.5	a	13.4	a	0.2271
Jun-12	11.1	a	12.1	a	11.2	a	10.6	a	0.6660
Aug-12	11.3	a	11.1	a	11.4	a	12.6	a	0.5434
Sep-12	9.88	a	10.7	a	11.5	a	11.0	a	0.6065
Nov-12	10.2	a	11.8	a	10.2	a	10.8	a	0.3160
Dec-12	11.8	a	13.2	a	13.8	a	32.9	a	0.4704
Feb-13	12.7	a	11.6	a	12.4	a	11.1	a	0.4256
Mar-13	12.8	a	13.1	a	11.7	a	11.6	a	0.3348
Average	11.6	a	12.9	a	13.3	a	13.8	a	0.1551

*Row means followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, $\alpha = 0.05$).

Table 2.9. Monthly comparisons of dead fine root N concentration (g kg^{-1}) among different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11	12.0	a	14.5	a	14.9	a	13.9	a	0.1270
Aug-11	11.9	a	12.8	a	13.9	a	12.7	a	0.4026
Sep-11	16.1	a	16.4	a	16.1	a	15.0	a	0.5267
Nov-11	17.0	a	14.8	a	15.5	a	14.0	a	0.1638
Dec-11	12.8	a	15.2	a	15.9	a	14.8	a	0.0912
Jan-12	14.4	a	15.0	a	17.6	a	14.3	a	0.0902
Mar-12*	12.8	a	13.6	ab	17.4	b	17.1	b	0.0033
Apr-12*	12.2	a	14.0	ab	17.0	b	13.5	ab	0.0060
May-12*	12.6	a	13.6	ab	15.5	b	14.1	ab	0.0406
Jun-12	12.2	a	13.6	a	13.2	a	10.4	a	0.0760
Aug-12*	11.3	a	12.8	ab	14.6	a	12.5	ab	0.0455
Sep-12	12.0	a	11.6	a	11.6	a	10.7	a	0.8424
Nov-12	11.8	a	11.9	a	14.1	a	12.2	a	0.2994
Dec-12	10.6	a	14.1	a	14.0	a	12.8	a	0.5709
Feb-13*	14.4	a	14.3	a	14.7	a	8.99	b	0.0016
Mar-13	12.9	a	12.6	a	12.7	a	12.5	a	0.9926
Average*	12.9	a	13.8	a	14.9	b	13.1	a	<0.0001

*Row means followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, $\alpha = 0.05$).

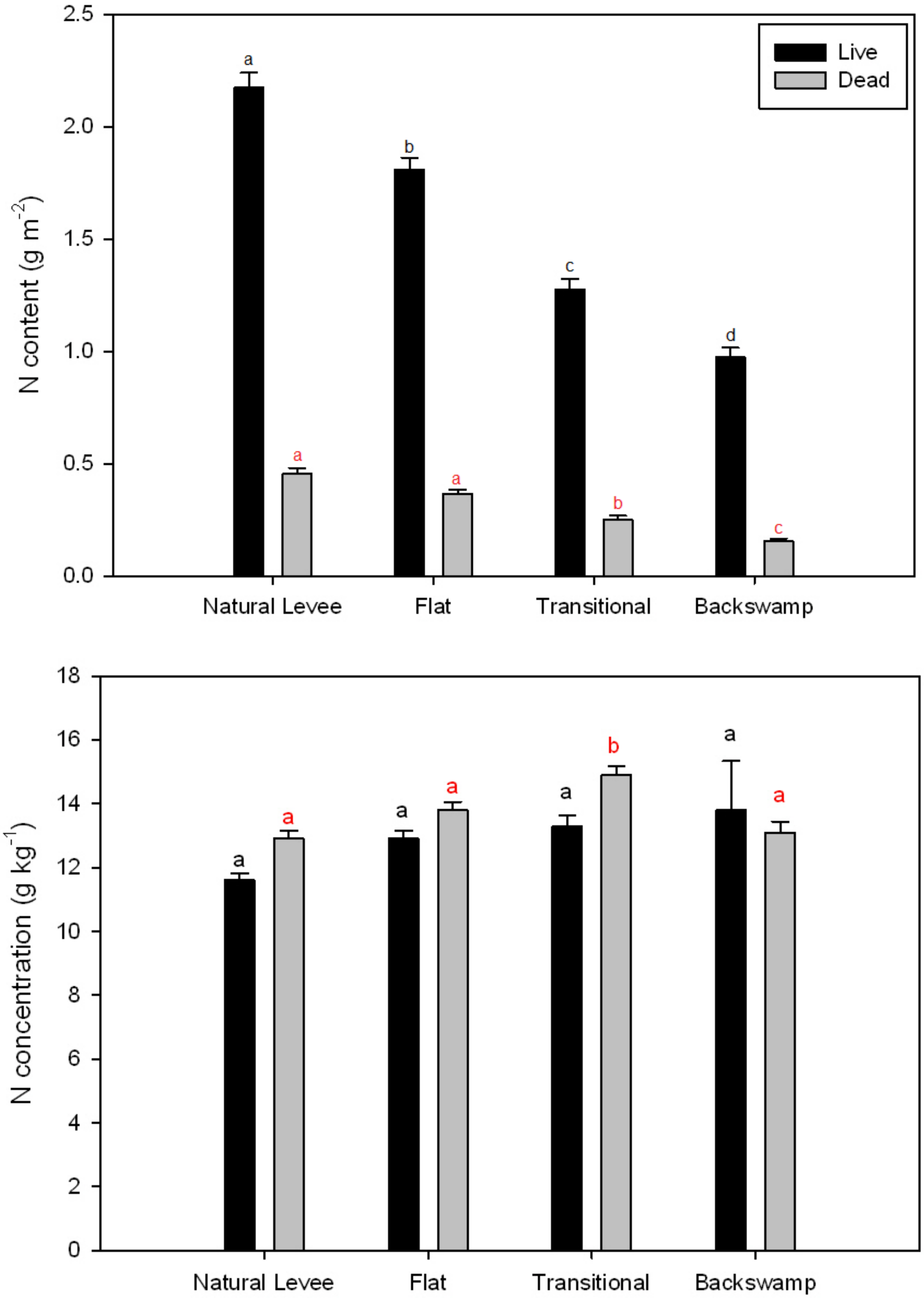

Figure 2.10. Live and dead fine root N content and N concentration by microsite. Different letters denote significant differences among microsites of either live or dead roots (Tukey's HSD, α = 0.05).

Table 2.10. Monthly comparisons of live fine root P concentration (g kg^{-1}) among different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11	3.20	a	2.85	a	2.85	a	2.43	a	0.2217
Aug-11*	3.80	a	3.10	ab	2.47	b	2.23	b	0.0008
Sep-11	3.51	a	3.06	a	2.00	a	2.32	a	0.0680
Nov-11*	3.91	a	3.32	ab	2.34	b	2.53	ab	0.0246
Dec-11	3.92	a	3.31	a	2.49	a	2.45	a	0.0425
Jan-12*	3.66	a	3.09	ab	2.33	b	2.48	ab	0.0177
Mar-12	3.26	a	2.69	a	2.01	a	2.14	a	0.0946
Apr-12	3.06	a	3.10	a	2.27	a	2.16	a	0.1893
May-12*	3.32	a	2.94	ab	2.22	b	2.25	b	0.0101
Jun-12	3.19	a	3.21	a	2.38	a	2.41	a	0.0454
Aug-12*	3.27	a	2.70	a	2.50	ab	1.70	b	0.0009
Sep-12*	3.58	a	3.04	a	1.73	b	1.83	b	0.0009
Nov-12*	3.32	a	3.20	a	1.64	b	1.92	ab	0.0033
Dec-12*	3.86	a	3.78	a	2.65	ab	2.17	b	0.0071
Feb-13*	3.19	a	2.83	ab	2.19	b	2.39	ab	0.0271
Mar-13*	3.94	a	2.92	ab	1.88	b	1.98	b	0.0001
Average*	3.50	a	3.07	b	2.25	c	2.20	c	<0.0001

*Row means followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, α = 0.05).

Chapter 3:

Nutrient limitation of fine root biomass in an old-growth floodplain forest at Congaree National Park, SC, USA

Abstract

The specific goals of this research are to determine the degree to which N or P, or both, may be limiting net primary production in this ecosystem. Fine roots and microbial biomass were studied across an elevational and wetness gradient in the Congaree National Park, SC. Elevation decreased and wetness increased across the following microsite types—natural levee, flat, transitional, and backswamp. In-growth coring was used, with four fertilizer treatments (control, N, P, and N + P) to provide a relative index of root growth. Fine root productivity decreased as elevation decreased and wetness increased, with the natural levee being the most productive and the backswamp being the least productive. N+P fertilization treatments significantly increased fine root productivity compared to the control treatment across entire study site. This study suggests that N and P co-limit fine root productivity in this floodplain forest. Drought effects were also observed during this study, indicating that water availability has a greater effect on both fine root productivity and microbial biomass than does N or P.

Key words: fine roots, nutrient limitation, in-growth cores, fertilization, microbial biomass, elevational gradient, floodplain forest

Nutrient availability is one of the key processes that controls productivity of all forest types around the world. Net primary productivity (NPP) in forests is often limited by low levels of nutrient availability (Binkley, 1986). According to Vitousek et al. (2010), nutrient limitation can be demonstrated by meaningful additions of an element in biologically available forms that cause an increase in the rate of a certain biological process, such as fine root growth. Many studies have focused on understanding the relationship between plant growth and soil fertility (e.g. Ostertag, 2001; LeBauer and Treseder, 2008; Alvarez-Clare et al., 2013). Nutrient limitations in forests influence not only productivity but also microbial populations which consequently control C allocation (Nadelhoffer et al., 1985). Globally, forest NPP is thought to be mainly limited by N, but some forests may transition from N to P as a primary growth limitation due to increased atmospheric N inputs (Vitousek and Howarth, 1991; Vitousek et al., 1997; Neatrour et al., 2008). N and P, in combination often limit productivity in most forest ecosystems (Vitousek and Howarth, 1991; Vitousek et al., 2010).

Human activities have increased the availability of N and P in many ecosystems, altering the amount of nutrients that are entering forested ecosystems, ultimately affecting nutrient transformations and cycles (Sundareshwar et al., 2003). Anthropogenic N additions have nearly doubled the global flux of N to the biosphere (LeBauer and Treseder, 2008). Vitousek et al. (1997) estimate that N deposition rates may increase another two or three-fold before reaching a plateau. Experimental additions of some nutrients affect N fixation, (Augusto et al., 2013), denitrification (Parkin, 1987), microbial respiration (Wallenstein et al., 2006), and many other ecosystem processes. Fine root production and turnover along with associated microbial activity are important in belowground C sequestration and nutrient cycling in forests (McClaugherty et al., 1982). Variable inputs of N and P can alter the amount of C sequestered and change amounts of these nutrients that are cycled through a system. As an example, when N input was increased, fine root mortality increased and production and longevity of fine roots decreased, while addition of N-free fertilizer (S and micronutrients) extended fine root longevity in a Norway spruce fertilization study (Majdi and Kangas, 1997).

Nutrient limitation is demonstrated when productivity is increased by the addition of a specific nutrient (Tanner et al., 1998). This generalization is based on the idea that plant tissue traits are directly related to growth costs and resource return times (Chapin, 1980). If tissues are expensive to generate because of limiting nutrients or slow uptake of C, then those tissues should be longer-lived because it may take longer to return the resources used to generate them. An example of this occurs when plants inhabiting infertile soils exhibit long-lived leaves with low C-gaining capacities (Ostertag, 2001). Likewise, plants on fertile soils have leaf tissues that are short-lived before nutrients are recycled (Ostertag, 2001). It is often assumed that fine roots will show similar responses to those of leaves in relation to nutrient availability (Chapin, 1980). If sites are nutrient rich, plants will respond by producing more fine roots in those areas (Jackson and Caldwell, 1989; Raich et al., 1994). Increasing nutrient availability should increase belowground NPP and root turnover rates. It has been suggested that this type of growth response might be specific to particular nutrients and could be used to examine growth limitations (Cuevas and Medina, 1986; Cuevas and Medina, 1988).

Nutrient limitation has a distinct relationship with productivity in forested floodplains (Schilling and Lockaby, 2006). Fine roots are important in regulating biogeochemical cycles in all ecosystem types and are essential to understanding how these systems respond to global climate change. Fine root production depends on the environmental aspects that govern an ecosystem; any stressor, especially drought and nutrient limitation, can cause shifts in fine root biomass. As N availability increases, the proportion of total biomass dedicated to roots may decrease, but belowground NPP increases in N-limited situations (Nadelhoffer, 2000). Vogt et al. (1996) concluded that more N is returned to the soil through fine root decomposition than by leaf litter decomposition. With additions of plant available N, plant community composition may shift to favor more competitive species, such as invasive and non-native species (Maurer and Zedler, 2002).

With increasing drought and urbanization stress in the southeastern United States, problems are likely to arise concerning forest production, especially involving water availability and augmented nutrient loads. Vogt et al. (1993) examined the use of fine roots as indicators of stress on forested ecosystems compared to aboveground biomass. As precipitation decreases, ecosystems that are subjected to stresses such as water and/or nutrient stress should be good candidates for using roots as bioindicators of changing stress levels (Vogt et al., 1993). Water often represents the primary limiting factor to production, but secondarily, N often is the nutrient that limits NPP (Vitousek and Howarth, 1991).

