EFFECTS OF SEDIMENTATION ON PRODUCTIVITY, NUTRIENT CYCLING, AND COMMUNITY COMPOSITION IN RIPARIAN FORESTS ASSOCIATED WITH EPHEMERAL STREAMS AT FT. BENNING, GA, USA

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Rachel Lynn (Cosgriff) Jolley, daughter of John Cornelius and Carolyn Lee (Humphreys) Cosgriff, was born May 28, 1974, in Pasedena, CA. The fourth of seven children, Rachel graduated from Christiansburg High School in 1992. She graduated from Brigham Young University (Provo, UT) with a Bachelor of Science degree in Conservation Biology (emphasis is Wildlife Biology) in 1998, and received her Masters of Science degree in Botany and Range Science in 2000. After working four years as the Botany Lab Manager at Utah Valley State College (Orem, UT), Rachel began her doctoral studies at Auburn University in June, 2004. She married Buck Jolley, son of David and Linda (Henderson) Jolley, in 2000.

DISSERTATION ABSTRACT

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The societal value of riparian forests in improving water quality by trapping sediments and pollutants is well understood. However, it is not clear how sedimentation impacts the overall integrity of riparian systems. In an effort to understand the consequences of sedimentation in riparian forests, a 5-year study was performed at Ft. Benning, GA. The specific objectives were to quantify above- and belowground forest productivity along a gradient of sedimentation rates and disturbance classes, determine how biogeochemical processes and nutrient circulation in riparian forests are affected by sediment deposition, and examine how differing rates of sedimentation drive changes in the understory, midstory, and overstory canopy layers in riparian forests. Significant declines in litterfall, woody biomass production, fine root production, LAI, and shrub biomass were found in response to as little as 0.1-0.4 cm yr^{-2} sedimentation. Soils in plots with the greatest sedimentation rates (i.e. highest sediment disturbance) were lower in nutrients, CEC, temperature, and moisture, and higher in bulk density, percent sand, and pH. Highly disturbed plots also had lower decomposition rates, net N mineralization rates, microbial C and N, and had higher NUE, PUE, and nutrient resorption proficiency and efficiency. A marked decline in nutrient circulation rates corresponded to current sedimentation rates between 0.1-0.4 cm yr^{-1}. Measures of community composition revealed proportionally more annual, exotic, and upland species in the understory of plots receiving high sediment deposition (HD) compared with reference (RF) plots. Shade-intolerant and N-fixing species had greater biomass in the midstory of HD plots; suggesting an increase in early-seral and opportunistic species. Increased overstory mortality was associated with high sedimentation rates, though increased understory light levels associated with overstory mortality was not the main driver of species changes in the understory. Edaphic factors, such as soil texture, moisture, and temperature, correlated to species changes in all three forest layers, suggesting that changes in soil physical properties associated with sedimentation are substantial enough to drive changes in the entire forest community. Decreased sediment retention (measured as increased sediment export) was found with increasing sedimentation rates. This study demonstrated that sedimentation rates are linked to declines in forest productivity, nutrient circulation, and changes in the vegetative community of riparian forests. Increased sedimentation rates may compromise the water purifying function of these forests.

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CHAPTER I

INTRODUCTION

Riparian forests have long been known to be ecologically important, acting as an interface between terrestrial and freshwater ecosystems. Naiman and Decamps (1997) describe riparian forests as the "most diverse, dynamic and complex biophysical habitats on the terrestrial portion of the planet." These areas act as safe sites for regional flora during dry periods, and also provide greater diversity of mammals, birds, and herptofauna (Plantico, 1984; Conner, 1994; Naiman and Decamps, 1997; Hupp, 2000).

One of the greatest societal benefits provided by riparian forests is that of maintaining and improving water quality. Healthy riparian zones are essential in the maintenance of water quality, acting as nutrient filters for streams and reducing sediment loads. One of the primary functions of riparian and wetland systems is that of sediment retention. As sediment-laden flows leave the main water channel and enter a forested wetland, velocities slow due to forest vegetation and deposition occurs (Olde Venterink et al., 2006). However, land use changes over the past 200 years have threatened the function of riparian forest ecosystems. Brinson et al. (1981b) estimated that over 70% of riparian forests in the U.S. have been lost since presettlement time. An estimated 23% were lost between 1950 and 1980 (Abernethy and Turner, 1987). Those remaining have been modified by timber harvest, agriculture, highway construction, and channelization (Bazemore et al., 1991; Hupp and Bazemore, 1993). This loss of riparian forest translates into loss of species diversity, flood storage capacity, groundwater recharge, and water quality (Plantico, 1984; Bren, 1993). Benke (1990) estimated that 98% of the rivers and streams in the continental United States are currently degraded enough to be unworthy of federal designation as wild or scenic rivers. As the loss and degradation of these forest systems continue, the importance of protecting remaining riparian forest increases. Therefore, it is essential to understand how anthropogenic disturbances affect the integrity and function of these systems.

By their nature, riparian forests are subject to alluviation as streams overflow banks. However, with the increase in land development and disturbance over the past 50 years, there has been a corresponding increase in movement of eroded materials into wetland systems (Hupp and Bazemore, 1993; Kleiss, 1996; Koning, 2004). In general, sediment supply and movement are direct responses to changes in hydrology, climate, and land use (Cahoon and Turner, 1989; Naiman and Decamps, 1997). The ability of a riparian forest to trap sediment is highly variable in both time and space, depending largely on hydrologic load, geomorphology, and vegetation cover. Agriculture, urbanization, and roads are major contributors to changes in sedimentation, and each may alter surface runoff flows and sediment loads (Ewing, 1996; Grace et al., 1998; Vargo et al., 1998; Elliot and Tysdal, 1999; Grace, 2002; Gruszowski et al., 2003).

In forest systems, unpaved forest roads not only alter sediment flows, but are also the major source of sediment. Forest road systems have been found to have erosion rates 1 to 3 times greater than undisturbed areas and could account for as much as 90% of soil erosion on forested lands (Grace, 2002). This is largely due to loss of surface cover, concentrated flow, interception of subsurface flow, destruction of soil structure, and increased slopes.

The ability of a system to trap sediments is dependent on the root mass and vegetation available, contributing to surface roughness (Naiman and Decamps, 1997; Naiman et al., 2000; Rybczyk et al., 2002; Olde Venterink et al., 2006). Schlosser and Karr (1981) found a significant decrease in suspended solids, phosphorus concentrations, and turbidity in streams associated with riparian vegetation. Barfield (1998) found that riparian filter strips removed over 90% of the sediment and chemicals in an experimental karst watershed. Kleiss (1996) found that bottomland hardwood forest along the Cache River in eastern Kansas (an area that represents only 3% of the watershed) was able to trap approximately 14% of the sediment that entered the river.

Much of the N and P inputs from agriculture and urban runoff are trapped in riparian forests, substantially reducing nutrient inputs into aquatic ecosystems. Braskerud (2002a; 2002b) found that constructed wetlands in first- and second-order streams in Norway retained an average of 21-44% of P inputs and 3-15% of N inputs. Peterjohn and Correll (1984) found that N retention of riparian forests was 89% compared to 8% in croplands and P retention was 80% compared to 41% in croplands. They also estimated the removal of particulates in riparian forests at 11 kg ha^{-1} organic N, 0.83 kg ha^{-1} dissolved ammonium-N, 2.7 kg ha^{-1} nitrate-N, and 3.0 kg ha^{-1} total particulate P. Lowrance et al. (1984) reported the conversion of inorganic N from crop fields to organic N through subsurface flow to the forest riparian zone.

Rates of sediment deposition vary greatly, depending on geomorphology (Hupp and Bazemore, 1993), hydrology (Darke and Megonigal, 2003; Lecce et al., 2004), topography (Asselman and Middelkoop, 1998; Craft and Casey, 2000), season (Lecce et al., 2006), vegetation (Barfield et al., 1998; Horvath, 2004; Lecce et al., 2006), and management practices of a given area (Anderson and Mitsch, 2006; Lecce et al., 2006). Studies have found sedimentation in forested riparian wetlands to range from 0.02 cm yr^{-1} to as much as 8.0 cm yr^{-1} (Cooper et al., 1987; Hupp and Morris, 1990; Hupp and Bazemore, 1993; Hupp et al., 1993; Kleiss, 1996; Rybczyk et al., 2002). Van der Valk et al. (1983) found that historic rates in an Alaskan wetland were approximately 0.3 cm yr^{-1}. Similar historic rates were found along the Cache River system in the coastal plain of eastern Arkansas (Hupp, 2000) and for an undisturbed wetland forest there (Hupp and Morris, 1990).

The general trend in all studies, however, is that recent sediment deposition rates are increasing compared with historical, pre-industrial rates (Bazemore et al., 1991; Grace, 2002). Kleiss (1996) found average rates as high as 2.64 cm yr^{-1} during 1988-1990 compared with the highest average rate of 0.36 cm yr^{-1} over the previous 25 years on the Cache River. Heimann and Roell (2000) found a similar increase in a riparian wetland in northern Missouri, with a rate of 0.29 cm $year^{-1}$ during the 1950s, 0.51 cm $year^{-1}$ during the 1960s, and 1.04 cm $year^{-1}$ in the period from 1970 to 1997. Bazemore et al. (1991) also found an increase in sedimentation rates near road crossings in Tennessee. A study of floodplain sedimentation on the upper Mississippi Valley found that rates in small tributary watersheds (<700 km^2) increased by at least an order of magnitude over the last 200 years (i.e., from 0.2 mm yr^{-1} prior to agriculture to between 2 and 20 mm yr^{-1}) (Knox, 2006).

Forest Productivity

Generally, bottomland hardwood forests have greater standing crop biomass and biomass production rates than nearby uplands (Brinson et al., 1980; Conner, 1994). In Southeastern US forests, net primary productivity (NPP) ranges between 2-20 Mg ha^{-1} yr^{-1} (Cahoon and Turner, 1989; Conner, 1994; Megonigal et al., 1997). The effect of sediment deposition on NPP in bottomland hardwood forests is largely unknown. Some researchers have suggested that sedimentation can actually increase productivity through the deposition of nutrient-laden sediments (Odum, 1979; Brown, 1981). However, Megonigal et al. (1997) found that any benefits from the additional nutrients were negated by the physiological stresses associated with flooding.

Several ecologists have hypothesized that sediment deposition may have effects similar to flooding by limiting gas exchange in roots through burial (Kozlowski et al., 1991; Kleiss, 1993; Ewing, 1996; Hupp, 2000; Cavalcanti, 2004). In a greenhouse study, Koning (2004) found no significant effects on vegetation biomass production (above and below ground) or root to shoot ratios with a one-time input of 1 cm of sediment. However, 2 cm of sediment caused decreased aboveground biomass but no changes in root to shoot ratio. Cavalcanti (2004) found decreasing productivity and higher overstory mortality in catchments with long-term sedimentation rates as low as 0.2 cm yr^{-1} over a 25-year period.

Belowground NPP (BNPP) is more difficult to measure than aboveground NPP (ANPP), and therefore fewer studies describe BNPP. However, BNPP represents significant nutrient circulation in forest systems, perhaps as much or more than litterfall (Baker et al., 2001a; Clawson et al., 2001). Eissenstat and Yanai (2002) suggest a conservative estimate of 33% of global net primary productivity is accounted for by fine-root production, but it has also been estimated to be as great as 50% (Vogt et al., 1986; Nadelhoffer and Raich, 1992; Côté et al., 1998; Price and Hendricks, 1998; Jones et al., 2003). Decreased fine root dynamics may be an indicator of stress to a forest system. Cavalcanti (2004) found fine root productivity declined sharply with sedimentation rates as low as 0.3 cm yr $^{-1}$. To date, this has been the only study correlating fine root productivity with sediment deposition rates.

Biogeochemistry

A driving factor in riparian forest function is nutrient circulation within the forest. The flow and rates of biogeochemical processes and nutrient exchanges will drive changes in productivity and community composition. Within forest systems, major nutrient pools are found in plant biomass, forest floor, belowground litter, soil organic matter, soil microbial biomass, and available inorganic nutrients. These pools are affected by and/or drive plant productivity, litter production, litter decomposition, nitrogen (N) mineralization, microbial immobilization, leaching, denitrification, N_2-fixation, and plant uptake (Idol et al., 2003). A key question is how the inflow of sediments may affect nutrient circulation within a forest system. Lockaby et al. (2005) found a reduction in decomposition rates, microbial C and N, and net N mineralization rates with long-term sedimentation rates as low as 0.2 cm yr^{-1} over a 25 year period. It is reasonable to assume that a threshold exists beyond which the stress of alluviation outweighs the subsidy provided by greater available nutrients.

Decomposition represents a significant flux in nutrient cycling in a forest system by determining nutrient availability for plant uptake (Swift et al., 1979). In systems where decomposition is limited, nutrients and organic matter will be tied up in the forest floor, negatively impacting productivity (Swift et al., 1979; Xiong and Nilsson, 1997). Therefore, analysis of decomposition rates can evaluate overall ecosystem function. Because decomposition rates are dependent on soil factors, sediment deposition could severely alter plant decay rates. Sedimentation may compact detritus, reduce gas exchange, suppress organismal activity, and transport surface-bound chemicals (Vargo et al., 1998).

Soil microbial organisms may be negatively influenced by sediment deposition in a similar manner. Microbial biomass is affected by changing substrate quality, quantity, and environmental conditions, and therefore can be used as a sensitive indicator of changes in substrate quality and quantity (Li et al., 2004). Sediment inflow may affect microbial communities by altering soil temperature, moisture, and bulk density.

In most forest systems, nitrogen (N) and phosphorus (P) are the primary limiting nutrients (Vitousek, 1982; 1984) and are essential to biomass production (Fisher and Binkley, 2000). Plant-available N is largely dependent on the rate of net N mineralization. For example, Reich et al. (1997b) found a strong positive correlation between forest productivity and N mineralization rates. It is unclear how sedimentation may affect net N mineralization, though there is likely an indirect effect since net N mineralization is primarily determined by the size of the microbial community and the level of N uptake by plant roots, both of which have been shown to decrease with increasing sedimentation (Cavalcanti and Lockaby, 2005; Lockaby et al., 2005). However, there is evidence that net N mineralization may be significantly reduced by soil compaction (Li et al., 2003; Tan et al., 2005), which may increase as a result of alluviation.

The degree to which forest productivity is influenced by nutrient availability has been shown to vary greatly based on species, site, and hydrology (Aerts, 1996; Killingbeck, 1996; Kobe et al., 2005; Schilling and Lockaby, 2005; 2006). Forest production efficiency is often measured by the amount of carbon (C) fixed per unit of nutrient uptake. An indicator of nutritional limitations to NPP in riverine forests is the ratio of N to P (Lockaby and Conner, 1999). Narrow N:P ratios may indicate N-deficient systems. Another indication of nutrient deficiency in a system is increased internal efficiency. Nutrient resorption or retranslocation is the capability of a system to internally recycle nutrients from leaves prior to senescence (Aerts, 1996; Killingbeck, 1996; Kobe et al., 2005; Schilling and Lockaby, 2006). It has been suggested that high internal recycling may compensate for low ecosystem recycling (Lugo et al., 1990a). There have been no studies relating sediment deposition to nutrient efficiency in a riparian forest system.

Community Composition

Plant community composition can change rapidly following disturbance. Because plant species vary greatly in resource use, allocation, and phenology, changes in plant community composition can also affect ecosystem processes such as nutrient cycling, productivity, and decomposition (Vitousek, 1986; Mahaney et al., 2004a). Very few studies relate community composition to sediment deposition in bottomland hardwood forests (Cavalcanti, 2004). However, the effects of sediment burial on seed germination have been thoroughly studied. Seedling emergence is reduced by as little as 0.5-2.0 cm of burial (Welling and Becker, 1990; Bonis and Lepart, 1994; Jurik et al., 1994; Gleason et al., 2003; Barry et al., 2004; Mahaney et al., 2004b; Peterson and Baldwin, 2004; Petru and Menges, 2004; Zheng et al., 2005). There are also indications that germination of larger seeds is more indifferent to burial than smaller seeds (Barry et al., 2004; Mahaney et al., 2004b), indicating that sedimentation would likely shift community composition toward large-seeded species.

Although sedimentation generally reduces seed germination, little is known about the effect of sedimentation on subsequent growth and survival of plant species (Kent et al., 2001). This is because individual species respond differently to the stress of sediment deposition (Mahaney et al., 2004b). Mahaney et al. (2004b) found that, although emergence was decreased in many species, sedimentation did not alter the subsequent growth of individual plants that successfully emerged. They suggest that the decrease in emergence lowers interspecific competition, providing more resources to individuals that emerge. Koning (2004) compared sediment depths in relation to community composition, but found no significant differences in community composition. A similar study by Ewing (1996) found some sedge species to have lower belowground biomass under sedimentation (though total biomass was not significantly different), as well as a lower rate of photosynthesis.

Similar to other ecosystem disturbances, sedimentation is likely to promote the growth of early-seral and opportunistic species (Kent et al., 2005). Cavalcanti (2004) found that riparian forests receiving greater sedimentation had a higher proportion of shrubs and seedlings than forests with little or no sedimentation. Of these shrubs and seedlings, there was a greater proportion of shade-intolerant and nitrogen-fixing species.

In dune succession, early colonizers are often specialized dune species which, following burial, have stimulated photosynthetic rates and greater above- and belowground biomass (Shi et al., 2004; Kent et al., 2005; Perumal and Maun, 2006). Many wetland species respond to seasonal flooding and resulting sedimentation events by forming adventitious roots, by stem buttressing, or through increased root flexibility (Naiman and Decamps, 1997).

Objectives

Although the importance of riparian forests in improving water quality by trapping sediments and pollutants is well documented, the effect of these deposited sediments on the overall integrity of the riparian system is less understood (Jurik et al., 1994; Cavalcanti, 2004; Koning, 2004; Cavalcanti and Lockaby, 2005; Lockaby et al., 2005). Specifically, at what critical level does sediment accumulation becomes a stress rather than a subsidy to the functional integrity of the system? In an effort to understand the consequences of sedimentation in riparian forests, a 5-year study was performed at Ft. Benning, GA, to determine how increasing sedimentation affects above- and belowground productivity, nutrient cycling, and vegetative community composition. The specific objectives were to:

1) Quantify above- and belowground forest productivity changes along a gradient of sedimentation rates and disturbance classes.
2) Determine how biogeochemical processes and nutrient circulation in riparian forests are affected by sediment deposition.
3) Examine how differing rates of sedimentation drive changes in the understory, midstory, and overstory canopy layers in riparian forests.

This dissertation is divided into three main topics: forest productivity, biogeochemical processes, and community composition, with each topic comprising an individual chapter. Chapter 2 describes changes in forest productivity along a gradient of sedimentation rates and within three disturbance classes. Forest productivity was estimated using litterfall, annual increases in woody biomass, and fine root productivity. Leaf-area index (LAI) also was measured in an effort to provide an alternative metric for land managers in evaluating how sedimentation may affect riparian forest productivity. Specific sedimentation thresholds corresponding to marked declines in productivity are defined.

Chapter 3 explores how sedimentation impacts the nutrient filtering function of riparian forests. Biogeochemical processes such as decomposition and N mineralization are quantified along a gradient of sedimentation rates and within three disturbance classes. This chapter also explores nutrient circulation within the forests through patterns of nutrient use efficiency, nutrient resorption, microbial carbon and N, and nutrient levels in foliar and fine root tissues. Declines in biogeochemical processes and nutrient circulation are correlated to specific thresholds of sedimentation.

The impact of sedimentation on the vegetative community composition is discussed in Chapter 4. Each layer of the forest canopy is evaluated separately in order to compare differing responses to environmental factors associated with sedimentation. Changes in species functional groups are described among disturbance classes and overall community diversity, richness, and evenness are compared along sedimentation gradients. The chapter also reports how the ability to trap and retain sediment changes with increasing sedimentation rates. This information offers insight into how disturbance from sedimentation differs from other common forest disturbances in driving changes in species composition. The tolerance of individual species to sedimentation is also evaluated in order to provide managers with restoration options.

Chapter 5 provides a summary of the research and results contained in each chapter. Implications for land managers and recommendations for further research are also presented.

CHAPTER II

IMPACTS OF SEDIMENT DEPOSITION ON RIPARIAN FOREST PRODUCTIVITY

Abstract

Riparian forests serve an essential function in preserving water quality through the filtering of sediments and nutrients from surface runoff. However, little is known about the impact of sediment deposition on productivity in riparian forests. Sediment inputs may act as a subsidy to forest productivity by providing additional nutrients for plant uptake or may act as a stress by creating anoxic soil conditions. This study determined how sediment deposition affected riparian forests along ephemeral headwater streams at Ft. Benning, GA, USA. Above- and belowground productivity, LAI, and standing crop biomass were compared along a gradient of current sedimentation rates in 17 riparian forests. Annual litterfall production was determined from monthly collections using 0.25 m^{-2} traps; woody biomass was determined from annual DBH measurements using species-specific allometric equations; fine root productivity was determined using sequential coring; LAI was measured by expanding specific leaf area by annual litterfall production; and shrub biomass was determined using species-specific biomass equations based on height and root collar diameter. Significant declines in litterfall, woody biomass production, fine root production, LAI, and shrub biomass were found with as little as 0.1-0.4 cm yr^{-2} sedimentation. We conclude that the levels of sedimentation in this study do not subsidize growth in riparian forests, but create a stress similar to that found under flooded conditions.

Key words: riparian forest, sedimentation, NPP, fine roots, LAI, woody biomass production, litterfall

Introduction

Riparian and wetland forests serve an essential role in preserving water quality. The primary function of these systems is to retain sediments, nutrients, and pollutants, which would otherwise degrade water quality. However, land use changes over the past century have threatened riparian forest ecosystems. Brinson et al. (1981b) estimated that over 70% of U.S. riparian forests have been lost since pre-settlement time, with an estimated 23% lost between 1950 and 1980 (Abernethy and Turner, 1987). Those remaining have been modified by timber harvest, agriculture, highway construction, and stream channelization (Bazemore et al., 1991; Hupp and Bazemore, 1993). This loss of riparian forest translates into reduced species diversity, flood storage capacity, groundwater recharge rates, and water quality (Plantico, 1984; Bren, 1993). As the loss and degradation of these forest systems continue, the importance of protecting remaining riparian forests increases. Therefore, it is critical to understand how anthropogenic disturbances threaten the integrity and functions of these systems. Although the importance of riparian forests in sediment retention is well documented (Hupp and Morris, 1990; Hupp and Bazemore, 1993; Kleiss, 1993; Kleiss, 1996; Wardrop and Brooks, 1998; Craft and Casey, 2000; Heimann and Roell, 2000), the effect of sediment deposition on the overall integrity of riparian systems is less well understood (Jurik et al., 1994; Cavalcanti, 2004; Koning, 2004; Lockaby et al., 2005). Sedimentation in forested riparian wetlands ranges from 0.02 to as much as 8.0 cm yr^{-1} (Cooper et al., 1987; Hupp and Morris, 1990; Hupp and Bazemore, 1993; Hupp et al., 1993; Kleiss, 1996; Wardrop and Brooks, 1998; Heimann and Roell, 2000; Rybczyk et al., 2002), with the highest rates associated with headwater floodplains (Wardrop and Brooks, 1998). These sediments carry nutrients (Olde Venterink et al., 2006), which could act as either a stress through microbial immobilization or subsidy for vegetation through plant nutrient uptake (Naiman and Decamps, 1997; Hupp, 2000; Baker et al., 2001b). Several studies have suggested that the import of nutrient-laden sediments may increase forest productivity by subsidizing existing nutrients (Odum, 1979; Megonigal et al., 1997). However, it has also been suggested that sedimentation may create stressful anoxic soil conditions similar to flooding. The purpose of this study was to determine how sediment deposition affects the productivity of riparian forests. Specifically, at what critical level does sediment accumulation becomes a stress rather than a subsidy?

The subsidy-stress hypothesis introduced by Odum (1979) suggests that short-duration floods benefit wetland forests with additional nutrients and water, whereas long-term flooding decreases productivity due to the physiological stress associated with anoxic soil conditions. While this hypothesis was later found to be inadequate in describing NPP patterns in Southeastern US floodplain forests (Megonigal et al., 1997), importation of nutrient-laden sediments may provide an important subsidy to forest production. Riparian forests associated with eutrophic redwater systems are known to be more productive than oligotrophic blackwater systems due to higher nutrient and sediment loads (Lugo et al., 1990b; Lockaby and Conner, 1999; Schilling and Lockaby, 2006). Wetlands receiving sediments from wastewater effluent have also shown higher fertility and productivity (Brown, 1981; Hesse et al., 1998; Day et al., 2006; Effler et al., 2006).

Systems that are deficient in both N and P may benefit from increased nutrient importation associated with low levels of sedimentation (Vitousek and Howarth, 1991;

Lockaby and Conner, 1999). However, it has been suggested that burial of stems by high rates of sediment deposition may create anoxic conditions, similar to the stress posed by flooding (Ewing, 1996; Kleiss, 1996; Cavalcanti, 2004; Cavalcanti and Lockaby, 2005; Lockaby et al., 2005). In a precursor to the present study, Cavalcanti and Lockaby (2005) found decreased above- and belowground productivity with long-term sedimentation rates as low as 0.2-0.3 cm yr^{-1} over a two-decade period.

Net Primary Productivity (NPP)

Net primary productivity (NPP) is "the annual gain of energy and matter by plant systems" (Swift et al., 1979), or the net gain in chemical energy from photosynthesis (Brinson et al., 1981a). Although most studies have been limited to aboveground estimates, total NPP includes both aboveground NPP (ANPP) and belowground NPP (BNPP), and is measured as the production of flowers, fruits, leaves, twigs, branches, stems and roots during a specific time period (Brinson et al., 1981a).

Generally, bottomland hardwood forests have greater biomass and biomass production rates than nearby uplands (Brinson et al., 1980; Conner, 1994). In southeastern forests, ANPP ranges from 2-20 Mg ha^{-1} yr^{-1} (Cahoon and Turner, 1989; Conner, 1994; Megonigal et al., 1997). Estimates of ANPP are generally based on measurements of annual woody biomass production and annual litterfall. Higher ANPP values have been reported for sites associated with inputs of water, oxygen, and nutrients by floodwaters or wastewater effluent (Hesse et al., 1998; Lockaby and Conner, 1999; Clawson et al., 2001; Day et al., 2006; Olde Venterink et al., 2006; Schilling and Lockaby, 2006), while continuous flooding has been associated with lower ANPP (Megonigal et al., 1997). Fertilization of nutrient-limited sites often results in higher

ANPP, LAI, and photosynthetic efficiency (Conner, 1994; Lawlor, 1995; Albaugh et al., 1998; Harrington et al., 2001).

Although it has been suggested that BNPP may account for as much as 50-75% of total NPP (Vogt et al., 1986; Nadelhoffer and Raich, 1992; Côté et al., 1998; Price and Hendricks, 1998; Badalucco and Kuikman, 2001; Jones et al., 2003) and approximately 30-50% of carbon fixed by plants, it is rarely reported in forest productivity estimates (Baker et al., 2001a; Clawson et al., 2001). This is largely due to the difficulty and expense associated with frequent sampling. Most studies that do incorporate fine root productivity are limited to less that two years in duration and do not sample frequently enough to account for fine root dynamics (Newman et al., 2006). Therefore, although BNPP represents a significant allocation of energy and nutrients, there exists only a limited understanding of fine root productivity and dynamics in riparian forests. Because fine root productivity is more dynamic than ANPP (Albaugh et al., 1998; Baker et al., 2001a; Eissenstat and Yanai, 2002), it may be a more useful indicator of site fertility and forest stress.

Carbon Allocation

Trees may shift resources to leaves, roots, and stems differentially when under stress. Fine root production and turnover can be highly variable in forest systems, responding to changes in abiotic resources (Vogt et al., 1998). Uren (2001) suggests that, when under stress, plants may contribute greater resources to root production. Therefore, an indication of forest stress may be not only decreased productivity, but shifts in resource allocation. Understanding how carbon resources are allocated both above- and belowground may be one of the keys in understanding ecosystem responses to various environmental stresses.

In riparian forests, the three most dominant environmental stresses include flooding, nutrient fluxes, and sedimentation. Studies have indicated that flooding may lead to increased ANPP, particularly in wood biomass (Conner and Day, 1976; Megonigal and Day, 1988; Lugo et al., 1990b; Megonigal and Day, 1992; Clawson et al., 2001) and a decrease in BNPP (Megonigal and Day, 1988; Powell and Day, 1991; Baker et al., 2001a; Clawson et al., 2001). It is has been suggested that fine roots may have a lower tolerance for the low oxygen conditions imposed by flooding (Brinson, 1990) and flooding may stimulate the growth of stems to provide greater surface area for gas exchange (Brown et al., 1979).

It is generally believed that increased nutrient availability may also cause a shift in C allocation from belowground to aboveground (Nadelhoffer et al., 1985; Albaugh et al., 1998; Fisher and Binkley, 2000). However, it appears that the relationship between soil fertility and carbon allocation is not as straight-forward as once believed. Nadelhoffer et al. (1985) found that sites with high N mineralization rates had a higher proportion of very fine roots as well as a lower proportion of litterfall productivity.

Very few studies relate sediment deposition to biomass production. Several suggest that sediment deposition may have an effect similar to flooding by limiting gas exchange in roots through burial and suffocation (Kozlowski et al., 1991; Kleiss, 1993; Ewing, 1996; Hupp, 2000; Cavalcanti and Lockaby, 2005). In a precursor to the present study, Cavalcanti and Lockaby (2005) found lower NPP in catchments receiving as little as 0.2 cm yr $^{-1}$ of sediment deposition over a 25-year period.

Objective

The objective of this study was to understand how sedimentation may act as both a subsidy and a stress in the productivity of riparian forests associated with headwater ephemeral streams. We tested the following hypotheses:

1) Riparian forests receiving low levels of sedimentation will exhibit greater productivity than those receiving no sediment inputs, due to the greater nutrient availability associated with sedimentation.
2) A critical threshold of sedimentation exists, above which sediment accumulation will become a stress to the system rather than a subsidy.
3) High levels of sedimentation will drive a shift in carbon allocation from below- to aboveground, similar to that caused by flooding.

Study Site

The study was conducted at Fort Benning Military Installation, near Columbus GA (Fig.1). This U.S. Army installation occupies 73,503 ha in Chattahoochee, Muscogee, and Marion counties of Georgia, and Russell county of Alabama. Fort Benning lies within the lower Piedmont and the upper Coastal Plain physiographic regions, however, only areas within the Coastal Plain were used in this study. All study areas chosen were associated with ephemeral riparian streams. The study areas are occupied primarily by uneven-aged deciduous or mixed hardwood/pine forests. Common species in the hardwood bottoms were red maple (*Acer rubrum* L.), hazel alder (*Alnus serrulata* (Ait.) Willd.), flowering dogwood (*Cornus florida* L.), titi (*Cyrilla racemiflora* L.), sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.), sweetbay (*Magnolia virginiana* L.), wax myrtle (*Morella cerifera* (L.)Small), blackgum

(*Nyssa sylvatica* Marsh.), and water oak (*Quercus nigra* L.). Upland forests are dominated by long-leaf pine (*Pinus palustris* P. Mill.), loblolly pine (*Pinus taeda* L.), and various oak species (*Quercus incana* Bartr., *Q. marilandica* (L.) Muenchh., *Q. phellos* L., *Q. laevis* Walt., *Q. falcata* Michx.). Uplands were primarily managed as long-leaf pine ecosystems with periodic prescribed burns every 1-3 years. Riparian soils included the Bibb (coarse-loamy, siliceous, active, acid, thermic Typic Fluvaquents) and Chastain (fine, mixed, semiactive, acid, thermic Fluvaquentic Endoaquepts) series. Upland soils included the Troup (loamy, kaolinitic, thermic Grossarenic Kandiudults), Lakeland (thermic coated Typic Quartzipsamments), and Cowart (fine-loamy, kaolinitic, thermic Typic Kanhapludults) series (Soil Survey Staff, 2004). Annual mean precipitation is approximately 123 cm yr^{-1}, with driest months in October and November, and wettest months in March and July. Mean annual temperature is 24.3° C, with lowest temperatures observed in January and highest temperatures in July (cdo.ncdc.noaa.gov/ dlyp/DLYP). During the period of this study (2001-2006), 2001 and 2006 had below average annual precipitation and 2003 and 2005 had above average precipitation (ncdc.noaa.gov/IPS/LCDPubs).

Ft. Benning military installation was first designated in 1918, with significant land acquisitions in the 1940s. Prior to becoming a military base, the land was predominantly in row crop agriculture dominated by cotton production. Poor soil conservation practices led to excessive erosion, which is still evidenced by landscape scars and gullies. Current erosion is primarily due to military traffic on unpaved forest roads and trails. This sediment is carried into riparian forests, where increased surface roughness causes the channels to slow and widen. Evidence of sedimentation included alluvial fans and partially buried tree stems.

Two circular plots (0.04 ha) were established in riparian forests along each of nine ephemeral streams in March 2002, for a total of eighteen plots. Study areas were selected to span a range of sediment deposition, from no visible sedimentation to high sedimentation. In April 2004, in an effort to better represent the range of sediment deposition, five plots were dropped from the study and new plots were added along four additional streams, yielding a total of seventeen plots along twelve ephemeral streams.

Methods

Rates of Deposition

Historical deposition rates were measured using a modification of the dendrogeomorphic method described by Hupp and Morris (1990). In July 2003, three to four saplings (8 to 10 cm in diameter) per plot were excavated to the depth of the root collar of the tree. Cross sections of the root collar and at the soil surface were used to determine the age of the tree and its age at burial. A sedimentation rate was determined by dividing the sediment depth by the years of deposition. This was repeated in March 2004 for new plots added to the study. Current sedimentation rates were obtained using a modification of the sediment disks described by Kleiss (1993). Metal washers were welded to the center of 1.22 m rebar segment, which were inserted into the soil so that the washer was flush with the surface of the soil. As sediment was deposited, monthly depth measurements were taken by inserting a small rod into the soil until it contacted the washer. Plots were assigned to disturbance categories based on current sedimentation rates: highly disturbed (HD, ≥ 1.0 cm yr^{-1}), moderately disturbed (MD, $0.1 < 1.0$ cm yr^{-1}), and reference plots (RF, ≤ 0.1 cm yr^{-1}).

Forest Productivity

Aboveground net primary productivity (ANPP) was estimated annually by summing litter production and woody biomass production. Litter production was estimated by collecting litterfall from three 0.25 m^2 litterfall traps in each study plot. Litterfall traps were made of treated lumber and lined with 2-mm nylon mesh. In plots receiving high sedimentation or frequent flooding, traps were elevated 30 cm above the ground with wooden stakes. Traps were installed in original plots during March 2002 and in new plots during July 2004. Collections were made on a monthly basis through December 2006. Litterfall was collected, oven-dried, and separated by component (leaf, stem, reproductive, and other) before weighing. Annual litter production was estimated by summing average monthly litterfall for a 12-month period.

Woody biomass production was estimated using species-specific biomass equations. Stem biomass was estimated each winter by measuring diameter at breast height (DBH, approximately 1.3 m) of all trees ≥ 5 cm in diameter. Trees were identified according to species and tagged with individual numbers at DBH. Diameters were measured at the same point each year. Original and new plots were inventoried beginning December 2002 and December 2004 through 2006, respectively. Stem biomass production for hardwood species was calculated from allometric equations developed by the USDA Forest Service for the Gulf Atlantic Coastal Plains (Clark et al., 1985) and pine species biomass equations were adapted from Ter-Mikaelian and Korzukhin (1997). All woody plants less than 5 cm DBH and over 10 cm in height were considered shrubs. Shrub biomass was estimated using shrub equations (Elliot and Clinton, 1993) based on root crown diameter and height measurements.

Belowground NPP (BNPP) was estimated using sequential coring of fine roots (Vogt and Perrson, 1991). In each plot, two samples were collected from a relatively homogeneous subplot (approximately 0.005 ha). In order to discern any peaks in production or fine root turnover, collections were made every six weeks from February 2002-July 2003 and from April 2004-December 2006. Sampling pipes were inserted into the soil to a pre-marked depth (11 cm), then rotated to break the sample away from the soil column below. The cores were extracted and any roots extending beyond the base of the core were carefully cut away. The 11 cm depth was chosen based on the study of Powell and Day (1991), in which they found significantly more root biomass in the top 10 cm of the soil. Cores were then transferred to a plastic bag and stored on ice until they could be processed in the laboratory. Fine roots (<3mm diameter) were manually extracted with a low pressure wash through a screen. Once extracted, roots were classified and divided by life class (dead or alive) and diameter class (0.1-1.0 mm, 1.1-2.0 mm, and 2.1-3.0 mm). Live and dead roots were determined by color and texture standards outlined by Böhm (1979) and Bledsoe et al. (1999). Root lengths were estimated using the line-intersect method outlined by Böhm (1979) for each life and size class. Roots were then dried at 70°C for at least 72 hours and weighed. Total laboratory processing time varied between 2-4 weeks from the time of collection. Fine root production was estimated by summing any positive significant ($\alpha=0.05$, using a pair-wise t-test) differences in mean fine root biomass between sample dates (1998). This method does not account for growth and mortality between sample dates and, consequently, the production estimates are conservative (Vogt et al., 1998; Fahey et al., 1999).

Leaf Area Index

Leaf area index was determined by collecting freshly senesced foliage from the most common trees in each plot during November and December 2006. Leaf area was measured using a Delta T video imaging system (Delta-T Devices LTD, Burwell, Cambridge, England). Leaves were then oven-dried (70° C for 72hours) and weighed. Leaf area index (LAI) was calculated by multiplying sampled leaf area by the annual foliar litterfall production.

Precipitation

Precipitation and temperature data were obtained from the Columbus, GA airport (ncdc.noaa.gov/IPS/LCDPubs). Relative moisture conditions were determined using the Palmer drought index (www.drought.noaa.gov/palmer.html) for each week from January 2001 through December 2006. This index calculates drought or excess moisture conditions based on normal temperature and precipitation of the area.

Statistical Analysis

Statistical analyses utilized SAS software version 9.1. Regression analysis was used to assess relationships between sedimentation rates and productivity (PROC REG, SAS Institute 2002-2003). Mean comparisons of productivity between disturbance classes were performed using analysis of variance (ANOVA) (PROC GLM, SAS Institute 2002-2003), with 2 degrees of freedom. Following significant ANOVA results, Tukey’s mean comparison test was performed. Differences between means were considered statistically significant at $\alpha=0.05$. Significant differences in mean fine root biomass between sampling dates were determined using paired t-tests. Data sets not meeting normality criteria (i.e., non-normal distribution) were transformed using the natural log.

Results and Discussion

Sedimentation

Historical sedimentation rates ranged from 0 to 4 cm yr^{-1} over a 25-year period and current sedimentation rates ranged from <0.01 to 5.5 cm yr^{-1} (Table 1). Similar sedimentation rates have been found in other US forested wetland studies. Using the dendrogeomorphic technique, Hupp et al. (1993) found historic sedimentation rates ranging from 0.7 to 5.7 cm yr^{-1} over an 80-year period along the Chickahominy River, Virginia. Using the same technique, historical sedimentation rates in Black Swamp, Arkansas were estimated to be 0.28 cm yr^{-1} over a period of 19 years (Hupp and Morris, 1990) and Hupp and Bazemore (1993) found mean rates of 0.24-0.28 cm yr^{-1} over 28 years in Tennessee. Using ^{137}Cs, Cooper et al. (1987) found historical sedimentation rates (over 20 years) in ephemeral streams of 0.25-1.0 cm yr^{-1} in North Carolina forested wetlands. Wardrop and Brooks (1998) found current sedimentation rates (over a 12-month period) as high as 8 cm yr^{-1} in headwater floodplains of Pennsylvania using erosion pins.

Mean current sedimentation rates were 0.05 (± 0.03), 0.4 (± 0.11), and 2.9 (± 0.39) cm yr^{-1} on reference (RF), moderately disturbed (MD), and highly disturbed (HD) plots, respectively. ANOVA showed that HD plots had significantly greater current sedimentation rates than MD and RF sites ($F_{df2,\,76}=50.9$, $p<0.01$), though MD and RF plots did not differ significantly. Equivalent current sediment mass rates ranged from 0.5 to 996 Mg ha^{-1} yr^{-1} (Table 1). Mean mass sedimentation rates were 4.0 (± 1.64), 55.2 (± 15.6), and 505 (± 69.0) Mg ha^{-1} yr^{-1}, on RF, MD, and HD plots, respectively.

Over the 5-year period of this study, long-term historic rates estimated from the previous 25-year period were only weakly positively correlated to current rates (r^2=0.22, p<0.01). This was surprising since studies comparing long-term rates (dendrogeomorphic technique) to current sediment rates (clay pad markers) in Arkansas (Kleiss et al., 1989; Hupp and Morris, 1990) found a strong correlation between rates, though current rates were consistently higher than historic long-term rates. Results from the first half of this study (Phase 1, Jan 2002- July 2003) showed a much greater correlation between historic and current sedimentation rates (r^2=0.59, p<0.01) (Lockaby et al., 2005).

Precipitation Patterns

Annual precipitation varied from 24.7 cm below the 30-year average in 2006 to 21.8 cm above the 30-year average in 2005 (Fig. 2). During the study period, winter months had lower than average precipitation and summer months had above average precipitation. The Palmer drought index indicated drought conditions in the winter months of 2002-03 and during the summer of 2006 (Fig. 3).

Litterfall

In analyses of ANPP, plot D12A was omitted as an outlier, due to unusually high litterfall and woody biomass productivity, which was significantly (p<0.001) higher than other plots in its disturbance class. This plot was also found to be an outlier in related aquatic, vegetation, and nutrient cycling studies. This plot also showed indications of high hydraulic conductivity, which may explain some of the differences between this plot and others.

Mean annual litterfall production ranged between 197 and 774 g m^{-2} yr^{-1} (Table 1). HD plots had significantly ($F_{df2,\,72}$=11.0, p<0.01) lower litterfall production than RF and MD plots (Table 2). Annual litterfall production was negatively correlated to sedimentation rates (r^2=0.49, p<0.01), with a marked decline corresponding to current sedimentation rates between 0.1 and 0.4 cm yr^{-1} current sedimentation rates (Fig. 4). Similar declines in litterfall have been reported as indicators of forest stress associated with continual flooding. Megonigal et al. (1997) reported that leaf litter was 38% less in continuously flooded plots than in intermediate and dry plots in South Carolina and Louisiana. Clawson et al. (2001) also found less litterfall biomass in poorly drained sites versus drier sites in floodplain forests along the Flint River, GA. However, in a summary of forested wetlands, Lugo et al. (1990a) reported that litterfall production was similar between riverine wetlands and continuously flooded basin wetlands.

In this study, litterfall values for RF plots (774 g m^{-2} yr^{-1}) were similar to those reported elsewhere for Southeastern floodplain forests. Meier et al. (2006) found averages between 759 and 870 g m^{-2} yr^{-1} in a Louisiana floodplain forest, while Conner (1994) reported a range from 420 to 574 g m^{-2} yr^{-1} in floodplain forests from other studies in the Southeast. Schilling and Lockaby (2006) reported 480 and 500 g m^{-2} yr^{-1} from the floodplains of the Satilla (a blackwater system) and Altamaha (a redwater system) Rivers in Georgia.

Throughout the 5-year study, litterfall was consistently highest in November (175.5 ± 8.0 g m^{-2}) and lowest in February (9.7 ± 1.4 g m^{-2}), with the exception of peak litterfall in September 2004 that corresponded with high winds associated with rain bands from Hurricane Ivan (Fig. 5). ANOVA showed significant differences in litterfall between seasons ($F_{df3,842}=165$, $p<0.01$) and disturbance classes ($F_{df2, 842}=17.3$, $p<0.01$), with a significant interaction between seasons and classes ($F_{df6, 842}=3.27$, $p<0.01$). HD plots had significantly lower litterfall compared to MD and RF plots during the fall and spring, but classes did not differ during winter and summer.

ANOVA showed that monthly variation in litterfall did not differ among disturbance classes ($F_{df2, 35}=0.97$, $p=0.52$) although HD plots had less monthly variation than MD or RF plots. There were no significant differences in annual litterfall among years across all disturbance classes ($F_{df4, 71}=0.62$, $p=0.65$), or among years within each disturbance class (HD: $F_{df4, 18}=0.42$, $p=0.79$; MD: $F_{df4, 21}=0.63$, $p=0.65$; RF: $F_{df4, 22}=1.24$, $p=0.32$).

Leaf litterfall ranged from 139-589 g m^{-2} (Table 1) and was significantly ($F_{df2, 22}=36.2$, $p<0.01$) lower in HD plots compared to RF and MD plots (Table 2). Leaf litterfall represented approximately 80% of total litterfall, a percentage consistent with other reports (Clawson et al., 2001; Schilling and Lockaby, 2005; Meier et al., 2006). Leaf litterfall in RF plots averaged 550 g m^{-2} yr^{-1}, which was within ranges previously reported in the Southeast: 553 (Brown, 1981), 420-574 (Conner, 1994), 395-689 (Megonigal et al., 1997), and 487-548 (Meier et al., 2006) g m^{-2} yr^{-1}.

Patterns of monthly and seasonal leaf litterfall closely followed those of total litterfall, with peak leaf litterfall in November, and lowest leaf litter in February.

ANOVA indicated that leaf litter varied significantly by disturbance class ($F_{df2, 842}$=8.4, p<0.01) and by season ($F_{df3, 842}$=216, p<0.01), with a significant interaction between class and season ($F_{df10, 842}$=4.2, p<0.01). Seasonal differences in litterfall among disturbance classes were only significant during spring and fall, when HD plots had significantly less leaf litterfall production than MD or RF plots ($F_{df2,22}$=8.3 and $F_{df2,22}$=17.6, respectively, p<0.01). There were no significant differences in leaf litterfall between years.

Reproductive litterfall (flowers, fruits, and seeds) ranged from 6.0 to 151.0 g m^{-2} yr^{-1} (Table 1). Reproductive litterfall in HD plots differed significantly from RF plots ($F_{df2, 22}$=10.7, p<0.01) (Table 2). Linear regression analysis of reproductive litterfall and current sedimentation rates showed a significant negative relationship (r^2=0.49, p=0.01).

Reproductive litterfall had greater monthly variation than leaf litter (Fig. 6a). Across all classes and years, peaks in reproductive litterfall occurred in March-April and again in September- November. Reproductive litter was the least in June and July. Seasonally, reproductive litter in RF and MD plots was significantly lower in winter than in spring ($F_{df3, 842}$=2.8, p=0.04) (Fig. 6b). ANOVA indicated a significant interaction between class and season ($F_{df6, 842}$=4.4, p<0.01). Within seasons, RF plots had significantly higher reproductive litter than HD plots in summer ($F_{df2, 177}$=9.5, p<0.01) and spring ($F_{df2, 177}$=7.2, p<0.01), but not in winter or fall (Fig. 6b). HD plots showed no significant differences between seasons, but MD plots were significantly higher in spring than in fall, winter, or summer ($F_{df3, 842}$=10.9, p<0.01); and RF plots were significantly higher in summer than in winter ($F_{df3, 842}$=3.0, p=0.03).

Seasonal patterns in reproduction are most likely due to differences in species composition and forest structure among disturbance classes. RF plots produced high reproductive biomass in all seasons except winter. This may be due to a higher proportion of mature trees, especially oak species, yellow poplar, sweetgum, and large pines, which contribute reproductive biomass in different seasons (personal observations). Oaks have little spring flower biomass, but may have large mast productions in the late summer and fall. Yellow poplars produce large flowers in the spring and dry samaras throughout the summer, sweetgum drop large fruits during the summer and fall, and pines drop cones year-round. MD plots had significantly higher reproductive biomass in the spring. These plots had fewer mature trees and more shrubs and smaller trees, such as black cherry (*Prunus serotina* Ehrh.), fetterbush (*Lyonia lucida* (Lam.) K. Koch), possumhaw (*Viburnum nudum* L.), swamp doghobble (*Leucothoe racemosa* (L.) Gray), and blueberry (*Vaccinium* spp.). Most of these species flower and fruit earlier to contribute to higher biomass of reproductive litterfall in spring. HD plots were consistently low in reproductive biomass. These plots were highest in shrub biomass and were dominated by hazel alder and wax myrtle, which produce little in the way of floral biomass and drop fruits and woody catkins during the winter months.

Leaf-area Index

Leaf-area index (LAI) varied between 1.8 and 7.9 and showed a significant decline with increasing sedimentation rates ($r^2= 0.77$, $p<0.01$) (Fig. 7). Leaf-area index in HD plots was significantly ($F_{df2,13}=6.6$, $p=0.01$) less than RF plots (3.9 ± 1.1 and 7.9 ± 0.7, respectively), while MD plots were not significantly different from either HD or RF plots (6.6 ± 0.7). LAI values in RF and MD plots were similar to the range reported by Vose et al. (1995) in mixed-hardwood forests of the Southern Appalachians in North Carolina. Similar rates were reported by Newman et al. (2006) in xeric (3.5) and mesic

(7.9) communities of mixed deciduous forests in southeast Kentucky. LAI is often used as a major determinant of photosynthetic (Barclay, 1998) and production (Lawlor, 1995) rates in forests. In a study of cypress forests in Florida, Brown (1981) found very low LAI values in cypress domes (0.5-3.4), where transpiration rates were also very low, compared to a cypress floodplain forest (LAI values averaging 8.5). Brown suggested that low LAI reduces transpiration, which may compensate for environmental stress. Our regression results indicate a sharp decline in LAI values at sedimentation rates between 0.1-0.4 cm yr^{-1} (Fig. 7).

Woody Biomass Productivity

Annual woody productivity ranged from 7.1 to 538 g m^{-2} yr^{-1} (Table 1). Woody biomass increments on RF plots (538 g m^{-2} yr^{-1}) fell within the low range of values reported from floodplain forests in the Southeast US. Total stem wood production in floodplain forests was reported to be 1,086 g m^{-2} yr^{-1} in cypress forests of Florida (Brown, 1981), 800-900 g m^{-2} yr^{-1} from a range of floodplain studies across the Southeast US (Conner, 1994), and between 775 and 1,108 g m^{-2} yr^{-1} on a Georgia floodplain (Clawson et al., 2001). Megonigal et al. (1997) reported average woody biomass production between 200 and 800 g m^{-2} yr^{-1} in South Carolina and Louisiana, compared to 800-900 g m^{-2} yr^{-1} in other studies across Southeastern bottomland hardwood forests.

Woody biomass production was negatively correlated to sedimentation rates (r^2=0.35, p<0.01) (Fig. 8). However, other studies have shown that woody biomass production alone may not be a good indicator of flooding stress, due to differential shifts in biomass allocations. In floodplain forests of Louisiana and South Carolina, Megonigal et al. (1997) found no significant difference in woody biomass production between flooding regimes. Clawson et al. (2001) found significantly higher woody biomass production on poorly-drained sites versus drier sites along the Flint River in Georgia, and Lugo et al. (1990a) report lower woody biomass production in poorly-drained basin wetlands than in riverine wetlands.

Between 2002 and 2006, annual woody biomass production varied significantly among years ($F_{df4, 58}$=5.3, p>0.01), with productivity in 2004 being significantly greater than 2003. However, only MD and RF classes reflected these annual differences. In HD plots, there was no significant annual variation in wood production ($F_{df4, 68}$=0.75 p=0.62). There were also no significant interactions between years and disturbance classes ($F_{df8, 58}$=0.13, p=0.99).

Mean standing crop woody biomass in RF plots from 2001 to 2006 was 171 Mg ha^{-1}, which was significantly ($F_{df2, 87}$= 34.3, p<0.01) greater than MD or HD plots (91.1 and 58.8 Mg ha^{-1}, respectively). There was no significant annual variation in woody biomass standing crop overall ($F_{df5, 84}$=1.27 p=0.11) or within each disturbance class (RF: $F_{df5, 18}$ =0.05 p=0.99, MD: $F_{df5, 18}$=0.2 p=0.96, HD: $F_{df5, 18}$=0.07 p=0.99). There was also no interaction between disturbance classes and years ($F_{df10, 79}$=0.13 p=0.99). Regression analysis revealed a significant negative relationship between standing crop woody biomass and current sedimentation rates (r^2=0.39, p<0.01), with a marked decrease at between 0.1-0.4 cm yr^{-1} (Fig. 9).

Tree density ranged from 125 to 2,800 trees per hectare. ANOVA results indicated no significant differences among disturbance classes ($F_{df2, 14}$=0.18 p=0.84). Regression analysis indicated no significant relationship between tree density and sedimentation rates (r^2=0.0 p=0.95). In mountainous streams in Southern Japan, Ito et al.

(2006) found lower tree densities in areas with high sedimentation rates compared with areas receiving lower sediment inputs.

In the current study, tree mortality was measured as the percent of trees that died each year. From 2001-2006, mean annual mortality across all plots ranged from 0 to 12% (Fig. 10). HD plots had the highest annual mortality (5.4 ± 1.6 %), followed by MD plots (2.1 ± 0.7 %), and RF plots (1.8 ± 0.8%). Differences among disturbance classes were not significant. However, there was a significant, positive relationship between annual mortality and current sedimentation rates ($r^2=0.72$, $p<0.01$) (Fig. 10). In floodplain forest of South Carolina and Louisiana, Megonigal et al. (1997) found the highest proportion of dead trees in plots with chronic flooding stress. These plots had undergone recent changes in hydrology and the existing species were not those adapted for flood conditions. In our study, increased mortality rates in HD sites may indicate prolonged stress, most likely due to low gas exchange in the roots associated with sediment burial, as evidenced by low fine root biomass in these same plots.

Comparison by disturbance class indicated that HD plots had significantly less annual wood production compared to RF plots ($F_{df2,\,87}=5.2$, $p<0.01$) (Table 2). This was probably because trees found in RF plots were larger than trees in MD and HD plots ($F_{df2,\,38}=7.86$, $p<0.01$, Fig. 11). MD and RF plots had a greater proportion of large trees (> 30 cm DBH) ($F_{df2,\,56}=20.3$, $p<0.01$, Fig. 11a). In comparing woody biomass productivity, there was no difference among disturbance classes within smaller size classes (5-15 cm DBH) ($F_{df2,63}=0.8$, $p=0.46$). However, with increasing tree diameters, production in HD plots decreased and production in MD and RF plots increased (Fig. 11b). In large-diameter trees (>25 cm DBH), HD plots had significantly less production than MD and RF plots ($F_{df2, 63}$=5.1, p=0.01).

Aboveground NPP

There was a strong, negative correlation between ANPP and increasing sedimentation rates (r^2=0.63, p<0.01) (Fig. 12a). ANPP did not vary significantly from year to year across all plots ($F_{df4, 64}$= 0.98, p=0.43). However, within RF plots, ANPP was significantly ($F_{df4, 22}$=5.8, p<0.01) higher in 2004 than in 2002, 2003, and 2006 (2005 did not differ from other years). MD and HD plots showed no significant annual differences (MD: $F_{df4, 9}$=1.53, p=0.27; HD: $F_{df4, 23}$=0.12, p=0.97).

ANPP values ranged between 204 and 1142 g m^{-2} yr^{-1} (Table 1), with HD plots being significantly lower in both litterfall and woody biomass than MD and RF sites (Table 2). Although HD plots had lower ANPP rates than those reported elsewhere in the Southeast US, MD and RF plots averaged 1,042 g m^{-2} yr^{-1}, which were within ranges reported for forests in the Southeast US (Table 3). Similar reductions in ANPP have been reported for studies monitoring the effect of flooding stress. Megonigal et al. (1997) found that continuously flooded forests had significantly lower ANPP (675 g m^{-2} yr^{-1}) than intermediate and dry plots (1,070 and 1,038 g m^{-2} yr^{-1}, respectively) in floodplain forests of Louisiana and South Carolina. In a comparison of wetland types, Lugo et al. (1990a) reported that continuously flooded basin wetlands had lower mean ANPP (596 g m^{-2} yr^{-1}) than riverine wetlands (1,265 g m^{-2} yr^{-1}). However, Clawson et al. (2001) found higher ANPP in poorly drained sites (1,672 g m^{-2} yr^{-1}) than in intermediate (1,393 g m^{-2} yr^{-1}) and somewhat poorly drained (1,459 g m^{-2} yr^{-1}) sites. These values were largely driven by high woody biomass production, while both litterfall and fine root production were reduced in poorly drained sites.

Belowground NPP

BNPP ranged from 5.6 to 288 g m^{-2} yr^{-1} (Table 1) and was significantly less in HD plots compared to MD and RF plots ($F_{df2, 29}$=16.4, p<0.01) (Table 2). These values were similar to those found in studies comparing different levels of flooding stress. Clawson et al. (2001) reported BNPP values (for roots < 2 mm diameter) of 56, 130, and 211 g m^{-2} yr^{-1} in somewhat poorly drained, intermediate, and poorly drained sites, respectively. Baker et al. (2001a) found 90, 181, and 154 g m^{-2} yr^{-1} on poorly drained, intermediately drained, and well drained sites, respectively (for roots ≤ 3 mm). In the Great Dismal Swamp of Virginia, BNPP estimates were 135, 139, 345, and 490 g m^{-2} yr^{-1} (for roots < 2 mm diameter) (Powell and Day, 1991) and 333, 369, 691, and 691 g m^{-2} yr^{-1} (for roots < 10 mm diameter) (Montague and Day, 1980) for communities aligned with decreasing wetness. Newman et al. (2006) also found higher BNPP in more xeric sites of southeast Kentucky compared with mesic sites. For each of these studies, the authors suggest that anaerobic soil conditions in wetter sites contributed to lower BNPP estimates.

There was a strong negative relationship between BNPP and current sedimentation rates (r^2=0.80, p<0.01) (Fig. 12b). Along a gradient of increasing sedimentation rates, there was a shift from belowground to aboveground productivity (r^2=0.76, p<0.01) (Fig. 13). Lugo et al. (1990a) suggested flooding stress may cause a shift from belowground to aboveground NPP, under the assumption that root biomass and production are often greatest in well-aerated soils and least in anaerobic conditions.

Megonigal and Day (1992) found that continuously flooded cypress allocated greater resources to aboveground biomass compared to periodically flooded cypress, though total biomass did not differ between the two treatments. Clawson et al. (2001) found that, on poorly drained sites, fine root productivity was lowest and stem biomass was the highest in a comparison of ANPP and BNPP along three wetness types on the Flint River floodplain in Georgia. Baker et al. (2001a) also compared fine root productivity in three wetness types in South Carolina and found lowest productivity in poorly drained sites. Powell and Day (1991) reported less fine root production in wetter sites (maple-gum and cypress) than in drier sites (mixed-hardwood sites) in the Great Dismal Swamp of Virginia.

Fine root standing crop biomass was measured as the total root biomass at each sampling period. Mean standing crop biomass varied between 5.9 and 564.2 g m^{-2} for live roots and between 10.7 and 505.1 g m^{-2} for dead roots (Table 1). Standing crop biomass for both live and dead roots differed significantly among disturbance classes (live: $F_{df2,\ 798}=274$, $p<0.01$; dead: $F_{df2,\ 759}=165$, $p<0.01$). For live and dead roots, RF plots had means of 295 and 264 g m^{-2}, MD plots had means of 175 and 189 g m^{-2} and HD plots had means of 46.1 and 38.7 g m^{-2}, respectively. Fine root standing crop biomass in HD plots showed very low temporal dynamics for either live or dead roots; MD plots showed greater dynamics, while RF plots showed very dynamic patterns in both live and dead root standing crop biomass (Fig. 14).

Theoretically, plant growth is maximized when roots are produced in the most favorable soil patches and shed when water and nutrient absorption are no longer efficient (Eissenstat and Yanai, 2002). Therefore, forests with high productivity should also have higher fine root turnover (Eissenstat and Yanai, 2002). Results from this study indicated a marked difference between temporal patterns in fine root standing crop biomass among disturbance classes (Fig. 14), with RF plots showing highly dynamic temporal patterns and HD plots showing very little variation through time. These patterns indicate rapid root turnover in RF plots and less root turnover in HD plots. It has been suggested that forests with slow root turnover are adapted to more nutrient-poor sites due to the high cost of continually replacing roots (Eissenstat and Yanai, 2002). Our results indicate that fine root turnover was less in forests receiving high levels of sediment inputs.

In general, root turnover is much greater in warmer climates (Fitter, 2002) and, therefore, more frequent sampling is required to track turnover rates (Baker et al., 2001a). This study measured dead and live root biomass approximately every six weeks from February 2002 to July 2003 and from April 2004 to December 2006, for a total of 33 samples.

Temporal patterns in standing crop biomass found in RF plots (Fig. 14c) were similar to those found in other studies (Schilling et al., 1999, Clawson et al., 2001, Powell and Day, 1991), with peaks in live root biomass in the spring (March-April) and fall (November-December) of each year. Dead root biomass peaked in August-September and January-February of each year. One exception was a peak in dead roots from October to December of 2006, which corresponded to a decrease in live roots during this same period. Precipitation data indicate that this period followed a period of drought conditions (Fig. 3), suggesting that root production may be driven by precipitation to a certain extent.

In northern hardwood forests, spring and fall peaks in fine root production are governed largely by temperature (Burke and Raynal, 1994). However in southern floodplain forests where temperatures are generally mild, hydrology and precipitation may play a larger role. In South Carolina, Baker et al. (2001a) found increased root mortality on all sites during periods of drought. In the present study, a comparison of live root standing crop biomass in RF plots and precipitation patterns for each preceding month reveal close similarities (Fig. 15), indicating that fine root production may be closely tied to precipitation.

The lack of temporal dynamics in HD plots may reflect increased stress in these plots. Fine roots dynamics in areas associated with frequent flooding are also less dynamic than in drier sites. Results from Powell and Day's study (1991) in the Great Dismal Swamp, show similar peaks in the summer and late fall-winter for mixed hardwoods sites, but little seasonal variation in the wetter maple-gum and cypress sites. Fine root dynamics along the Flint River , GA (Clawson et al., 2001), also reflected peaks in live root biomass in spring, early fall, and winter in somewhat poorly drained sites, while poorly drained sites showed very little seasonal variation. In addition, Jones et al. (1996) found no seasonal patterns in fine root production along blackwater streams in Alabama, which experienced frequent flooding. There were no seasonal peaks in fine root biomass exhibited in HD plots of the present study (Fig. 14), suggesting that high sedimentation rates may impose a stress similar to that of flooding.

Fine root standing crop biomass differed within and among diameter size classes (0.1-1.0 mm, 1.1-2.0 mm, and 2.1-3.0 mm). Standing crop biomass was greater in RF plots compare to MD and RF plots (Table 4). In the smallest diameter class, (0.1-1.0 mm diameter) roots showed greater variability among disturbance classes in both live and dead categories than roots of larger diameter classes (Fig. 16). Fine root standing crop biomass was negatively correlated to current sedimentation rates in both live and dead roots and had the strongest relationship in the smallest diameter class (live roots: $r^2=0.86$; dead roots: $r^2=0.89$, $p<0.01$) (Fig. 17).

Mean root length was correlated to current sedimentation rates only in the smallest diameter class (0.1-1.0 mm) for both live ($r^2=0.73$, $p<0.01$) and dead ($r^2=0.81$, $p<0.01$) roots (Fig.18). Root length in this diameter class varied significantly among disturbance classes, with live VF roots showing significant differences among all three classes ($F_{df2,\,819}=24.7$, $p<0.01$) and dead VF roots significantly lower in HD plots ($F_{df2,\,765}=39.6$ $p<0.01$). Mean root lengths for live VF roots in HD, MD, and RF plots were 245 (± 20.2), 1094 (± 69.5), and 1910 (± 104) m m^{-2}. The highest biomass was also found in the smallest size class (Fig. 16). Because finer roots are more efficient at nutrient uptake, it has been suggested that an increase in small diameter roots may indicate nutrient deficient soils (Eissenstat and Yanai, 2002). However, roots of the smallest size class in this study were proportionally greater than roots of the other two diameter classes within each disturbance class.

Total NPP

Total NPP ranged from 175 to 1,500 g m^{-2} yr^{-1} (Table 1). HD plots had significantly lower NPP ($F_{df2,\,13}=16.3$, $p<0.01$) than MD and RF plots (Table 2). There was a significant negative relationship between NPP and increasing sedimentation ($r^2=0.76$, $p<0.01$) (Fig. 19).

Shrubs

Shrub biomass varied widely among plots, between 24 and 3,464 g m^{-2} (Table 1). Shrub biomass differed significantly among all disturbance classes ($F_{df2,29}$=30.7, p=0.01), with class means of 297 (± 62.8), 1,500 (± 658), and 2,090 (± 330) g m^{-2} for RF, MD, and HD plots, respectively. There was a positive relationship between increasing shrub biomass and increasing sedimentation (r^2=0.34, p<0.01) (Fig. 20a). There was no significant variation between years in shrub biomass across all disturbance classes or within disturbance classes.

Stem density (including shrubs and trees) ranged from 0.95 to 14 stems m^{-2} (Table 1). HD plots had significantly ($F_{df2, 184}$=7.8, p<0.01) higher total stem density than MD and RF plots. Mean stem densities of HD, MD, and RF plots were 8.1 ± 0.1, 3.9 ± 0.4, and 4.8 ± 0.4 stems m^{-2}, respectively. Regression analysis showed a significant positive correlation between stem density and sedimentation rates (r^2=0.23, p<0.01) (Fig. 20b). Lugo et al. (1990b) reported higher stem densities in areas of poor drainage. Brown et al. (1979) suggested that this may be a response to flooded conditions, where there is little gas exchange. Both studies suggest that higher stem densities allow greater surface area for gas exchange. Kent et al. (2001) found that most shrubs in dune systems shift resources from belowground to aboveground during burial stress. In our study, we found a weak, but significant positive relationship between stem densities and increasing sedimentation rates (r^2=0.10 p<0.01). This may be further evidence that high sedimentation rates are restricting gas exchange in the soil. Increased stem densities may also be a consequence of high tree mortality, which created canopy openings for stem regeneration.

Forest Productivity

Although we expected to see an increase in forest productivity with moderate levels of sedimentation, we found that both ANPP and BNPP were highest in RF plots receiving less than 0.1 cm yr^{-1} current sedimentation. Regression analysis clearly indicated a sharp decline in productivity with rates as low as 0.1-0.4 cm yr^{-1}, which appeared to be a consistent threshold. Although other studies have found increased forest productivity associated with nutrient-rich sediment from flooding or waste-water (Hesse et al., 1998; Rybczyk et al., 2002; Day et al., 2006), results from this study indicate that sediment deposition from upland erosion acts as a stress rather than a subsidy even at very low levels. It should be noted, however, that this study represents sediment depositions entering a system which had been under sedimentation stress for many years, as evidenced by many large gully scars. This cumulative effect may be a strong driver of associated declines in productivity.

Another factor which may have contributed to declines in productivity was the nature of the deposited materials. Rather than silt, sediments at Ft. Benning are coarse sand, which greatly increase soil bulk density in depositional areas (bulk density averaged close to 1.7 and 1.4 Mg m^{-3} in HD and MD plots, compared to 1.1 Mg m^{-3} in RF plots). Such high bulk density can severely limit root growth (Unger and Kaspar, 1994; Kozlowski, 1999; Freddi et al., 2007). These coarse sands were also limited in clays, which have been shown to influence the cation exchange capacity (CEC) in soils (Manrique et al., 1991; Parfitt et al., 1995)

There are no indications that depositional material at Ft. Benning carries significant nutrient sources. Sediments in this study originated from roads and were not associated with agricultural fields or other sources of nutrient inputs. Brinson et al. (1980) suggest that sediments from headwater streams have fewer nutrient inputs compared with sediments from agricultural runoff, wastewater effluence, and alluvial swamps.

Conclusions

Results from this study suggest that current sedimentation rates greater than 0.1-0.4 cm yr^{-1} are associated with significant declines in both aboveground and belowground forest productivity (hypothesis 2). Similar results were found using historic, long-term sedimentation rates. We found no evidence that sediment inputs improved forest productivity even at very low levels (hypothesis 1). Areas associated with high sedimentation rates exhibited many of the same forest responses that have been observed with flooding stress, including a shift from belowground to aboveground productivity (hypothesis 3). It is likely that sedimentation may cause low soil oxygen conditions that are similar to those caused by flooding.

The potential for reduced forest production due to sedimentation disturbances poses a concern for land managers. Results from this study suggest that productivity declined at sedimentation rates between 0.1-0.4 cm yr^{-1}. However, this threshold may vary regionally and in different ecosystems. It it important to note that these rates were found in forests that have been receiving continuous sediment inputs over a long period of time.

In order to determine how sedimentation may impact forested areas, land managers need a metric. From the metrics used in this study, monitoring LAI may prove to be the most useful metric for land managers. LAI is relatively simple to measure and showed a tight correlation to sedimentation rates and forest productivity. Sedimentation rates similar to those reported here are fairly common in riparian forests across the Southeast, especially in agricultural areas or areas experiencing increased urbanization. Therefore, it is critical for land managers to understand how sedimentation may be affecting productivity in these forests.

Acknowledgments

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Table 1. Summary of sedimentation rates and productivity associated with each plot in riparian forests at Ft. Benning, GA, 2004-2006.

Parameter			HD						MD						RF		
Plot ID	**D12B**	**F1WAd**	**K11d**	**F3**	**D12A**	**I3Bd**	**F1Wb**	**K11c**	**I3C**	**F1E**	**F4Ac**	**I3Ad**	**F1WAc**	**F4C**	**I3Bc**	**F4Ad**	**I3Ac**
Current Sedimentation Rate (cm yr^{-1})	5.52	4.38	3.96	1.85	1.39	0.78	0.46	0.43	0.23	0.15	0.14	0.11	0.09	0.01	0.01	0.00	0.00
Historic Sedimentation Rate (cm yr^{-1})	2.07	1.15	1.71	1.97	4.00	0.32	1.29	0.50	2.06	0.20	0.00	1.48	0.00	0.00	0.00	0.00	0.00
Current Sedimentation Rate (g m^{-2} yr^{-1})	0.99	0.77	0.7	0.33	0.22	0.11	0.08	0.07	0.04	0.01	0.07	0.02	0.01	<0.01	<0.001	<0.001	<0.001
Twigs (g m^{-2} yr^{-1})	66.3	20.8	31.7	63.1	94.5	76.4	43.3	46.1	57.9	92.8	58.0	116	84.9	100	103	57.6	60.6
Leaves (g m^{-2} yr^{-1})	187	139	279	351	589	509	419	472	414	472	468	571	504	449	518	588	521
Reproductive Tissues (g m^{-2} yr^{-1})	46.6	6.0	18.5	40.6	66.7	50.7	34.5	52.1	37.0	31.0	38.1	65.4	27.3	60.5	151	68.8	56.8
Annual Litterfall (g m^{-2} yr^{-1})	300	197	357	462	749	645	506	589	519	612	572	755	660	643	774	715	647
Annual Woody Biomass Production (g m^{-2} yr^{-1})	117	73	137	183	300	256	226	232	226	242	227	301	255	255	386	357	321
ANPP (g m^{-2} yr^{-1})	592	204	509	722	1,152	898	1,060	805	978	952	1,008	1,142	1,089	1,055	1,094	1,085	956
BNPP (g m^{-2} yr^{-1})	21.8	5.6	40.0	60.4	166.6	125	163	5.5	118	225	165	288	165	213	133	265	163
NPP (g m^{-2} yr^{-1})	614	210	549	783	1318	1,023	1,223	811	1,096	1,177	1,173	1,431	1,254	1,268	1,227	1,349	1,120

Shrub Standing Crop Biomass (g m^{-2})	3,465	808	806	4,109	1,607	1,614	6,890	162	29	1,433	100	160	359	239	747	24	294
Stem Density (stems m^{-2})	14.0	9.03	3.39	10.5	0.98	0.95	4.34	5.24	1.79	2.36	6.77	2.68	3.48	4.80	3.38	3.75	1.17
Tree Standing Crop Biomass (Mg ha^{-1})	807	15	149	929	1,148	372	1,396	365	909	1,283	2,690	1,382	2,274	1,582	1,599	905	1,172
Fine Root Standing Crop Biomass, Dead (g m^{-2})	15.5	12.6	24.5	83.4	52.2	175	101	49.2	161	464	332	153	235	360	191	292	192
Fine Root Standing Crop Biomass, Live (g m^{-2})	8.9	12.6	15.9	96.2	88.2	193	176	54.3	171	272	244	177	241	538	257	343	192

Table 2. Mean net primary productivity (NPP) in reference (RF), moderately disturbed (MD), and highly disturbed (HD) plots from 2002-2006. Means followed by different letters across classes are significantly different by Tukey's HSD (α=0.05). Standard errors in parentheses.

Measured variable	Disturbance Class			D.F.$_{\text{error}}$	F-value	P-value
	RF	**MD**	**HD**			
Productivity (g m^{-2} yr^{-1})						
Litterfall	672 (19.4)^{a}	619 (19.1)^{a}	384 (26.7)^{b}	64	11.0	<0.01
Leaf	550 (39.2)^{a}	533 (39.1)^{a}	343 (37.1)^{b}	64	14.9	<0.01
Reproductive	67.6 (11.0)^{a}	46.6 (4.2)^{ab}	34.7 (5.7)^{b}	64	21.1	<0.01
Woody biomass	381 (25.0)^{a}	331 (30.0)^{ab}	229 (46.5)^{b}	70	5.22	<0.01
Aboveground	1,053 (29.6)^{a}	950 (41.4)^{a}	613 (53.2)^{b}	66	36.0	<0.01
Belowground	184 (19.2)^{a}	154 (28.9)^{a}	58.9 (19.3)^{b}	120	42.2	<0.01
Total	1,237 (32.5)^{a}	1,104 (71.5)^{a}	672 (114)^{b}	13	16.3	<0.01

Table 3. Comparison of aboveground net primary productivity estimates from the Southeastern United States.

Location	Forest type	ANPP ($g\ m^{-2}\ yr^{-1}$)	Source
GA	Bottomland hardwood forests (<0.1 cm yr^{-1} sedimentation)	1042	Present study
LA and S C	Floodplain forests	500-1300	Megonigal et al. 1997
Throughout the Southeast	Floodplain forests	267-1607	Conner 1994
GA	Floodplain forests, redwater	1020	Schilling and Lockaby 2006
GA	Floodplain forests, blackwater	830	Schilling and Lockaby 2006
GA	Floodplain forest, redwater	1393-1672	Clawson et al. 2001
Throughout the Southeast	Basin wetlands	596	Lugo et al. 1990a
Throughout the Southeast	Floodplain forests	1265	Lugo et al. 1990a

Table 4. Summary of mean fine root standing crop biomass for each disturbance class within each diameter class and type for fine roots collected in riparian forests at Ft. Benning, GA, from 2002 to 2006. Standard errors are shown in parentheses. Significant differences using ANOVA are shown in bold. Different letters represent significant differences in means by Tukey's HSD (α=0.05).