Determining the extent of nutrient limitation can be problematic because of variability (Neatrour et al., 2008). Mixed-species stand responses may be highly variable causing difficulty in interpreting results (Raich et al., 1994). Studies testing the changing roles of N and P limitation along with varying microtopography in a floodplain forest are scarce, especially those that involve both fine root production and microbial biomass. This study was conducted in the Congaree National Park and used an experimental approach to test the effects of N and P amendments on fine roots and microbial biomass. We focused on the growth response and activity of fine roots (roots with a diameter of <3 mm) because of their role in belowground C cycling and their potentially rapid response to fertilization treatments. N and P fertilization trials at different elevations were implemented to determine which nutrient was most limiting to the system and whether limitation changes with microsite wetness.

METHODS AND MATERIALS

Site Description and Fine Root Sampling

This study was conducted at Congaree National Park in Richland County near Columbia, SC (33°47’0” N, 80°47’0” W) (Fig. 3.1). This park contains the largest intact expanse of old growth bottomland hardwood forest communities in the United States (Zhao et al., 2006) centering on a 8991 ha portion of the east bank of the Congaree River and contains trees estimated to be older than 200 years (Wohl et al., 2011). The oldest loblolly pines (*Pinus taeda*) are >247 years old and the oldest baldcypress (*Taxodium distichum*) are 700-1000 years old (Wohl et al., 2011). Congaree National Park contains two major forest types that are influenced primarily by hydrologic regime (Allen et al., 2005). Sweetgum (*Liquidambar styraciflua*), American holly (*Ilex opaca*), oak species (*Quercus* spp.), sugarberry (*Celtis laevigata*), green ash (*Fraxinus pennsylvanica*), elm species (*Ulmus* spp.), red maple (*Acer rubrum*), and other hardwood species, as well as loblolly pine, inhabit areas that are infrequently flooded or flooded for a short period of time (Allen et al., 2005). Species composition in frequently flooded sloughs is dominated by baldcypress, black gum (*Nyssa sylvatica*), Chinese privet (*Ligustrum sinense*), loblolly pine, pawpaw (*Asimina triloba*), pond cypress (*Taxodium ascendens*), swamp tupelo (*Nyssa biflora*), sweetgum, water tupelo (*Nyssa aquatica*), and water oak (*Quercus nigra*), among others (Allen et al., 2005).

Soil series in this portion of the Park include Chastain and Congaree soil series (Soil Survey Staff, 2012). Chastain soils are fine, mixed, semiactive, acid, thermic Fluvaquentic Endoaquepts that are typically poorly drained and have frequent or occasional periods of inundation by water. These soils occur farther from the natural levee in the backswamp. Congaree soils are fine-loamy, mixed, active, nonacid, thermic Oxyaquic Udifluvents that are well to moderately drained and occur closer to the natural levee of the floodplain of the Congaree River (Soil Survey Staff, 2012).

Twenty circular plots (4.0 m diameter) were distributed among four transects in a portion of the Park that has limited access by the public. The sites were grouped into four microsite types, classified according to distance from the river and elevational changes with five plots in each microsite. The microsites included natural levee, flat, transitional, and backswamp (Fig. 3.1). The natural levee was chosen as the highest elevation and best drained microsite, while each subsequent microsite decreased in elevation and increased in soil wetness. The natural levee and flat tended to have a more open canopy and denser understory. Soils on the natural levee had lower soil moisture content, lower clay, and higher base saturation and CEC (cmol kg^{-1}). The backswamp tended to have a more closed canopy, with larger older trees, and a less dense understory. Soils within the backswamp tended to have a higher soil moisture content and clay percentage, and lower base saturation and CEC (cmol kg^{-1}) (Table 3.1).

Monthly climate data were collected from the nearest continuous monitoring station at the Columbia Metropolitan Airport, South Carolina (National Oceanic and Atmopsheric Administration, National Climatic Data Center, Asheville, NC, USA). Variables collected included precipitation (mm), mean daily air temperature (°C), and Palmer drought severity index (PDSI) values.

Fine Root Nutrient Limitation

Nutrient limitation on fine root dynamics was tested in the summer 2012 and fall 2012. The in-growth core method (Vogt and Persson, 1991; Vogt et al., 1998) was implemented for this portion of the project. This process replaces a soil core removed from the ground with root free soil from the same site. Each in-growth core was formed by removing a soil core (diameter of 8 cm to a depth of 11 cm), and placing it directly into a fiber glass mesh screen bag of the same size. The root free soil is contained in the screen bag to allow roots to grow into the bag and a relative estimate of production can be obtained from the in-growing roots. Four in-growth core treatments (control, N, P, and N+P) with two replications were installed at each plot. N was added to each core at a rate of 300 kg ha^{-1} and 50 kg ha^{-1} of P. Nutrients were added to 15 grams of sand and then added to each in-growth core before they were inserted back into the ground. These rates amounted to 0.331 grams N and 0.125 grams P per core. Cores remained in the soil for approximately four months (April 2012-August 2012; August 2012-January 2013), then were collected using a shovel; any roots extending outside of the mesh bag were cut off. Samples were then returned to the laboratory to be processed. Samples were stored at 4˚C to preserve live roots until extraction from cores. Only live roots were separated and collected from in-growth cores. Live roots are described as flexible, normally contain many lateral branches, and are white in color (Powell and Day, 1991). Cores were rinsed with tapwater to extract roots and then roots were sorted. Samples were then oven-dried at 70˚C for at least 72 hours and weighed. Weights were converted to g m^{-2} to an 11 cm depth.

Fine Root Nutrient Analysis

Samples were ground to pass a 0.40 mm sieve to evaluate C, N, and P concentrations and contents. Total C and N were quantified using thermal combustion (Perkin-Elmer 2400 series II CHNS/O analyzer; Perkin Elmer Corp., Norwalk, CT, USA). Concentrations of P were measured only for the natural levee and flat since there was insufficient sample (< 0.25 g per core) to calculate P concentrations for the transitional and backswamp microsites. Total P samples were dry-ashed and analyzed using the vanadomolybdate procedure (Jackson, 1958; Clawson et al., 2001). Total P was detected using a Spectronic 501 spectrophotometer (Milton Roy Co., Rochester, NY, USA) and total C, N, and P contents were calculated as a product of root dry weight and nutrient concentration.

Microbial Biomass C and N

Microbial biomass was estimated using the chloroform-fumigation method (Vance et al., 1987). Soil subsamples were taken from one set of in-growth cores collected for biomass from each plot during summer 2012 and fall 2012. All samples were sieved and roots were removed. For fumigated samples, 18.5 grams of moist soil were exposed to $CHCl_3$ for 24 hour and then extracted with 125 mL of 0.5 mol L^{-1} K_2SO_4. Unfumigated samples were extracted within 2 days after being collected. The soil-K_2SO_4 suspension was shaken for half an hour and then filtered and put in the freezer for at least 48 hours until analysis. After being thawed, samples were analyzed for organic C and N using a Shimadzu TOC-V and total N combustion analyzer (Shimadzu Scientific Instruments, Columbia, MD). Differences between fumigated and unfumigated samples represented microbial C and N.

Soil Analysis

Soil data were collected for each floodplain microsite, including depth to shallow water table, bulk density, percent sand, percent clay, organic matter, pH, CEC and base saturation (Table 2.1). Soils on the study plots were described from auger cores to a depth of 100 cm (Schoeneberger et al., 2002). Four soil cores per plot were collected to a depth of 11 cm for laboratory analyses. Cores were oven dried at 105°C to calculate bulk density using the core method (Soil Survey Staff, 2004). Soil pH was calculated from air dried subsamples using a 1:1 soil-deionized water slurry (Soil Survey Staff, 2004). Major extractable element concentrations

(Ca, Fe, K, Mg, Mn, Na, P, Zn) were quantified using inductively coupled plasma atomic emission spectroscopy (ICP-AES) after double extraction (Mehlich-1; Mehlich, 1953) and cation exchange capacity (CEC) was calculated. The percent base saturation was determined as the ratio of extractable bases to CEC. Total soil C and N contents were quantified using thermal combustion (Perkin-Elmer 2400 series II CHNS/O analyzer; Perkin Elmer Corp., Norwalk, CT, USA). Soil particle distribution (texture) was quantified using the hydrometer method as described by Gee and Bauder (1986).

Statistical Analysis

Differences in fine root biomass, fine root C and N concentration and content, fine root P concentration, and microbial biomass C and N content were examined using least means squares (PROC MIXED, SAS Institute, Inc. 9.2 2002-2008). Tukey's Range Test was used to test for differences among fertilization treatments for fine root production, nutrient concentrations and contents, and microbial biomass. Differences were considered statistically significant at $\alpha = 0.05$. T-tests were performed to determine differences between seasonal responses to fertilization treatments.

RESULTS

Precipitation Patterns

Annual temperature was similar to the 30-year average. The winter, fall, and summer months had lower than average precipitation and the spring months had higher than average precipitation during the study period. The Palmer drought index indicated that moderate drought conditions occurred from June 2011 to April 2012 (Fig. 3.2).

Fine Root Nutrient Limitation

Fine root biomass varied for the control, N, P, and N+P treatments, 57.9, 73.5, 84.7, and 71.6 g m^{-1}, respectively, although only the N+P treatment was significantly different from the control at the 0.05 level (Table 3.2). C and N concentrations in fine roots varied slightly but did not show any statistical differences among fertilization treatments (Tables 3.2). Fine root C and N content followed similar trends to fine root biomass, where the control and N+P treatments were statistically different, with the control having the least response and the N+P treatment having the greatest response (Table 3.2). P concentration for fine roots was only calculated for the natural levee and flat due to small amount of sample to process and did not show any statistical differences between fertilization treatments (Table 3.2).

Fine root production was also examined among microsites for fertilization treatments. The control treatment produced the most fine root biomass on the natural levee which was significantly greater than both the transitional and backswamp microsites (Table 3.3). For the N treatment, the value for the natural levee was statistically greater than values for all the other microsites (Table 3.3). When the P treatment was observed, the natural levee was significantly greater than the transitional and backswamp microsites, as well as the flat being significant greater than the backswamp (Table 3.3). The natural levee was significantly greater than both the transitional microsite and backswamp, and the flat was significantly greater than the transitional microsite for the N+P treatment (Table 3.3).

Fine root C concentration was significantly less between the transitional microsite and both the natural levee and flat (Table 3.3). Fine root C content showed significant differences among microsite types for all treatments, following similar patterns as fine root biomass. For the control, P, and N+P treatments, the natural levee produced significantly greater C contents in roots than both the transitional and backswamp microsites (Table 3.3). For the N treatment, fine root C content was significantly greater on the natural levee than all other microsites (3.3).

Fine root N concentration was statistical different among all treatments. The flat had significantly greater N concentration in roots than the backswamp (Table 3.3). The N treatment had the highest fine root N concentration on the transitional microsite, and was significantly greater than the natural levee (Table 3.3). The P treatment showed the same trends as the N treatment, except that the transitional microsite had a fine root N concentration that was statistically greater than that of both the natural levee and the backswamp (Table 3.3). The N+P treatment produced fine root N concentrations that were significantly greatest on the transitional and flat microsites and least on the backswamp microsite (Table 3.3).

Seasonal comparisons showed that fine root productivity was greater in the fall 2012 than summer 2012 across all microsite positions (Fig 3.3), and when all microsites were averaged there was a significant difference between seasons for both the control and N+P treatments (Fig. 3.4). Although not significant when separated by microsite, fine root C content followed similar trends to fine root biomass with fall 2012 having larger C contents than summer 2012 (Fig. 3.5). When microsites were averaged for the control and N+P treatments, fall 2012 was significantly greater than summer 2012 (Fig. 3.6). Fine root N content showed the same seasonal trends as biomass and C content across all microsites with fall 2012 being greater than summer 2012 (Fig. 3.7). When all the microsites were averaged, the mean fine root N content was significantly greater in fall 2012 than the summer 2012 for the control and N+P treatments (Fig. 3.8).

Microbial Biomass

Microbial biomass C content did not show any significant effects of fertilization treatment, microsite type, or season, this probably due to sample variability. For microbial biomass N, the control treatment had the greatest microbial N content, followed by N+P, P, and finally N treatments (124, 119, 115, and 107 mg kg^{-1}), with the control being significantly greater than the N treatment (Table 3.2). For the control and N treatments, microbial N content decreased from the natural levee towards the backswamp, with both the natural levee and flat microsites being statistically greater than the transitional and backswamp microsites (Table 3.3). The P treatment produced microbial N contents that were statistically greatest on the natural levee and flat compared to the backswamp (Table 3.3). Microbial N content was greatest on the natural levee and decreased towards the backswamp for the N+P treatment with the natural levee being statistically greater than the transitional microsite and backswamp, as well as the flat being statistically greater than the backswamp (Table 3.3). Microbial N content did not show any significant differences when seasonal comparisons were observed (Figs. 3.11, 3.12).

DISCUSSION

General circulation models (GCMs) used in the Southern Forest Futures Project predict warmer temperatures, ranging from 19.3-20.2°C, and more variable precipitation, ranging from 912-1106 mm, by 2060 in the southeastern United States (McNulty et al., 2011). Coupled with predicted increases in evapotranspiration, agriculture and urbanization (Simmons et al., 2007), deforestation (Osterkamp and Hupp, 2010), and reservoir construction (Hupp et al., 2009), climate change has the potential to damage floodplain forested systems by greatly decreasing productivity and nutrient and sediment storage.

Alterations to the landscape, through flow regulation resulting from dam construction and stream channelization, could lead to changes in sediment supply conditions (Hupp et al., 2009). Floodplains are also affected by dam construction and the downstream impacts to these landscapes include severe reductions in flood frequency, peak flows, flood duration and peak discharge, and sediment transport, as well as altered timing of floods and increased periods of low flows (Williams and Wolman, 1984). One of the most obvious changes associated with urbanization is the engineering of stream channels, where natural streams are replaced by concrete channels; this feature alters hydrology and urban stream channels show indications of downcutting (Henshaw and Booth, 2000). Groffman et al. (2003) states that downcutting results when large volumes of water scour out sediment in the channel that has accumulated during cultivation of farmland or residential construction in the watershed area.