Diameter Class	**Type**	**Disturbance Class**					
		HD	**MD**	**RF**	**DF error**	**F-statistic**	**P-value**
mm			**g m^{-2}**				
0.1-1.0	Live	24.8 $(2.1)^{c}$	90.5 $(4.5)^{b}$	153 $(6.7)^{a}$	817	249	**<0.01**
	Dead	20.2 $(2.1)^{b}$	119 $(7.5)^{a}$	140 $(7.1)^{a}$	764	157	**<0.01**
1.1-2.0	Live	9.5 $(1.1)^{c}$	43.0 $(2.9)^{b}$	64.8 $(3.8)^{a}$	610	76.0	**<0.01**
	Dead	7.7 $(0.8)^{c}$	31.5 $(2.5)^{b}$	50.1 $(3.1)^{a}$	598	62.6	**<0.01**
2.1-3.0	Live	12.8 $(2.2)^{c}$	54.0 $(5.6)^{b}$	92.4 $(5.6)^{a}$	475	20.0	**<0.01**
	Dead	10.2 $(1.5)^{b}$	39.5 $(3.9)^{b}$	73.8 $(4.5)^{a}$	473	12.1	**<0.01**

Figure 1. Location of study area and 17 plots in riparian forests at Ft. Benning, GA.

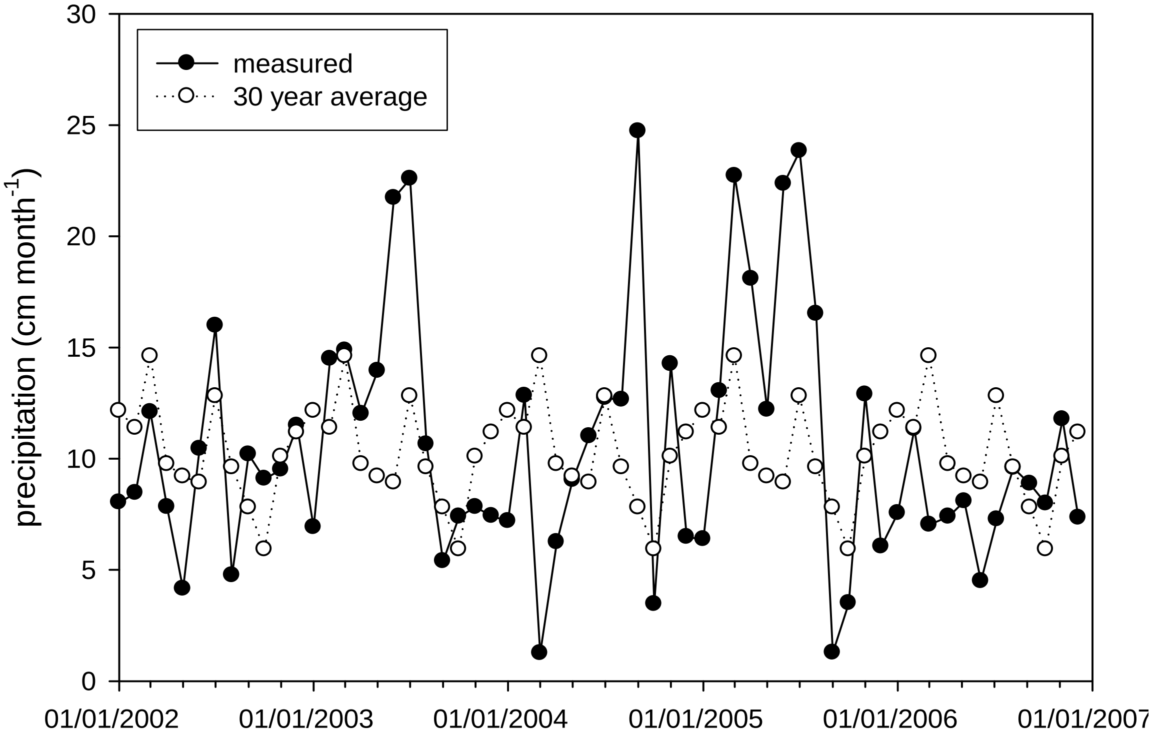

Figure 2. Monthly precipitation totals for Columbus, GA regional airport 2002 through 2006 (solid circle) and the 30-year average (open circle).

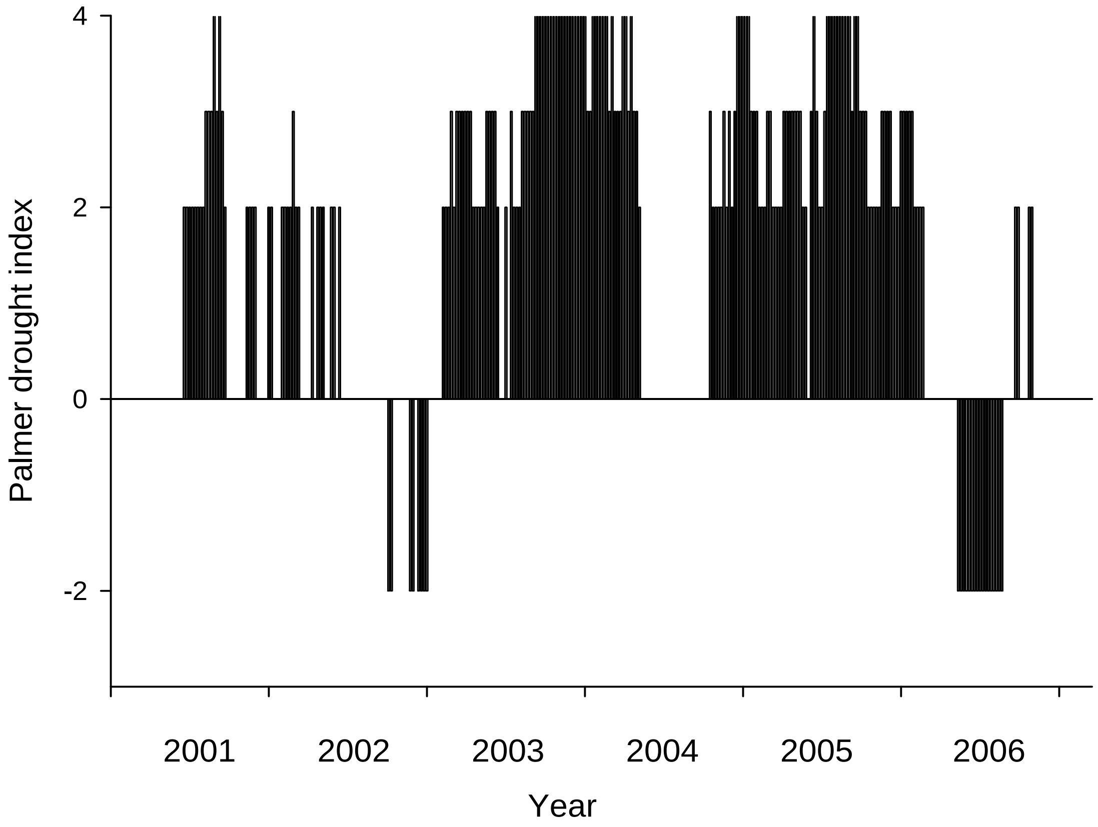

Figure 3. Palmer drought indices for 2001-2002. Positive bars indicate excess moisture, negative bars indicate drought.

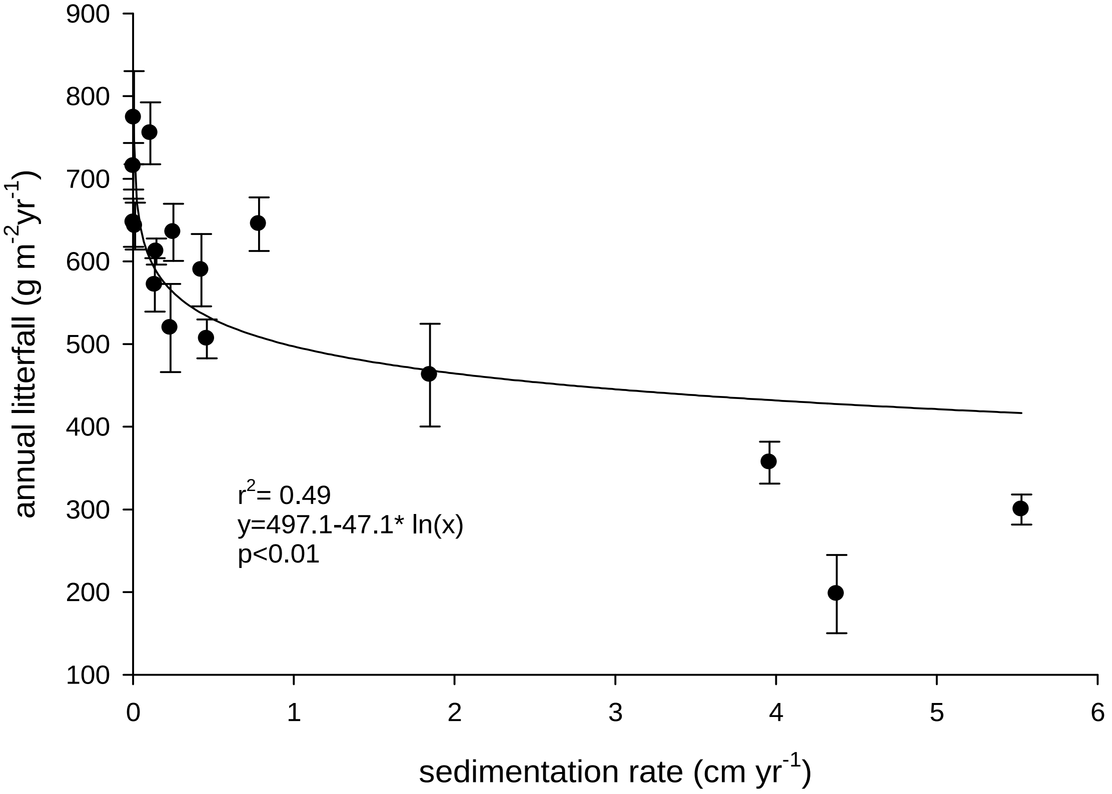

Figure 4. Regression relationship between litterfall production (2002-2006) and current sedimentation rates. Vertical bars indicate standard errors.

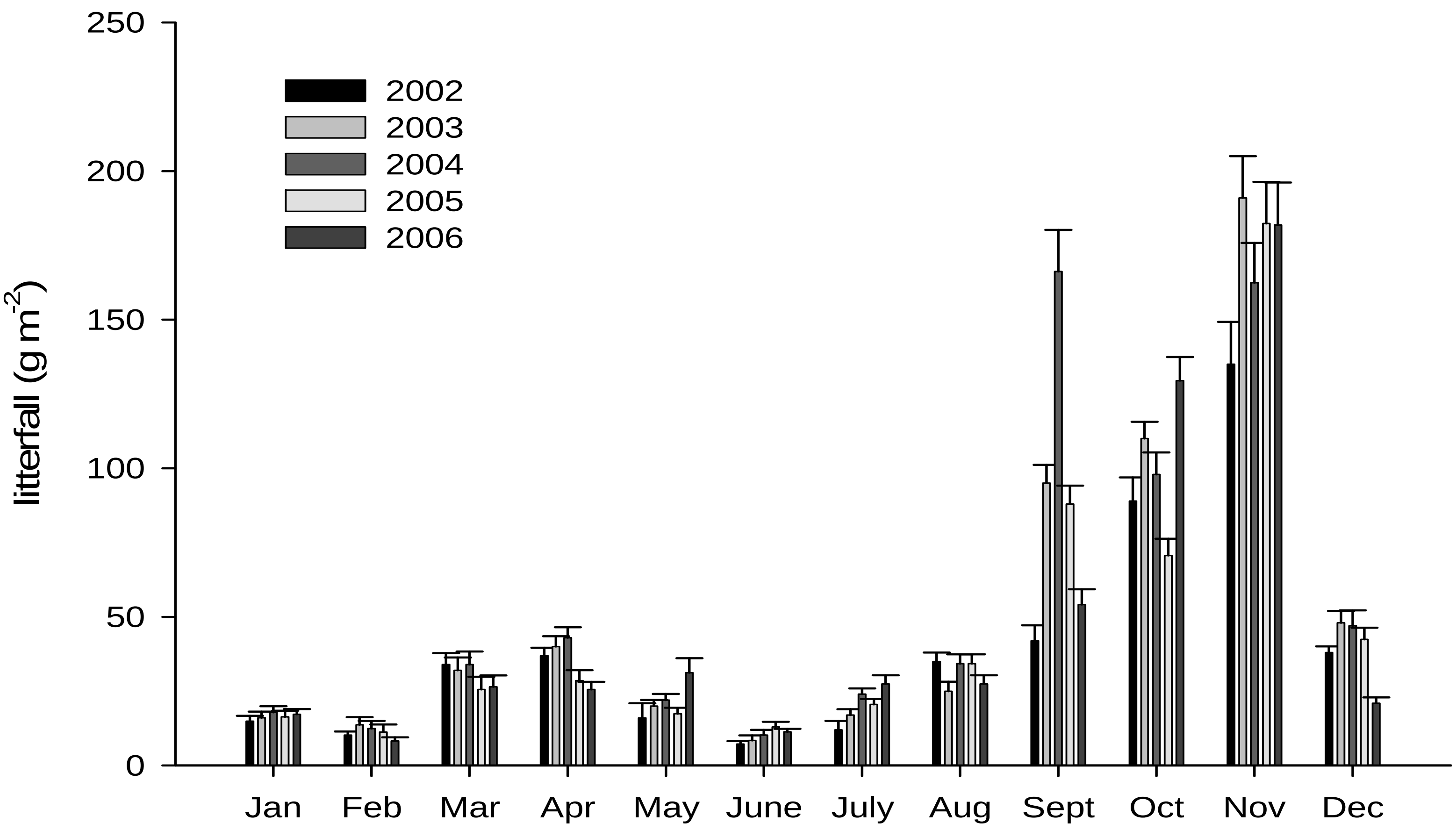

Figure 5. Litterfall production averaged across all plots by month and year. Vertical bars indicate standard errors.

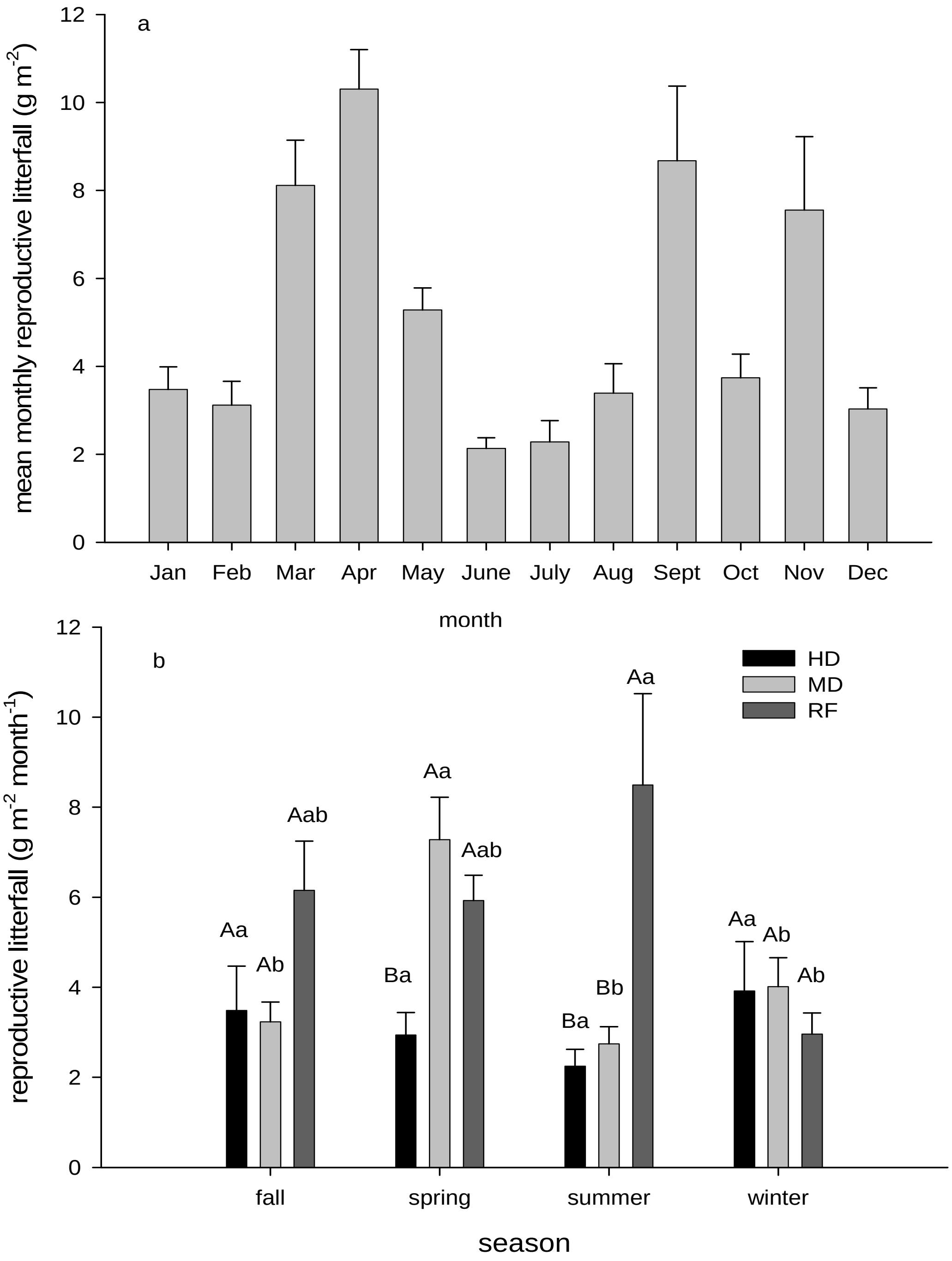

Figure 6. Mean monthly reproductive litterfall mass (2002-2006) a) averaged across all plots and b) by disturbance class and season. Uppercase letters represent significant differences between disturbance classes within seasons and lowercase letters represent significant differences between seasons within disturbance classes. All comparisons were analyzed using Tukey's HSD ($\alpha=0.05$). Vertical bars indicate standard errors.

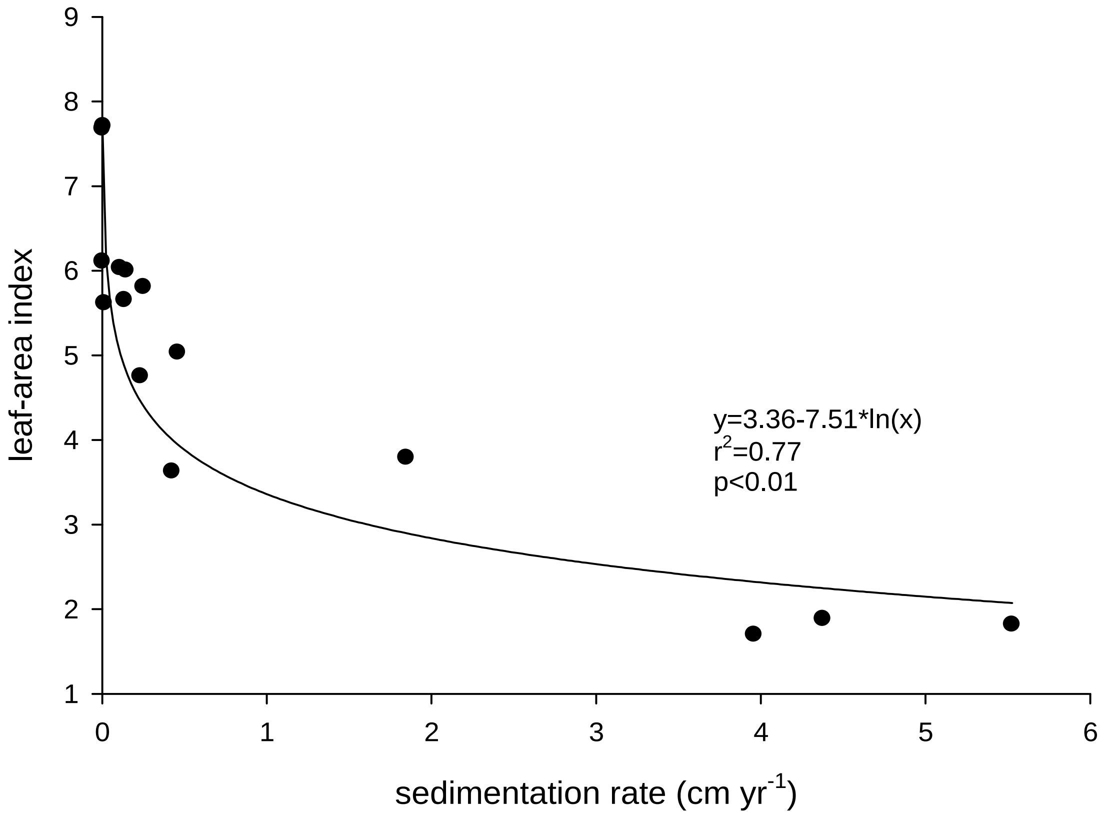

Figure 7. Regression relationship between leaf-area indices and current sedimentation rates.

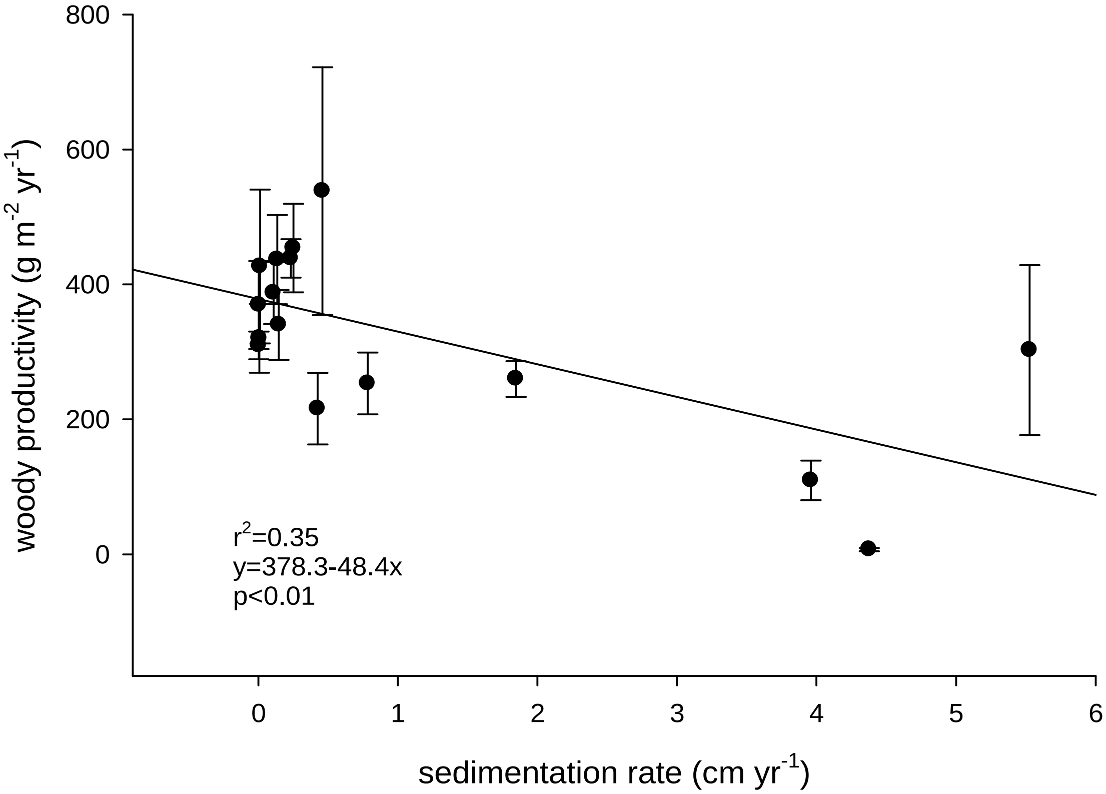

Figure 8. Regression relationship between current sedimentation rate and annual woody biomass production (2002-2006). Vertical bars indicate standard errors.

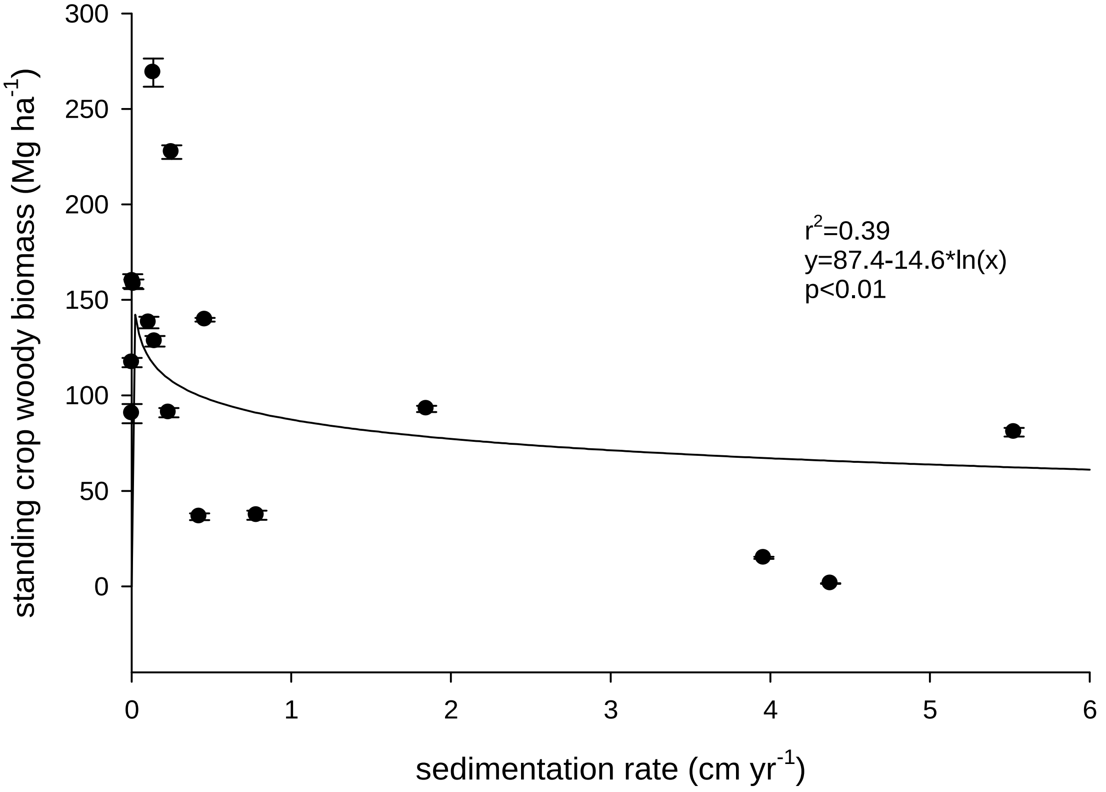

Figure 9. Regression relationship between mean standing crop woody biomass (2001-2006) and current sedimentation rates. Vertical bars indicate standard errors.

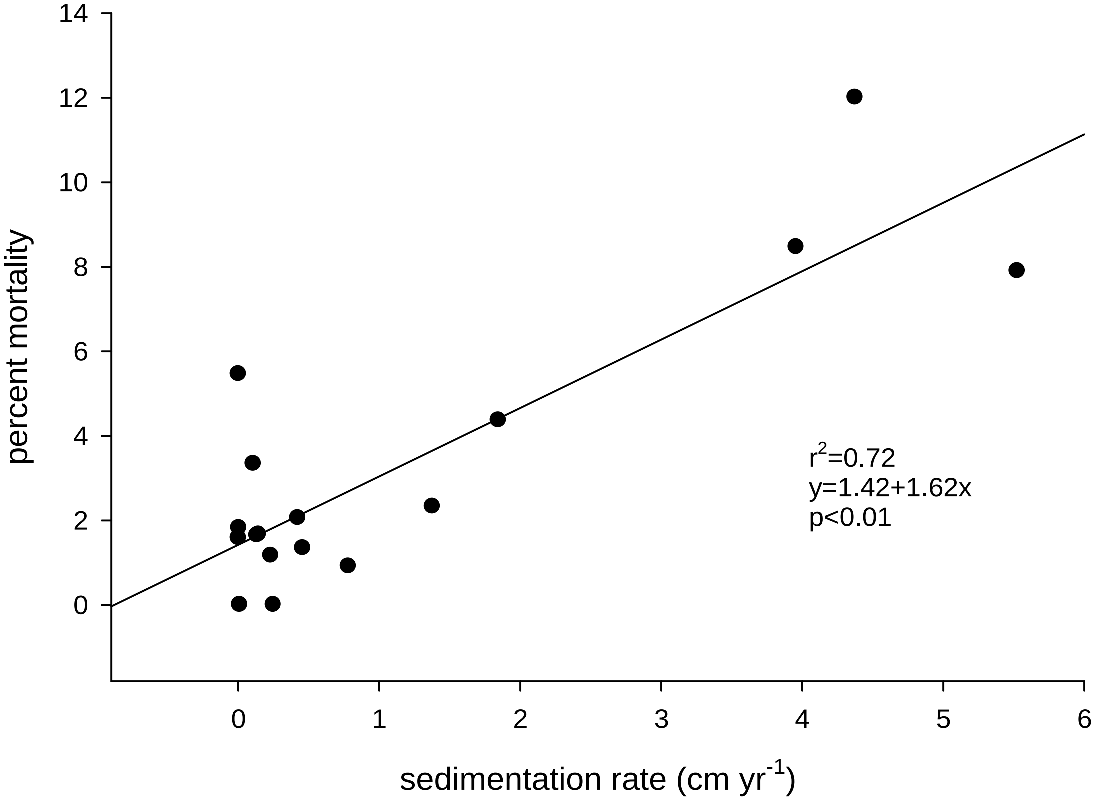

Figure 10. Regression relationship between tree mortality (2002-2006) and current sedimentation rates.

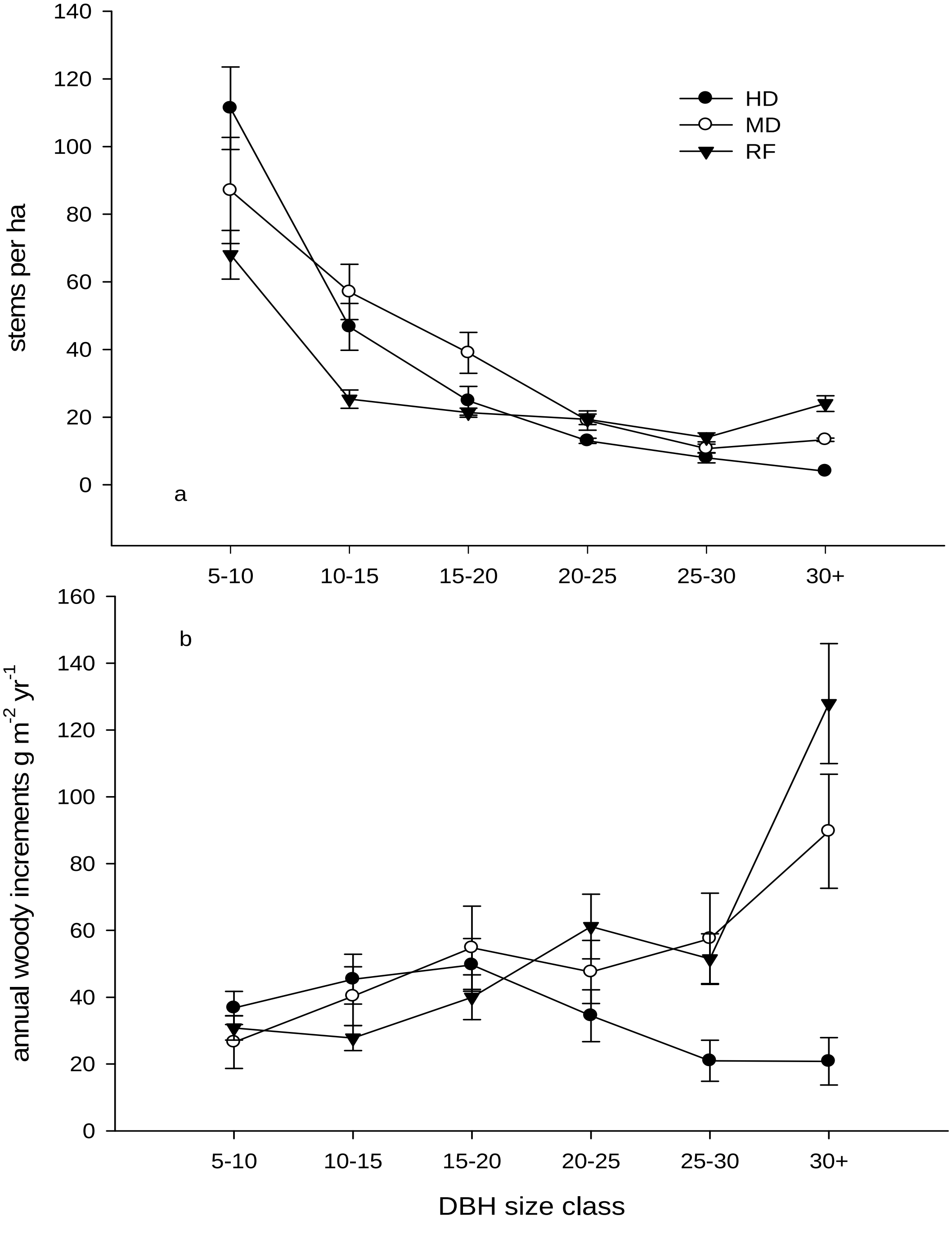

Figure 11. Comparisons of a) stem density and b) woody biomass production across stem diameter classes among disturbance classes. Triangles represent RF plots, open circles represent MD plots, and filled circles represent HD plots. Vertical bars indicate standard errors.

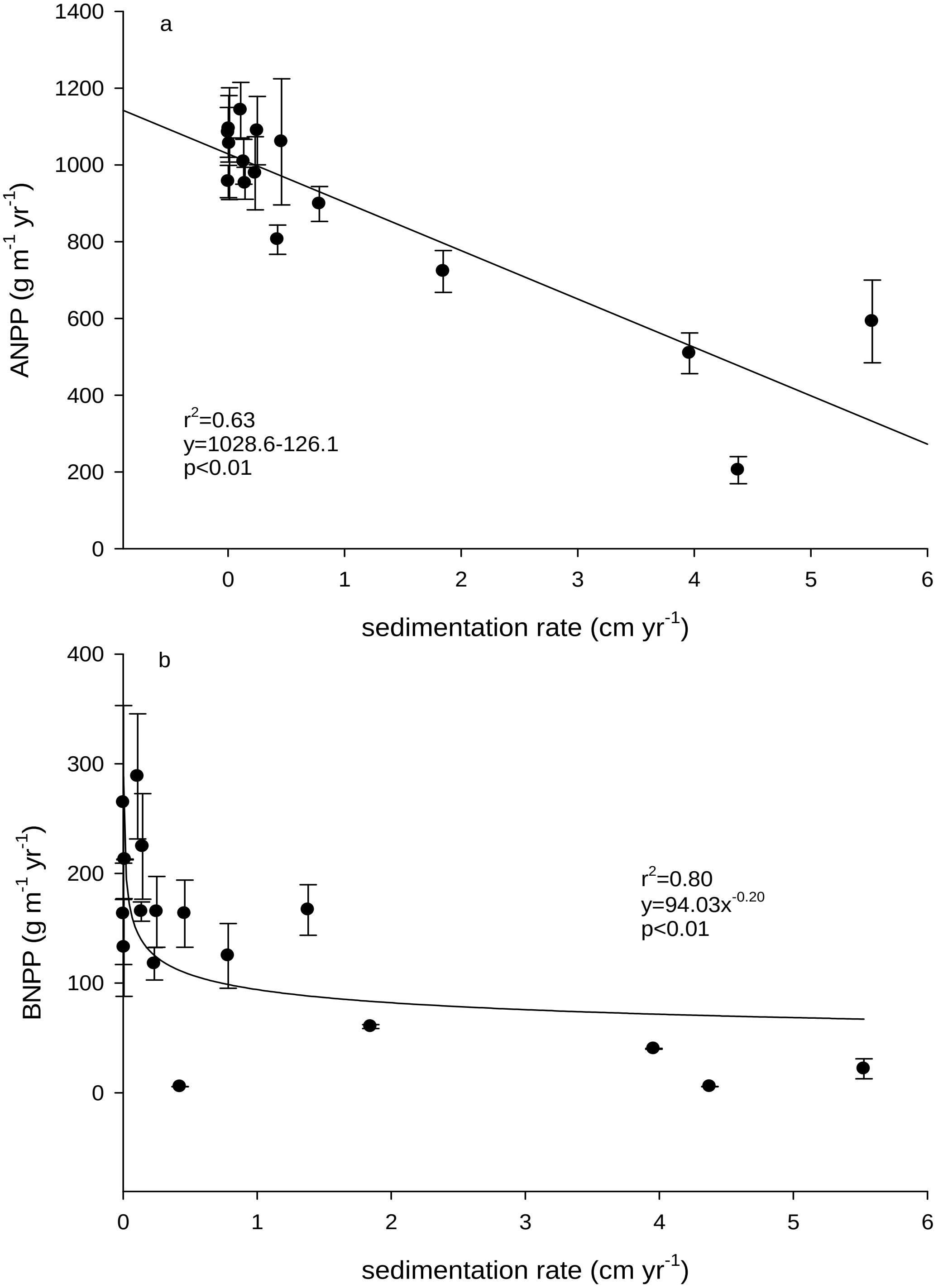

Figure 12. Regression relationship between a) aboveground net primary productivity and b) belowground net primary productivity (2002-2006) and current sedimentation rates. Vertical bars indicate standard errors.

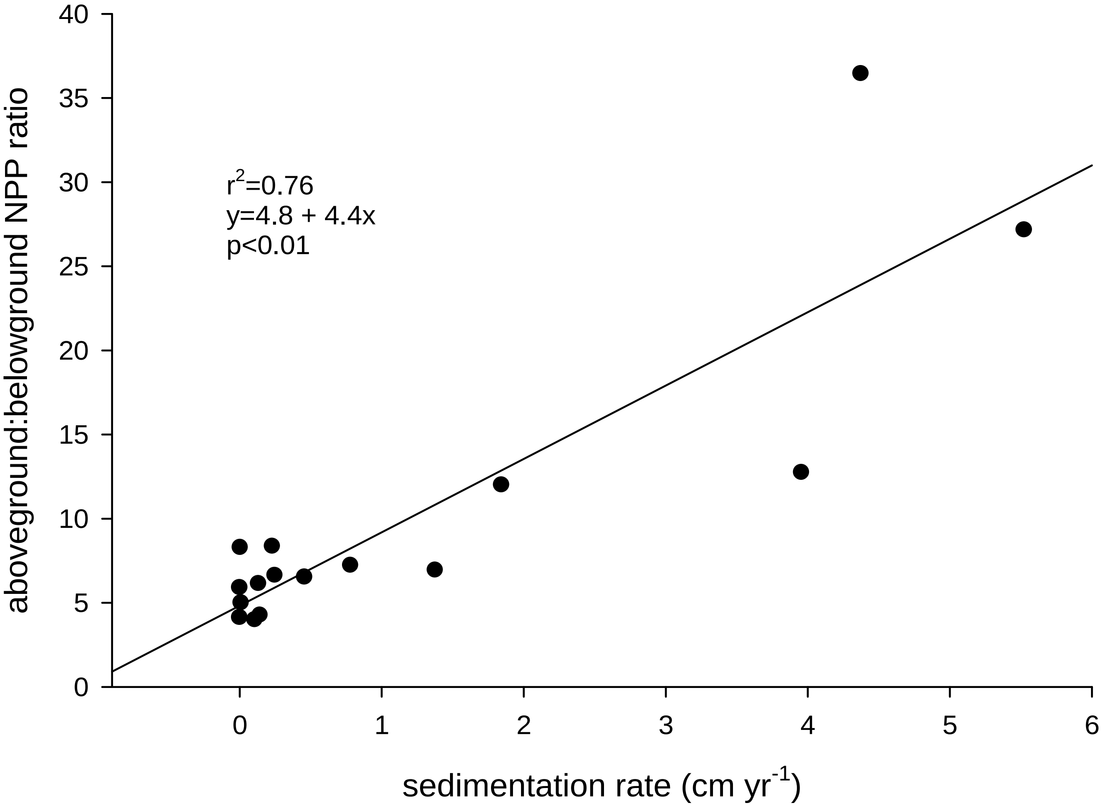

Figure 13. Regression relationship between ratio of ANPP to BNPP (2002-2006) and current sedimentation rates.

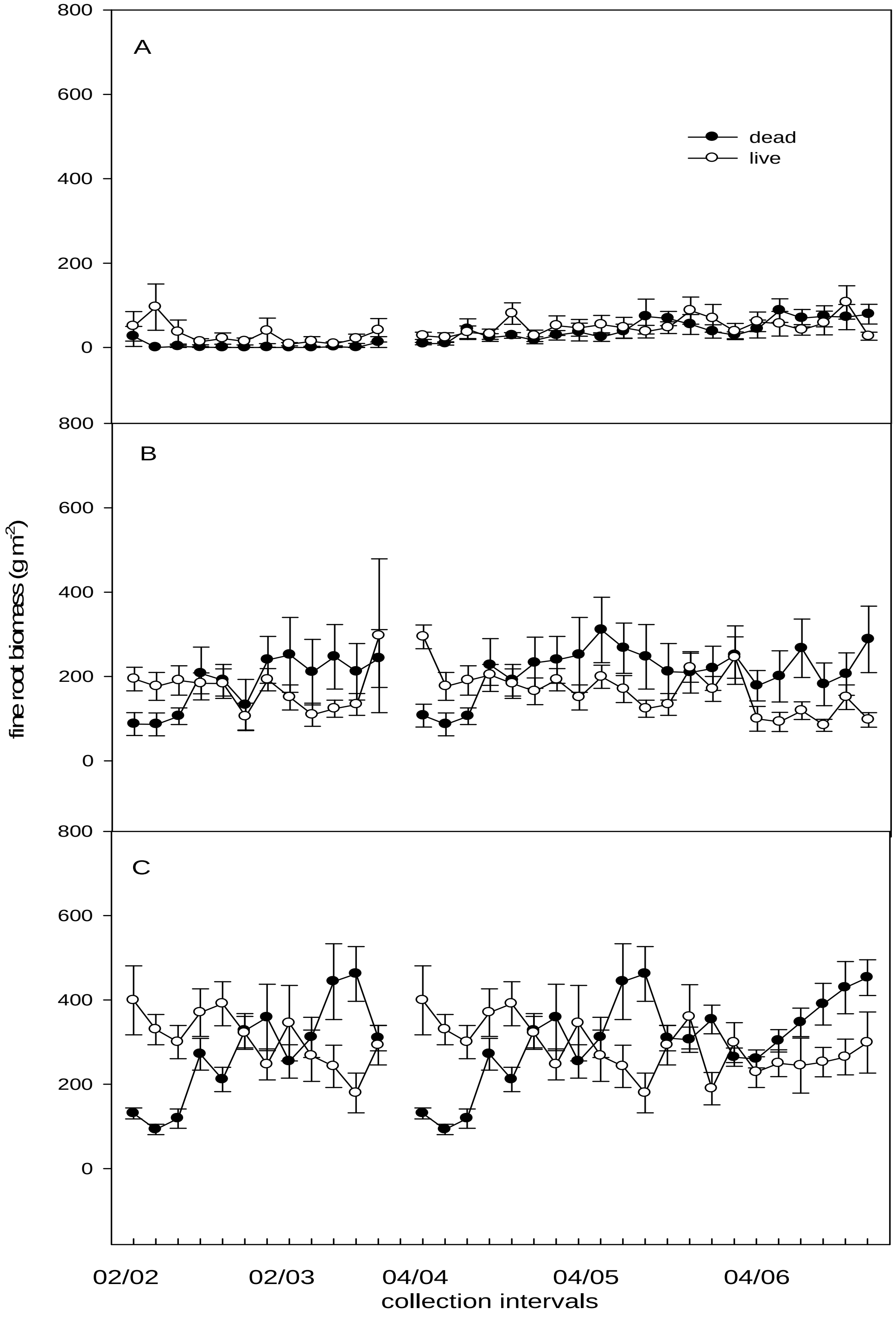

Figure 14. Fine root standing crop biomass (0.1-1.0 mm diameter) at each collection date in (A) HD, (B) MD, and (C) RF plots. Black circles represent dead roots, hollow circles represent live roots. Vertical bars indicate standard errors.

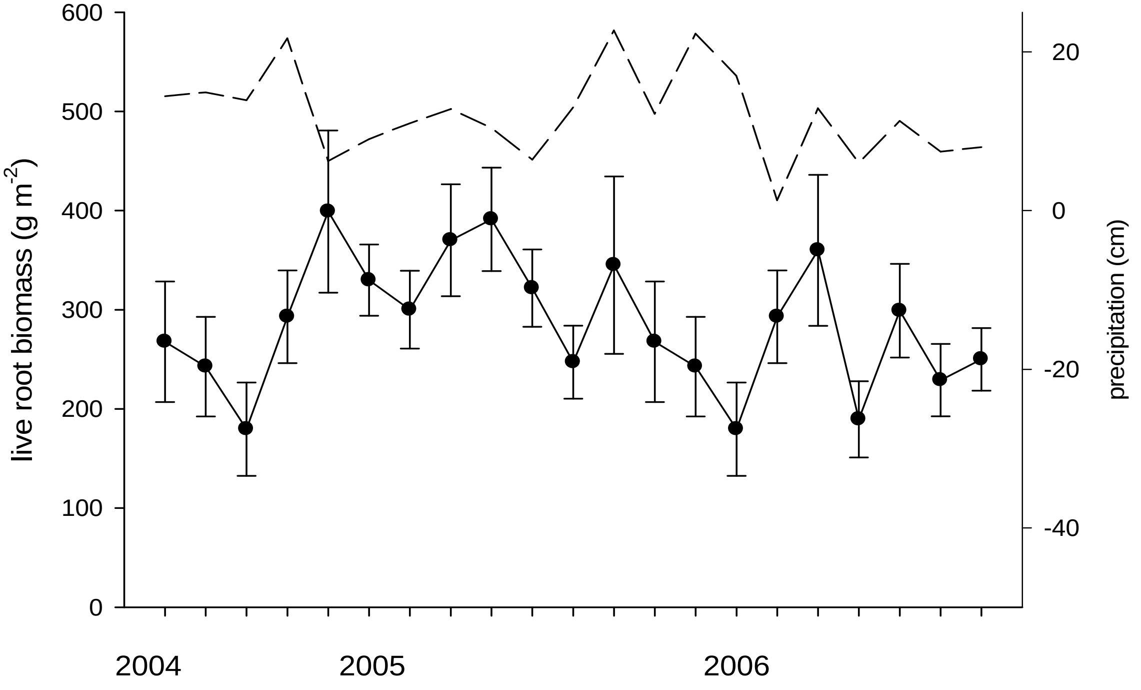

Figure 15. Relationship between live root standing crop biomass in RF plots (solid line) and precipitation for the month preceding each collection (broken line). Vertical bars indicate standard errors.

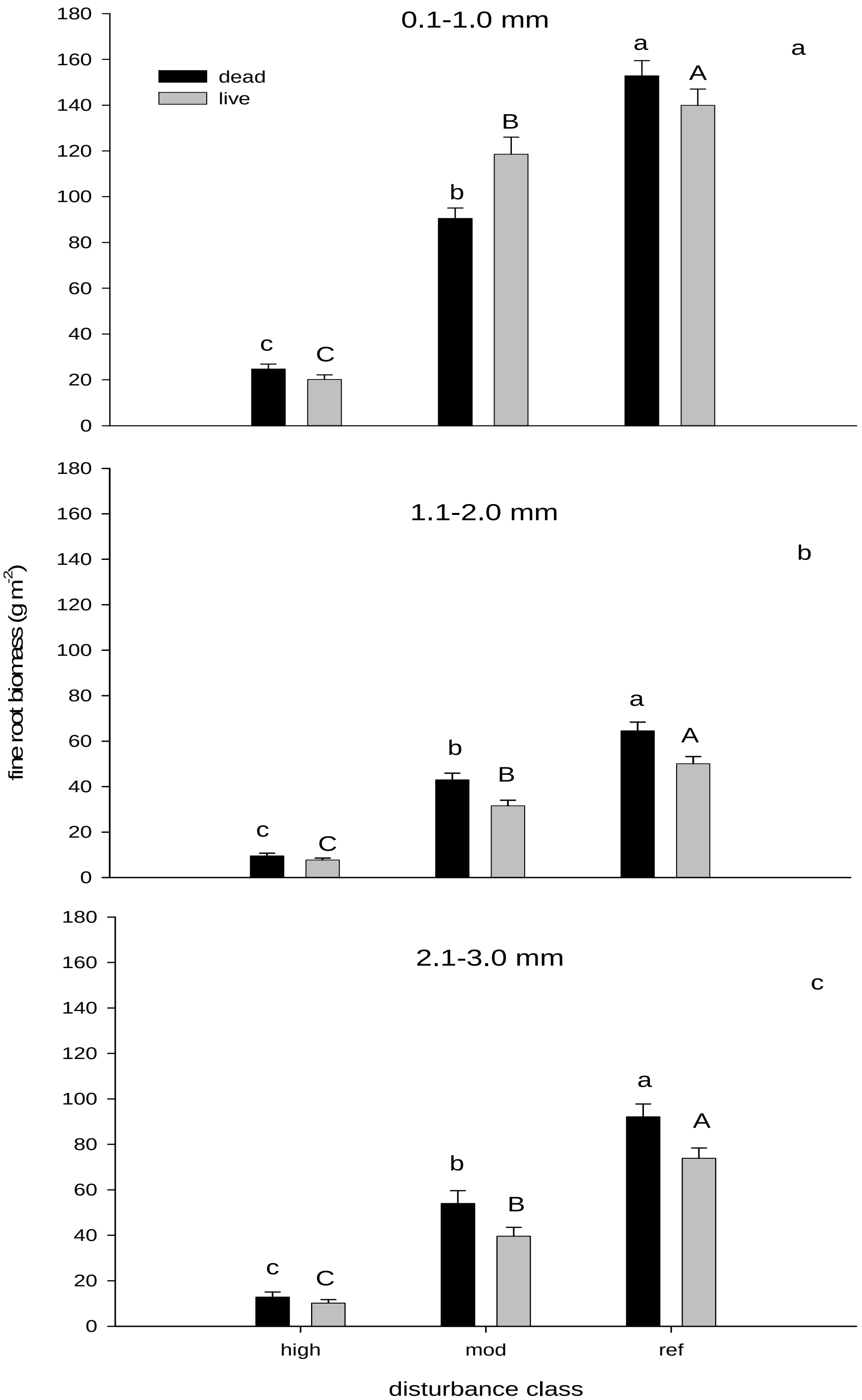

Figure 16. Fine root standing crop biomass (2002-2006) by disturbance class for diameter classes: a) 0.1-1.0 mm, b) 1.1-2.0 mm, and c) 2.1-3.0 mm. Lowercase letters represent significant differences among disturbance classes for dead roots and uppercase letters represent differences among disturbance classes for live roots by Tukey's HSD ($\alpha=0.05$). Vertical bars indicate standard errors.

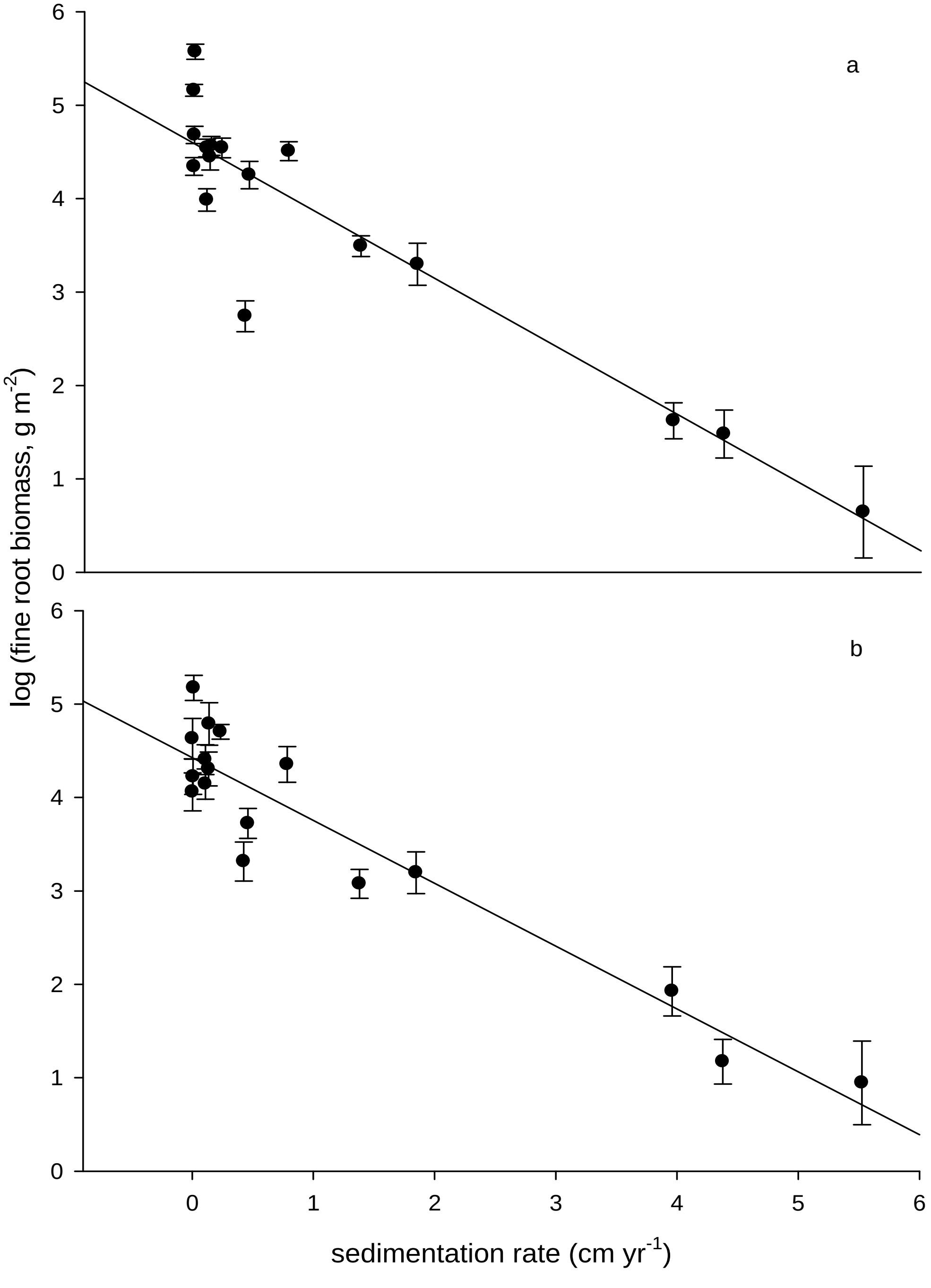

Figure 17. Regression relationship between a) live and b) dead root biomass (0.1-1.0 mm diameter size class) and current sedimentation rates. Vertical bars indicate standard errors.

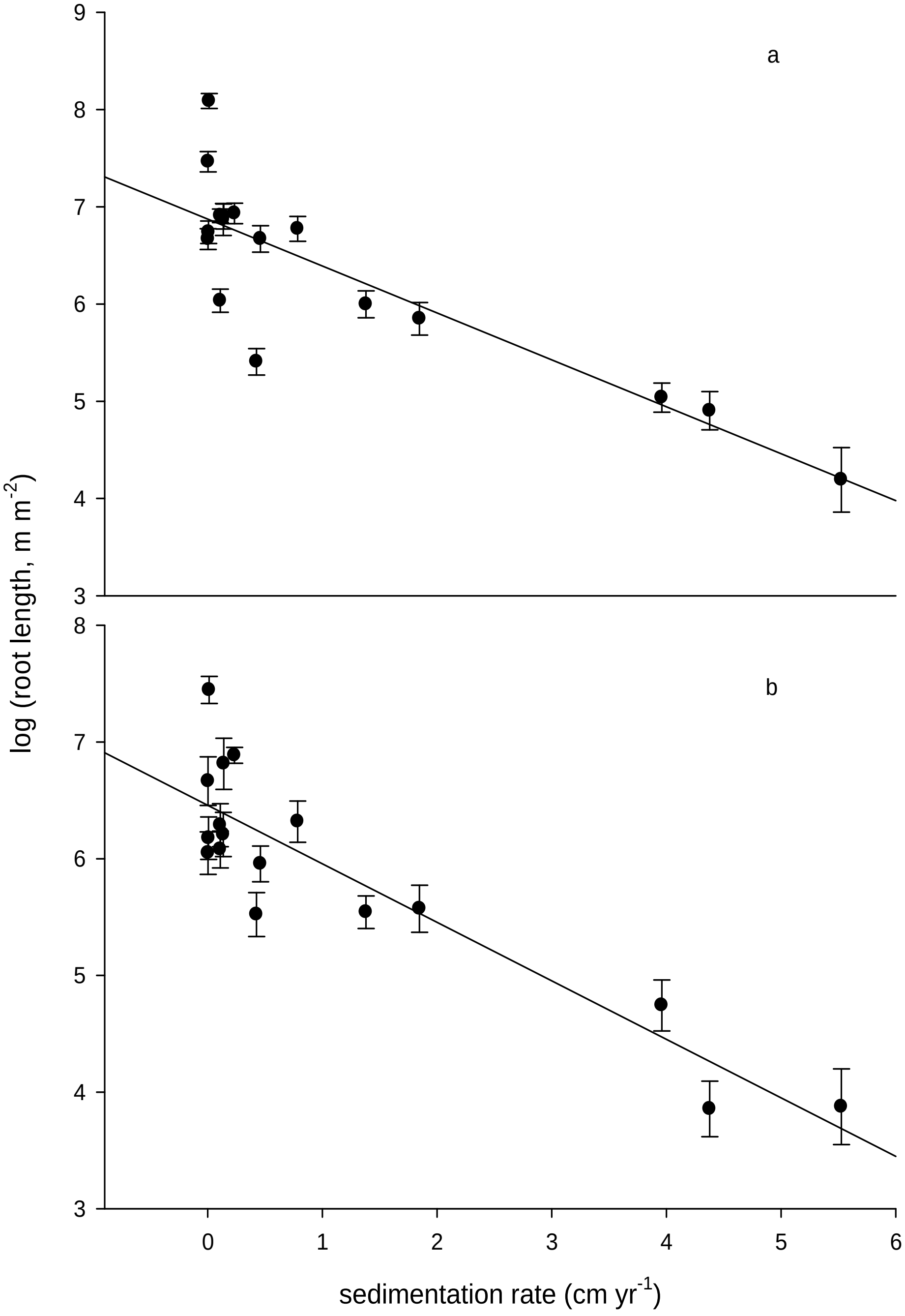

Figure 18. Regression relationship between a) live root length and b) dead root length and current sedimentation rate in very fine roots (0.1-1.0 mm diameter). Vertical bars indicate standard errors.

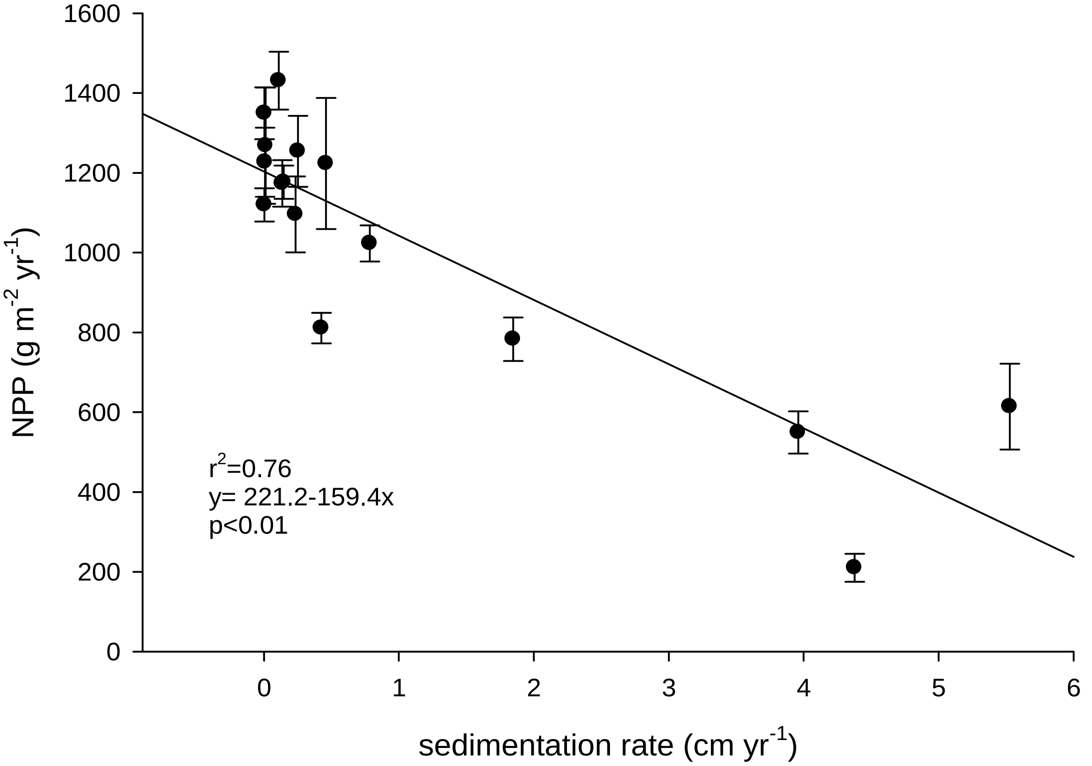

Figure 19. Regression relationship between NPP (2002-2006) and current sedimentation rates. Vertical bars indicate standard errors.

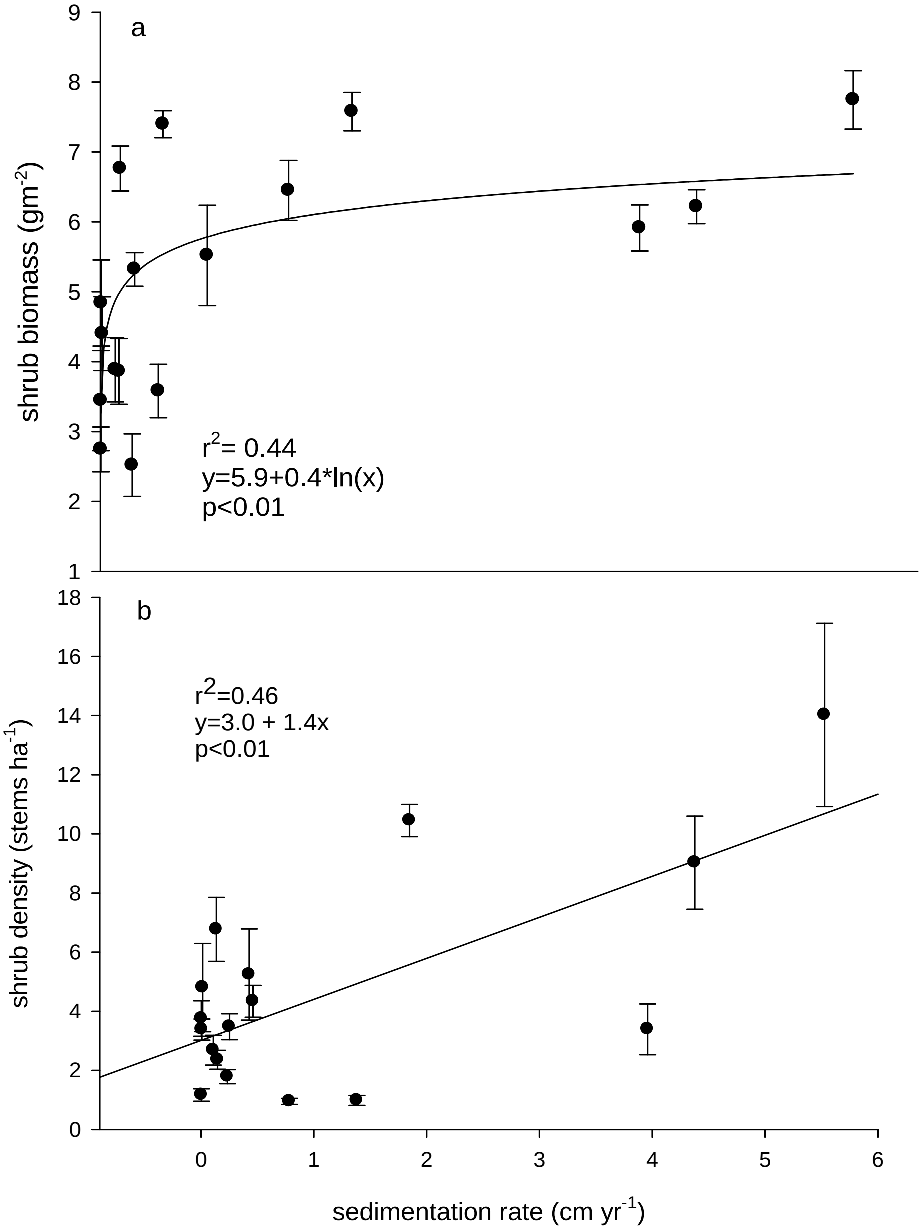

Figure 20. Regression relationship between a) annual shrub biomass and b) stem density (2003-2006) and current sedimentation rates. Vertical bars indicate standard errors.

CHAPTER III

EFFECTS OF SEDIMENT DEPOSITION ON THE BIOGEOCHEMICAL PROCESSES OF RIPARIAN FORESTS

Abstract

The importance of riparian forests in maintaining water quality through the retention of sediments and nutrients is well understood, however, little is known about how sediment deposition affects the integrity of these systems. It has been suggested that sediment deposition in riparian forests may act as either a stress or a subsidy for biogeochemical processes. Impacts of sediment deposition on nutrient dynamics in riparian forests were studied along ephemeral streams at Ft. Benning, GA. Seventeen plots receiving varying rates of sedimentation were evaluated on the basis of decomposition rates, N mineralization, microbial C and N, and foliar and fine root nutrients. Decomposition rates were measured using the litterbag technique; N mineralization rates were determined using the *in situ* method; microbial biomass was measured by chloroform fumigation; plant tissue N and C were measured using a Perkin Elmer Analyzer; and plant tissue P was determined using acid digestion. Soils were analyzed for pH, nutrients, CEC, and bulk density. Soils in plots with the highest sedimentation rates (highly disturbed, HD) were lower in soil nutrients, cation exchange capacity (CEC), temperature, and moisture, and higher in bulk density, percent sand, and pH. HD plots also had lower decomposition rates, net N mineralization rates, microbial

C and N, and had higher NUE, PUE, and nutrient resorption proficiency and efficiency. Declines in biogeochemical processes and nutrient circulation corresponded to current sedimentation rates between 0.1-0.4 cm yr^{-1}. The results of this study imply that even low levels of sediment deposition in sediment-stressed riparian forests may cause a decline in soil quality and significantly impact biogeochemical processes in these forests. Because rates of sedimentation similar to those found in this study are commonly found in riparian forests associated with upland erosion, it is critical to protect these important systems from upland erosion.

Key words: riparian forest, sedimentation, biogeochemistry, nitrogen mineralization, decomposition, microbial biomass, forest floor, nutrient use efficiency, nutrient resorption

Introduction

One essential function of riparian forest systems is that of water filtration through sediment and nutrient retention. Riparian vegetation modifies sediment transport by entrapping materials or by changing hydraulics of the channel due to surface roughness. Nutrients are transformed through vegetation uptake and microbial activities or are retained in sediments (Naiman and Decamps, 1997). Because riparian systems play a critical role in maintaining water quality, understanding how anthropogenic disturbances may limit this function is vital to protecting this ecosystem service.

It has been well established that N and P inputs from agriculture and urban runoff are trapped in riparian forests, substantially reducing nutrient inputs to aquatic ecosystems. Treated wastewater effluent flowing through a Louisiana tidal wetland showed a 79% reduction in total N and 88% reduction in total P (Day et al., 2006), where a constructed riparian wetland in Norway retained an average of 21-44% of P (Braskerud, 2002a) and 3-15% of N (Braskerud, 2002b) inputs. Barfield et al. (1998) found that riparian filter strips removed over 90% of the sediment and chemicals in an experimental karst watershed, and Peterjohn and Correll (1984) found N and P retention of riparian forests to be 89% and 80%, respectively. They also estimated the removal of particulates in riparian forests at 11 kg ha^{-1} organic N, 0.83 kg ha^{-1} dissolved ammonium-N, 2.7 kg ha^{-1} of nitrate-N, and 3.0 kg ha^{-1} total particulate P (Peterjohn and Correll, 1984). Kleiss (1996) found that a bottomland hardwood forest along the Cache River in eastern Kansas (an area that represents only 3% of the watershed) was able to trap approximately 14% of the sediment that entered the river. Lowrance et al. (1984) showed that inorganic N was converted to organic N in subsurface flows from crop fields to forest riparian zones.

There is little known about the effect of sediment deposition on riparian forests, and specifically, how it may impact the nutrient filter function (Cavalcanti, 2004; Koning, 2004; Lockaby et al., 2005). Imported sediments often carry adsorbed nutrients (Olde Venterink et al., 2006; Zhang and Mitsch, 2007), which could act as either a stress or subsidy for forest ecosystems (Naiman and Decamps, 1997; Hupp, 2000; Baker et al., 2001b). Many studies have suggested that nutrients associated with imported sediments may increase soil fertility and thus subsidize forest productivity (Odum, 1979; Brown, 1981; Megonigal et al., 1997; Hesse et al., 1998; Day et al., 2006; Effler et al., 2006). Bottomland hardwood forests may benefit from increased nutrient import associated with low levels of sedimentation in systems that are often deficient in both N and P (Vitousek and Howarth, 1991; Lockaby and Conner, 1999). However, the stress caused by sedimentation may impede plant uptake of increased nutrients. In a precursor to the present study, Lockaby et al. (2005) and Cavalcanti and Lockaby (2005; 2006) found decreased production, decomposition, N mineralization, and microbial C and N with a 25-year sedimentation rate as low as 0.2-0.3 cm yr^{-1}. The present study focused on the influence of sediment deposition from upland erosion on nutrient circulation in bottomland riparian forests. Key functions studied include litter decomposition, net N mineralization and immobilization in microbial biomass, nutrient resorption, and nutrient use efficiency.

Decomposition

A major indicator of forest health and productivity is foliar decomposition and nutrient cycling. Decomposition represents a significant flux in nutrient cycling in a forest system because it determines carbon and nutrient availability for plant uptake (Swift et al., 1979). In systems where decomposition is limited, nutrients and organic matter are tied up in the forest floor and productivity may be decreased (Swift et al., 1979; Hobbie, 1992; Xiong and Nilsson, 1997). Therefore, decomposition rates can serve as indicators of overall ecosystem function. For example, conifer leaves show less nutrient leaching and slower breakdown than deciduous leaves, young leaves decay faster than old leaves, and nutrients leach faster from senesced leaves than from green leaves (Lockaby et al., 1996; Xiong and Nilsson, 1997; Baker et al., 2001b).

In general, litter quality is the most significant factor in decomposition. Leaf litter tends to decompose faster in species occupying nutrient-rich sites than in species growing on nutrient-poor sites (Hobbie, 1992; Berendse, 1994). Therefore, changes in plant nutrient uptake or species composition may affect decomposition rates (Berendse, 1994). The ratio of N to P is a valuable indicator of litter quality. Optimum N:P ratios are approximately 10:1 for decomposer organisms; beyond 10, the detritus may be less palatable to decomposers (Lockaby and Conner, 1999). Nitrogen also seems to play a critical role in initial decay rates, while high lignin ratios will slow decay in later stages (Swift et al., 1979; Salamanca et al., 1998). In general, the narrower the ratios of C:N, C:P, N:P, and lignin:N, the better the litter quality and the faster the decomposition rate (Gower and Son, 1992; Baker et al., 2001b; Chimney and Pietro, 2006).

Abiotic factors such as soil moisture, pH, temperature, nutrient regimes, and aeration also play a major role in decomposition rates (Swift et al., 1979; Vargo et al., 1998). These factors not only determine how quickly nutrients can leach from a system, but also the species diversity of detritivores in the soil (Zimmer, 2002). Soil moisture is key to the growth and survival of all soil fauna (Swift et al., 1979). Flooding can either stimulate or inhibit decay rates of litter, depending on the length of inundation. Decomposition proceeds more quickly in areas receiving brief pulses of flooding rather than prolonged flooding (Lockaby et al., 1996; Baker et al., 2001b) and slows where waterlogged, anaerobic conditions exist (Brinson et al., 1981a). Temperature is also critical to decomposition rates. Although decomposing organisms have adapted to nearly all temperature zones, warmer and wetter climates favor a greater abundance of soil organisms (Swift et al., 1979). Soil aeration also accelerates decomposition by promoting the abundance of soil organisms. More detritivores have been found in aerobic than in anaerobic soils (Swift et al., 1979).

Because decomposition rates are so dependent on soil factors, including aeration, sediment deposition could severely alter litter decay rates. In a study of several riparian forest systems, Baker et al. (2001b) found the lowest decomposition rates in the Cache River, Arkansas, which Hupp (2000) found to have elevated sedimentation rates. Sedimentation and burial compacts detritus, reduces gas exchange, suppresses organismal activity, and may transport surface-bound chemicals (Vargo et al., 1998). Therefore, sedimentation can alter decomposition patterns through changes in temperature, soil moisture, aeration, and nutrient fluxes. Because long-duration flooding has been found to inhibit decomposition (Baker et al., 2001b), it is generally hypothesized that sediment burial reduces aeration in a similar manner. Increased sedimentation may also affect decomposition rates by altering the micro- and macro-fauna responsible for decomposition (Reice, 1974).

Although riparian forests of headwater streams receive some of the highest sedimentation rates (Wardrop and Brooks, 1998), very little is known about how decomposition and nutrient cycling are affected. During part 1 of the present study, Lockaby et al. (2005) found a significant negative correlation between decomposition rates and long-term sedimentation rates in riparian forests associated with ephemeral and headwater streams. They found a significant decline in decomposition rates with historic sedimentation rates (estimated over a 25-year period) as low as 0.2-0.3 cm yr^{-1}. So far, this has been the only study comparing decomposition rates in headwater streams receiving varying rates of sedimentation.

Nitrogen Mineralization and Microbial Biomass

In most forest systems, N is the primary limiting nutrient (Vitousek, 1982; 1984), essential in both foliar and biomass production. Plant-available N is largely dependent on the rate of net N mineralization. Reich et al. (1997b) found a strong correlation between forest productivity (NPP) and net N mineralization rates. Berendse (1994) found a similar correlation in the heathlands of Northern Europe, relating the increase in N mineralization rates during 50 years of succession to increased production. Rates of net N mineralization are controlled largely by the amount of labile organic C available as an energy source to soil microbes. In C-rich soils, all available mineralized N will be used by microbe populations, resulting in net N-immobilization (Badalucco and Kuikman, 2001; Gurlevik et al., 2004).

Microbial biomass is affected by changing substrate quality and environmental conditions, making it useful as a sensitive indicator of changes in substrate quality and quantity (Li et al., 2004). Vegetation community composition and structure can influence microbial biomass, since plants often compete with microbes for limited available N (Zak et al., 1994; Badalucco and Kuikman, 2001). Microbial activity is generally greater in association with high-quality vegetation, due to the higher content of water-soluble sugars and organic and amino acids in higher-quality litter (Brimecombe et al., 2001; Uren, 2001; Li et al., 2004). The use of herbicides to control vegetation growth has been found to result in lower microbial C and lower C:N ratios (Li et al., 2004).

Nutrient Cycling

The addition of nutrient-bound sediments may affect how nutrients are circulated in a forest system. In forests, major nutrient pools include plant biomass, forest floor litter, belowground litter, soil microbial biomass, and available inorganic N. These pools are controlled by plant productivity, litter production, litter decomposition, N mineralization, microbial immobilization, leaching, denitrification, N_2-fixation, and plant uptake (Idol et al., 2003). In general, forests are primarily limited by N and P (Vitousek and Howarth, 1991; Fisher and Binkley, 2000). The patterns through which these nutrients are circulated in a forest system may offer clues concerning nutrient limitations.