The combination of reduced infiltration in impervious urban areas and stream incision can reduce groundwater levels in floodplains, called hydrologic drought, which will ultimately affect soil, plant, and microbial processes (Groffman et al., 2003). Along with a lower groundwater level, Hupp et al. (2009) suggests that in future years floodplain surfaces may become flatter because sediment trapping may occur primarily in the backswamp leading to a higher floodplain with little to no topographical relief, which in turn decreases connectivity. This will affect hydroperiod and ultimately nutrient loading and cycling with negative impacts on plant diversity and productivity (Hupp et al., 2009).

Drought may have contributed to the lack of variation in fine root response to fertilization treatments (Table 3.3, Fig. 3.3). Water stress throughout the study period may have suppressed root growth during summer 2012, showing that ultimately water was the most limiting factor for root growth. Nutrient supply and other factors like soil moisture and saturation are controlled by temperature and precipitation (Tanner et al., 1998). Data suggest that fine root biomass was controlled by drought stress because fine root biomass increased significantly following increased precipitation during fall 2012. In upland temperate forests, fine root production is always influenced by temperature and moisture (Burke and Raynal, 1994), while in southern floodplain forests fine root production and mortality are controlled by both temperature and precipitation, as well as hydrologic regime (Mitsch and Gosselink, 2007). More frequent severe droughts, combined with increased water demand for a growing population, could stress forested ecosystems more than nutrient limitation in parts of the southeastern United States (Lockaby et al., 2011).

In temperate floodplain forests, co-limitation by both N and P may occur. Elser et al. (2007) found that many ecosystems are near the point where both N and P are equally limiting plant growth. This study was similar, in that root production along the Congaree River floodplain increased significantly with the N+P fertilization treatment compared to the control, suggesting that the system may be co-limited by N and P. Multiple resource limitation occurs when the addition of several nutrients causes an increase in production or biomass (Vitousek et al., 2010). Many studies have shown that synergistic interactions exist between limited supplies of N and P across aquatic and terrestrial ecosystems (Elser et al., 2007; Harpole et al., 2011). P supply constrains the rates of N fixation in many ecosystems since when P additions occur, N availability is increased in both aquatic and terrestrial ecosystems (Schindler, 1977; Crews et al., 2000). On the other hand, additions of N allow microbes to produce more extracellular phosphatase enzymes that bind to P in soil organic matter (Treseder and Vitousek, 2001; Wang et al., 2007), which increases the local availability of P. Vitousek et al. (2010) points out that these interactions are asymmetric; P supply affects the quantity of N within ecosystems by affecting N fixation, while more phosphatase enzymes affect the rate of P cycling but not the quantity of P in the system. This process yields ecosystems in which plants are both limited in N and P (Elser et al., 2007).

Increased temperatures and more variable precipitation may create drier floodplain microsites and, in backswamps, a shift from anaerobic soil conditions to aerobic conditions as the floodplain becomes flatter and drier. Alterations in hydrology, like a lower groundwater table, can cause aerobic conditions in soils that were previously mapped as hydric (Groffman et al., 2003). This can cause shifts in microbial communities from obligate anaerobes to facultative anaerobes and/or aerobes. Our results suggest that prolonged drought increased microbial C and N activity during summer 2012, because during those months the soils were drier so that more aerobe species were present. After soil moisture increased in fall 2012 (when the area was no longer in drought) microbial communities became suppressed (Fig. 3.10).

Alteration of soil profiles in floodplain forests can have major effects on N and C mineralization. Soil moisture content may influence N and C mineralization through effects on the amount of substrate delivered to the microbial community (Curtin et al., 2012). Increasing temperatures may cause an increase in C mineralization due to an increase in aerobic microbial activity (MacDonald et al., 1995; Zak et al., 1999; Curtin et al., 2012); this would be especially prominent in the top layers of the soil where conditions are driest. Groffman et al. (2003) showed that aerobic urban forested floodplain soils with deep groundwater tables had high levels of NO_3^- and nitrification, a process that produces NO_3^- through microbial processes, along with low levels of denitrification, an anaerobic process that consumes NO_3^-, compared to reference soils in forested watershed with shallow water tables. Curtin et al. (2012) found that N mineralization significantly increased with increasing temperatures and most of the mineralized N accumulated as NO_3-N, even though nitrifiers are less tolerant of moisture stress than are ammonifiers (Paul and Clark, 1996). Ricker (2013) conducted an N mineralization experiment in Congaree National Park (overlapping our study period) and found that net N mineralization showed seasonal variations with the greatest mineralization in the summer months (Fig. 3.13). Regional drought produced aerobic soil conditions, which resulted in NO_3-N being the main product of N mineralization in all seasons. NH_4-N was produced in the hydric soils on the transitional microsite and backswamp due to spring flood pulsing (Ricker, 2013).

Hydrology is a controlling factor in many ecological communities (Dixon and Turner, 2006). Consequently, flood regime changes are most often associated with the decline of bottomland hardwood forests (Alldredge and Moore, 2012). It is well known that slight changes in elevation can alter the composition, richness, and diversity of plant species (Sharitz and Mitsch, 1993; Naiman et al., 2005; Kupfer et al., 2010). Floodplain plants are selective to where they establish because they are sensitive to alterations in flooding frequency and duration, as well as soil type (Battaglia and Sharitz, 2006). Since bottomland hardwood tree species differ in their tolerance to flooding (Wharton et al., 1982; Kozlowski, 2002), changes in flood regime could create changes in plant communities. Altered hydrologic regimes could cause a decline in obligate wetland species, which could eventually be replaced by non-wetland species once the older, larger plants die off, consequently changing forest composition and structure (Kupfer et al., 2010), especially in areas that are lower on the landscape because they are most susceptible to drier conditions. This species shift may take between 100-200 years to take place (Hughes, 1997). Groffman et al. (2003) found that throughout the Gwynns Falls watershed near Baltimore, MD, riparian zones were becoming drier, providing sites more favorable for germination and growth of upland species instead of native wetland species. This shift in species would have dramatic effects on ecosystem processes and services provided by wetland vegetation.

CONCLUSION

These data suggest that fine root biomass and fine root C content responded positively to the N+P treatment compared to the control treatment. Insignificant differences among the N and P treatments may be due to the large sample variances in the data. Microbial biomass N responded negatively to the N treatment compared to the control. Further study of nutrient limitation in bottomland hardwood floodplain forests is needed to understand how these systems will react to potential anthropogenic changes in N and P: this includes a larger sample number as well as a longer study period. In addition, the study also suggests that future changes in climate may have negative effects on nutrient cycling and C storage in floodplain forests, as shifts from being N limited to P limited may occur as well as changes in microbial metabolism throughout the floodplain.

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TABLES AND FIGURES

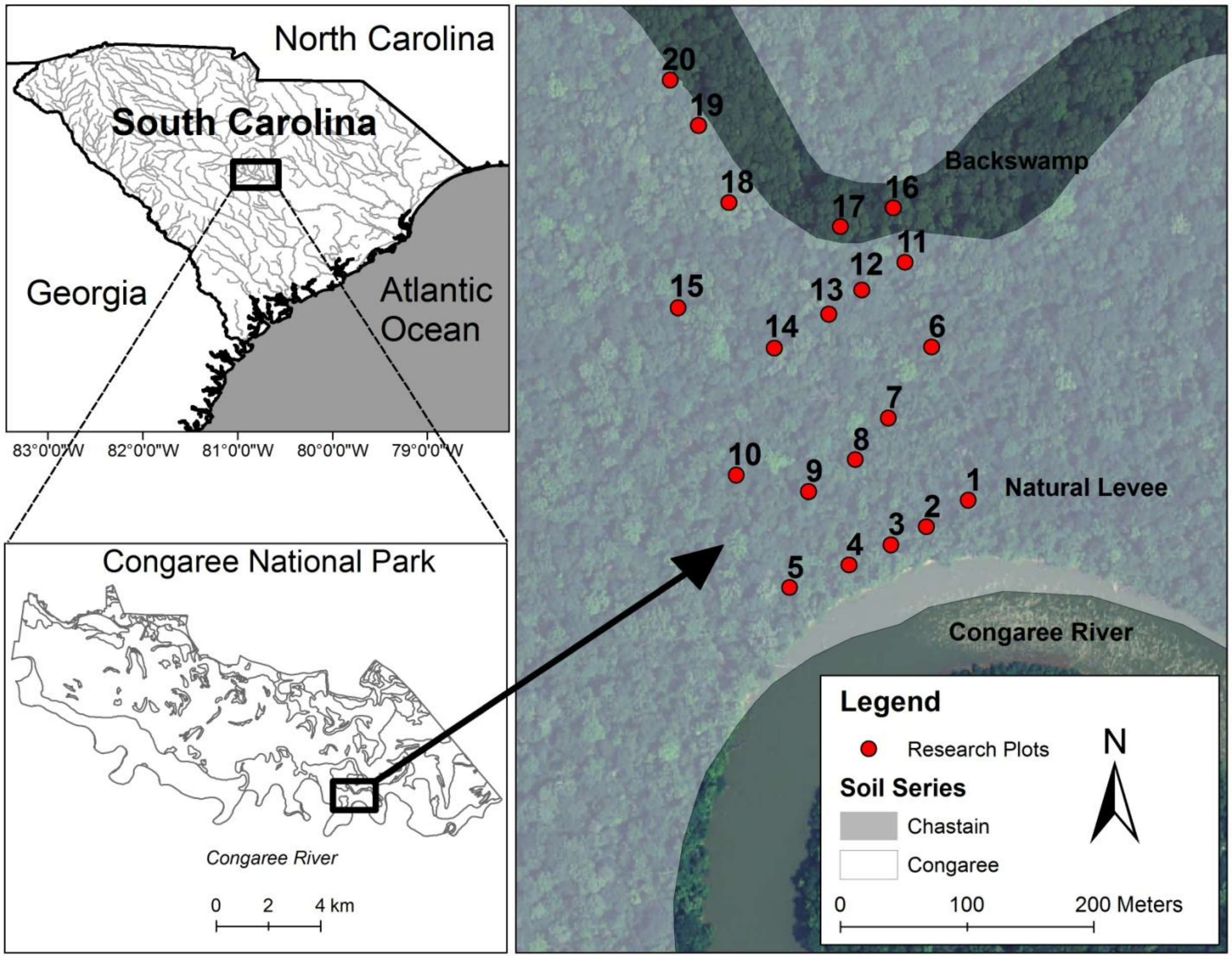

Figure 3.1. Location of Congaree National Park and research plots.

Table 3.1. Mean soil characteristics for each floodplain microsite, standard error is shown in parentheses (n = 5, per landscape). ***Mean values by column with different letters are significantly different (Tukey's HSD, α = 0.05). Source: Ricker, 2013.***

			Toposequence Soil Characteristics (0-10 cm)							
Microsite	**Plots**	**Depth to SHWT (m)†**	**Bulk Density (Mg m-3)**	**Sand (%)**	**Clay (%)**	**Organic Matter (%)**	**Soil pH**	**CEC (cmol kg^{-1}) ‡**	**Base Saturation (%)‡**	**C:N Ratio**
Levee	1-5	0.85 (0.07) a	1.02 (0.02) a	5 (0.4) a	26 (2.0) a	6.8 (0.40) a	5.91 (0.08) a	16.6 (1.1) a	88.5 (1.4) a	12.6 (0.3) a
Flat	6-10	0.82 (0.12) a	0.92 (0.05) a	8 (0.9) a	27 (0.5) a	8.2 (0.37) a	5.72 (0.17) a	17.0 (1.4) a	84.7 (2.7) a	11.6 (0.4) a
Transitional	11-15	0.44 (0.04) b	1.03 (0.03) a	7 (0.8) b	39 (1.0) b	7.5 (0.78) a	5.01 (0.05) b	12.2 (0.7) b	62.4 (2.4) b	11.9 (0.4) a
Backswamp	16-20	0.13 (0.02) c	0.96 (0.04) a	6 (0.9) c	45 (1.4) c	6.9 (0.89) a	5.11 (0.08) b	12.1 (0.5) b	64.7 (2.9) b	12.6 (0.5) a

†Depth to seasonal high water table (SHWT), interpreted as depth to common (>2%) redox depletions

‡Calculated from Mehlich-1 (double acid) extracts

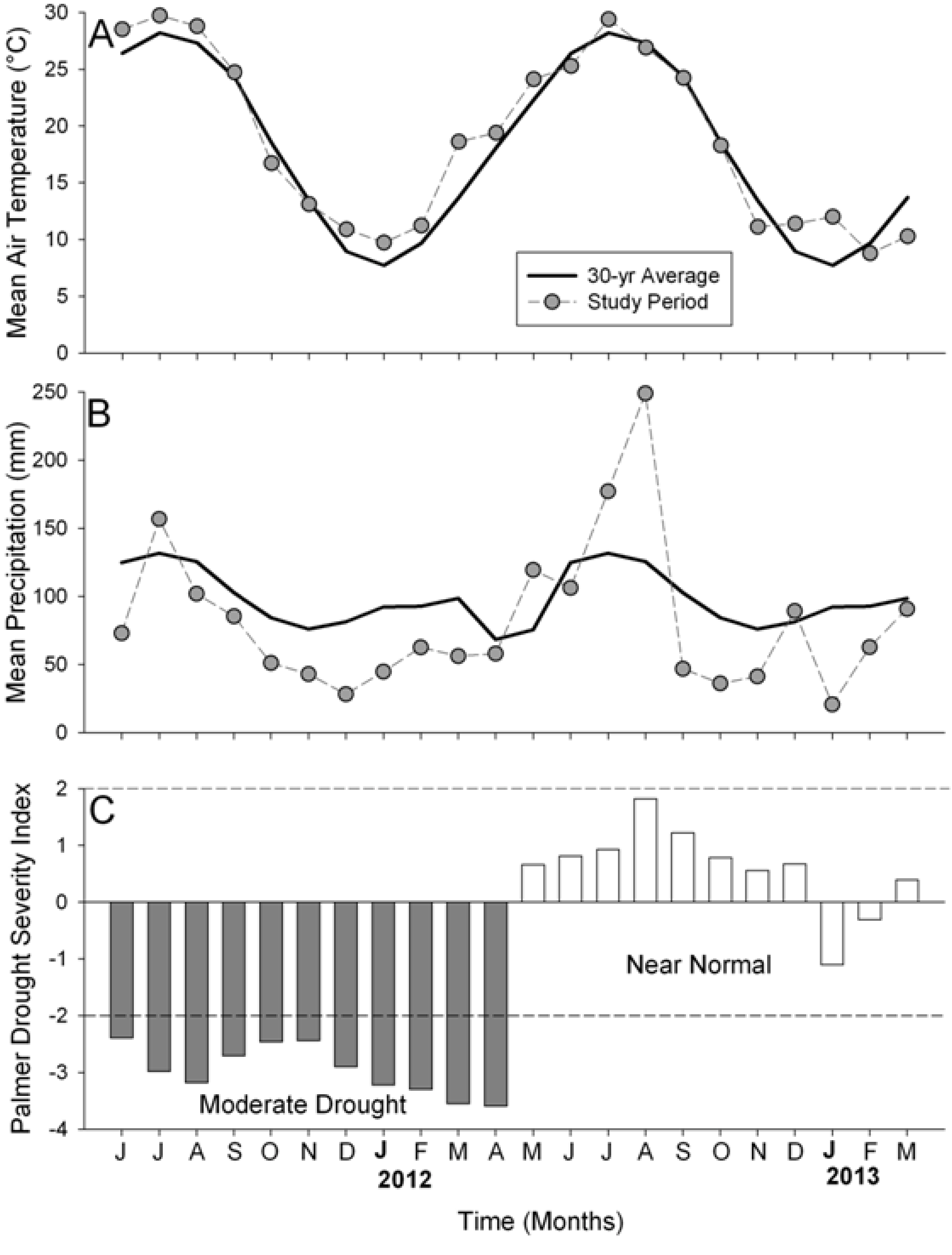

Figure 3.2. Monthly air temperature, precipitation, and Palmer drought severity index during the study period for the Columbia Metropolitan Airport, SC. ***Source: U.S. Department of Commerce-National Oceanic & Atmospheric Administration.***

Table 3.2. Least means squares estimates and differences fine root dynamics and microbial biomass (±SE) for different fertilization treatments across entire study site.

	Fertilization Treatment			
Variable	**Control**	**N**	**P**	**N+P**
Fine Root Biomass (g m^{-2})	57.9 (7.91) a	73.5 (9.96) ab	84.7 (8.80) ab	71.6 (10.6) b
Fine Root C Concentration (g kg^{-1})	330 (7.45) a	339 (7.89) a	341 (6.04) a	337 (6.70) a
Fine Root C Content (g m^{-2})	2,010 (290) a	2,518 (348) ab	2,520 (317) ab	2,910 (371) b
Fine Root N Concentration (g kg^{-1})	135 (3.68) a	14.1 (3.86) a	13.8 (4.24) a	13.3 (3.01) a
Fine Root N Content (g m^{-2})	77.6 (10.3) a	96.3 (11.7) ab	91.1 (10.0) ab	109 (13.3) b
Fine Root P Concentration (g kg^{-1})	2.43 (0.142) a	2.44 (0.0976) a	2.73 (0.132) a	2.53 (0.0896) a
Microbial Biomass C (mg kg^{-1})	627 (62.3) a	536 (51.5) a	577 (68.1) a	639 (70.5) a
Microbial Biomass N (mg kg^{-1})	124 (7.88) a	107 (7.44) b	115 (7.91) ab	119 (7.59) ab

*Row means followed by different lowercase letters indicate significant differences among fertilization treatments (Tukey's HSD, $\alpha = 0.05$).

Table 3.3. Least means squares estimates for fine root dynamics and microbial biomass (±SE) by microsite.

	Control	N	P	N+P
Fine Root Biomass (g m^{-2})				
Natural Levee	97.7 (25.6) a	145 (28.8) a	129 (23.5) a	151 (29.0) a
Flat	76.1 (10.5) ab	77.6 (11.8) b	86.3 (10.5) ab	107 (19.3) ab
Transitional	24.0 (7.47) b	27.8 (6.97) b	43.1 (12.5) bc	39.4 (9.47) c
Backswamp	33.7 (5.94) b	43.9 (8.57) b	27.7 (7.83) c	40.6 (6.99) bc
Fine Root C Concentration (g kg^{-1})				
Natural Levee	358 (10.6) a	345 (14.8) a	357 (13.5) a	355 (8.89) a
Flat	351 (8.85) a	345 (12.4) a	353 (5.67) a	336 (10.6) a
Transitional	293 (17.2) b	338 (17.0) a	334 (12.1) a	347 (14.3) a
Backswamp	320 (16.3) ab	328 (20.0) a	321 (14.2) a	310 (16.8) a
Fine Root C Content (g m^{-2})				
Natural Levee	3,510 (909)a	4,940 (984) a	4,620 (851) a	5,330 (1,010) a
Flat	2,640 (348) ab	2,620 (419) b	3,030 (358) ab	3,580 (654) ab
Transitional	802 (292) b	948 (261) b	1,450 (402) b	1,350 (236) b
Backswamp	110 (231) b	1,600 (348) b	1,020 (334) b	1,370 (266) b
Fine Root N Concentration (g kg^{-1})				
Natural Levee	13.3 (0.523) ab	12.7 (0.520) b	11.9 (0.391) b	12.9 (0.521) ab
Flat	15.1 (0.691) a	14.7 (0.552) ab	14.4 (0.358) ab	13.8 (0.654) a
Transitional	13.7 (1.07) ab	15.7 (1.05) a	16.1 (1.01) a	14.8 (0.628) a
Backswamp	11.9 (0.618) b	13.3 (0.638) ab	12.8 (0.822) b	11.5 (0.369) b
Fine Root N Content (g m^{-2})				
Natural Levee	120 (28.3) a	173 (31.5) a	145 (23.6) a	184 (32.2) a
Flat	115 (18.1) a	110 (15.0) ab	119 (12.7) a	149 (29.5) a
Transitional	38.7 (14.7) b	41.9 (11.1) b	66.8 (19.1) b	57.1 (9.48) b
Backswamp	37.8 (6.12) b	61.7 (13.3) b	34.9 (9.09) b	47.7 (8.95) b
Fine Root P Concentration (g kg^{-1})				
Natural Levee	2.98 (0.181) a	2.74 (0.181) a	2.78 (0.191) a	2.74 (0.181) a
Flat	2.66 (0.185) a	2.52 (0.185) a	2.81 (0.185) a	2.58 (0.185) a
Microbial C Content (mg kg^{-1})				
Natural Levee	857 (184) a	605.11(185.49) a	802.71(184.49) a	825.69(184.49) a
Flat	708 (61.6) a	666.41(61.60) a	677.34(61.60) a	579.81(61.60) a
Transitional	418 (94.6) a	378.40(94.61) a	689.99(94.61) a	524.07(94.61) a
Backswamp	526 (132) a	492.51(132.42) a	386.61(132.42) a	379.44(132.42) a
Microbial N Content (mg kg^{-1})				
Natural Levee	168 (12.5) a	132 (12.5) a	142 (12.5) a	154 (12.5) a
Flat	152 (12.4) a	141 (12.4) a	142 (12.4) a	131 (12.4) ab
Transitional	95.5 (17.5) b	78.3 (17.5) b	119 (17.5) ab	92.2 (17.5) bc
Backswamp	81.7 (7.13) b	77.0 (7.13) b	72.9 (7.13) b	81.3 (7.13) c

*Column means followed by different lowercase letters indicate significant differences among microsites for a given fertilization treatment (Tukey's HSD, α = 0.05).

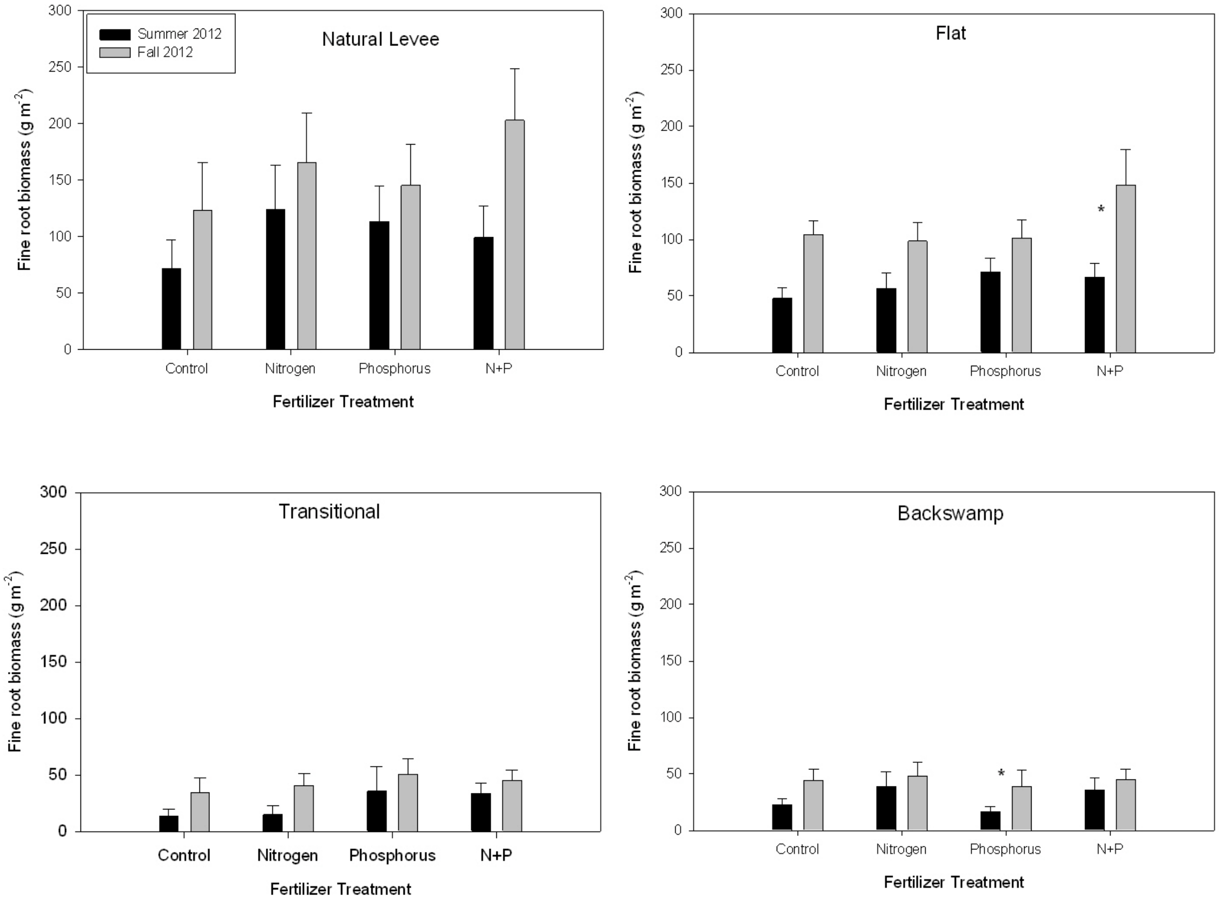

Figure 3.3. Fine root biomass (±SE) response to control, N, P, and N+P fertilization treatments using in-growth cores by microsite. ***denotes significant difference between seasons (t-test, α = 0.05).***

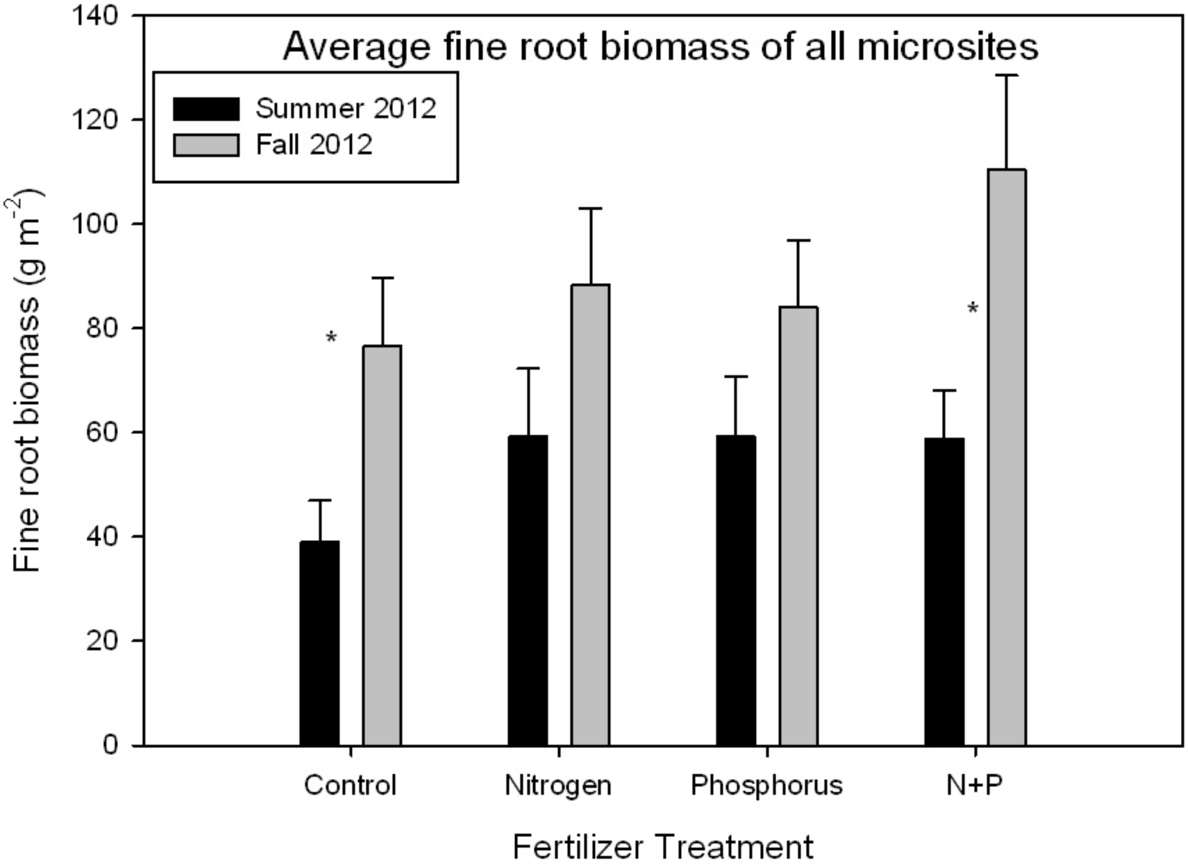

Figure 3.4. Average fine root biomass (±SE) response to control, N, P, and N+P fertilization treatments using in-growth cores. ****denotes significant difference between seasons (t-test, α = 0.05).***