Internal nutrient recycling is often measured as nutrient resorption efficiency (defined as the ratio of nutrients in green versus senesced leaves) (Aerts, 1996; Killingbeck, 1996). The greater proportion of a nutrient that a plant is able to resorb prior to leaf abscission, the greater the supply of nutrients available for immediate use, and the less dependent the plant is on nutrient uptake from the soil. Although it seems advantageous that plants growing on nutrient-poor sites would have higher resorption efficiencies, no consistent trend has been found in the literature (Aerts, 1996; Reich et al., 1997a; Kobe et al., 2005). In contrast, it has been suggested that plants growing under luxuriant N regimes accumulate more “mobile” forms of nutrients, which are more easily recycled, whereas plants in nutrient-stressed environments have a larger proportion of nutrients in structural, insoluble form (Fisher and Binkley, 2000). Aerts (1996) found that deciduous species had higher resorption efficiencies than evergreen species. He suggests that species adapted to nutrient-poor sites may conserve nutrients through longer leaf retention (i.e., evergreen species) more so than through internal recycling mechanisms. Reich et al. (1997a) also found a negative correlation of resorption with leaf life span (i.e., deciduous vs. evergreen). However, within species, there has been no consistent trend of increasing resorption efficiency with decreasing fertility (Kobe et al., 2005).

Several authors have suggested that resorption efficiency measurements may be an inadequate index. Reich et al. (1997a) poses that ratios could be driven by either numerator or denominator, resulting in very different species having similar efficiencies. Killingbeck (1996) suggests that resorption proficiency (concentration of nutrients in senesced leaves) may be a better indication of internal recycling than resorption efficiency because it reflects the biochemical limits of nutrient resorption, which is not subject to temporal variations in nutrient concentrations and timing of sample collections.

Foliar nutrient concentrations can greatly affect productivity. Reich et al. (1997a) found positive correlations between maximum photosynthesis rate, respiration rate, specific leaf area, and foliar N concentration. The efficiency of forest systems can also be evaluated by measuring nutrient-use efficiency, specifically, N-use efficiency (NUE) and P-use efficiency (PUE). This is determined by measuring the amount of carbon (C) fixed per unit of nutrient uptake (Vitousek et al., 1982; 1984). Schilling and Lockaby (2006) found that NUE and N:P ratios were good indicators of N limitations in forest productivity in red-water and black-water systems. They found that the nutrient-use efficiecy of base cations was greater in a more nutrient-deficient blackwater system. However, no studies have compared how nutrient-use efficiency or nutrient resorption is affected by increased sedimentation.

Study Objectives

In this study, we measured how differing rates of sedimentation affected the biogeochemistry of riparian forests associated with headwater ephemeral streams. The specific objectives of this study were to compare decomposition rates, net N mineralization rates, microbial biomass, plant nutrients, internal nutrient recycling, and nutrient-use efficiency along a gradient of sedimentation rates. We hypothesized that low levels of sediment deposition may increase soil fertility through the import of nutrient-bound sediments, which would be reflected in faster decomposition rates, greater N mineralization rates, greater microbial biomass, greater concentration of plant nutrients, and less efficient internal recycling and nutrient-use efficiencies. However, high levels of sediment deposition may alter biogeochemical functions by creating anoxic soil conditions. This stress may be reflected in slower decomposition rates, low N mineralization rates, less microbial biomass, lower concentrations of plant nutrients, and more efficient internal recycling and nutrient-use efficiencies.

Study Site

This study was conducted at Fort Benning Military Installation, near Columbus GA, a U.S. Army installation that occupies 73,503 ha in Chattahoochee, Muscogee, and Marion counties of Georgia and Russell county of Alabama (Fig. 1). Fort Benning lies within the lower Piedmont and the upper Coastal Plain physiographic regions, but only areas within the Coastal Plain were used in this study. All study areas chosen were associated with ephemeral riparian streams. The study areas are composed primarily of uneven-aged deciduous or mixed hardwood/pine forests. Common species in the hardwood bottoms are red maple (*Acer rubrum* L.), hazel alder (*Alnus serrulata* (Ait.) Willd.), flowering dogwood (*Cornus florida* L.), titi (*Cyrilla racemiflora* L.), sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.), sweetbay (*Magnolia virginiana* L.), wax myrtle (*Morella cerifera* (L.) Small), blackgum (*Nyssa sylvatica* Marsh.), and water oak (*Quercus nigra* L.). Upland forests are dominated by long-leaf pine (*Pinus palustris* P. Mill.), loblolly pine (*Pinus taeda* L.), and various oak species (*Quercus incana* Bartr., *Q. marilandica* (L.) Muenchh, *Q. phellos* L., *Q. laevis* Walt., *Q. falcata* Michx.). Uplands are primarily managed as long-leaf pine ecosystems with periodic prescribed burns every 1-3 years.

Riparian soils included the Bibb (coarse-loamy, siliceous, active, acid, thermic Typic Fluvaquents) and Chastain (fine, mixed, semiactive, acid, thermic Fluvaquentic Endoaquepts) series. Upland soils included the Troup (loamy, kaolinitic, thermic Grossarenic Kandiudults), Lakeland (thermic coated Typic Quartzipsamments), and Cowart (fine-loamy, kaolinitic, thermic Typic Kanhapludults) series (Soil Survey Staff, 2004). Annual mean precipitation is approximately 123 cm yr^{-1}, with driest months in October and November, and wettest months in March and July. Mean annual temperature is 24.3° C, with lowest temperatures observed in January and highest temperatures in July (cdo.ncdc.noaa.gov/ dlyp/DLYP). During the period of this study (2001-2006), 2001 and 2006 had below average annual precipitation and 2003 and 2005 had above average precipitation (ncdc.noaa.gov/IPS/LCDPubs).

Ft. Benning Military Installation was first designated in 1918, with significant land acquisitions in the 1940s. Prior to becoming a military base, the land was predominantly in row-crop agriculture. Poor soil conservation practices led to excessive erosion, which is still evidenced by landscape scars and gullies. Current erosion is primarily due to military traffic on unpaved forest roads and trails. This sediment is carried into bottomland riparian forests, where it is deposited as channels widen. Evidence of active sedimentation included alluvial fans and partially buried tree stems.

Methods

Eighteen circular plots (0.04 ha) were established in riparian forests along nine ephemeral streams in March 2002. Study areas were chosen to span a range of sediment deposition, from no sedimentation to high sedimentation. In April 2004, in an effort to get a better representation of the range of sediment deposition, five plots were dropped from the study and four new plots were added, yielding a total of seventeen plots along twelve ephemeral streams.

Rates of Deposition

Historical deposition rates were measured using a modification of the dendrogeomorphic method described by Hupp and Morris (1990). In July 2003, three to four saplings (8 to 10 cm in diameter) showing signs of burial were excavated to the depth of the root collar of the tree in each plot. Cross sections of the root collar and at the soil surface were used to determine the age of the tree and its age at burial. A sedimentation rate was determined by dividing the sediment depth by years of deposition. This was repeated in March 2004 for the new plots added to the study. Current sedimentation rates were obtained using a modification of the sediment disks described by Kleiss (1993). Metal washers were welded to the center of 1.22 m rebar segments, which were inserted into the soil so that the washer was flush with the surface of the soil. As sediment was deposited, monthly measurements were taken by inserting a small rod into the soil until it contacted the washer. Plots were assigned to disturbance categories based on current sedimentation rates: highly disturbed (HD, ≥ 1.0 cm yr^{-1}), moderately disturbed (MD, 0.1 - 1.0 cm yr^{-1}), and reference plots (RF, ≤ 0.1 cm yr^{-1}).

Temperature and Precipitation

Air and soil temperatures were measured using Hobo temperature/light dataloggers (Onset Computer Corporation, Bourne, MA). Two dataloggers were placed arbitrarily within each plot and housed in a plastic waterproof container approximately 1.5 m off the ground. Each datalogger also had a cable with a soil temperature sensor, which was buried approximately 15 cm below the soil surface. Data were downloaded every 2-3 months using a Hobo shuttle (Onset Computer Corporation, Bourne, MA).

Precipitation and temperatures data were downloaded from the Columbus, GA airport weather station (ncdc.noaa.gov/IPS/LCDPubs).

Decomposition

Two consecutive decomposition studies were conducted. Study 1 ran from April 2002 to March 2003, and study 2 ran from April 2004 to July 2005. Decomposition rates were compared for 11 plots using the litterbag technique described by Swift et al. (1979). Foliar litterfall was collected in the fall of 2001 and the fall of 2003 using tarps suspended approximately 1 m from the ground on each plot. Leaves were then air-dried, sorted by species, and weighed to determine species composition of each plot. Twenty 20 cm by 20 cm litterbags per plot were filled with 10 grams of the plot-specific species composition and placed on the forest floor at each plot. The litterbags were made from mesh nylon, with a finer mesh (1-mm openings) on the bottom to keep plant materials in, and a larger mesh (6-mm openings) on top to allow entry by macroarthropods. During study 1, litterbags were collected at weeks 0 (for handling loss estimates and initial C, P, and N content), 2, 4, 10, 16, 25, 36, and 48. During study 2, bags were collected at weeks 0, 1, 2, 4, 11, 16, 24, 36, 48, and 64. When collected, bags were carefully placed into re-sealable plastic bags and transported back to the laboratory on ice. Litterbags were kept in a cooler until processing (1-2 days). Any soil, moss, or roots were carefully removed and the contents of the bags were oven-dried at 70° C for 48 hours. N and P concentrations were analyzed from the litter in each collection. The annual decomposition rate, k, was derived from the exponential decay formula, $-k=\ln(X/X_0)/t$ (X=final dry wt, X_0=initial dry weight) (Swift et al., 1979). Net immobilization and mineralization for N and P was calculated by plotting the percent of original N and P remaining at each collection time. Net immobilization was estimated by calculating the graph area where nutrient concentrations exceeded original concentrations (area of the graph above 100%). Net mineralization was estimated by calculating the graph area where nutrient concentrations declined below initial concentrations (area of graph below 100%). This allowed for relative comparisions of net immobilization and mineralization among plots.

Forest Floor Litter

Forest floor litter samples were collected in August 2006 and February 2007. Four 0.1-m^2 samples of forest floor litter (all organic materials to the mineral soil surface) were collected from all plots to estimate total annual maximum and minimum forest floor prior to and post leaf senescence. Samples were oven-dried at 70° C for 72 hours and weighed. Differences in mass of forest floor litter between the two sampling periods were used as a crude second estimate of annual forest floor turnover rates.

Nitrogen Mineralization and Microbial Biomass

Nitrogen mineralization was estimated using the *in situ* method (Hart et al., 1994). Samples were collected at approximately 3-month intervals between July 2003 and October 2006 for original plots and on the same schedule beginning August 2004 for new plots. Two randomly placed soil cores were taken at a depth of approximately 7.5 cm within the same quadrant of each plot (an area approximately 0.01 ha). The soil from each core was divided between two polyethylene bags (about 150 mL of soil in each bag), one of which was reburied to a depth of about 7.5 cm and incubated for approximately 30 days. Pre-incubation and post-incubation samples were put on ice and

Microbial biomass was estimated using the chloroform-fumigation technique (Vance et al., 1987). Soil sub-samples were taken from the non-incubated samples collected for N-mineralization. For fumigated samples, 18.5 g of moist soil was exposed to chloroform ($CHCl_3$) for 24 hours and then extracted with 125 mL of 0.5 *M* potassium sulfate (K_2SO_4). Non-fumigated samples were extracted within 2 days of collection in the same manner. The soil-K_2SO_4 suspension was shaken for 1 hour and then filtered and frozen for at least 48 hours until ready for analysis. Organic C and N extracts were analyzed using a Shimadzu TOC-V and total N combustion analyzer (Shimadzu Scientific Instruments, Columbia, MD) and Apollo 9000 combustion TOC analyzer with TN module (Teledyne Tekmar Instruments, Mason, OH). Microbial C and N were calculated as the differences between fumigated and unfumigated samples.

Plant and Soil Nutrient Analyses

Plant tissues from litterfall (see Chapter 2), forest floor, and decomposition samples were analyzed to find C, N, and P concentrations. Fine roots were analyzed only

Resorption efficiency was estimated by comparing nutrient content of green leaves with that of senesced leaves from each plot. Green leaves were collected from mid-canopy of the 3-4 most common trees in each plot in July 2006. Senesced leaves were collected from litterfall traps in November and December 2006. Leaf area and green weights were measured, then leaves were oven-dried (70° C for 72 hours) and re-weighed. Oven-dried leaves were ground and analyzed for C, N, and P. Resorption efficiency was determined by comparing the nutrient content in green leaves with that of abscised leaves and determining the percentage of each nutrient that was reabsorbed prior to leaf senescence. Resorption proficiency was determined as the concentration of N and P in abscised leaves.

Soil samples were collected in May 2003 and again in March 2006 and sent to the Auburn University Soil Testing Laboratory. Soils were analyzed for pH, CEC, P, K, Mg, Ca, Al, B, Cu, Fe, Mn, Na, and Zn. Analysis of K, Ca and Mg were performed using an atomic absorption (AA) spectrophotometer, while cations and P samples were determined by inductively coupled argon plasma spectrophotometry (ICAP). Bulk density was measured in September 2004 using a 5-cm diameter double-cylinder push probe. Three samples were taken from each plot (0-7.5cm depth), dried to a constant mass at 105° C

Statistical Analyses

Statistical analyses were done using SAS software version 9.1 (SAS Institute, Cary, NC). Linear relationships between variables were determined using regression analysis (PROC REG, SAS Institute 2002-2003). Decomposition rates were determined using nonlinear regression analysis (PROC NLIN, SAS Institute 2002-2003) on natural-log transformed data. Analysis of variance (ANOVA) (PROC GLM, SAS Institute 2002-2003) was performed to find differences in means among disturbance classes. Following significant ANOVA results, Tukey's HSD test was performed. Differences between means were considered statistically significant at $\alpha=0.05$. Data were log-transformed when necessary to meet the assumptions of normality.

Results and Discussion

Sedimentation Rates

Mean current sedimentation rates were 0.05 ± 0.04, 0.38 ± 0.11, and 2.89 ± 0.39 cm yr^{-1} on reference (RF), moderately disturbed (MD), and highly disturbed (HD) plots, respectively. Historical sedimentation rates ranged from 0 to 4 cm yr^{-1} over a 25-year period (Table 1). Current sedimentation rates ranged from <0.01 to 5.53 cm yr^{-1} (Table 1). Historical rates were only weakly correlated to current rates ($r^2=0.22$, $p=0.05$). Comparisons among disturbance classes showed that current sedimentation rates in HD plots (2.89 ± 0.39 cm yr^{-1}) were significantly greater ($F_{df2, 76}$=50.88, p<0.01) than MD (0.38 ± 0.11 cm yr^{-1}) and RF (0.08 ± 0.04cm yr^{-1}) plots.

Temperature and Precipitation Patterns

Differences in abiotic factors among disturbance classes, such as temperature and soil texture, may have been driving factors in observed differences in biogeochemical processes such as decomposition, nutrient cycling, and N mineralization. From 2002-2006, annual precipitation varied from 24.7 cm below the 30-year average in 2006 to 21.8 cm above the 30-year average in 2005. During the study period, winter months had lower than average precipitation and summer months had above average precipitation. The Palmer drought index indicated drought conditions during the fall and winter of 2002-03, and a more extensive drought during the spring-summer of 2006 (Fig. 2).

Mean air temperatures were compared among disturbance classes. No clear relationship existed between air temperatures and current sedimentation rates, though RF plots had significantly ($F_{df2, 391,528}$=50.8, p<0.01) higher daytime temperatures (21.6 ± 0.2 °C) than HD and MD plots (20.0 ± < 0.1 and 19.8 ± 0.1 °C, respectively) (Fig. 3). Nighttime temperatures (2300 hours) showed the reverse pattern, with MD plots significantly warmer ($F_{df2, 394,125}$=134, p<0.01) than HD and RF plots (14.5 ± 0.1, 12.9 ± <0.1, and 11.5 ± 0.2 °C, respectively). The mean range in air temperatures between 1100 and 2300 hours differed significantly ($F_{df2, 398,152}$=234, p<0.01) among disturbance classes. RF plots had the greatest mean range in daily temperatures (10.4 ± 0.02 °C), followed by HD (7.5 ± 0.01 °C), and MD plots (5.4 ± 0.01 °C). The dense mid- and understory of MD plots may have helped to moderate daily air temperature fluctuations in the understory canopy.

Soil temperatures differed significantly among disturbance classes ($F_{df2,\ 388,125}$ =381.2, p<0.01). Mean annual soil temperatures were highest in RF plots (17.4 ± 0.01 °C), followed by MD (17.2 ± 0.01 °C) and HD (16.6 ± 0.01 °C) plots. There was a significant interaction ($F_{df10,\ 280,951}$=990, p<0.01) between seasons and disturbance class. In spring and summer, soil temperatures were cooler in RF plots, whereas soil temperatures were warmest in RF plots during fall and winter. There was a significant negative relationship (r^2=0.41, p<0.01) between soil temperatures and sedimentation rates (Fig. 4).

Soil temperature was likely influenced by a combination of light penetration and forest floor insulation. In RF plots, soil temperatures were significantly warmer than MD and HD plots during months of leaf senescence. During the growing season, when there was less light penetration, soil temperatures of RF plots were significantly cooler than MD and HD plots. However, the opposite pattern was observed in HD plots, which received light levels similar to MD and RF plots, but had the coolest soil temperatures during months of leaf senescence. Differences in seasonal soil temperatures between RF and HD plots may be due to differences in forest floor biomass. HD plots had less forest floor biomass to moderate seasonal soil temperatures (Table 2). Differences in soil temperature may also be attributed to soil color. In an experimental wetland study, Koning (2004) hypothesized that air temperature may be increased by increased albedo from sediments. In the present study, plots receiving high sedimentation had very light-colored soils and cooler air temperatures, whereas reference plots had much darker soils and higher daytime air temperatures.

Soil Texture and Chemistry

In the present study, soil texture was strongly correlated to current sedimentation rates due to the sandy nature of depositional materials. Disturbance classes differed significantly in soil texture (Table 3). The percentage of sand increased with increasing sedimentation, while the percentage of silt and clay decreased (Fig. 5). Soil texture showed an abrupt change at sedimentation rates between 0.1-0.4 cm yr^{-1}, which corresponded to similar changes in soil pH, soil moisture, bulk density, CEC, and soil macronutrients.

Soil texture is often a driving force in biogeochemical processes in forests due to its influence on water-holding capacity, aeration, and organic matter retention. It has also been suggested that the textural composition of sediment may influence N supplies in soils (Pinay et al., 1995). Sandy soils generally exhibit higher moisture stress, higher bulk densities, and fewer available nutrients (Fisher and Binkley, 2000). In this study, soil moisture also differed significantly ($F_{df2, 519}$=21.7, $p<0.001$), with RF plots having significantly higher % moisture than MD and HD plots (Table 3).

Soils of all plots were acidic, with pH ranging between 4.2 and 5.9 (Table 1). There was a significant, positive, non-linear relationship between soil pH and current sedimentation rates (r^2=0.53, $p<0.01$). Among disturbance classes, pH in RF plots was significantly less ($F_{df2, 14}$=3.9, p=0.04) than HD plots (4.48 ± 0.09 versus 5.22 ± 0.31), likely due to the proportional decrease in clay in RF soils (Fig 5). The decline in clay content was also likely responsible for lower CEC and clay-associated nutrients such as K, Al, and Mg (Table 1) (Fisher and Binkley, 2000). There was a significant, negative, non-linear relationship between soil cation exchange capacity (CEC) and current sedimentation rates (r^2=0.27, p<0.01). CEC in RF plots was significantly higher than in HD plots ($F_{df2, 14}$=3.54, p=0.05), with RF plots averaging 4.64 (± 0.82) meq $100g^{-1}$ and HD plots averaging 1.90 (± 0.94) meq $100g^{-1}$. There was a marked decline in K (r^2=0.0.21, p=0.07) and Mg (r^2=0.20, p=0.08) with sedimentation rates between 0.1-0.4 cm yr^{-1} (Fig. 6).

There was a significant, positive, non-linear relationship between soil bulk density (sampled at a depth of 0-7.5 cm) and current sedimentation rates (p<0.01, r^2=0.37) (Fig. 7), with a marked increase in bulk density corresponding to a current sedimentation rate near 0.5 cm yr^{-1}. Bulk density among disturbance classes differed significantly ($F_{df2, 48}$= 21.9, p<0.01), with averages of 1.05 (± 0.10), 1.46 (± 0.06), and 1.74 (± 0.03) Mg m^{-3} in RF, MD, and HD plots, respectively. Greater bulk density has been shown to decrease activities in roots, aerobic microbes, and to reduce water infiltration rates (Fisher and Binkley, 2000).

Decomposition

Over the 5-year study period, two consecutive decomposition studies were monitored over a period of 48 and 64 weeks, respectively. Results from both decomposition studies indicated a decline in nutrient turnover from litter decomposition with increased sedimentation.

Study 1 began in April 2002 (Lockaby et al., 2005) and study 2 in April 2004. Study 1 showed a significant negative, non-linear relationship (r^2=0.62, p=0.04) between decomposition rates (*k*) and historic sedimentation rates (averaged over a 25-year period). A rapid decline in decomposition rates was correlated with historic sedimentation rates between 0.2 and 0.3 cm yr^{-1}. In study 2, however, there was no significant relationship between *k* and sedimentation rates (r^2=0.01, p=0.62) and no significant difference in decomposition rates among disturbance classes ($F_{df2, 9}$=0.25, p=0.48). There was a strong positive relationship between current sedimentation rates and percent mass and nutrients remaining after 64 weeks (Fig. 8) however, which was not observed in study 1.

Our results indicated distinct differences in decomposition patterns between study 1 and study 2, which may be a result of differences in both litter quality and precipitation during each study period. A comparison of C:N ratios in the litter between the two studies indicated significant ($F_{df1, 16}$=10.6, p<0.01) differences in litter quality. Litter C:N ratios in study 1 were greater (mean of 71.6 ± 5.2), indicating lower litter quality, compared with study 2 (mean C:N ratio of 53.1 ± 2.4). This was likely due to precipitation differences between the years in which the litterfall was produced for each study. Annual precipitation in 2001 was 97.6 cm, which was 25.8 cm below the 30-year average, whereas annual precipitation in 2003 was 144.9 cm, 21.8 cm above the 30-year average. Differences between these two studies suggest that precipitation may a strong driver of litter quality, as measured by C:N ratios. Precipitation during each study period also varied, with study 1 (2001-2001) spanning a period of drought and study 2 (2004-2005) spanning a period of above-average precipitation (Fig. 2).

Decomposition rates from study 1 had a significant negative relationship with litter C:N (r^2=0.34, p<0.01), which has also been found in other studies (Conn and Dighton, 2000; Chimney and Pietro, 2006). However, there was no significant relationship between litter quality and decomposition rates during study 2. The effects of sedimentation on decomposition rates may not have been evident during study 2 due to high litter quality and ample precipitation, which may have masked any effects of sedimentation. It appears, however, that low litter quality and drought conditions during study 1 were further exacerbated by the stress of sedimentation. Percent nutrients remaining at the end of study 1 also indicated that both N and P were being immobilized, suggesting N and P limitations even in RF plots (Fisher and Binkley, 2000).

Although *k*-rates in study 2 did not exhibit effects of sedimentation rates, mass and nutrients remaining at the end of the study showed strong, positive, linear relationships with sedimentation rates (Fig. 8). The decline in nutrient release during decomposition will result in a decline of available nutrients for plant growth. A decline in mass loss and nutrient release was also found in early-successional forests compared with primary forests in Mexico (Cárdenas and Campo, 2007).

Several studies have focused on changes in decomposition as a function of litter burial. Conn and Dighton (2000) found that buried litter showed increased decomposition (compared with surface litter) through increased fungal colonization in the New Jersey Pinelands. Wang et al. (1994) found that decomposition rates of cattails in wetlands had lower initial mass loss in buried litter (compared to surface litter), but after 9 months, there was no significant difference between treatments. However, Vargo et al. (1998) found that a one-time application of 0.2 cm of coarse sediment was enough to inhibit the decay of emergent wetland species by 10% and multiple sediment applications showed significantly less decomposition. Litterfall buried under sediment also showed significantly lower N concentration.

Mineralization/immobilization Patterns

A comparison of N and P immobilization and mineralization patterns during study 2 indicated no significant relationships between the net immobilization of N or P

(r^2=0.003, p=0.87) or P mineralization (r^2=0.34, p=0.08) of nutrients in decomposition litterbags and sedimentation rates. There was a significant negative, linear relationship (r^2=0.58, p=0.01) however, between N mineralization within decomposition litterbags and sedimentation rates. There were no significant differences among disturbance classes in net immobilization (N: $F_{df2,7}$=0.05, p=0.95; P: $F_{df2,7}$=0.91, p=0.45) or mineralization (N: $F_{df2,7}$=0.8, p=0.49; P: $F_{df2,7}$=0.43, p=0.66) patterns of nutrients. Numerically, RF plots had the lowest net P immobilization and MD plots had the highest net P mineralization (Fig. 9). The ratios of P mineralization to immobilization and N mineralization to immobilization were not significantly different among disturbance classes (p: $F_{df2,7}$=0.68, p=0.54; N: $F_{df2,7}$=1.55, p=0.28).

Forest Floor

Forest floor litter was compared between its maximum (late winter) and minimum (late summer) biomass (Table 2). Maximum biomass values were significantly higher in RF plots compared to HD plots. Minimum values did not differ by disturbance classes, suggesting that forest floor turnover in RF plots was greater than that of MD and HD plots. Nitrogen content did not vary by disturbance class; however P content was significantly greater in RF plots compared with HD plots during the late winter collection, but did not differ among disturbance classes in the late summer. The greatest percent change between maximum and minimum forest floor values for biomass and nutrient contents were found in RF plots, though differences were not significant. Although differences in forest floor turnover (percent change between maximum and minimum values) were not significant among disturbance classes, numerical differences indicated that forest floor in RF plots had greater decomposition and nutrient release than

MD or HD plots (Table 2). A comparison of nutrients indicated that both P and C concentrations increased as forest floor decomposition progressed, while N concentration decreased.

Lockaby and Conner (1999) suggested that optimal N:P ratios for forest floor are approximately 10:1 for decomposer organisms. In the present study, mean forest floor N:P ratios were 5.0, 5.5, and 7.0 for RF, MD, and HD plots, respectively. These ratios indicate that all plots may be N-limited. The higher ratios in HD plots may reflect the greater P-limitations associated with lower clay content in those soils (Huffman et al., 1996).

N Mineralization

Net N mineralization rates ranged from 50 to 233 g ha^{-1} day^{-1}, which are within the lower range of rates reported for studies in North Carolina (Wright and Coleman, 2002; Li et al., 2003; Gurlevik et al., 2004). Nitrogen mineralization varied seasonally and by disturbance class. Peaks of N mineralization occurred during summer months for RF and MD plots, and in the spring for HD plots. Temporal variation in N mineralization was also less dynamic in HD plots than in RF and MD plots (Fig. 10a). Net N mineralization in HD plots averaged 88.4 (± 16.7) g ha^{-1} day^{-1}, which was significantly ($F_{df2, 665}$=10.6, $p<0.01$) less than in MD or RF plots (138± 17.6 and 173± 18.9 g ha^{-1} day^{-1}, respectively) (Fig. 10b).

Seasonally, differences among disturbance classes were strongest during the summer and fall. As has been found in other studies, highest rates of net N mineralization occurred during the warmest months (summer, spring > fall > winter) ($F_{df3, 453}$=24.6, $p<0.01$) (Idol et al., 2003; Li et al., 2003; Gurlevik et al., 2004). In the present study, decreased soil temperatures in HD plots may have contributed to the lower rates of net N mineralized (Fisher and Binkley, 2000). Regression analysis indicated a significant, but very weak, negative, non-linear relationship between current sedimentation rates and mean N mineralization rates ($r^2=0.06$, $p<0.01$).

Studies by Vitousek et al. (1982) and Joshi et al. (2006) found that net N mineralization rates were correlated with N in foliar tissues, suggesting that N mineralization may play a role in the uptake of N into plant tissues. In the present study, net mineralized N did not correlate with foliar N concentrations. However, N mineralization rates did show trends similar to those of foliar N content, which reflected greater ANPP in plots receiving less sedimentation (see Chapter 2). Both ANPP and BNPP (see Chapter 2) exhibited significant positive, linear relationships with N mineralization rates ($r^2=0.56$ and 0.60, $p<0.01$, respectively, Fig. 11). Reich and Nadelhoffer (1989) and Newman et al. (2006) also found correlations between ANPP and N mineralization rates. Nadelhoffer et al. (1985) found a positive relationship between BNPP and N mineralization rates, but such a relationship was not evident in the study by Newman et al. (2006).

Net N mineralized is influenced by soil nutrients, root exudates, microorganisms, and physical soil properties such as aeration and compaction. It has been suggested that labile C in roots may be an important determinant of net N mineralization rates through an increase in soil microbial activities (Vitousek et al., 1992; Gurlevik et al., 2004). In the present study, fine root C concentration had a significant, positive relationship with net N mineralization rates ($r^2=0.47$, $p<0.01$, Fig. 12). The reduction in root biomass associated with HD plots would also reduce the root exudates entering the rhizosphere.

It has also been suggested that soil compaction may affect net N mineralized through the reduction of aerobic microbial activities (Kozlowski, 1999; Li et al., 2003; Tan et al., 2005). Although other field studies have not found significant differences in net N mineralization rates with increased soil compaction (soil bulk density above 1.5 Mg m^{-3}) (Li et al., 2003; Tan et al., 2005; Tan and Chang, 2007), results of this study indicated a significant difference ($t=-1.95$, $p=0.05$) in N mineralization rates (117.0 g ha^{-1} day^{-1}) in compacted plots (bulk density above 1.5 Mg m^{-3}) versus less compacted plots (159.0 g ha^{-1} day^{-1}). High bulk densities in the current study were largely due to high proportions of sand rather than mechanical compaction.

Sandy soils also have decreased soil moisture (Bristow et al., 1984; Pinay et al., 1995; Vetterlein et al., 2007), which may affect N mineralization rates (Cassman and Munns, 1980; Pinay et al., 1995). In a comparison of two riparian forests of similar vegetation and habitat, Pinay et al. (1995) found that sandy soils had lower moisture retention, N mineralization potential, nitrate, organic N, and N uptake by plants.

In the present study, soil moisture had a significant positive linear relationship with N mineralization rates ($r^2=0.47$, $p< 0.01$). Similar results were found by Li et al. (2003), who reported that poorly drained soils had higher mineral soil C and N and contributed to higher N mineralization rates. The effect of sedimentation on net N mineralization is likely an indirect effect since N mineralization is primarily determined by the microbial community and the uptake of mineralized N by plant roots, both of which have been shown to decrease with increasing sedimentation.

Microbial Biomass

Microbial N averaged between 5 and 42 µg g^{-1} and microbial C averaged between 30 and 280 µg g^{-1}. These values are lower than those reported for soils associated with loblolly pine in eastern North Carolina (Allen and Schlesinger, 2004; Li et al., 2004), but within ranges reported for sandy soils in a coastal forest in Taiwan (Chen et al., 2005) and a coastal swamp in Louisiana (Poret-Peterson et al., 2007).

Microbial C differed significantly among disturbance classes ($F_{df2, 668}$=208, p<0.01). Mean values for microbial C were 29.4 ± 2.8, 143 ± 8.7, and 278 ± 11.4 µg g^{-1} for HD, MD, and RF plots, respectively. Mean values for microbial N were 5.29 ± 0.6, 22.4 ± 1.4, and 42.1± 1.7 µg g^{-1} for HD, MD, and RF plots, respectively. Microbial C:N ratios were significantly ($F_{df2, 644}$=261, p<0.01) wider in HD plots compared to MD and RF plots (9.3 ± 1.3, 7.45 ± 0.44, and 7.36 ± 0.31, respectively).

Regression analysis indicated significant, negative, non-linear relationships between sedimentation rates and microbial C (r^2=0.23, p<0.01) and N (r^2=0.17, p<0.01). Microbial C and N exhibited marked declines corresponding to current sedimentation rates between 0.1 and 0.4 cm yr^{-1} (Fig. 13), corresponding to the point of change in soil texture. Lower moisture content in sandy soil may be a driving factor in the decline of microbial biomass (Swift et al., 1979). There were also significant, negative, linear relationships between microbial C and N and soil bulk density (r^2=0.87, p<0.01 and r^2=0.85, p<0.01, respectively) (Fig. 13). Li et al. (2003) also found a reduction in microbial biomass with increased bulk densities in North Carolina associated with soil compaction. DeBusk et al. (2005) found a decrease in microbial biomass along upland ridges at Ft. Benning, GA, associated with soil compaction due to heavy foot traffic.

In general, microbial populations are thought to be reduced in areas with high temperature variations (Swift et al., 1979; Schilling et al., 1999). However, in this study, highest temperature fluctuations were found in RF plots, which also had highest microbial biomass. It is possible that RF plots had higher soil organic matter compared with MD and HD plots, which may support higher populations of microbial biomass.

It has often been suggested that net N mineralization rates should be negatively correlated to microbial biomass since soil microbes compete with plants for mineralized N (Hart et al., 1994; Fisher and Binkley, 2000; Badalucco and Kuikman, 2001; Brimecombe et al., 2001). In the present study, microbial C and N had significant, positive, linear relationships with net N mineralization rates ($r^2=0.53$, $p=0.001$ and $r^2=0.55$, $p=0.001$, respectively). This apparent relationship between microbial biomass and net N mineralization may be due to shared soil requirements necessary for N mineralization and microbial populations. Low soil moisture and aeration, which may be more common in the sandy soils of HD plots, would prove harsh environments for both N mineralization and soil microbe populations. Taylor et al. (1999) found that microbial biomass changes were most closely associated with soil moisture, though others have shown no correlation (Chang et al., 1995; Tonon et al., 2005). Because microbe populations depend on plant C as a major source of energy, it was expected that microbial biomass would exhibit significant relationships with plant productivity. Zak et al. (1994) reported a positive relationship between microbial C and ANPP in a diversity of ecosystems across North America. In the present study, both ANPP and BNPP (see

Chapter 2) had significant, positive, linear relationships with microbial biomass (r^2=0.34, p=0.01 and r^2=0.26, p=0.04, respectively), however fine root C content had the strongest positive, linear relationship with microbial C and N (r^2=0.68, p<0.01 and r^2=0.61, p<0.01, respectively).

There have been varying results in studies comparing microbial biomass in different disturbance treatments. The most common studies examine the effects of harvesting disturbance, mainly organic matter removal and compaction. Li et al. (2004) found that organic matter removal (whole tree and forest floor) decreased microbial N but did not affect microbial C or C:N ratios. In British Columbia, Canada, Tan et al. (2005) found that removal of forest floor reduced microbial biomass, though not significantly. Microbial biomass has been reported to increase (Lundgren, 1982; Entry et al., 1986) as well as decrease (Schilling et al., 1999) following clearcutting. Schilling et al.(1999) suggest that the different responses in these studies probably correspond to changes in temperature and soil moisture in response to different climates or variations within a climate zone. In the southeastern United States, declines in microbial biomass were probably caused by high soil temperatures and drying of the soils (Schilling et al., 1999), whereas increased soil temperatures in boreal forests may promote microbial communities (Lundgren, 1982; Entry et al., 1986). Timber harvest increases gaps in the canopy, leading to wider temperature ranges which may create more harsh environmental conditions for some microbial populations (Swift et al., 1979; Brimecombe et al., 2001). In the present study, however, temperature fluctuations did not seem to play a significant role in microbial biomass since RF plots had the highest fluctuations and the highest microbial biomass.

Microbial C and N showed strong, negative, linear relationships with soil bulk density (Fig. 14). Other studies have shown that the effect of soil compaction on microbial biomass varies regionally. Compaction had no effect on microbial communities in subtropical or Mediterranean climates (Busse et al., 2006), but did reduce communities in North Carolina (Li et al., 2003). Tan et al. (2005) and Mariani et al. (2006) found than compaction did not affect microbial biomass and only slightly reduced microbial N for a short time in an experimental forest in British Columbia. Impacts of soil disturbance, including compaction by military activities and erosional deposition, were consistently shown to result in decreased microbial activity at Ft. Benning, GA (DeBusk et al., 2005). DeBusk et al. (2005) found a decrease in microbial biomass, microbial respiration, and an increase in the microbial carbon: total C ratio with increasing soil disturbance (mainly compaction resulting from foot traffic) in both upland and bottomland soils. As part of the present study, Lockaby et al. (2005) also found a significant decline in microbial biomass associated with increased sediment deposition in riparian forests at Ft. Benning, GA.

Foliar Nutrients

Regression analysis showed no significant relationships between foliar nutrient concentrations and sedimentation rates. However, mean nutrient concentration and total nutrient content in litterfall differed among disturbance classes (Table 4). RF and MD plots had significantly higher C concentration than HD plots, suggesting that HD plots were less productive in fixing carbon. Concentrations of P did not differ among disturbance classes and N concentrations were significantly greater in RF and HD plots than in MD plots. This was likely due to the greater density of N-fixing shrubs found in

HD plots compared to MD plots (see Chapter 4). Litterfall N varied temporally, with highest N concentrations in 2003 and lowest in 2006 ($F_{df4,\,875}$=14.5, $p<0.01$). Annual variations in N concentrations reflected patterns similar to those found in annual precipitation, with higher N concentrations in years of higher precipitation. One exception was 2005, which had the highest annual rainfall but did not exhibit the highest N concentration.

Total P, N, and C content were significantly higher in RF plots compared to HD plots (Table 4). Differences in nutrient content tended to be driven by differences in litterfall biomass. RF plots had significantly greater foliar biomass than MD and HD plots (see Chapter 2). Differences in nutrient contents among disturbance classes were largely driven by differences in biomass. Vitousek et al. (1982) suggested that sites with litterfall N content less than 40 kg ha^{-1} yr^{-1} must have higher N resorption efficiencies or function on lower N concentrations. In our study, litterfall N content in HD plots fell into that range and exhibited numerically higher resorption efficiencies than were found in MD and HD plots.

Ratios of N:P were narrow for all disturbance classes (Table 4). HD plots had the highest N:P ratio (10) and MD plots had the lowest (7.7). N:P ratios showed a general increase with increasing current sedimentation rates (Fig. 15). Lockaby and Conner (1999) suggest that N:P less than 12 may indicate N deficiency. In this study, nearly all plots had N:P ratios less than 12, with the exception of two HD plots with very low P concentrations. These results suggest that all plots may be N-deficient. C:N ratios were wide across all plots (Table 4), suggesting N-limitation and increased potential for N-immobilization (Vitousek et al., 1982) in all plots. MD plots had significantly wider C:N ratios than RF or HD plots, reflecting lower N concentration in these plots.

Nutrient Resorption

Nutrient resorption was compared using green and senesced leaves from the most common tree species in each plot. RF plots had significantly ($F_{df2,\,7}$=3.56, p=0.04) higher N concentration in senesced leaves, indicating a lower resorption proficiency (5,970 ± 474 mg kg^{-1}) than MD (4,430 ± 460 mg kg^{-1}) and HD (4,610 ± 334 mg kg^{-1}) plots (Fig. 16). Mean N resorption efficiency was also significantly lower ($F_{df2,\,7}$=3.3, p=0.05) in RF plots (63.6 ± 2.4%) compared to MD (72.4 ± 2.3%) and HD (68.3 ± 3.6 %) plots (Fig. 16). Differences among disturbance classes in P proficiency and efficiency were not significant ($F_{df2,6}$=0.15, p=0.84; and $F_{df2,\,6}$=0.31, p=0.75, respectively). Mean P concentration in senesced leaves had a significant (r^2=0.50, p<0.01), negative relationship with sedimentation rates (Fig. 17), indicating an increase in P resorption proficiency with increasing current sedimentation rates.

The primary mechanisms for nutrient recycling within a forest system are: 1) retranslocation, 2) return to forest floor by leaching, and 3) return to forest floor by litter-fall (Lugo et al., 1990b). Except for leaching, each of these mechanisms is controlled biologically. Lugo et al. (1990b) and Odum (1984) suggest that highly efficient biotic recycling may be a response to low environmental recycling efficiencies. Berendse (1994) hypothesized that slower decomposition in nutrient-poor environments may be a side effect of a plant's adaptation to reduce nutrient losses through resorption of longer-lived leaves. In the present study, HD plots had lower forest floor turnover and a decrease in mass loss through decomposition, suggesting that nutrients were likely less available in the soil.

Several studies have indicated that nutrient resorption increases in nutrient-limited systems. Cárdenas and Campo (2007) found an increase in P resorption proficiency in P-limited tropical forests. Schilling and Lockaby (2006) found that N resorption proficiency in a blackwater (low-nutrient system) and redwater (high nutrient system) floodplain forests did not differ significantly, but P and calcium proficiency were higher in the nutrient-limited blackwater system. Cárdenas and Campo (2007) also found that N and P concentration in mature leaves reflected soil nutrient availability along a forest succession gradient in Mexico. They found that P concentration in senesced leaves was lower in the early-successional forest, where soils were less fertile, than in late-successional or primary forests. Harrington et al. (2001) also found higher PUE and NUE in nutrient-limited sites in Hawaii. A review of nutrient efficiency rates by Aerts (1996) found the mean resorption efficiency was 50% for N (n=287) and 52% for P (n=226). Our results indicated much higher resorption efficiencies in N (61-77%), suggesting N deficiency in all plots (Lugo et al., 1990a). Overall, results from this study suggest that all plots may be N deficient, while P deficiency is likely highest in MD and HD plots.

Nutrient Use Efficiency

Nutrient use efficiency, measured as litterfall biomass per unit of nutrient, was calculated for both N (NUE) and P (PUE). There was no significant relationship between NUE and current sedimentation rates (r^2=0.04, p=0.75) or between NUE and litterfall productivity (r^2=0.12, p=0.89). Although N resorption values indicated that HD plots may be the most deficient in both N and P, MD plots had significantly ($F_{df2,\,851}$=19.1, p<0.01) higher NUE than RF and HD plots (Fig. 18a). The lower NUE in HD plots may be due to the high number of N-fixing shrubs in HD plots, which contribute to litterfall. Resorption values were calculated using only dominant tree species, none of which were N-fixers, while NUE was based on litterfall nutrients, which represented both trees and shrubs. Killingbeck (1996) suggested that N-fixing plants are generally less efficient at recycling nutrients. Cárdenas and Campo (2007) found no difference in N resorption among forest successional stages in Mexico and attributed this to the dominance of N-fixing trees common among all forests. HD plots had significantly ($F_{df2,\,794}$=14.5, p<0.01) higher PUE than MD or RF plots (Fig. 18b). When plotted against litterfall productivity, there was a trend for HD plots to have high PUE and low litterfall productivity (Fig. 19), suggesting that HD plots may be more P deficient than MD and RF plots. Overall, high NUE and PUE values in MD and HD plots suggests deficiencies in N and P there.

Fine Root Nutrients

Fine root nutrients differed significantly among disturbance classes in both live and dead classes (Table 4). Fine root nutrient content was driven largely by biomass, which was significantly greater in RF plots (RF>MD>HD) for both live and dead roots (see Chapter 2). Fine root C concentration was highest in RF plots and lowest in HD plots for both live and dead roots (Table 4). Fine root N, however, showed the opposite trend, with highest N concentrations in HD plots. McClaughtery et al. (1982) found greater N concentration in roots associated with greater N in forest floor. However, this was not the case in our study. High N concentration in fine roots of HD plots was likely a result of a greater density of N-fixing shrubs in these plots. C and N concentrations in fine roots exhibited seasonal variability (Fig. 20). Live root C generally peaked in the spring and fall of each year, whereas C in dead roots peaked only in the spring. This corresponded to peaks in overall fine root biomass (see Chapter 2). Fine root N also peaked in the spring for both live and dead roots, with fewer fall peaks. N concentration exhibited a steep decline in all disturbance classes beginning in the summer of 2006, corresponding to the onset of a drought (Fig. 2). McClaughtery et al. (1982) found similar seasonal patterns in fine root C and N, which increased during the spring and autumn and decreased in winter.

Conclusions

This study indicates that current sedimentation rates greater that 0.1-0.4 cm yr^{-1} were associated with decreased nutrient content in plant biomass, increased internal recycling, increased nutrient use efficiencies, decreased nutrient turnover through decomposition, a decline in net N mineralization rates, and decreased microbial biomass. There was no indication that imported sediments contributed to increased soil fertility. Nutrient contents in plants, nutrient-use efficiencies, and immobilization patterns indicated that forests associated with high sedimentation may be more nutrient deficient than undisturbed soils. Deposition of sandy sediments increased bulk density and likely contributed to low soil moisture and aeration, creating more harsh environments for soil microbes which may lead to declines in biogeochemical processes such as decomposition and N mineralization. It it important to note that these rates were found in forests that have been receiving continuous sediment inputs over a long period of time.

Results of this study imply that even low levels of sediment deposition in riparian forests may cause a decline in soil quality and have a significant impact on biogeochemical processes. Declines in nutrient cycling will lead to reduced nutrients available for plant growth and forest productivity. Reduced productivity will, in turn, further decrease nutrient cycling, creating a negative feedback for forest growth. Decreased nutrient availability may also limit plant diversity, leading to an overall decline in biodiversity. Because similar rates of sedimentation are commonly found in riparian forests associated with upland disturbance, it is critical to protect these important habitats from upland erosion.

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Table 1. Summary of sedimentation rates and soil parameters associated with each plot in riparian forests at Ft. Benning, GA, 2004-2006.

	HD					MD							RF				
Plot	**D12B**	**F1Wd**	**K11d**	**F3**	**D12A**	**I3Bd**	**F1Wb**	**K11c**	**I3C**	**F1E**	**F4Ac**	**I3Ad**	**F1Wc**	**F4C**	**I3Bc**	**F4Ad**	**I3Ac**
Current Sedimentation Rate (cm yr^{-1})	5.52	4.38	3.96	1.85	1.39	0.78	0.46	0.43	0.23	0.15	0.14	0.11	0.09	0.01	0.01	0	0
Historic Sedimentation Rate (cm yr^{-1})	2.07	1.15	1.71	1.97	4.00	0.32	1.29	0.50	2.06	0.20	0.00	1.48	0.00	0	0	0	0
Current Sedimentation Rate (g m^{-2} yr^{-1})	0.99	0.77	0.70	0.33	0.22	0.11	0.08	0.07	0.04	0.01	0.07	0.02	0.01	<0.01	<0.001	<0.001	<0.001
% sand	92.1	94.8	95.0	94.6	93.3	87.3	88.5	85.4	89.2	92.9	78.3	74.6	89.6	78.3	79.2	92.5	43.3
%clay	4.58	2.50	2.08	2.08	3.75	4.58	5.42	5.83	4.17	0.83	8.75	11.67	2.92	7.08	8.75	1.67	29.6
%silt	3.33	2.71	2.92	3.33	2.92	8.13	6.04	8.75	6.67	6.25	12.92	13.75	7.50	14.6	12.1	5.83	27.1
%moist	16.4	10.3	6.51	13.4	12.6	11.3	12.8	8.4	28.3	55.3	59.3	16.5	32.2	28.6	11.7	20.1	21.5
pH	5.80	5.00	5.90	5.20	4.20	4.80	4.70	5.20	4.70	4.70	4.50	4.70	5.30	4.2	4.6	4.4	4.7
CEC (meq/100g)	0.77	0.94	1.27	0.87	5.67	2.65	3.05	2.46	1.95	4.60	6.93	4.25	3.60	6.11	4.37	2.85	2.95
P (mg ha^{-1})	0.00	1.00	5.00	1.00	3.00	3.00	2.00	4.00	1.00	2.00	0.00	1.00	2.00	4	2	2	2
K (mg ha^{-1})	26.0	21.0	37.0	16.0	82.0	36.0	33.0	48.0	34.0	55.0	48.0	89.0	46.0	135	63	25	46
Mg (mg ha^{-1})	24.0	11.0	20.0	13.0	53.0	23.0	17.0	34.0	13.0	38.0	26.0	57.0	37.0	97.0	50.0	11.0	34.0
Ca (mg ha^{-1})	63.0	27.0	135	30.0	156.0	74.0	56.0	137	39.0	52.0	49.0	122	204	233	98	22	110
Al (mg ha^{-1})	19.7	108	57.2	29.5	218.3	199	288	187	131	212	568	242	210	871	242	129	195
B (mg ha^{-1})	0.20	0.10	0.01	0.01	0.40	0.10	0.10	0.01	0.01	0.90	1.30	1.20	0.50	0.6	0.4	0.2	0.1
Cu (mg ha^{-1})	1.50	5.60	3.80	2.00	1.80	3.80	5.50	3.60	4.30	8.20	4.30	6.20	2.40	4.2	5.1	1.1	7.8
Fe (mg ha^{-1})	15.1	27.2	15.1	35.6	63.5	17.4	21.0	28.1	12.5	364	509	407	153	215	104	69	19.3

Mn (mg ha^{-1})	2.10	2.40	3.50	2.40	10.50	9.60	12.4	5.10	3.90	4.30	2.30	24.10	4.90	5.7	20.4	3.3	9.4
Na (mg ha^{-1})	18.1	20.9	18.6	18.2	26.9	20.5	19.1	21.4	18.3	41.1	29.8	29.1	31.0	46.4	19.8	23.1	23.5
Zn (mg ha^{-1})	0.30	0.70	1.20	0.01	1.20	0.90	1.60	0.90	1.00	1.90	2.50	3.50	0.20	3.9	2.1	0.01	3.1

Table 2. Analysis of variance (ANOVA) of forest floor biomass and nutrient content between forest floor maximum biomass, forest floor minimum biomass, and percent change between maximum and minimum values across disturbance classes at Ft. Benning, Ga. Different letters represent significant differences in means by Tukey's HSD (α=0.05). Standard errors are in parentheses.

forest floor g m^{-2}	disturbance class			$F_{df\ 2,\ 65}$	P-value
	high	moderate	reference		
dry weight					
maximum	241.4 (47.0) ^{b}	325.7 (27.7) ^{ab}	385.0 (27.5) ^{a}	4.36	0.02
minimum	167.8 (30.4) ^{a}	186.9 (25.5) ^{a}	191.7 (22.8) ^{a}	0.68	0.52
% change	27.7 (12.6) ^{a}	40.4 (6.0) ^{a}	51.4 (4.1) ^{a}	2.38	0.10
C content					
maximum	98.9 (21.2) ^{b}	133.4 (14.5) ^{ab}	158.7 (14.1) ^{a}	3.19	0.05
minimum	69.8 (14.4) ^{a}	77.3 (12.6) ^{a}	84.8 (10.7) ^{a}	0.35	0.71
% change	21.8 (14.0) ^{a}	36.6 (7.6) ^{a}	44.1 (8.0) ^{a}	1.29	0.28
N content					
maximum	1.1 (0.2) ^{a}	1.3 (0.2) ^{a}	1.5 (0.2) ^{a}	1.37	0.26
minimum	0.5 (0.1) ^{a}	0.4 (0.1) ^{a}	0.3 (<0.1) ^{a}	0.70	0.50
% change	65.7 (7.4) ^{a}	56.6 (10.7) ^{a}	70.7 (9.1) ^{a}	0.54	0.59
P content					
maximum	0.2 (<0.1) ^{b}	0.2 (<0.1) ^{ab}	0.3 (<0.1) ^{a}	3.45	0.04
minimum	0.2 (<0.1) ^{a}	0.2 (<0.1) ^{a}	0.2 (<0.1) ^{a}	0.31	0.74
% change	7.0 (20.4) ^{a}	9.3 (13.2) ^{a}	37.4 (6.8) ^{a}	1.65	0.2

Table 3. Comparison of soil texture and moisture across disturbance classes at Ft. Benning, GA. Different letters represent significant differences in means by Tukey's HSD (α=0.05). Standard errors are in parentheses.

soil composition	disturbance class			F df 2, 249	P-value
%	high	moderate	reference		
sand	92.0 (1.0) [a]	86.8 (0.9) [b]	81.8 (1.5) [c]	18.57	<0.01
silt	2.9 (0.4) [c]	7.7 (0.5) [b]	9.7 (0.7) [a]	33.32	<0.01
clay	5.1 (0.6) [b]	5.5 (0.5) [b]	8.5 (0.9) [a]	7.75	<0.01
moisture	11.4 (0.5) [c]	21.6 (2.8) [b]	28.8 (1.4) [a]	21.74	<0.01

Table 4. Analysis of variance (ANOVA) of nutrient concentrations and content in litterfall and fine roots across disturbance classes from 2002-2006 at Ft. Benning, Ga. Different letters represent significant differences in means by Tukey's HSD (α=0.05). Standard errors are in parentheses.

		Disturbance Class						DF_{error}	F	P-value
litterfall	**parameter**	**High**		**Moderate**		**Reference**				
	P (mg kg^{-1})	931	(31.4)^{b}	1,020	(22.9)^{a}	1,051	(19.0)^{a}	851	2.23	0.11
	N (mg kg^{-1})	9,113	(223)^{a}	7,547	(186)^{b}	8,671	(157)^{a}	851	18.2	<0.01
	C (mg kg^{-1})	480,413	(1,386)^{b}	484,390	(872)^{a}	483,981	(710)^{a}	850	4.62	0.01
	Pcont (g m^{-2})	3.9	(0.4)^{b}	5	(0.3)^{ab}	5.6	(0.4)^{a}	851	5.78	<0.01
	Ncont (g m^{-2})	29.7	(2.7)^{b}	37.7	(2.5)^{ab}	45.5	(2.9)^{a}	851	8.19	<0.01
	Ccont (g m^{-2})	1,754	(164)^{b}	2,691	(171)^{a}	2,854	(179)^{a}	850	11.3	<0.01
	N:P	10.8	(0.4)^{a}	7.7	(0.2)^{c}	8.8	(0.2)^{b}	850	19.1	<0.01
	C:N	63	(2.1)^{b}	83.7	(4.0)^{a}	62.7	(1.4)^{b}	849	19.8	<0.01
roots	**Ncont (g m^{-2})**									
	Live	0.5	(0.0)^{c}	1.6	(0.1)^{b}	2.6	(0.1)^{a}	776	87.1	<0.01
	Dead	0.4	(0.0)^{c}	1.8	(0.1)^{b}	2.3	(0.1)^{a}	778	52.3	<0.01
	Ccont (g m^{-2})									
	Live	23.3	(2.1)^{c}	86.8	(4.5)^{b}	147	(5.7)^{a}	791	48.1	<0.01
	Dead	19.7	(1.9)^{c}	86.5	(5.8)^{b}	121	(5.4)^{a}	788	82.1	<0.01
	N (mg kg^{-1})									
	Live	9,368	(207)^{a}	8,191	(149)^{b}	7,982	(390)^{b}	776	14.3	<0.01
	Dead	9,618	(209)^{a}	8,492	(133)^{b}	8,482	(129)^{b}	778	11.3	<0.01
	C (mg kg^{-1})									
	Live	432,142	(2,403)^{c}	450,615	(1,287)^{b}	466,694	(1,057)^{a}	791	65.3	<0.01

	Dead	424,960	(2,745)^{c}	437,430	(2,064)^{b}	462,255	(1,490)^{a}	788	42.3	<0.01
C:N										
	Live	46.1	(1.7)^{c}	55.0	(1.4)^{b}	58.5	(1.2)^{a}	772	53.3	<0.01
	Dead	44.2	(1.3)^{c}	51.5	(1.2)^{b}	54.5	(0.9)^{a}	782	28.3	<0.01

Figure 1. Location of study area and 17 plots in riparian forests at Ft. Benning, GA.

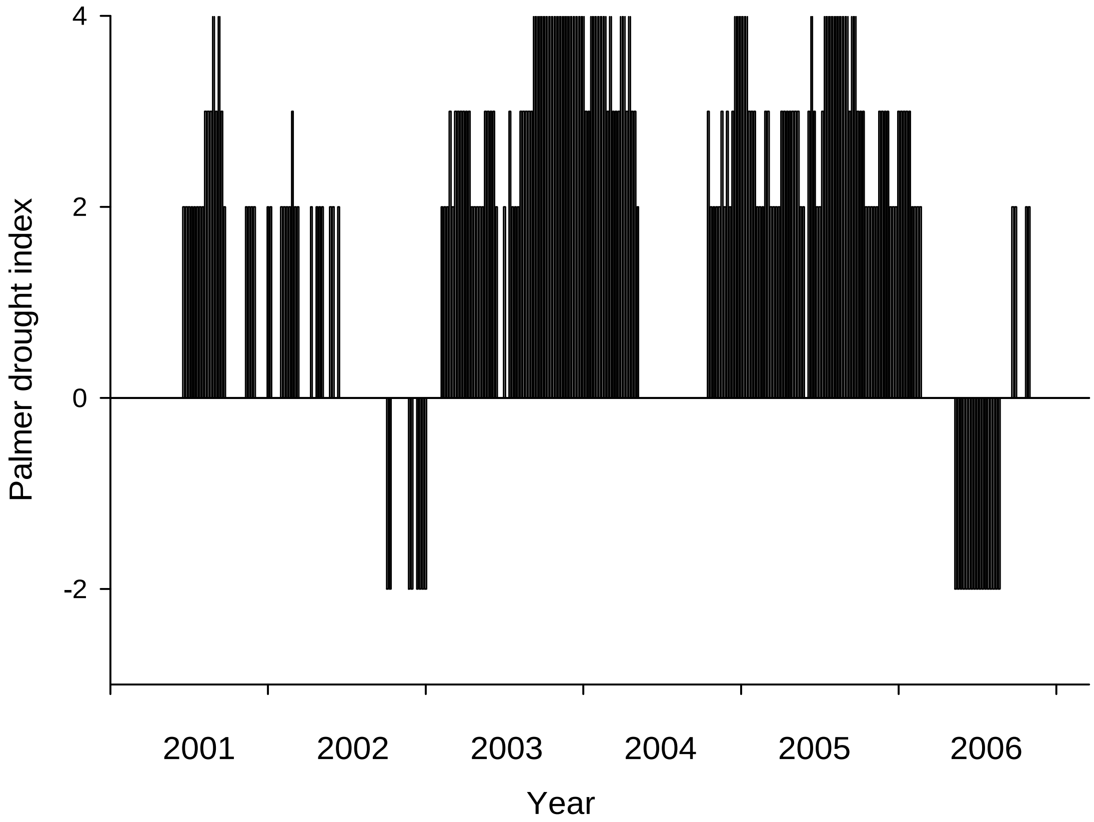

Figure 2. Palmer drought indices for 2001-2002. Positive bars indicate excess moisture, negative bars indicate drought.

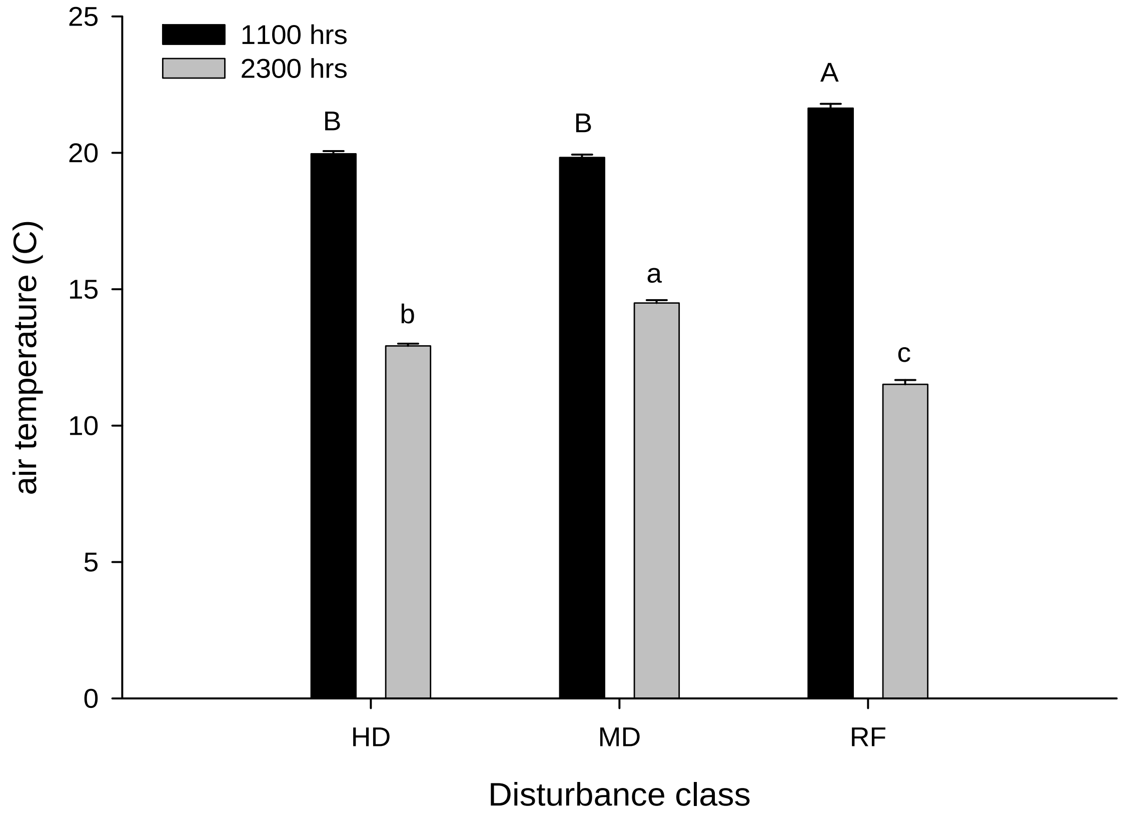

Figure 3. Comparison of understory day (1100 hours) and night (2300 hours) air temperatures among disturbance classes in riparian forests at Ft. Benning, GA, from July 2004 to December 2006. Uppercase letters indicate significant differences in daytime temperatures and lowercase letters indicate significant differences in nighttime temperatures among disturbance classes means by Tukey’s HSD (α=0.05). Vertical bars indicate standard error.

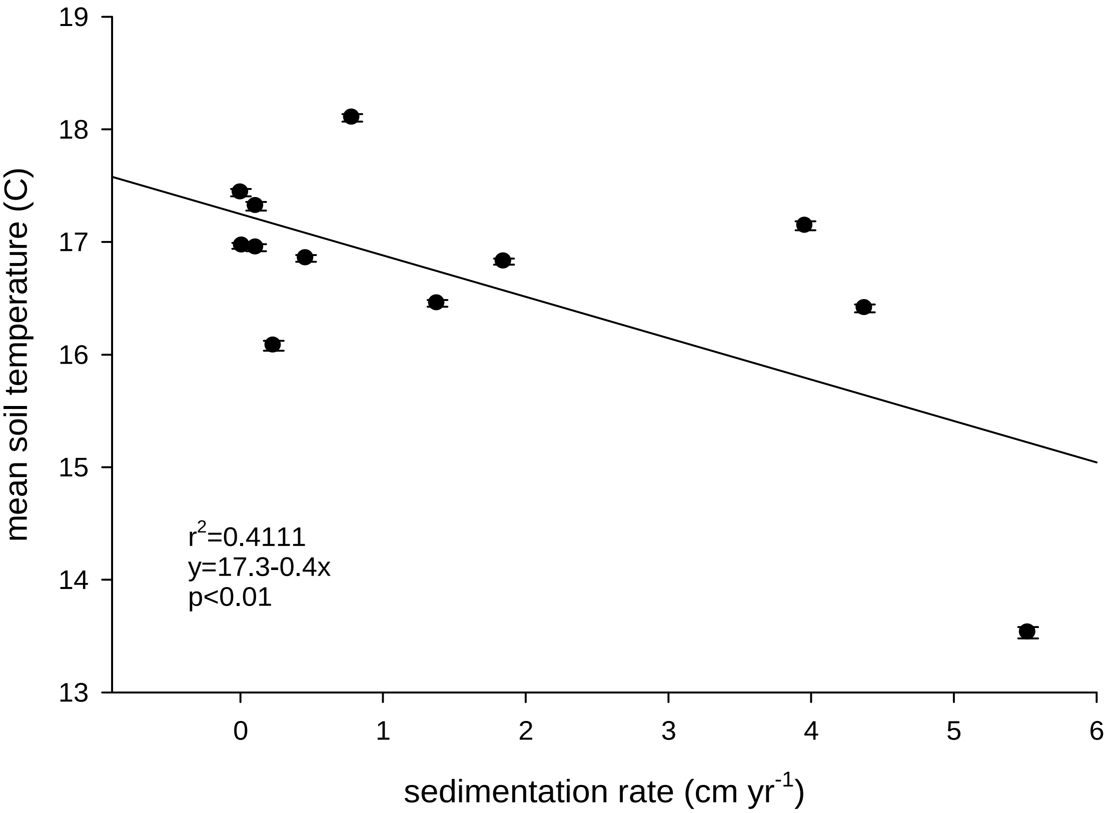

Figure 4. Regression relationship between current sedimentation rates and mean soil temperature in riparian forests at Ft. Benning, GA, from July 2004 to December 2006. Vertical bars indicate standard error.

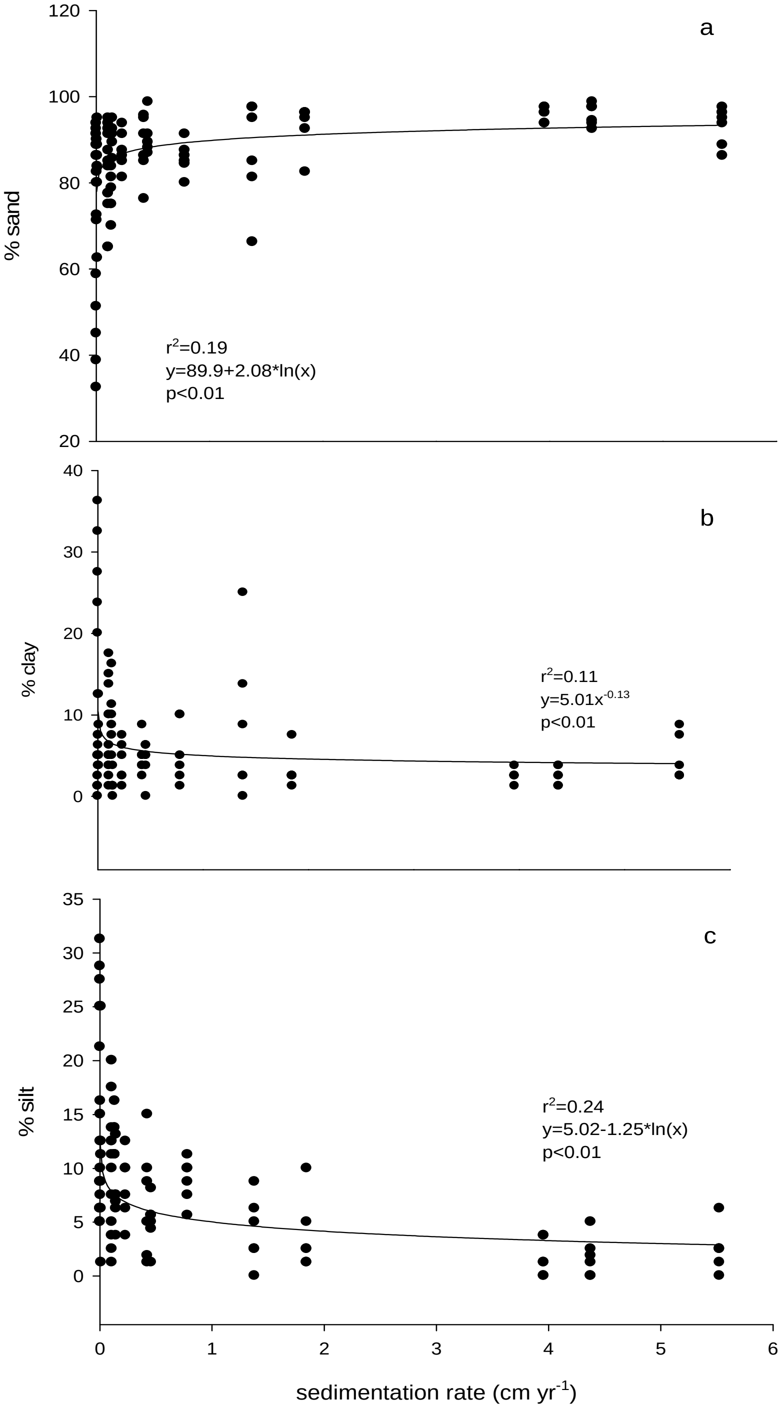

Figure 5. Regression relationships between current sedimentation rates and soil texture as measured by percent a) sand, b) clay, and c) silt in riparian forests at Ft. Benning, GA, 2002-2006.

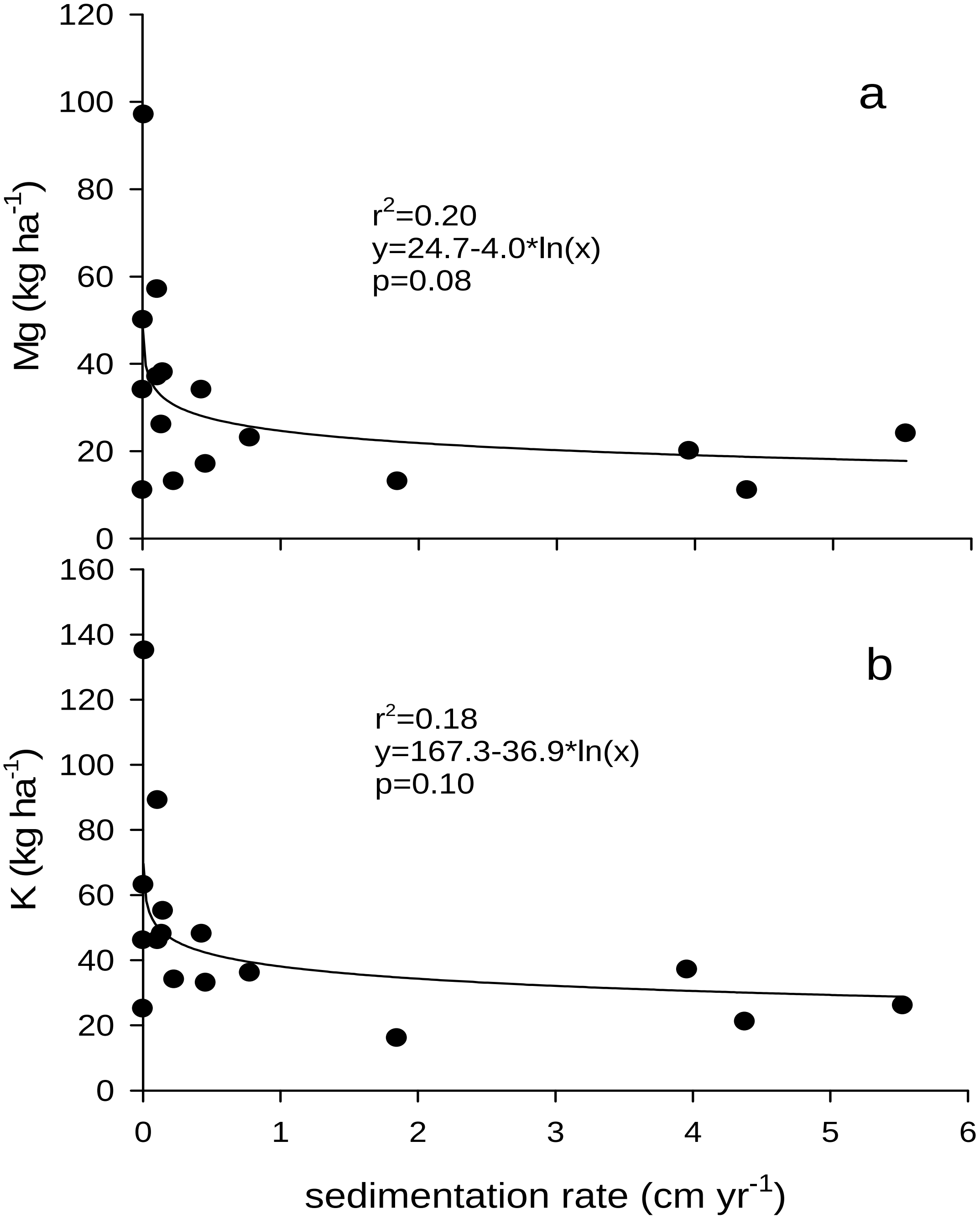

Figure 6. Regression relationships between current sedimentation rates and concentrations of a) Mg and b) K in riparian forests at Ft. Benning, GA.

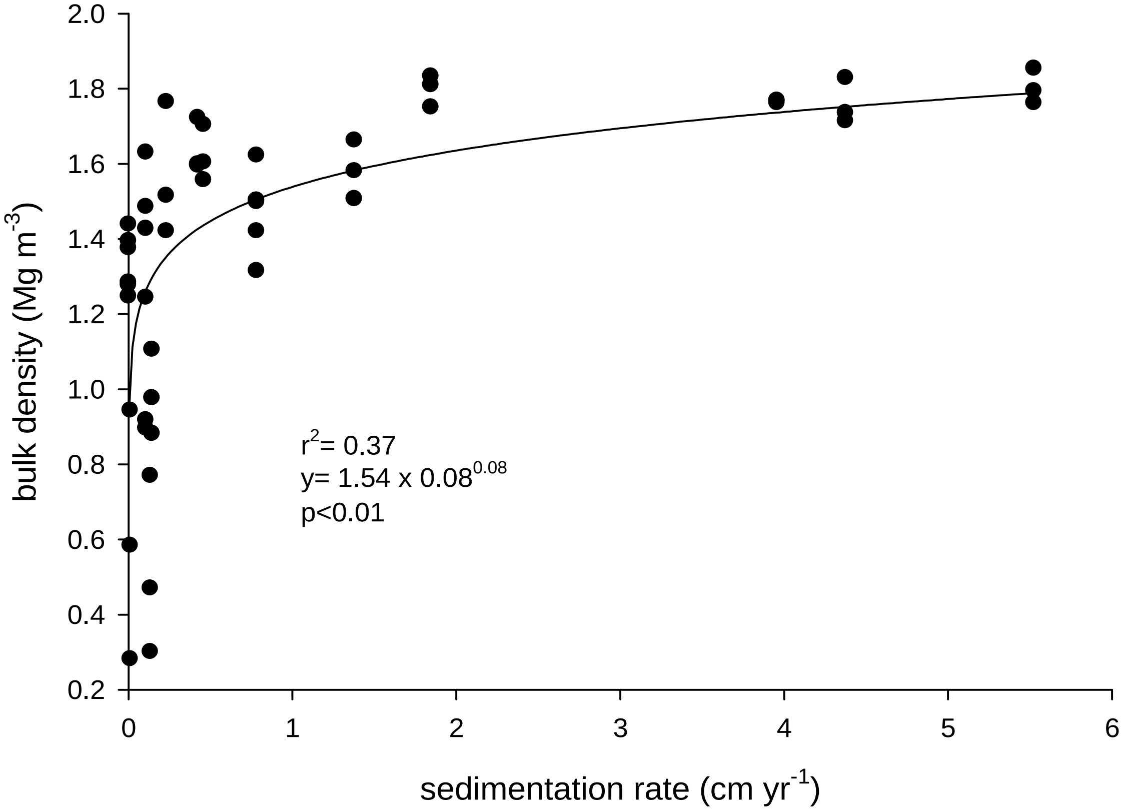

Figure 7. Regression relationship between current sedimentation rates and soil bulk density sampled at a depth of 0-7.5 cm in riparian forests at Ft. Benning, GA.