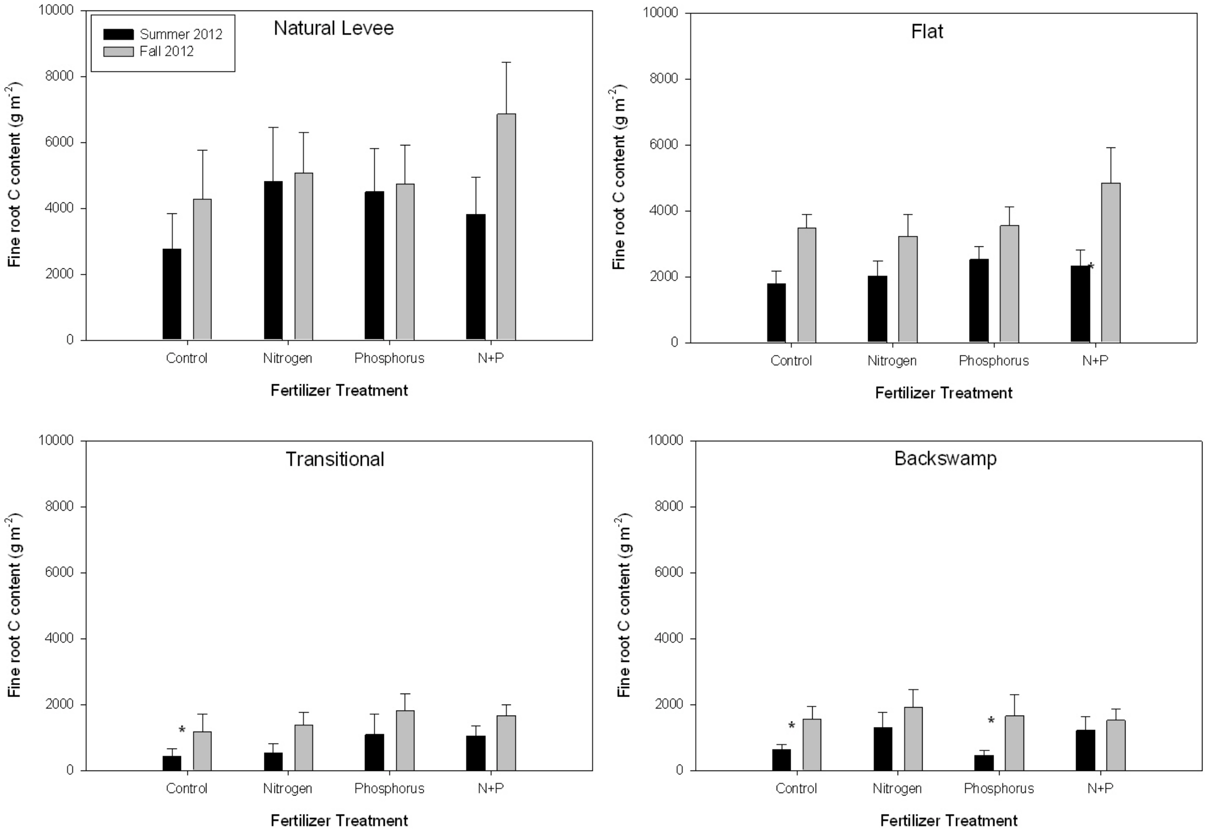

Figure 3.5. Fine root C content (±SE) response to control, N, P, and N+P fertilization treatments using in-growth cores by microsite. ****denotes significant difference between seasons (t-test, α = 0.05).***

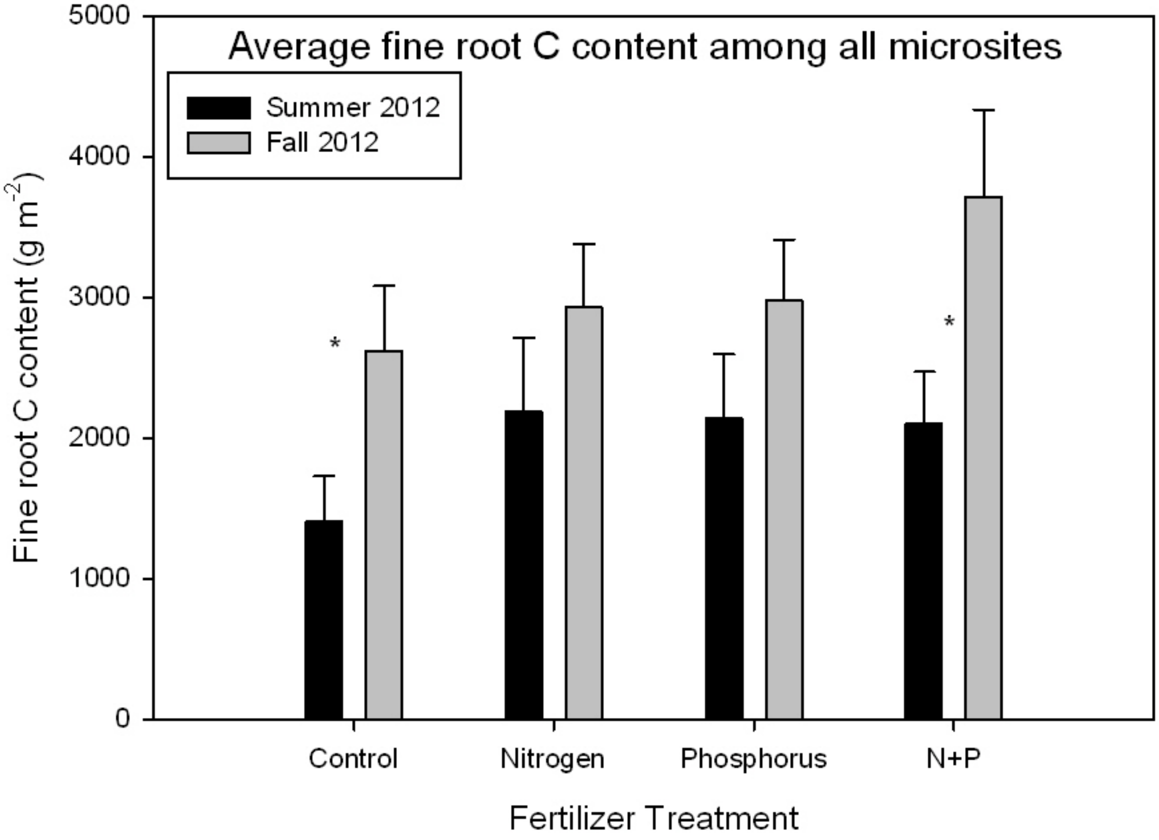

Figure 3.6. Average fine root C content (±SE) response to control, N, P, and N+P fertilization treatments using in-growth cores ****denotes significant difference between seasons (t-test, α = 0.05).***

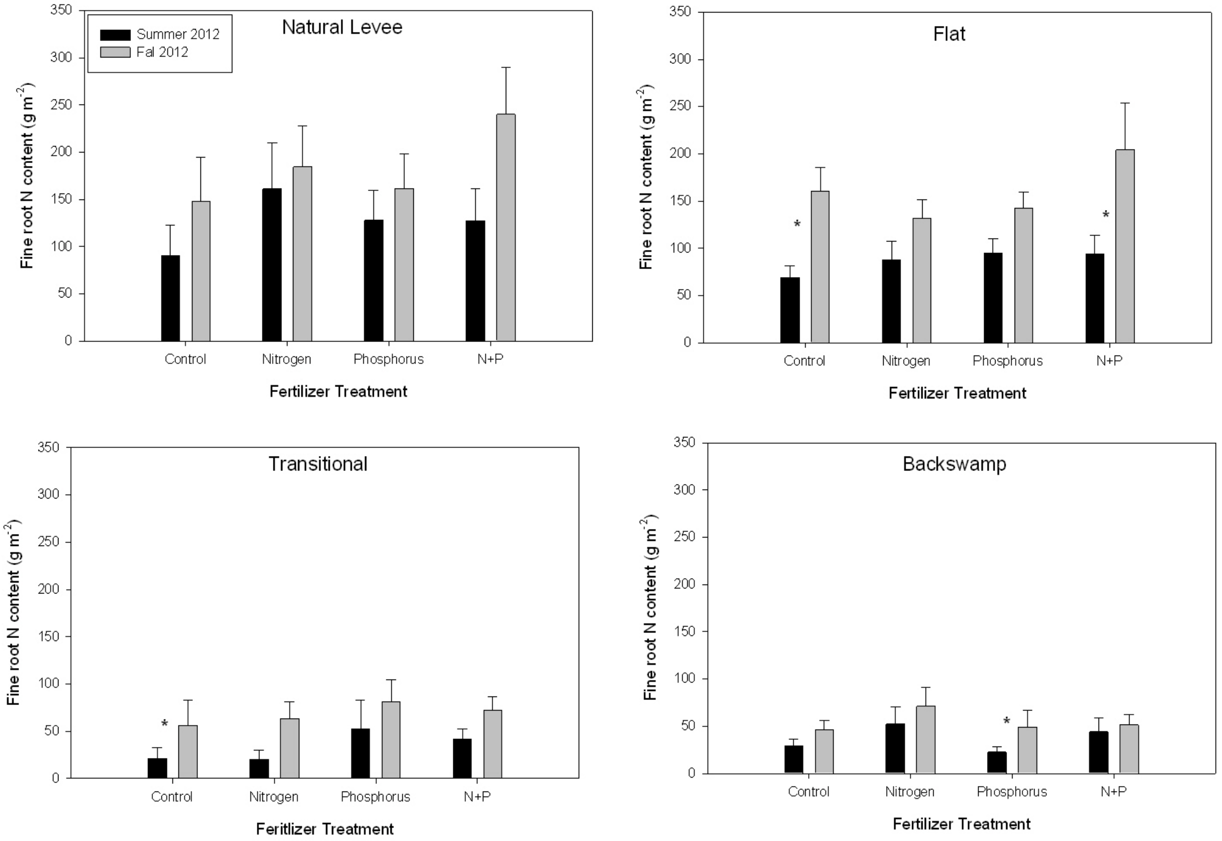

Figure 3.7. Fine root N content (±SE) response to control, N, P, and N+P fertilization treatments using in-growth cores by microsite. *denotes significant difference between seasons (t-test, α = 0.05).*

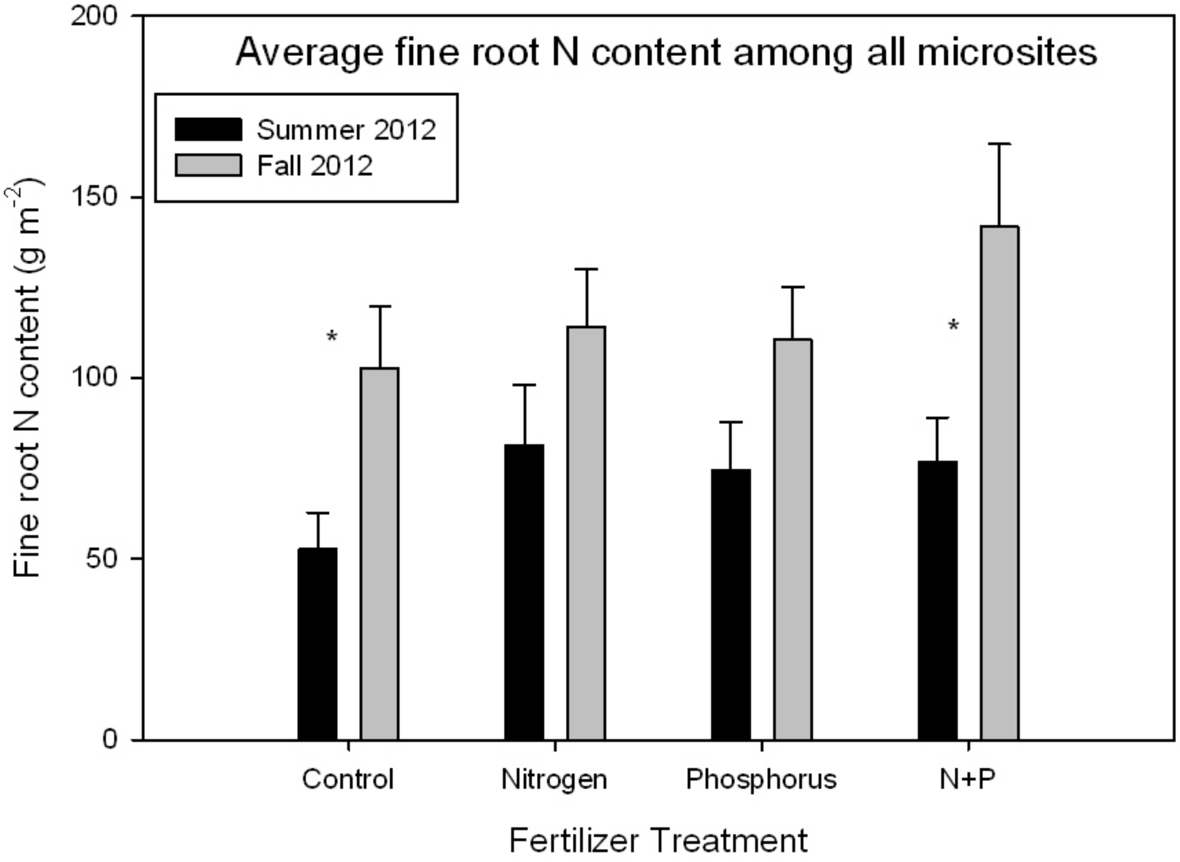

Figure 3.8. Average fine root N content (±SE) response to control, N, P, and N+P fertilization treatments using in-growth. ****denotes significant difference between seasons (t-test, α = 0.05).***