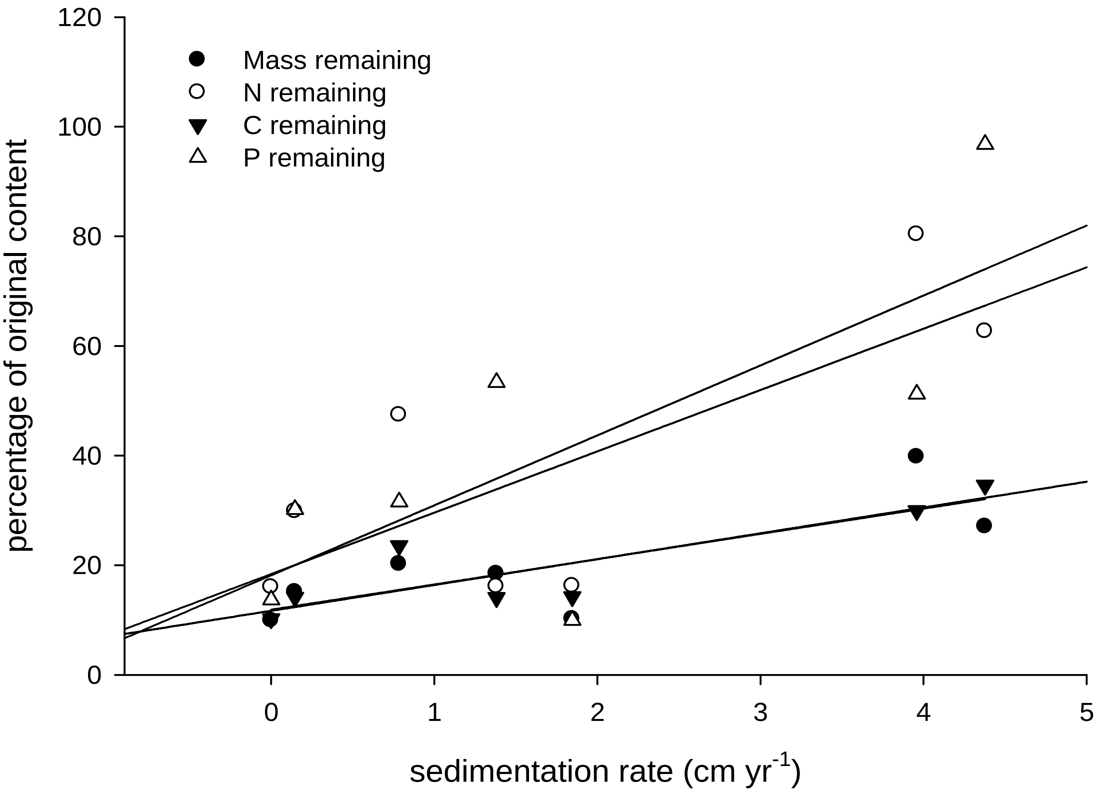

Figure 8. Regression relationships between current sedimentation rates and percent remaining of original mass (r^2= 0.62, p<0.01), N (r^2= 0.58, p<0.01), C (r^2= 0.75, p<0.01), and P (r^2= 0.57, p<0.01) after 64 weeks of decomposition in riparian forests at Ft. Benning, GA, April 2004 to July 2005.

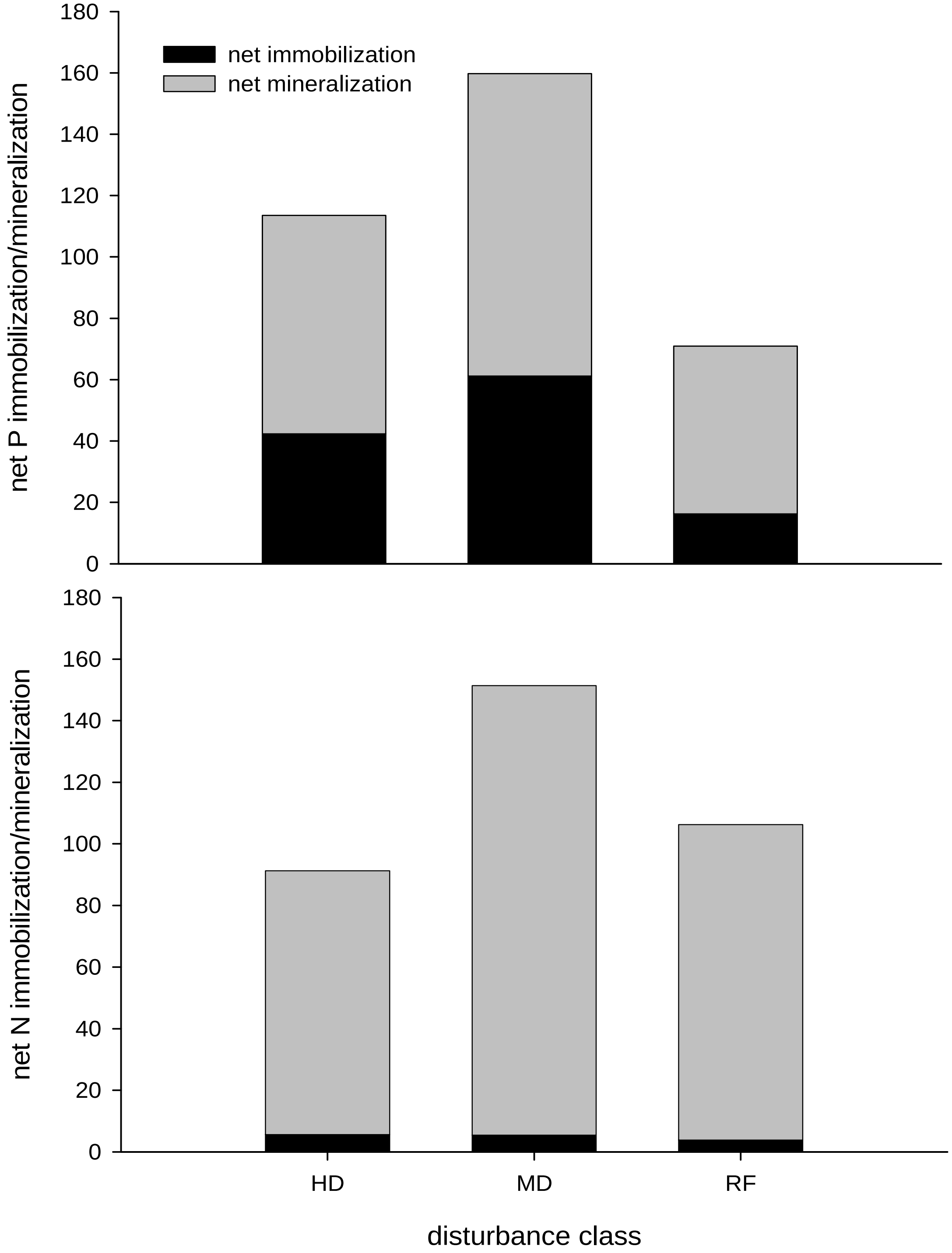

Figure 9. Comparison of N and P net immobilization and mineralization in decomposing litter in riparian forests at Ft. Benning, GA, from April 2004 to July 2005.

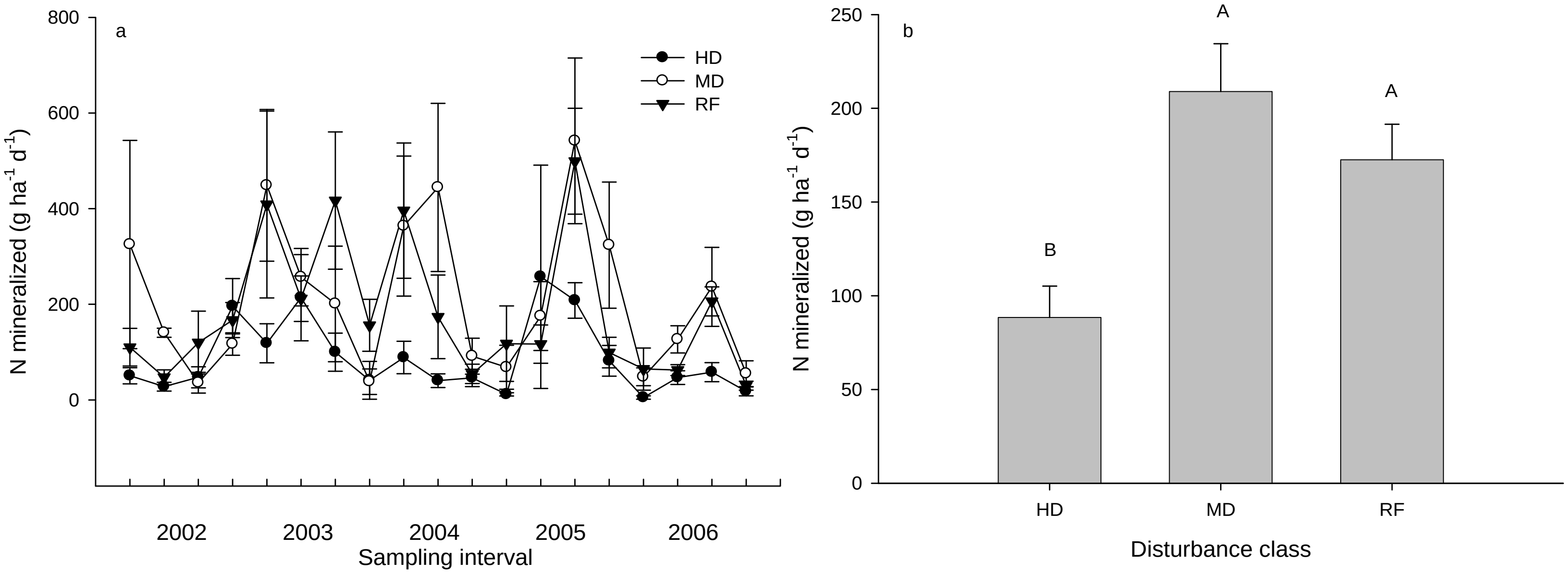

Figure 10. Comparison of nitrogen mineralization a) patterns and b) rates among disturbance classes in riparian forests at Ft. Benning, GA, from February 2002 to October 2006. Letters indicate significant differences in means by Tukey's HSD (α=0.05). Vertical bars indicate standard error.

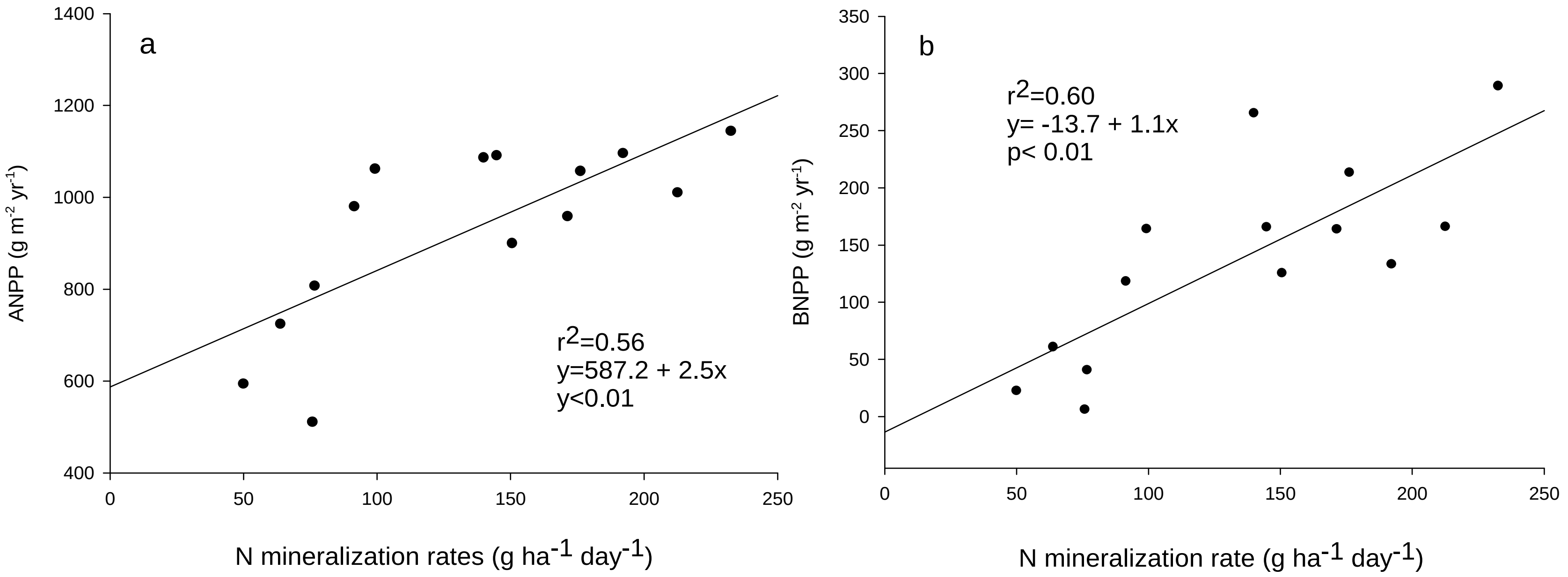

Figure 11. Regression relationship between mean a) ANPP and b) BNPP (see chapter 2) and mean N mineralization rates in riparian forests at Ft. Benning, GA, from February 2002 to October 2006.

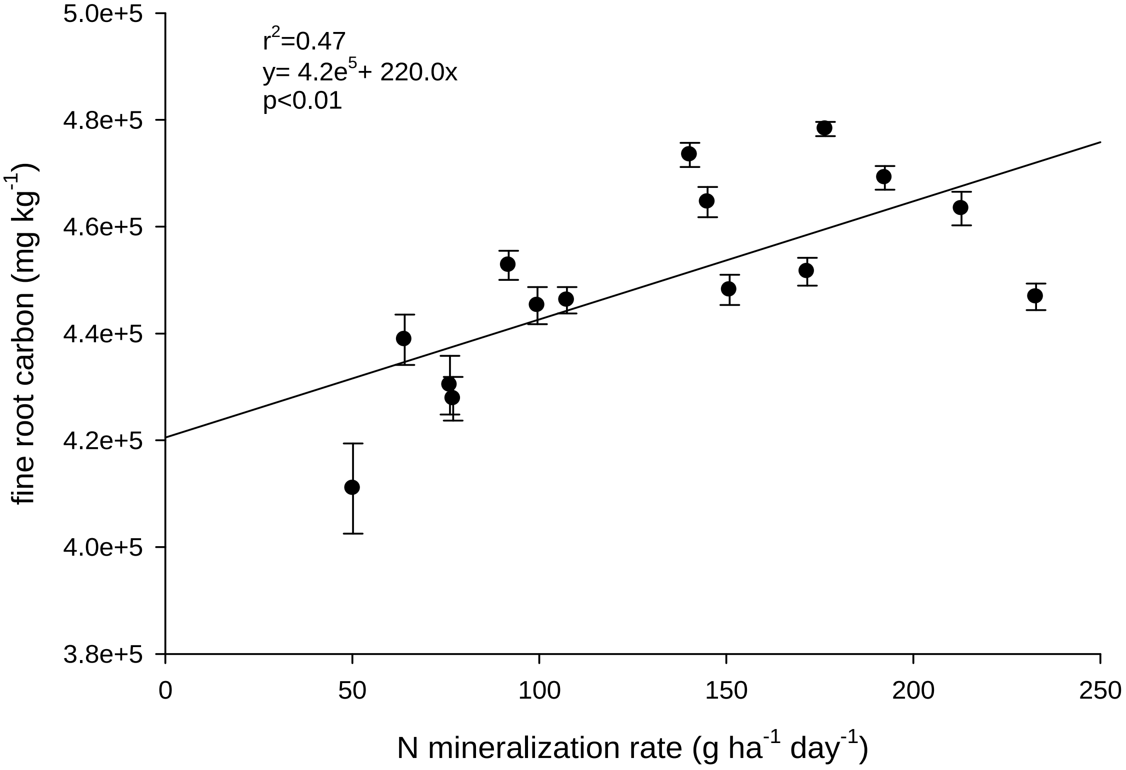

Figure 12. Regression relationship between fine root carbon concentration and mean N mineralization rates in riparian forests at Ft. Benning, GA, from February 2002 to October 2006. Vertical bars indicate standard error.

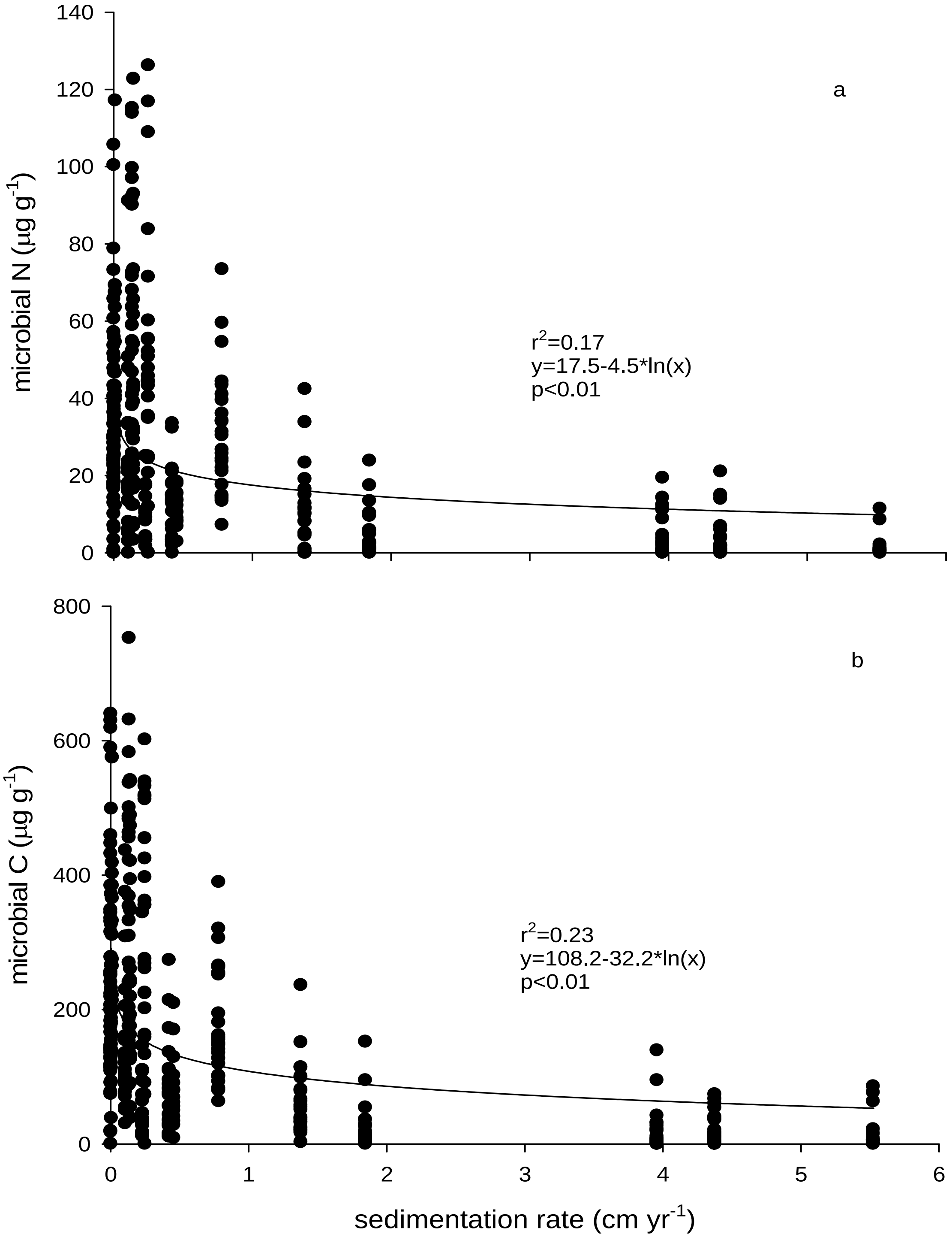

Figure 13. Regression relationship between current sedimentation and mean a) microbial N and b) microbial C in riparian forests at Ft. Benning, GA, from February 2002 to October 2006. Vertical bars represent standard error.

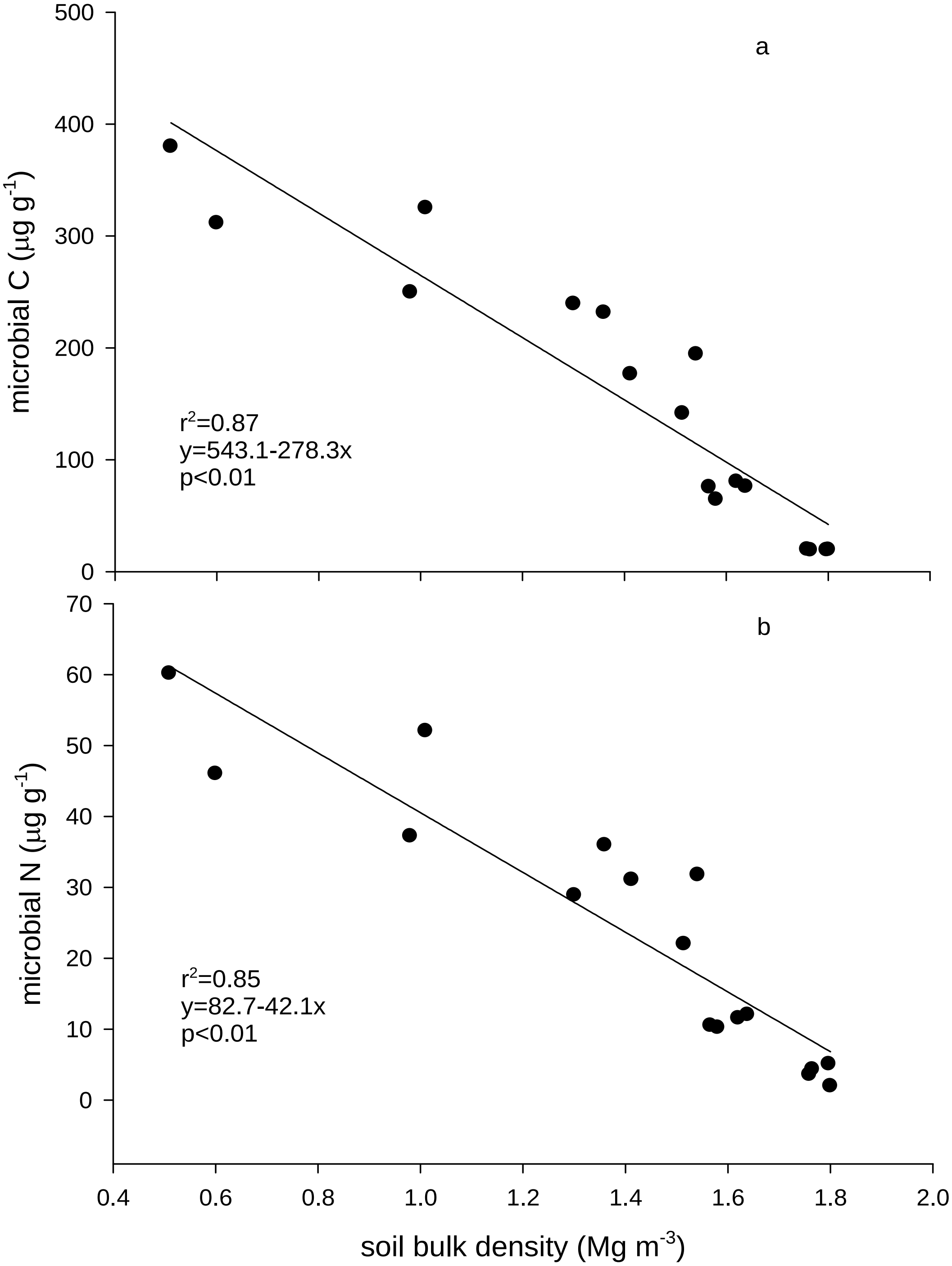

Figure 14. Regression relationship between microbial a) C and b) N and soil bulk density in riparian forests at Ft. Benning, GA, from February 2002 to October 2006.

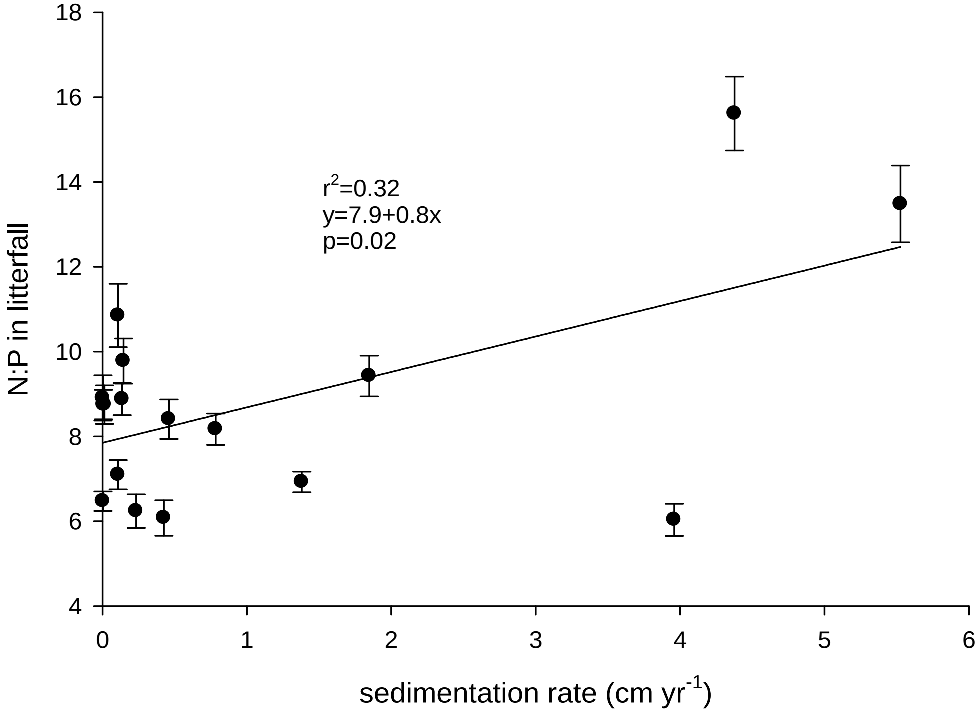

Figure 15. Regression relationship between current sedimentation rates and N:P ratio in litterfall in riparian forests at Ft. Benning, GA, from 2002 to 2006. Vertical bars indicate standard error.

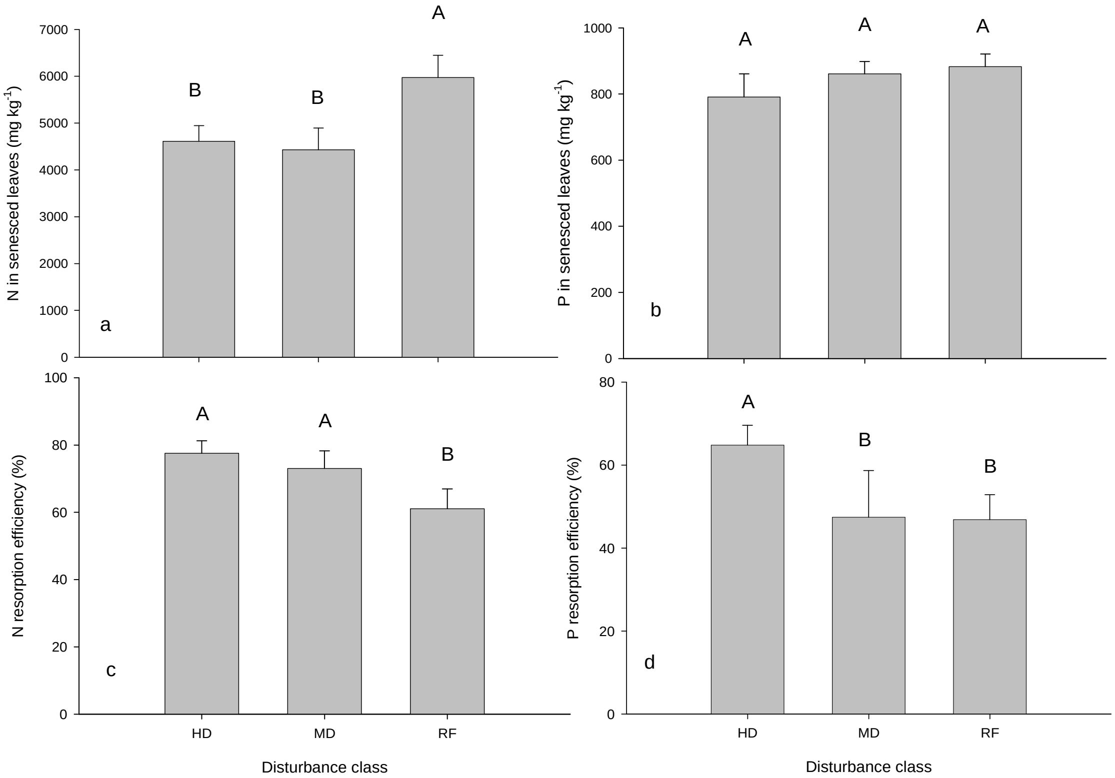

Figure 16. Comparison of a) N resorption proficiency, b) P resorption proficiency, c) N resorption efficiency, and d) P resorption efficiency among disturbance classes in riparian forests at Ft. Benning, GA measured in 2006. Different letters represent significant differences in means by Tukey's HSD (α=0.05). Vertical bars indicate standard error.

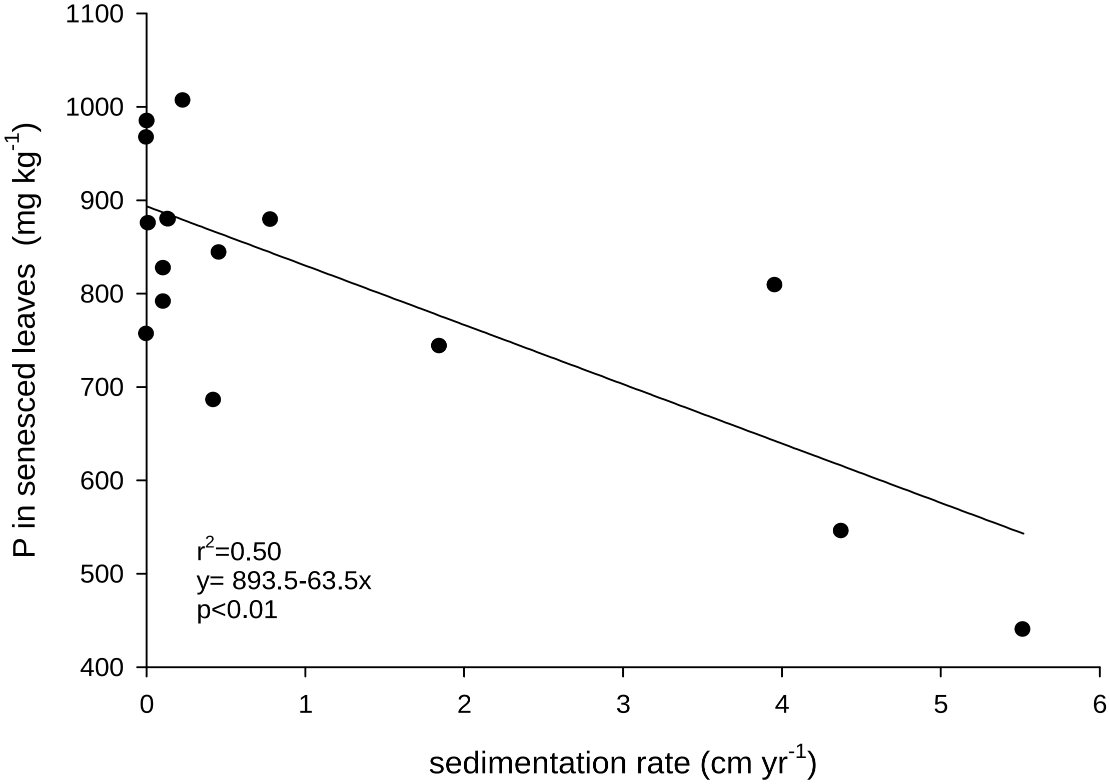

Figure 17. Regression relationship between current sedimentation rates and P resorption proficiency, expressed as P concentration in senesced leaves in riparian forests at Ft. Benning, GA, measured in 2006.

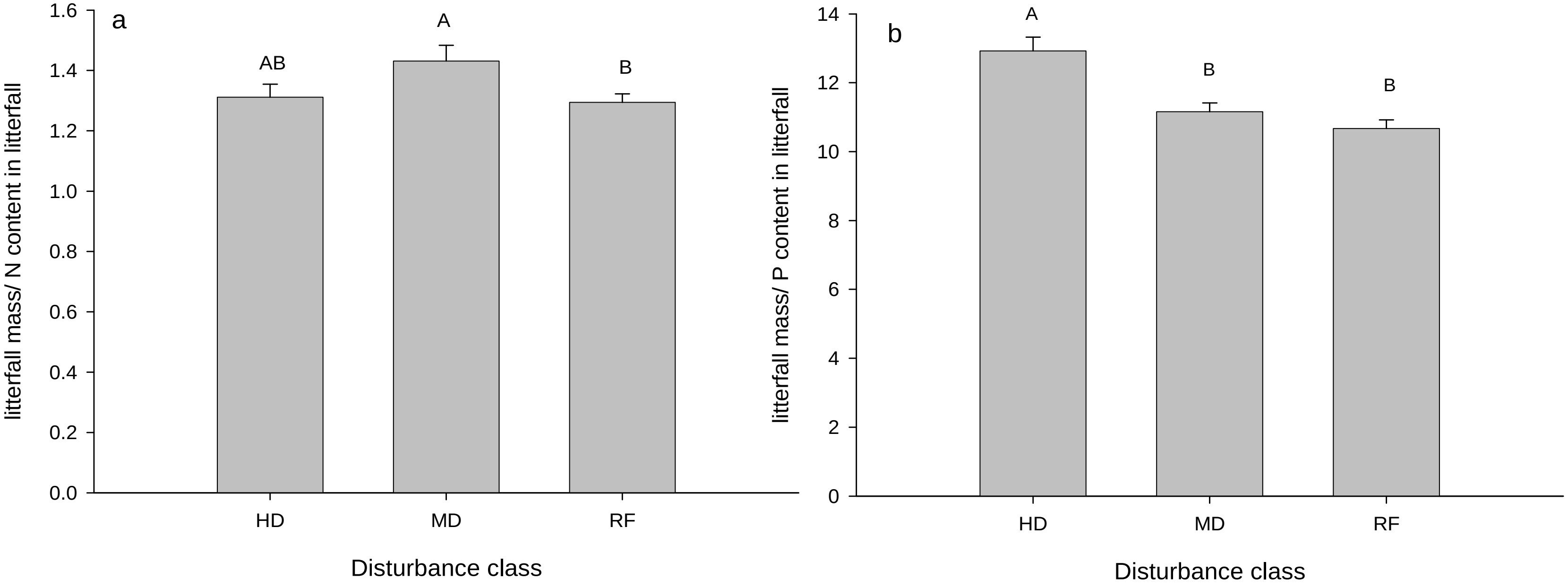

Figure 18. Comparison of a) N use efficiency (NUE) and b) P use efficiency (PUE) among disturbance classes in riparian forests at Ft. Benning, GA, from 2002 to 2006. Letters indicate significant differences in means by Tukey's HSD ($\alpha=0.05$). Vertical bars indicate standard error.

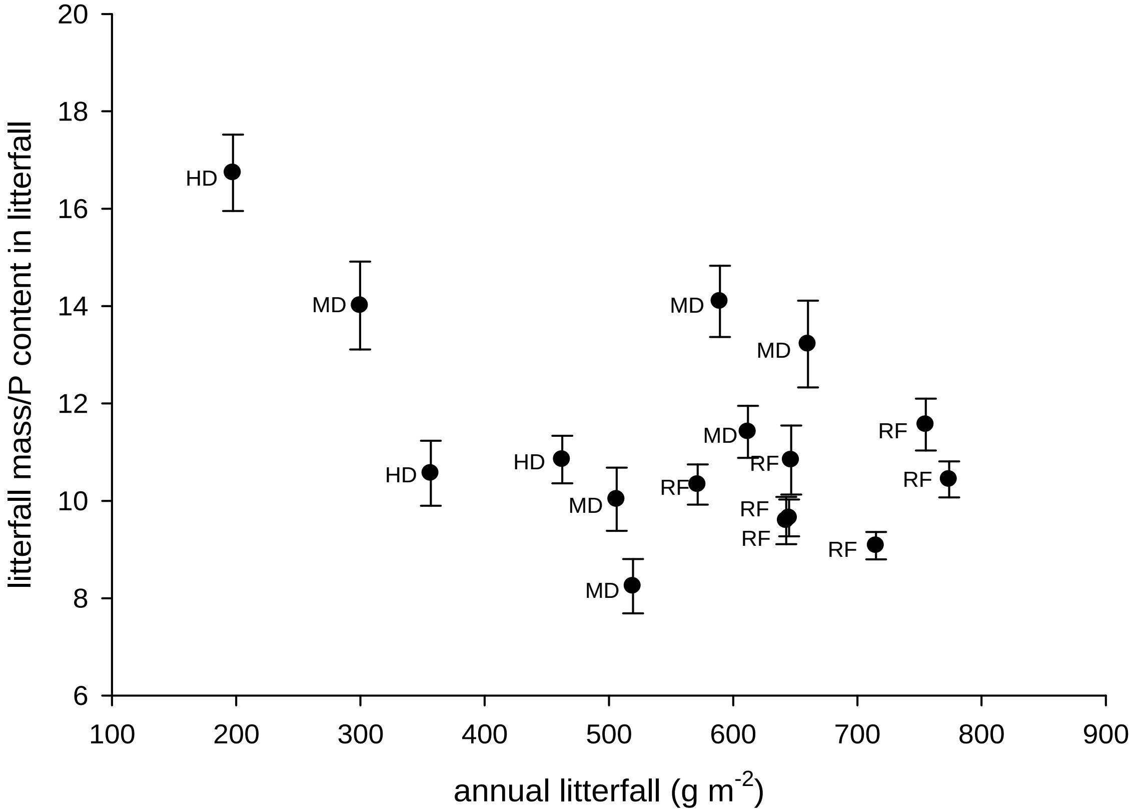

Figure 19. Relationship between P use efficiency and mean annual litterfall in riparian forests at Ft. Benning, GA, from 2002 to 2006. HD=highly disturbed, MD=moderately disturbed, and RF= reference plot. Vertical bars indicate standard error.