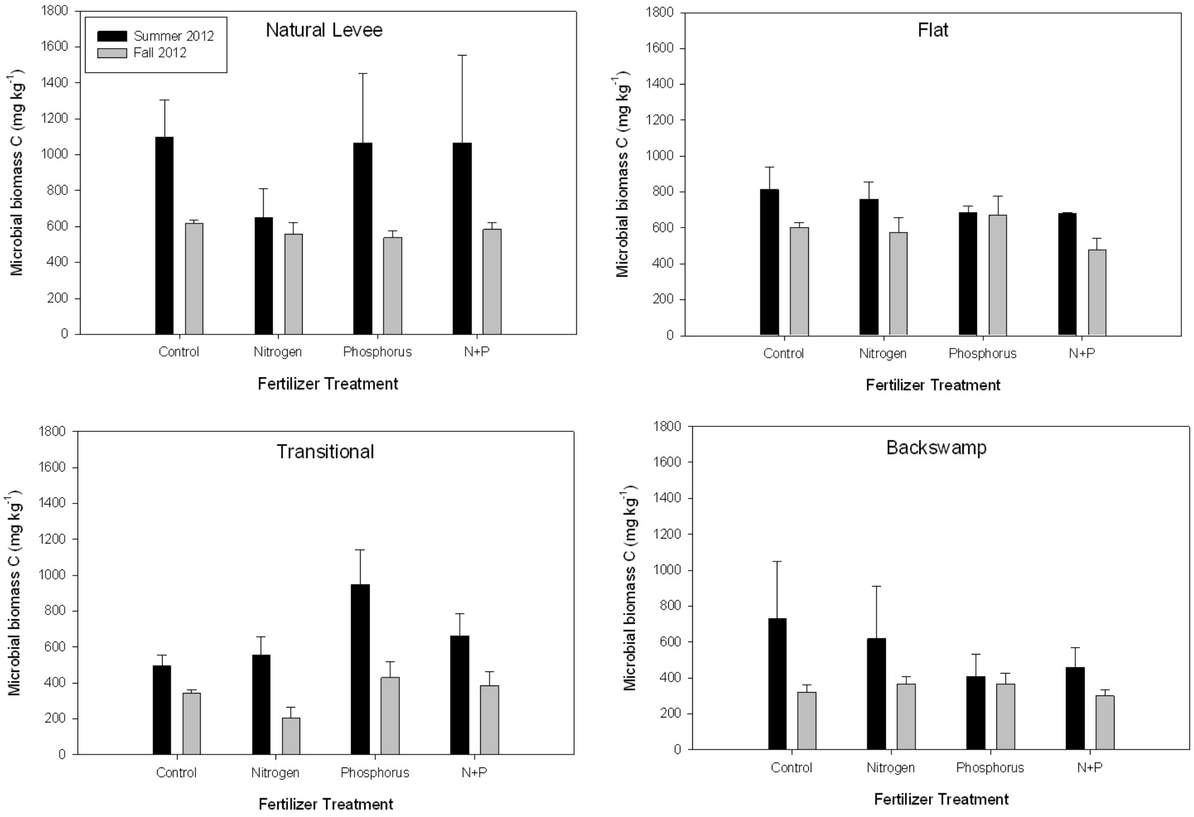

Figure 3.9. Soil microbial C content (±SE) response to control, N, P, and N+P fertilization treatments using in-growth cores by microsite. **denotes significant difference between seasons (t-test, α = 0.05).*

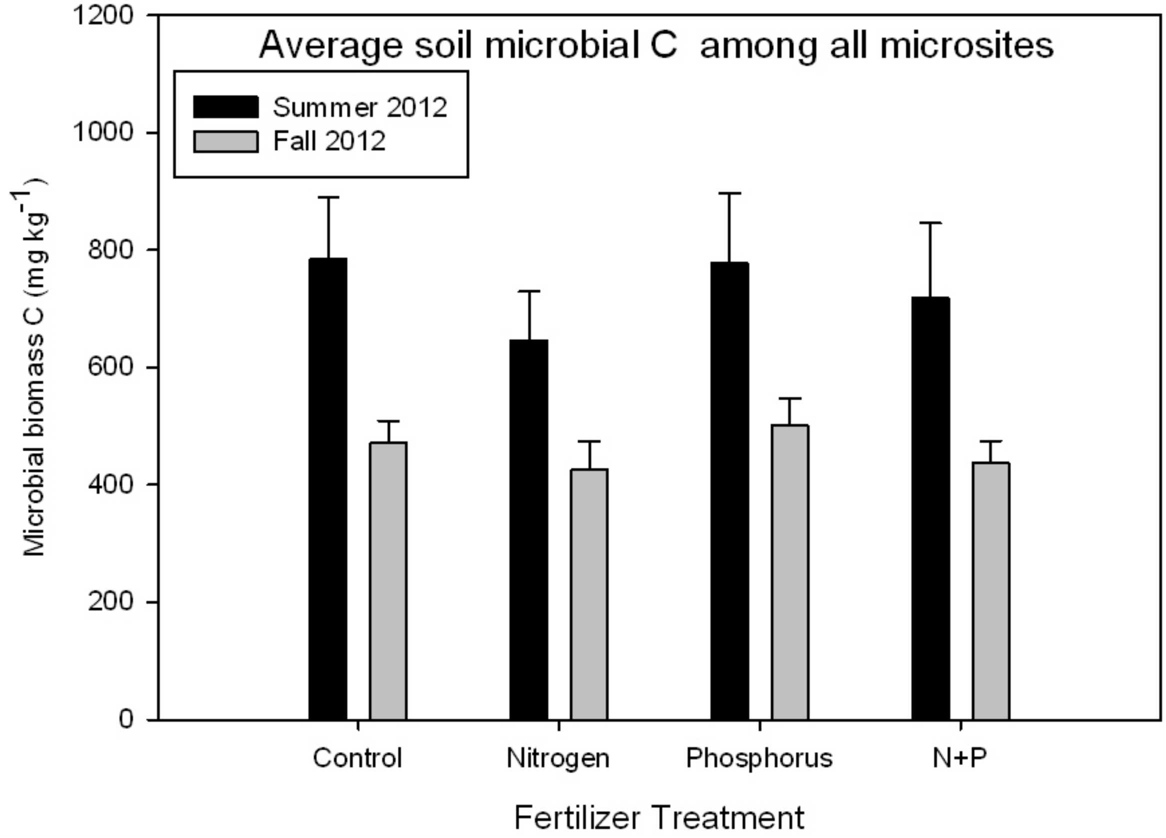

Figure 3.10. Average soil microbial C content (±SE) response to control, N, P, and N+P fertilization treatments using in-growth cores. ****denotes significant difference between seasons (t-test, α = 0.05).***

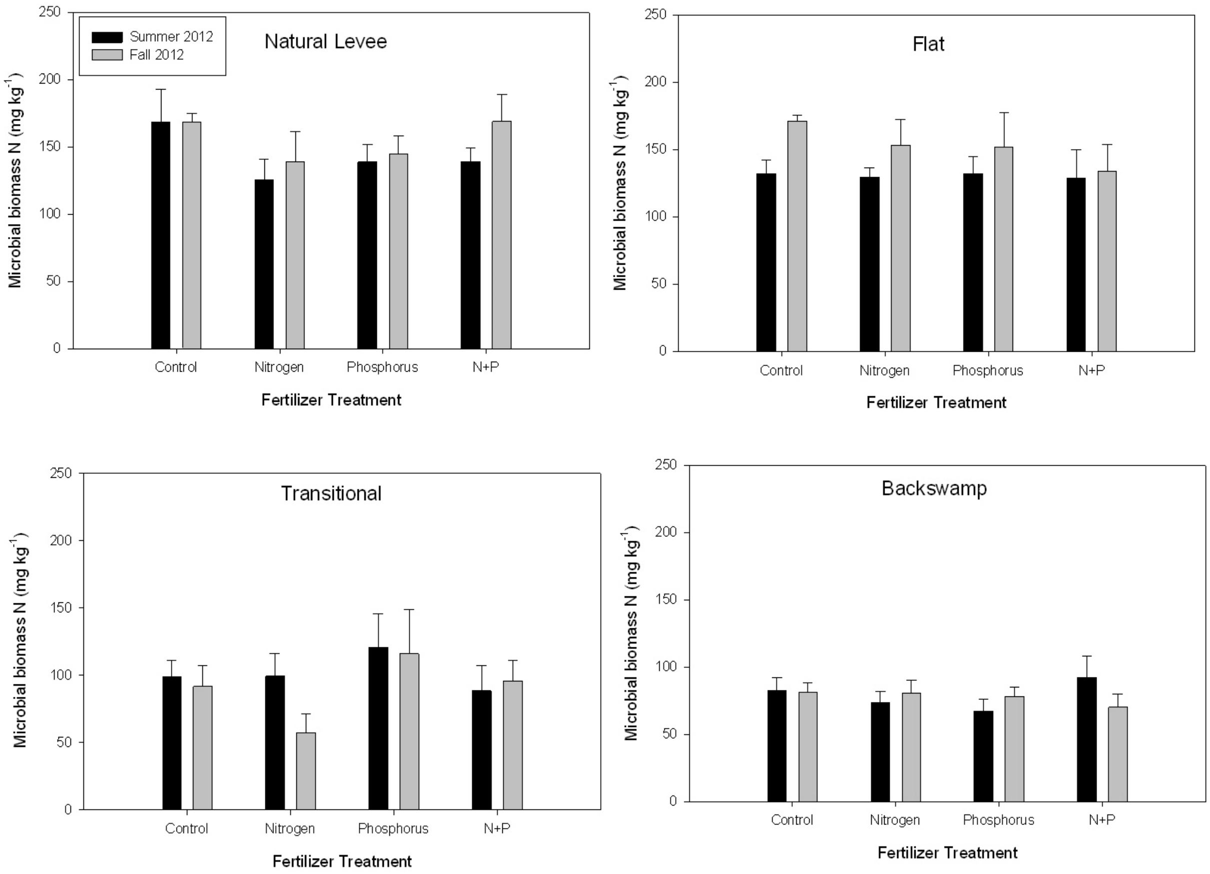

Figure 3.11. Soil microbial N content (±SE) response to control, N, P, and N+P fertilization treatments using in-growth cores by microsite. *_denotes significant difference between seasons (t-test, α = 0.05)._

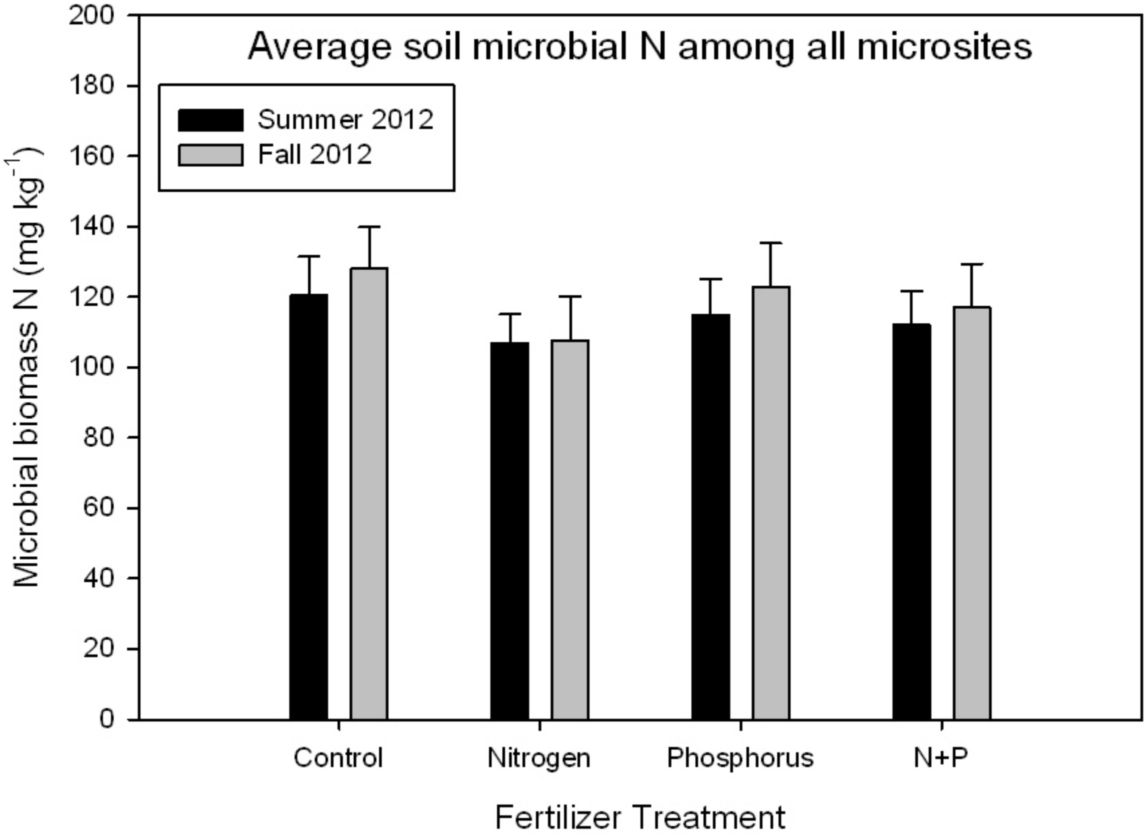

Figure 3.12. Average soil microbial N content (±SE) response to control, N, P, and N+P fertilization treatments using in-growth. **denotes significant difference between seasons (t-test, α = 0.05).*

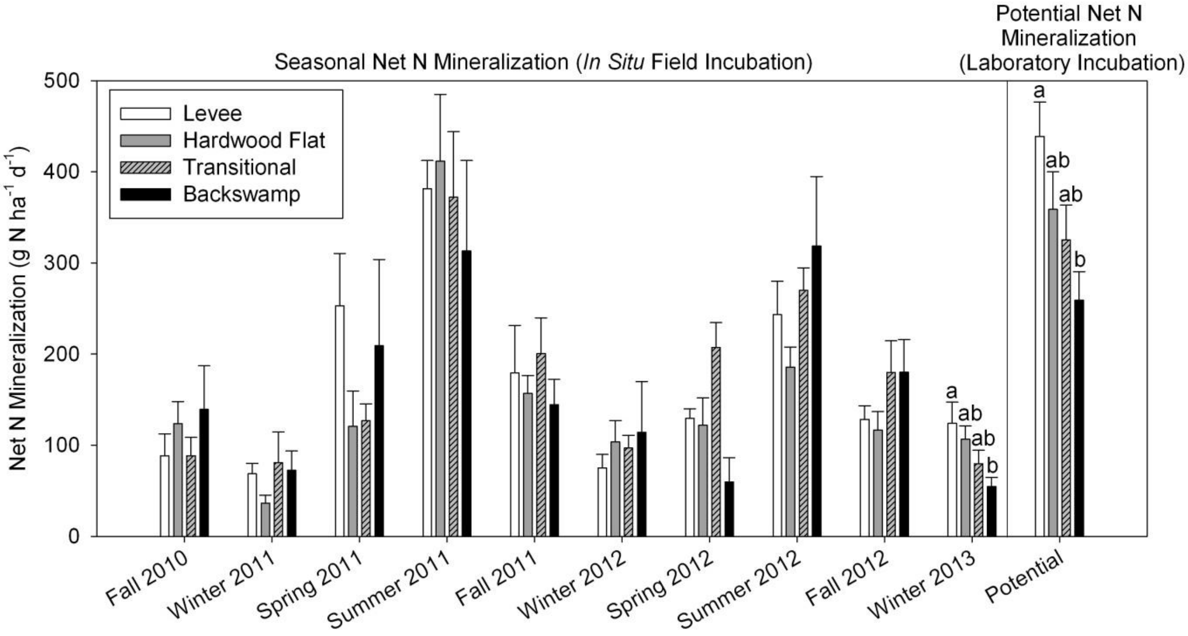

Figure 3.13. Mean net N mineralization rates (± 1 SE) separated by microsite (n = 10) from both *in situ* field incubations and laboratory analysis of potential net N mineralization. Means with different letters within each season are significantly different (Tukey's HSD, α = 0.05). *Source: Ricker, 2013.*

Chapter 4:

Summary and Conclusion

Study Objectives

The goal of this research was to understand how microtopography affects the function and structure of floodplain forests, specifically belowground productivity (BNPP). The study objectives were to: 1) determine fine root dynamics and quantify how belowground net primary production changes along a topographical sequence and wetness gradient, and 2) determine the degree to which N and P limit BNPP.

Fine Root Dynamics

Both BNPP and standing crop biomass of live fine roots decreased with decreasing elevation along the topographical sequence and increasing soil wetness. The greatest amount of fine roots occurred on the natural levee, decreasing significantly toward the backswamp which had the least amount of fine roots. Dead fine roots showed similar trends for standing crop biomass with the greatest amount of fine roots occurring on the natural levee and the least on the backswamp for over half the study period. Slight changes in elevation and soil wetness appeared to have a regulatory effect on both live and dead roots. Peaks in standing crop biomass were positively related to peaks in precipitation over the study period. Data suggested that fine root biomass was controlled by drought stress. Fine root C and N content reflected live and dead biomass trends, with the natural levee having the greatest C and N contents and the backswamp the lowest. Fine root N concentration was higher in dead roots than live roots on average. P concentrations decreased from the natural levee to the backswamp.

Nutrient Limitation

Data showed that fine roots responded positively to the N+P treatment compared to the control treatment. Non-significant differences among the N and P treatments may be due to the large sample variances in the data. C and N concentrations in roots did not show any statistical differences among fertilization treatments. C content followed similar trends to fine root biomass with the N+P treatment having the largest response. P concentration was only calculated for the natural levee and flat due to small amount of sample to process and did not show any statistical differences among fertilization treatments.

Microbial biomass C content responded the most for the N+P treatment followed by the control, P, and the N treatments. In response to all fertilization treatments, microbial C remained statistically unchanged. Microbial biomass N content appeared to be suppressed by fertilization treatments, especially the N treatment, with the control treatment having the greatest content, followed by N+P, P and finally N treatments. Microbial N content responded similarly for each fertilization treatment across the toposequence, with natural levee and flat having the greatest microbial N content and decreasing towards the transitional and backswamp microsites.

Seasonal trends show that fine root productivity was greater in the fall 2012 than summer 2012 across all landscape positions, and when all microsites were averaged there was a significant difference between seasons for both the control and N+P treatments. When all microsite types were averaged, fine root C and N contents for the control and N+P treatments followed similar trends to fine root biomass with fall 2012 having significantly larger C contents than summer 2012.

Synthesis and Future Directions

General circulation models (GMCs) used in the Southern Forest Futures Project predict warmer temperatures, ranging from 19.3-20.2°C, and more variable precipitation, ranging from 912-1106 mm, by 2060 in the southeastern United States (McNulty et al., 2011). Coupled with predicted increases in evapotranspiration, increases in agriculture and urbanization (Simmons et al., 2007), deforestation (Osterkamp and Hupp, 2010), and reservoir construction (Hupp et al., 2009), these increases have the potential to damage floodplain forested systems and may greatly decrease productivity, along with nutrient and sediment storage. Future drought may have a significant impact on forest productivity and C storage in the southeastern United States.

Among the topographic locations, data showed that lower elevation and increased soil wetness reduced total BNPP and belowground C storage in roots. Peaks in standing crop biomass were positively related to peaks in precipitation over the study period. Data from this study indicate that fine root biomass was controlled by drought stress. Drought stress is caused by warming temperatures and more variable precipitation data associated with climate change. Warming may cause a change in seasonality of root dynamics. These data also indicated that fine roots in Congaree National Park responded to the N+P treatment. Non-significant differences among the N and P treatments may be due to the large sample variances in the data, or trends may not have been observed due to co-limitation by both N and P.

In order to determine how future changes in precipitation and temperature may impact forest productivity, it is important that more studies to be conducted and encompass longer periods of time, especially regarding the belowground portion of these ecosystems. This study also indicates that further study of fertilization in bottomland hardwood floodplain forests is needed to understand how these systems will react to limitation or co-limitation of N and P.

Additionally, due to the complex and variable nature of biogeochemical processes, long-term studies should be implemented in order to gain a complete perspective on the effects of future predicted drought and nutrient limitation on floodplain forests.

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Appendix A: Representative photographs of study plots in Congaree National Park, SC, USA (33°47’0” N, 80°47’0” W)

Figure. 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 sweetgum (*Liquidambar styraciflua*), American sycamore (*Platanus occidentalis*), sugarberry (*Celtis laevigata*), and pawpaw (*Asimina triloba*). Photo credits: M.C. Ricker. *Source Ricker, 2013.*

Figure. A2. Photograph of study plot #6 representative of the moderately well drained hardwood flat microsite (painted marker represents the center of a 10 m diameter circular plot). Dominant overstory species include sweetgum (*Liquidambar styraciflua*), sugarberry (*Celtis laevigata*), and various bottomland oaks (*Quercus* spp.). The flat understory contained many switchcane (*Arundinaria gigantea* (Walter) Muhl. sub sp. *tecta* (Walter) McClure) brakes. Photo credits: M.C. Ricker. *Source Ricker, 2013.*

Figure. A3. Photograph of study plot #12 representative of the somewhat poorly drained transitional microsite (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 microsite understory was generally open and high water marks to 1.5 m were present on the tree trunks. Photo credits: M.C. Ricker. *Source Ricker, 2013.*

Figure. A4. Photograph of study plot #19 representative of the poorly drained backswamp microsite (painted marker represents the center of a 10 m diameter circular plot). The overstory was dominated by baldcypress (*Taxodium distichum*). The backswamp microsite understory was generally open and high water marks to >2.0 m were present on the tree trunks. Photo credits: M.C. Ricker. *Source Ricker, 2013.*

Appendix B: Chapter 2 Supplemental Data

Table. B1. Monthly comparisons for 0.1-1.0 mm diameter size class live fine root standing crop biomass (g m^{-2}) among the different microsites.

Date	Natural levee	Flat	Transitional	Backswamp	p-value
Jun-11*	62.31 a	47.18 a	39.81 ab	19.11 b	0.002
Aug-11*	64.50 a	52.15 ab	44.19 ab	25.28 b	0.0092
Sep-11*	61.31 a	65.89 a	38.62 ab	20.50 b	0.0022
Nov-11*	57.73 a	43.00 ab	44.19 ab	24.29 b	0.0431
Dec-11*	92.76 a	48.97 b	37.62 b	32.65 b	0.0009
Jan-12*	79.62 a	69.07 ab	38.42 ab	31.25 b	0.0083
Mar-12	85.00 a	71.06 a	63.90 ab	27.47 a	0.0731
Apr-12*	81.22 a	57.93 ab	35.23 b	38.22 ab	0.0319
May-12*	106.90 a	65.29 b	67.08 ab	38.02 b	0.0008
Jul-12*	107.37 a	72.06 ab	43.79 b	42.00 b	0.0007
Aug-12*	98.53 a	78.83 ab	52.95 bc	31.45 c	0.0013
Sep-12*	90.17 a	75.64 ab	38.62 bc	28.66 c	0.0004
Nov-12*	108.09 a	69.47 ab	32.05 b	31.05 b	0.0003
Dec-12*	107.29 a	83.21 ab	47.18 b	43.59 b	0.0168
Feb-13*	100.92 a	66.88 ab	33.64 b	33.04 b	0.0006
Mar-13*	106.50 a	51.16 b	34.84 b	34.64 b	0.0028

*Row mean followed by different lowercase letters indicate significant differences among microsite types (Tukey’s HSD, $\alpha = 0.05$).

Table. B2. Monthly comparisons for 0.1-1.0 mm diameter size class dead fine root standing crop biomass (g m^{-2}) among the different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11	19.31	a	15.73	a	11.35	a	9.16	a	0.0623
Aug-11*	29.26	a	20.11	ab	20.50	ab	8.96	b	0.0085
Sep-11*	22.49	a	19.91	ab	11.06	b	6.77	b	0.0005
Nov-11*	19.11	a	12.74	ab	8.96	b	5.97	b	0.0042
Dec-11*	23.49	a	16.92	ab	9.56	b	7.76	b	0.0011
Jan-12*	21.10	a	16.92	a	5.77	b	4.98	b	<0.0001
Mar-12*	16.92	a	16.52	ab	8.56	ab	7.56	b	0.0108
Apr-12	19.71	a	12.54	a	9.95	a	7.76	a	0.1615
May-12*	20.30	a	18.51	ab	16.32	ab	9.75	b	0.0474
Jul-12*	20.11	a	12.94	ab	8.16	b	7.37	b	0.0021
Aug-12*	21.30	a	16.12	ab	6.77	b	5.57	b	0.0007
Sep-12*	20.90	a	16.52	ab	7.96	b	6.37	b	0.0037
Nov-12*	24.88	a	14.13	b	3.98	c	4.98	c	<0.0001
Dec-12*	33.84	a	15.13	b	9.16	b	10.15	b	0.0004
Feb-13*	26.67	a	11.35	b	4.58	b	6.97	b	0.0003
Mar-13*	19.91	a	9.95	ab	6.37	b	4.38	b	0.0009

*Row mean followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, $\alpha = 0.05$).

Table. B3. Monthly comparisons for 1.1-2.0 mm diameter size class live fine root standing crop biomass (g m^{-2}) among the different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11	33.84	a	31.19	a	14.93	a	14.43	a	0.0149
Aug-11*	41.80	a	35.03	ab	30.52	ab	12.94	b	0.0397
Sep-11	43.20	a	52.55	a	34.04	a	17.63	a	0.0752
Nov-11*	40.61	ab	50.87	a	30.69	ab	14.73	b	0.0161
Dec-11*	55.94	a	36.43	ab	35.39	ab	19.11	b	0.0216
Jan-12*	50.16	a	39.61	ab	24.09	b	23.00	b	0.0227
Mar-12	46.67	a	43.00	a	31.85	a	21.23	a	0.1420
Apr-12	46.98	a	34.24	a	26.87	a	39.02	a	0.7017
May-12*	49.96	a	35.63	ab	32.65	ab	18.36	b	0.0124
Jul-12*	56.53	a	33.04	ab	28.09	ab	17.52	b	0.0081
Aug-12	41.80	a	30.96	a	33.09	a	21.15	a	0.3496
Sep-12	52.35	a	33.24	a	29.20	a	20.57	a	0.1480
Nov-12*	72.46	a	37.82	b	22.30	b	19.66	b	<0.0001
Dec-12*	58.13	a	34.04	ab	23.64	b	9.70	b	0.0017
Feb-13	39.21	a	33.84	a	32.65	a	20.65	a	0.3653
Mar-13*	51.31	a	36.49	ab	30.36	ab	15.92	b	0.0224

*Row mean followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, $\alpha = 0.05$).

Table. B4. Monthly comparisons for 1.1-2.0 mm diameter size class dead fine root standing crop biomass (g m^{-2}) among the different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11	16.37	a	9.36	a	10.95	a	6.97	a	0.1712
Aug-11*	25.08	a	10.15	b	8.76	b	9.38	b	0.0121
Sep-11	11.70	a	8.73	a	8.63	a	2.99	a	0.3599
Nov-11	7.47	a	12.94	a	8.67	a	5.47	a	0.6339
Dec-11	12.03	a	13.60	a	4.55	a	4.38	a	0.0956
Jan-12	11.09	a	4.02	a	12.23	a	5.19	a	0.4771
Mar-12	7.68	a	4.95	a	8.76	a	5.14	a	0.6353
Apr-12	10.84	a	4.78	a	2.49	a	4.78	a	0.1882
May-12	4.38	a	10.62	a	12.23	a	7.96	a	0.8066
Jul-12	3.98	a	14.73	a	6.97	a	4.31	a	0.1458
Aug-12	19.69	a	13.93	a	3.48	a	7.96	a	0.3153
Sep-12	8.36	a	11.28	a	7.11	a	4.98	a	0.4887
Nov-12	13.27	a	21.90	a	3.98	a	10.95	a	0.1687
Dec-12	7.96	a	5.97	a	9.62	a	2.65	a	0.3537
Feb-13	17.63	a	8.46	a	3.98	a	4.48	a	0.2455
Mar-13	18.31	a	9.95	a	9.56	a	5.31	a	0.5493

*Row mean followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, α = 0.05).

Table. B5. Monthly comparisons for 2.1-3.0 mm diameter size class live fine root standing crop biomass (g m^{-2}) among the different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11	47.77	a	38.04	a	37.82	a	46.18	a	0.8250
Aug-11	59.72	a	50.10	a	60.12	a	19.91	a	0.1783
Sep-11	96.88	a	44.68	a	60.86	a	41.01	a	0.2263
Nov-11	50.01	a	46.23	a	33.44	a	24.88	a	0.1631
Dec-11*	97.14	a	50.43	ab	45.78	ab	26.21	b	0.0336
Jan-12	91.35	a	65.69	a	50.05	a	44.29	a	0.3031
Mar-12*	102.52	a	65.12	ab	42.80	b	31.60	b	0.0108
Apr-012	58.23	a	65.09	a	35.33	a	63.70	a	0.2954
May-12	49.02	a	37.38	a	64.69	a	29.86	a	0.1069
Jul-12	65.69	a	68.79	a	45.45	a	32.10	a	0.1813
Aug-12	70.52	a	64.45	a	66.02	a	41.23	a	0.6330
Sep-12	87.98	a	64.36	a	43.79	a	40.67	a	0.1592
Nov-12*	88.03	a	43.59	b	64.27	ab	46.45	ab	0.0376
Dec-12	88.91	a	51.19	a	63.70	a	55.99	a	0.3562
Feb-13	99.31	a	59.47	a	67.35	a	42.69	a	0.1055
Mar-13	73.32	a	51.51	a	55.41	a	42.80	a	0.2737

*Row mean followed by different lowercase letters indicate significant differences among microsite types (Tukey’s HSD, α = 0.05).

Table. B6. Monthly comparisons for 2.1-3.0 mm diameter size class dead fine root standing crop biomass (g m^{-2}) among the different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11	25.21	a	24.68	a	29.53	a	15.92	a	0.7552
Aug-11	29.86	a	21.90	a	19.24	a	13.14	a	0.6345
Sep-11	25.21	a	14.73	a	20.30	a	.	.	0.4727
Nov-11	.	.	21.90	a	13.93	a	4.98	a	0.4298
Dec-11	13.93	a	13.93	a	16.59	a	.	.	0.9294
Jan-12	11.28	a	27.47	a	5.97	a	.	.	0.3351
Mar-12	.	.	25.08	a	.	.	10.95	a	0.4920
Apr-12	27.87	a	29.20	a	13.93	a	27.87	a	0.9342
May-12	39.81	a	31.19	a	.	.	5.97	a	0.6822
July-12	15.92	a	32.84	a	21.90	a	13.93	a	0.7212
Aug-12	20.57	a	29.86	a	11.94	a	43.79	a	0.0999
Sep-12	13.93	a	22.89	a	35.83	a	25.21	a	0.6177
Nov-12	20.90	a	19.91	a	5.97	a	.	.	0.4856
Dec-12	41.80	a	23.89	a	13.93	a	5.97	a	0.1330
Feb-13	.	.	5.97	.	7.96	.	.	.	.
Mar-13	.	.	25.88	a	11.28	a	3.98	.	0.2765

*Row mean followed by different lowercase letters indicate significant differences among microsite types (Tukey’s HSD, α = 0.05).

Table. B7. Monthly comparisons for total live fine root standing crop biomass (g m^{-2}) among the different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11*	120.03	a	109.48	ab	77.43	ab	53.75	b	0.0118
Aug11*	142.13	a	117.25	ab	101.72	ab	50.16	b	0.0172
Sep-11*	162.63	a	158.65	a	115.26	ab	53.35	b	0.0393
Nov-11*	138.35	a	116.52	ab	91.60	ab	58.92	b	0.0429
Dec-11*	245.84	a	130.78	b	92.36	b	67.48	b	0.0001
Jan-12*	212.00	a	161.24	ab	97.54	b	69.67	b	0.0047
Mar-12*	209.01	a	159.65	ab	126.80	ab	71.86	b	0.0232
Apr-12	174.77	a	157.26	a	128.19	a	90.37	a	0.0618
May-12*	196.07	a	151.48	a	134.56	ab	69.47	b	0.0019
Jul-12*	203.32	a	167.01	ab	94.55	b	86.99	b	0.0018
Aug-12*	189.70	a	158.25	ab	119.04	ab	77.24	b	0.0308
Sep-12*	230.51	a	147.50	ab	99.93	b	75.64	b	0.0020
Nov-12*	259.77	a	150.89	b	99.33	b	74.65	b	<0.0001
Dec-12*	245.44	a	153.08	ab	107.09	b	99.73	b	0.0008
Feb-13*	229.52	a	148.30	ab	106.10	b	88.58	b	0.0097
Mar-13*	196.67	a	125.21	ab	92.16	b	85.00	b	0.0176

*Row mean followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, α = 0.05).

Table. B8. Monthly comparisons for total dead fine root standing crop biomass (g m^{-2}) among the different microsites.

Date	Natural levee		Flat		Transitional		Backswamp		p-value
Jun-11	41.60	a	37.82	a	37.42	a	18.11	a	0.2010
Aug-11*	75.24	a	45.58	ab	30.66	b	21.70	b	0.0005
Sep-11*	39.41	a	35.13	a	28.07	ab	7.96	b	0.0045
Nov-11*	24.88	a	22.10	a	13.82	ab	9.16	b	0.0416
Dec-11*	39.89	a	29.26	ab	17.72	bc	9.95	c	0.0005
Jan-12*	34.47	a	33.47	ab	14.13	bc	7.85	c	0.0009
Mar-12	23.84	ab	32.53	a	12.94	ab	11.61	b	0.0251
Apr-12	35.035	a	23.69	a	17.92	a	10.15	a	0.0993
May-12	38.62	a	34.24	a	24.88	a	14.33	a	0.1479
Jul-12	26.87	a	23.69	a	21.10	a	11.35	a	0.2709
Aug-12*	45.19	a	27.47	ab	10.55	b	12.34	b	0.0003
Sep-12	27.87	a	26.48	a	20.11	a	16.92	a	0.4801
Nov-12*	37.03	a	18.31	b	7.17	b	6.17	b	<0.0001
Dec-12*	54.34	a	20.50	b	17.72	b	11.55	b	0.0005
Feb-13*	39.02	a	15.33	b	8.76	b	6.17	b	0.0005
Mar-13*	29.06	a	15.53	ab	14.531	ab	6.37	b	0.0742

*Row mean followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, α = 0.05).

Table. B9. Comparison of fine root turnover rates (calculated as BNPP/mean belowground standing crop) between microsites, standard error is shown in parentheses (n=10, per microsite).

Microsite	**Root Turnover (yr^{-1})**	
Natural Levee	3.50(0.19)	a
Flat	3.52(0.41)	a
Transitional	4.71(0.58)	a
Backswamp	4.81(0.50)	a

* Row mean followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, $\alpha = 0.05$).

Table. B10. Comparison of belowground net primary production between microsites, standard error is shown in parentheses (n=10, per microsite).

Microsite	Mean (g m^{-2})	
Natural Levee	684.85 (81.24)	a
Flat	482.05 (46.16)	ab
Transitional	431.13 (52.26)	b
Back Swamp	341.19 (32.66)	b

*Row means followed by different lowercase letters indicate significant differences among microsite types (Tukey's HSD, $\alpha = 0.05$).

Table. B11. Comparison of soil N over time, standard error is shown in parentheses (n = 80, 20 per microsite per collection). ***Source: Ricker, 2013.***

Date	**Mean N (mg/L)**	
Oct-10	9.98(0.84)	ab
Jan-11	5.34(0.33)	c
Apr-11	6.73(0.48)	bc
July-11	7.72(0.78)	bc
Oct-11	13.37(1.90)	a
Jan-12	8.72(1.08)	bc
Apr-12	7.83(0.48)	c
July-12	8.25(0.60)	bc
Oct-12	9.54(0.91)	b
Jan-13	5.59(0.34)	c

* Row means followed by different lowercase letters indicate significant differences among sampling dates (Tukey’s HSD, α = 0.05).

Appendix C: Chapter 3 Supplemental Data

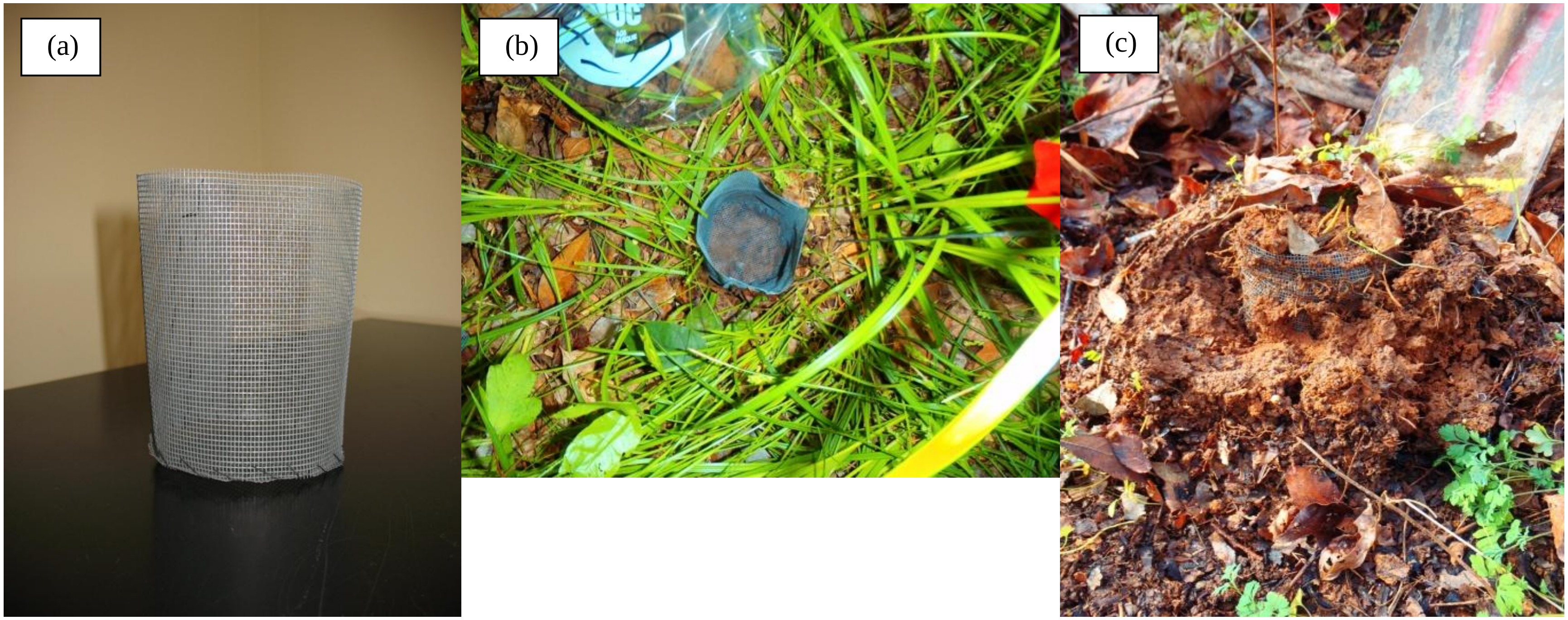

Figure. C1. Photographs of in-growth core (a), installation (b), and collection with spade (c). Photo credits: R. Governo (a) and L.D. Behnke (b, c).