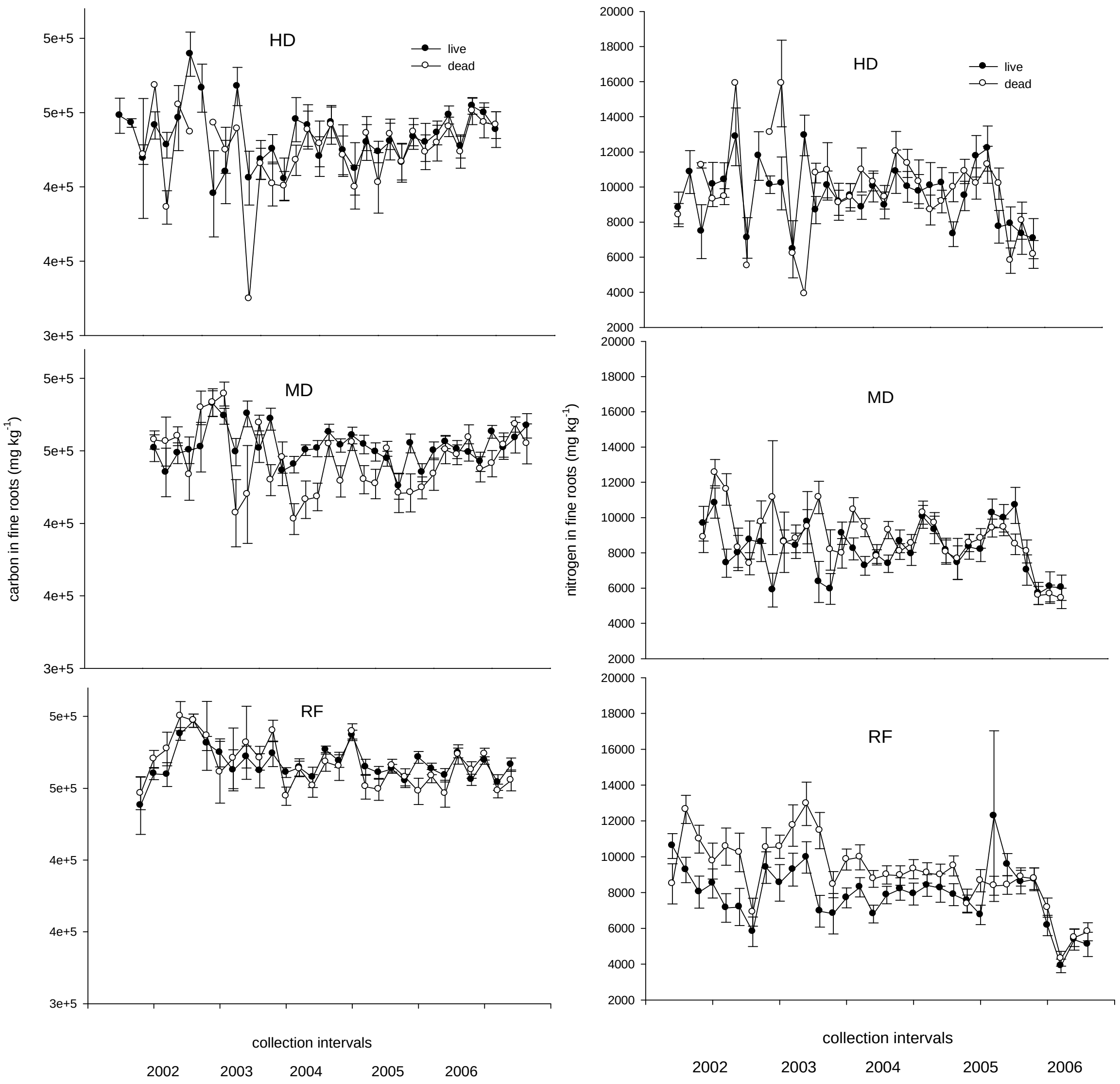

Figure 20. Temporal patterns in C and N concentrations in live and dead roots among disturbance classes. Vertical bars indicate standard error.

CHAPTER IV

CHANGES IN RIPARIAN FOREST COMPOSITION ALONG A SEDIMENTATION RATE GRADIENT

Abstract

Riparian forests are highly valued for maintaining water quality through the retention of sediments and nutrients. They also provide some of the most diverse and species-rich habitats in the world. What is largely unknown, however, is how sediment deposition affects both community composition and sediment retention in these forests. The objective of this study was to examine changes in community composition across a gradient of increasing rates of sedimentation in riparian forests at Ft. Benning, GA. Seventeen plots were established within riparian forests receiving between 0 and 5.5 cm yr^{-1} of sediment deposits. Species density and biomass estimates were collected annually from 2002-2006 for overstory and mid-story species within each plot. Measures of species cover and frequency were were also conducted annually (2004-2006) in the understory of each plot. Measures of community composition in the understory, midstory, and overstory layers of forests were compared to changes in environmental factors associated with sedimentation. Nested frequency and cover were measured in the understory, and biomass and density were measured in the mid- and overstory layers. In the understory, annual, exotic, and upland species had higher importance values in plots receiving high sediment deposition (HD) compared with reference (RF) plots. There were also greater densities of shade-intolerant and N-fixing species in the midstory of HD plots. Increased overstory mortality was associated with high sedimentation rates, though increases in understory light levels in these gaps were not the main driver of understory species changes. Edaphic factors, such as soil texture, moisture, and temperature, were positively correlated to species composition in all three forest layers, suggesting that changes in soil physical structure due to sedimentation may drive community-level changes in these forests.

Key words: community composition, riparian forest, sedimentation

Introduction

Riparian forests have long been known to be ecologically important, acting as interfaces between terrestrial and freshwater ecosystems and providing some of the most diverse and species-rich habitats in the world (Gregory et al., 1991; Naiman et al., 1993; Nilsson et al., 1994; Naiman and Decamps, 1997). One of the greatest societal benefits provided by riparian forests is that of maintaining and improving water quality (Schlosser and Karr, 1981; Peterjohn and Correll, 1984; Cooper et al., 1987; Naiman and Decamps, 1997). Riparian vegetation slows overland flows and traps sediments, thus acting as a nutrient filter and reducing stream sediment loads. Vegetation in riparian buffers can remove 80-90% of the sediments leaving agricultural fields (Peterjohn and Correll, 1984; Cooper et al., 1987; Daniels and Gilliam, 1996). The function of riparian vegetation in trapping sediments and stabilizing streams is highly valued, however, little is known about how sediment retention affects riparian forest community composition (Jurik et al., 1994; Cavalcanti, 2004; Koning, 2004; Lockaby et al., 2005).

By their nature, riparian forests are subject to alluviation as streams overflow their banks. However, increases in land development and disturbance result in corresponding increases in movement of eroded materials into wetland systems (Hupp and Bazemore, 1993; Kleiss, 1996; Meyer et al., 2003). Sedimentation in forested riparian wetlands ranges from 0.02 cm yr^{-1} to as much as 8.0 cm yr^{-1} (Cooper et al., 1987; Hupp and Morris, 1990; Hupp and Bazemore, 1993; Hupp et al., 1993; Kleiss, 1996; Wardrop and Brooks, 1998; Heimann and Roell, 2000; Rybczyk et al., 2002). The ability of a riparian forest to trap sediments is dependent on the forest vegetation, contributing to surface roughness, among other factors (Naiman and Decamps, 1997; Naiman et al., 2000; Rybczyk et al., 2002). Increased sedimentation may bury vegetation, decreasing surface roughness and the ability to trap additional sediment inputs (Hupp and Bazemore, 1993; Werner and Zedler, 2002). Previous sediment studies suggest that reduction of microrelief and vegetation burial decrease surface roughness and lead to a decline in sediment retention (Hupp and Bazemore, 1993; Werner and Zedler, 2002; Lockaby et al., 2005) and, consequently, increase sediment inputs to a stream via surface runoff. However, sediment export rates associated with surface roughness and sedimentation influx have not been quantified previously.

As with other types of forest disturbances, high sedimentation rates may cause shifts in community composition. Disturbances which increase overstory mortality create openings in the canopy layer, which may alter the microclimate associated with the understory, and creating greater coarse woody debris (Jurik et al., 1994). Sediment deposition may also affect community composition by altering ground surface microtopography, changing mineral soil substrate, damaging plants, and altering propagule availability (Roberts, 2004). Influx of sediments can reduce plant biomass and alter species diversity (Koning, 2004; Kent et al., 2005; Cavalcanti and Lockaby, 2006). It has been suggested that sedimentation will allow opportunistic and early-seral species to become established in gaps created by disturbance (Wardrop and Brooks, 1998; Levine and Stromberg, 2001; Cavalcanti and Lockaby, 2006). Because plant species vary greatly in resource use, allocation, and phenology, changes in community composition may also affect ecosystem processes, such as nutrient cycling, productivity, and decomposition (Vitousek, 1986; Hobbie, 1992; Mahaney et al., 2004a; Cárdenas and

Campo, 2007). Therefore, it is important to understand how differing rates of sedimentation may shift community composition of riparian forests.

Although headwater floodplains have some of the greatest rates of sedimentation (Wardrop and Brooks, 1998), few studies have investigated sedimentation effects on forest communities. For example, Cavalcanti (2004) showed an increase in N-fixing and shade-intolerant shrubs in riparian forests with high rates of sedimentation. Based on studies in coastal marsh or dune ecosystems (Kent et al., 2001), it is likely that the major factors influencing the vegetation community composition in riparian forests with high levels of sedimentation are seedling emergence, species adaptations to burial, species succession (Levine and Stromberg, 2001), and changes in abiotic soil conditions.

Classification of vegetation is a challenge to ecologists due to the innate complexity and diversity of plant communities. Often, this challenge has been addressed by classifying plant species into guilds or functional groups based on similar characteristics (Bazzaz, 1979; Grime, 1979; Barbour et al., 1998; Lyon and Sagers, 2003). Separation into functional groups based on the vertical layers in the forest vegetation (i.e., overstory, midstory, and understory) has been shown to be an effective means of incorporating similar morphology, position in a successional sere, and competitive status (Grime, 1993; Smith et al., 1993; Gilliam et al., 1995; Lyon and Sagers, 2003).

Most forest studies focus primarily on dominant overstory species, but understory species, especially herbaceous species (Hupp and Osterkamp, 1985; Bazemore et al., 1991; Smith, 1996; Nakamura et al., 1997; Coates, 2002; Hoshino et al., 2003; Yamashita et al., 2004), may be more useful indicators of changes in edaphic factors (Pregitzer and

Barnes, 1982; Decocq, 2002) due to their greater sensitivity to disturbance and soil fertility changes (Peterson and Rolfe, 1982; Moore and Vankat, 1986; Gilliam et al., 1995). In this paper, the response of each forest layer was analyzed in an attempt to understand the complexity of species response to environmental disturbance by sedimentation.

The relationship between seed burial and germination has been well studied. Generally, seed germination is dependent upon light, oxygen availability, soil temperature, and moisture (Bonis and Lepart, 1994; Jurik et al., 1994; Barbour et al., 1998; Gleason et al., 2003; Shi et al., 2004; Zheng et al., 2005). These cues are altered by sediment deposition, which may result in lower germination rates (Peterson and Baldwin, 2004). Soil microtopography contributes to the creation of "safe sites," (*sensu* Harper 1977) capable of trapping and protecting germinating seeds. However, sedimentation creates a very smooth soil surface, filling in and eliminating microrelief (Werner and Zedler, 2002). Studies of seed burial suggest that even small amounts of sediment may reduce emergence of small seeds (Welling and Becker, 1990; Bonis and Lepart, 1994; Jurik et al., 1994; Gleason et al., 2003; Barry et al., 2004; Mahaney et al., 2004b; Peterson and Baldwin, 2004; Petru and Menges, 2004; Zheng et al., 2005), indicating that sedimentation may favor large-seeded species over those with small seeds.

Study Objective

The overall goal of this work was to examine how differing rates of sedimentation may affect community composition in riparian forests associated with ephemeral headwater streams at Ft. Benning, GA. We hypothesize that sediment deposition above an unknown threshold will cause a shift in the plant community in favor of early-successional and ruderal species. This study compared species composition in the overstory, midstory, and understory layers of riparian forests along a gradient of sedimentation rates. The following questions were addressed: 1) How does sedimentation affect species richness, diversity, and evenness within each forest layer?; 2) How do individual species differ in their growth and productivity along a gradient of sedimentation rates?; 3) Does seed size affect species composition along a gradient of sedimentation rates?; 4) How do different sedimentation rates affect the abundances of functional species groups?; and 5) How does sedimentation affect the sediment-retention function of riparian forests?

Based on our study questions, we examined several hypotheses. Primarily, we hypothesized that fewer species would be able to tolerate high sedimentation rates. Therefore, we expected that species richness, diversity, and evenness would decline with increased sedimentation rates. We also expected that some species would increase in relative importance along a gradient of increasing sedimentation rates. We hypothesized that species emergence under high sedimentation would likely be a factor of seed size. Specifically, we hypothesized that species with large seeds would be better adapted to grow under high sedimentation rates than species with small seeds. As with other disturbance types, we expected a shift in community composition toward more early-seral species, such as annuals, shade-intolerant, and N-fixing species. Based on studies of dune systems (Kent et al., 2001; Franks and Peterson, 2003; Chen et al., 2005; Kent et al., 2005; Dech and Maun, 2006; Perumal and Maun, 2006), we hypothesized that sedimentation will favor species adapted to burial, specifically, woody perennial species over herbaceous species. Finally, we hypothesized that greater sedimentation rates would decrease surface roughness, thereby decreasing the ability of riparian forests to retain sediment and increasing the potential sediment export into perennial streams.

Study Site

The study was conducted at Fort Benning Military Installation, near Columbus GA (Fig.1). This U.S. Army installation occupies 73,503 ha in Chattahoochee, Muscogee, and Marion counties of Georgia and Russell county of Alabama. Fort Benning lies within the lower Piedmont and the upper Coastal Plain physiographic regions, however only areas within the Coastal Plain were used in this study. All study areas chosen were associated with ephemeral riparian streams. The study areas are occupied primarily by uneven-aged deciduous or mixed hardwood/pine forests. Common species in the hardwood bottoms were red maple (*Acer rubrum* L.), hazel alder (*Alnus serrulata* (Ait.) Willd.), flowering dogwood (*Cornus florida* L.), titi (*Cyrilla racemiflora* L.), sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.), sweetbay (*Magnolia virginiana* L.), wax myrtle (*Morella cerifera* (L.) Small), blackgum (*Nyssa sylvatica* Marsh.), and water oak (*Quercus nigra* L.). Upland forests are dominated by long-leaf pine (*Pinus palustris* P. Mill.), loblolly pine (*Pinus taeda* L.), and various oak species (*Quercus incana* Bartr., *Q. marilandica* (L.) Muenchh., *Q. phellos* L., *Q. laevis* Walt., *Q. falcata* Michx.). Uplands were primarily managed as long-leaf pine ecosystems with periodic prescribed burns every 1-3 years. Riparian soils included the Bibb (coarse-loamy, siliceous, active, acid, thermic Typic Fluvaquents) and Chastain (fine, mixed, semiactive, acid, thermic Fluvaquentic Endoaquepts) series. Upland soils included the Troup (loamy, kaolinitic, thermic Grossarenic Kandiudults), Lakeland (thermic coated Typic Quartzipsamments), and Cowart (fine-loamy, kaolinitic, thermic Typic Kanhapludults) series (Soil Survey Staff, 2004). Annual mean precipitation is approximately 123 cm yr^{-1}, with driest months in October and November, and wettest months in March and July (cdo.ncdc.noaa.gov/ dlyp/DLYP). Mean annual temperature is 24.3° C, with lowest temperatures observed in January and highest temperatures in July (cdo.ncdc.noaa.gov/ dlyp/DLYP). During the period of this study (2001-2006), 2001 and 2006 had below average annual precipitation and 2003 and 2005 had above average precipitation (ncdc.noaa.gov/IPS/LCDPubs).

Ft. Benning military installation was first designated in 1918, with significant land acquisitions in the 1940s. Prior to becoming a military base, the land was predominantly in row crop agriculture dominated by cotton production. Poor soil conservation practices led to excessive erosion, which is still evidenced by landscape scars and gullies. Current erosion is primarily due to military traffic on unpaved forest roads and trails. This sediment is carried into riparian forests, where increased surface roughness causes the channels to widen, water flow to slow, and sediment deposition. Evidence of sedimentation includes alluvial fans and partially buried tree stems.

Methods

Eighteen circular plots (0.04 ha) were established in riparian forests along nine ephemeral streams in March 2002. Study areas were chosen to span a range of sediment deposition, from no sedimentation to high sedimentation. In April 2004, in an effort to better cover the range of sediment deposition, five plots were dropped from the study and four new plots were added, yielding a total of seventeen plots along twelve ephemeral streams.

Rates of Deposition

Historical deposition rates were measured using a modification of the dendrogeomorphic method described by Hupp and Morris (1990). In July 2003, three to four hardwood saplings (8 to 10 cm in diameter) per plot were excavated to the depth of the root collar of the tree. Stem cross sections taken from the root collar and at the soil surface were used to determine the age of the tree and its age at burial. A sedimentation rate was determined by dividing the sediment depth by the years of deposition. This was repeated in March 2004 for new plots added to the study. Current sedimentation rates were obtained using a modification of the sediment disks described by Kleiss (1993). Metal washers were welded to the center of 1.22 m rebar segments, which were inserted into the soil so that the washer was flush with the surface of the soil. As sediment was deposited, monthly depth measurements were taken by inserting a small rod into the soil until it contacted the washer. Plots were assigned to disturbance categories based on current sedimentation rates: highly disturbed (> 1.0 cm yr^{-1}, HD), moderately disturbed (0.1 < 1.0 cm yr^{-1}, MD), and reference plots (< 0.1cm yr^{-1}, RF). Sedimentation rates were converted to mass measurements (g m^{-2}) by multiplying sediment depth by soil bulk density at each plot. Net sediment export was determined by summing any sediment lost between monthly measurements.

Community Composition

Understory community composition was surveyed annually from 2004 to 2006 in each plot. Plots were surveyed in mid-July when flowers and fruits of most species were available for ease of identification. All species less than 1 m in height were included in the understory survey. Permanent subplots (1-m^2) were placed every 5 meters along transects arranged along each cardinal direction from plot center, for a total of 8 subplots per plot. Large (20 cm) nails and pin flags were placed at each corner of each subplot so that subplots could be relocated. A 1-m^2 nested-frequency quadrat frame was used to determine a cover class score and a nested frequency score for each species in each subplot. Six cover classes were used based on visual estimates, as modified by Daubenmire (1959): 1) 0.1-2%, 2) 3-12%, 3) 13-25%, 4) 26-50%, 5) 51-75%, and 6) >75%. Nested frequency scores were determined according to the following: a score of 4 was given if the species was found within the smallest area (0.0009 m^2), 3 if the species was found in the next larger area (0.0625 m^2), 2 if found only in the second largest area (0.4375 m^2), and 1 if the species was only found in the largest area (1.0 m^2). The ten points identifying these areas along the frame were also used to collect cover point data. Cover point data included bare ground, litter, standing water, and vegetation.

Importance values (IVs) were calculated for each species in each plot as the sum of relative dominance (cover of each species/total cover of all species x 100%) + relative frequency (nested frequency score of each species/total nested frequency of all species x 100%) at each plot. Therefore, importance values were based on a maximum of 200%. Species were classified into groups based on lifespan (annual or perennial), growth form (herbaceous, grass, vine, or woody), origin (native or exotic), and wetland category (wetland or upland species) as designated in the Synthesis of the North American Flora (1999). Nomenclature follows the USDA PLANTS database (USDA, 2005). Species which could not be determined were identified to the genus level. Mean seed size was calculated by using the mean reported seed size for each species (Radford et al., 1968).

Midstory species were inventoried each June, from 2004 to 2006. All woody species < 5 cm diameter at breast height (DBH) and ≥ 1 m in height were included in this survey. Within each plot, four 1.80-meter radius subplots (0.001 ha) were placed along the perimeter of the plot at random compass bearings. A count was taken of each species meeting the size requirements. Biomass was estimated using species-specific allometric equations (Elliot and Clinton, 1993) based on root crown diameter and height measurements.

Overstory species were inventoried each winter by measuring diameter at breast height (DBH, approximately 1.3 m in height) of all trees ≥ 5 cm in diameter. Trees were identified according to species and tagged with individual numbers at DBH, and were measured at the same height each year. Original and new plots were inventoried beginning December 2002 and December 2004, respectively, and inventory continued through 2006. Stem biomass production for hardwood species was calculated from allometric equations developed by the USDA Forest Service for the Gulf Atlantic Coastal Plains (Clark et al., 1985) and pine species biomass equations were adapted from Ter-Mikaelian and Korzukhin (1997).

Environmental Variables

Environmental variables used in the analysis included air temperature, soil temperature, relative light intensity, soil bulk density, N-mineralization rate, soil texture, and soil pH. Air temperature, soil temperature, and relative light intensity were measured using Hobo temperature/light dataloggers at 1 hour intervals (Onset Computer Corporation, Bourne, MA). Two dataloggers were placed at each plot and housed in a plastic waterproof container approximately 1.5 m off the ground. A soil temperature sensor was attched to each data logger and was buried approximately 15 cm below the soil surface. Data were downloaded every 2-3 months using a Hobo shuttle (Onset Computer Corporation, Bourne, MA).

Soil bulk density was measured in September 2004 using a 5-cm diameter double cylinder push probe. Three samples were taken from each plot (0-7.5 cm depth), dried to a constant mass at 105° C, and weighed. The method for determining N-mineralization rates is described in Chapter 3. Soil pH was determined from soil samples collected in May 2003 and again in March 2006. Soil samples were collected in May 2003 and again in March 2006 and sent to the Auburn University Soil Testing Laboratory. Soils were analyzed for pH, P, K, Mg, Ca, Al, B, Cu, Fe, Mn, Na, and Zn. Analysis of K, Ca and Mg were performed using an atomic absorption (AA) spectrophotometer, while cations and P samples were determined by inductively coupled argon plasma spectrophotometry (ICAP). Bulk density was measured in September 2004 using a 5-cm diameter double-cylinder push probe. Three samples were taken from each plot (0-7.5cm depth), dried to a constant mass at 105° C for 48 hours and weighed. Three soil samples were taken at 5 depths (0-7.5, 7.5-15, 15-20, 25-30, and 35-40 cm) from each plot to calculate soil texture. Soil texture was determined using the hydrometer method (Gee and Bauder, 1986) to determine particle size distributions. Soil texture from 0-15 cm was determined using the hydrometer method (Gee and Bauder, 1986) to determine particle size distributions.

Statistical Analyses

To better understand the effects of sedimentation on community composition, vegetation data were evaluated in terms of: 1) overall species diversity, 2) IVs of functional groups along different environmental gradients, 3) multivariate analysis on species matrices, and 4) IVs of individual species along a gradient of sedimentation rates. Species diversity indices were calculated for overstory, midstory, and understory layers in each plot. Since ANOVA resulted in no significant differences between years, means were pooled across all years. For each forest layer, community diversity indices included species richness (S), Shannon's diversity index (H'), and Pielou's evenness (J'):

Shannon's diversity index (Shannon and Weaver, 1949) $H' = -\sum^{S} (p_i \ln p_i)$ (1)

Pielou's evenness (Pielou, 1966) $J' = \frac{H'}{H_{\max}}$ (2)

where p_i is the fraction of individuals belonging to the i-th species and $H_{\max}$ is the maximum level of diversity possible, measured as the natural log of S. Overstory and midstory species were compared using mean species biomass, and understory species were compared using IVs. Regression analysis was used to assess relationships between environmental variables and IVs or biomass of functional groups, using PROC REG (SAS-Institute, 2002-2003). Both linear and non-linear models were compared to determine best fit. Mean comparisons among disturbance classes were performed using analysis of variance (ANOVA) (PROC GLM, SAS Institute 2002-2003). Following significant ($p<0.05$) ANOVA results, Tukey's HSD test was performed to detect significant differences among means.

Both detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were used as complementary approaches (Gilliam et al., 1995; Odland and Moral, 2002; Lyon and Gross, 2005; He et al., 2007) to relate species composition to environmental variables such as sedimentation rate, bulk density, N-mineralization rate, and soil texture. Both analyses were done using PC-ORD 4.0 (McCune and Mefford, 1999), in which default options were used and rare species were down-weighted (McCune et al., 2002). The Monte Carlo permutation was used with CCA to test the null hypothesis that no relationship existed between the species and environmental matrices. Ordination analyses in the understory layer used IV data for each species, and biomass data were used for analyses of mid- and overstory layers.

Results

Sedimentation Rates

Current sedimentation rates ranged from <0.01 to 5.53 cm yr^{-1} (Table 1), which is within the range of sedimentation rates reported for riparian forests (Cooper et al., 1987; Hupp and Morris, 1990; Hupp and Bazemore, 1993; Hupp et al., 1993; Kleiss, 1996; Wardrop and Brooks, 1998; Heimann and Roell, 2000; Rybczyk et al., 2002). Mean current sedimentation rates on RF, MD, and HD plots were 0.05 ± 0.04, 0.38 ± 0.11, and 2.89 ± 0.39 cm yr^{-1}, respectively. Equivalent sediment mass rates ranged from 0.5 to 996

Mg ha^{-1} yr^{-1} (Table 1). Mean historical sedimentation rates (estimated over 25 years) ranged from 0 to 4.0 cm yr^{-1} (Table 1). Although significant, historical rates were only weakly correlated to current sedimentation rates ($r^2=0.22$, $p<0.01$).

Community Composition

A total of 120 species was found across all plots: 36 species of trees, 32 species of shrubs, 7 species of vines, and 45 species of herbs and grasses. Species present in all plots were *Quercus nigra*, *Smilax* spp., and *Vitis rotundifolia* Michx. Species present in greater than 75% of all plots were *Nyssa sylvatica, Liquidambar styraciflua*, *Pinus taeda*, *Acer rubrum*, *Magnolia virginiana*, and *Morella cerifera*.

Plots ranged in species richness from 21 to 45 species. Mean species richness (S) did not differ significantly among disturbance classes ($F_{df2,\,27}=0.29$, $p=0.76$). Total species richness had a quadratic relationship with sedimentation rate ($r^2=0.17$, $p<0.01$, Fig. 2). There was a significant, positive, linear relationship between species richness of the herbaceous layer (S_h) and current sedimentation rates ($r^2=0.55$, $p<0.01$), while tree species richness (S_t) had a significant, negative, linear relationship with sedimentation rate (Fig. 3). S_h was significantly greater in HD plots than MD and RF plots ($F_{df2,\,27} = 7.55$, $p<0.01$) ($r^2=0.49$, $p<0.01$), while differences in S_t were not significant ($F_{df2,\,13} =2.78$, $p=0.10$). Species richness of vines ($S_{v)}$ and shrubs (S_s) did not differ by disturbance class and showed no relationship with current sedimentation rate (Table 2).

Understory Layer

The understory layer was considered to be all plants ≤ 1 m in height. Disturbance classes did not significantly differ in *H’*, *S*, and *J’* values (Table 3). Relative importance values for understory species indicated that HD plots had a greater proportion of exotic ($F_{df2, 26}$ = 11.5, p<0.01) and annual species ($F_{df2, 69}$= 7.22, p<0.01) than RF plots. Among all plots, native species had significantly greater (t =-3.5, p<0.01) mean IVs than exotic species (29.6 ± 0.59 % and 17.8 ± 1.93 %, respectively). HD plots had a significantly greater proportion of exotic species (mean IV = 16.0% ± 0.9) compared to MD plots (mean IV= 5.14% ± 2.53), with no exotic species found in RF plots (Fig. 4). Conversely, native species had significantly lower ($F_{df2, 533}$=3.60, p=0.03) IVs in HD plots (mean IV=28.1 ± 1.03) compared with MD (mean IV=31.6 ± 0.98) and RF plots (mean IV=28.8 ± 1.02). Among all plots, perennial species had a significantly greater (t =-3.3, p<0.01) IV than annual species (29.8 ± 0.60 and 22.2 ± 2.04, respectively). Annual species made up a smaller proportion of the vegetation in RF plots compared with HD and MD plots and perennial species made up a smaller proportion of the vegetation in HD plots compared with RF and MD plots (Fig. 5). Importance values of herbs, grasses, and woody plants did not differ significantly among disturbance classes ($F_{df2, 99}$=1.50, p=0.23; $F_{df2, 92}$=0.83, p=0.44, $F_{df2, 781}$=0.34, p=0.71, respectively). However, when IVs of herbs and grasses were combined, HD plots had significantly lower proportions (IV= 18.2 ± 1.12) compared with MD (IV= 30.5 ± 2.80) and RF plots (IV= 31.6 ± 6.13) ($F_{df2, 99}$=12.8, p<0.01).

Disturbance classes differed in IVs of wetland species ($F_{df2, 648}$ =16.4, p<0.01). Wetland species were reduced in HD plots (IV=24.4 ± 0.92) compared to MD (IV= 33.1 ± 1.29) and RF plots (IV= 28.7 ± 1.19). Among all plots, wetland species made up 85% of all species present in the understory layer. Upland species IVs did not differ between

HD and MD plots ($F_{df1,\,45}$=0.72, p=0.62) and no upland species were present in RF plots (Fig. 6).

Mean seed size of understory species was used to determine whether seed size differed among disturbance classes. In contrast to predictions, larger seeded species were more frequently found in RF plots compared with HD and MD plots. The mean seed size of species present in RF plots was 9.4 ± 0.4 mm compared to 6.9 ± .26 and 6.3 ± 0.23 mm in MD and HD plots, respectively ($F_{df2,\,535}$ =4.93, p<0.01) (Fig. 7).

As expected, understory light intensity was greatest in plots with the greatest tree mortality rates. MD plots had significantly lower tree mortality ($F_{df2,\,425}$=7.54, p<0.0) compared to HD plots and significantly lower light understory light intensity ($F_{df2,\,380,888}$=348, p<0.01) compared to HD or RF plots (Fig. 8). Regression analysis revealed significant positive relationships between light intensity and sedimentation rate (r^2=0.40, p<0.01) and tree mortality and sedimentation rates (r^2=0.72, p<0.01). Total understory cover had a mean of 96 ± 12 % among all plots and did not differ by disturbance class ($F_{df2,\,93}$= 1.53, p=0.22).

Midstory Layer

The midstory layer consisted of all woody plants ≥ 1 m in height and ≤ 5 cm diameter at DBH. Therefore, some woody plants were considered part of the understory and midstory layers. There were 55 species of trees and shrubs present in the midstory layer among all plots. Among disturbance classes, mean *S*, *H'* and *J'* did not differ (Table 3), though stem density was significantly greater (F_{df2} =7.8, p<0.01) in HD plots (7.08 ± 0.85 stem m^{-2}) compared with MD (2.87 ± 0.36 stem m^{-2}) and RF plots (3.84 ± 0.36 stem m^{-2}).

Across all plots, shade-tolerant species had a significantly (t-statistic=-3.6, $p<0.01$) greater stem density than shade-intolerant species, with significantly greater densities (F_{df2}=5.06, $p<0.01$) in HD plots (2.78 ± 0.37 stems m^{-2}) compared with MD (1.44 ± 0.29 stems m^{-2}) and RF (2.1 ± 0.32stems m^{-2}) plots. Stem densities of shade-tolerant and shade-intolerant species did not differ in HD plots (F_{df1}=0.09, p=0.76), but in MD and RF plots there was a significantly lower density of shade-intolerant species compared with shade-tolerant species (F=4.04, p=0.05, and F=8.68, $p<0.01$, respectively) (Fig. 9).

Nitrogen-fixing species, such as *Morella cerifera* and *Alnus incana*, were most often found in the midstory layer. The stem density of nitrogen-fixing species significantly increased in plots receiving greater sediment deposition (Fig. 10, r^2=0.58, $p<0.01$). HD plots had significantly ($F_{df2, 184}$=16.2, $p<0.01$) greater densities of N-fixing species (2.4 ± 0.12 stems m^{-2}) compared with MD and RF plots (0.7 ± 0.04 and 1.1 ± 0.02 stems m^{-2}, respectively).

Overstory Layer

Across all plots, there were 25 species of trees found in the overstory layer. RF plots had significantly greater *H'* and *J'* compared with HD and MD plots (Table 3). There were significant negative relationships between *S* and current sedimentation rate (Fig. 11a, r^2=0.60, $p<0.01$), *H'* and current sedimentation rate (Fig. 11b, r^2=0.60, $p<0.01$), and *J'* and current sedimentation rates (Fig. 11c, r^2=0.65, $p<0.01$).

Unlike understory and mid-story layers, there were significant relationships between the overstory layer and environmental and biological gradients. Species diversity had significant linear relationships with N-mineralization rate (described in

Chapter 3) and soil bulk density (Fig. 12). Forest productivity (NPP, described in Chapter 2) had a non-linear relationship with *S* (Fig. 13). The point of decline in NPP in plots with the greatest S_t corresponded to plots with very high sedimentation rates. These plots also had high tree mortality rates (Fig. 8a), contributing to a decrease in NPP.

Species Ordination

Initial ordinations in all layers produced outliers from the two K11 plots, which were greater than half the axis-distance from the rest of the data along most axes in both DCA and CCA ordinations. These plots were located at higher elevations, were consequently drier and sandier, and had scrub-oak communities. These plant communities were distinct from those on all other plots and inclusion of these K11 plots resulted in compression of the other plots in the ordination graphs. Therefore, all ordinations were repeated with these outliers removed (Kent and Coker, 1992; Gilliam et al., 1995).

Detrended correspondence analysis (DCA) ordination in the understory layer accounted for 40.7% and 21.7% of the variation in species data in axis 1 and axis 2, respectively. The influence of soil texture on understory species composition was most strongly correlated to axis 1, with percent sand having a significant negative correlation with the first axis (Table 4). Soil temperature was most strongly correlated to axis 2. These relationships are reflected in the biplot vectors in Fig. 14. Plots did not cluster by disturbance classes. Bulk density and N mineralization rate were not significantly correlated to variation in plant species composition. Eigenvalues for canonical correspondence analysis (CCA) were similar to those of DCA, however only axis 2 had a significant eigenvalue (λ=0.35, p=0.03) according to the Monte Carlo permutation test.

In the midstory layer, DCA accounted for 90.0% and 35.2% of the variation in species data in axis 1 and 2, respectively. As with the understory layer, axis 1 was most strongly correlated to percent sand, though soil temperature also had a significant correlation with axis 1 (Table 4). Historical sedimentation rates and soil moisture were both significantly correlated to axis 2. As with the understory layer, there was no strong grouping of plots by disturbance class (Fig. 15). Axes 1 and 3 had significant eigenvalues in CCA, according to the Monte Carlo permutation test ($\lambda=0.88$, $p=0.03$ and $\lambda=0.45$, $p=0.03$, respectively).

In the overstory, DCA axis 1 and 2 accounted for 53.1% and 24.2% of the variation in the species data, respectively. Percent sand and soil temperature were significantly ($p<0.05$) correlated to axis 1, with soil moisture significantly ($p<0.05$) correlated to axis 2 (Table 4). Plots did not group by disturbance class (Fig. 16). In CCA ordination, only axis 2 had a significant eigenvalue ($\lambda=0.42$, $p=0.02$) and a significant species-environmental interaction (0.98, $p=0.03$), according to the Monte Carlo permutation test.

Sediment Retention

Net sediment export was calculated by subtracting total sediments exported from total sediment imported. Net sediment export was significantly ($F_{df2,\,84}=9.42$, $p<0.01$) greater in HD plots compared with MD and RF plots (-0.071 ± 0.001, -0.01 ± 0.001, and -0.01 ± 0.001 g m^{-2} yr^{-1}, respectively). The ability to retain trapped sediment declined with increasing sedimentation rates. Surface roughness was estimated by combining values of vegetation and litter cover (%) found by point cover estimates. Net sediment export had a significant negative relationship with surface roughness ($r^2=0.56$, $p<0.01$).

Surface roughness decreased with increasing sedimentation rates (r^2=0.67, p<0.01) (Fig. 17). The burial of vegetation and litter by sediment deposition likely led to very homogeneous soil surfaces with little microrelief. Although it has been suggested that sedimentation may lead to the loss of surface roughness and a reduction in sediment retention (Hupp and Bazemore, 1993; Werner and Zedler, 2002), sediment export rates and surface roughness measures have not previously been reported. The present study shows an inverse linear relationship between surface roughness and net sediment export (Fig. 17), indicating a loss in the sediment retention function of riparian forests associated with high sedimentation rates.

Discussion

Community Composition

Similar to other ecosystem disturbances, sedimentation may select for stress-tolerant and opportunistic species (Grime, 1973; Barbour et al., 1998; Wardrop and Brooks, 1998; Levine and Stromberg, 2001). The intermediate stress hypothesis suggests that species richness will be greatest at moderate ranges of environmental stress (Grime, 1979). This is generally interpreted to mean that high levels of stress create conditions too harsh for most species and that low levels of stress will favor only a few species through competitive exclusion (Rosenzweig and Abramsky, 1993; Vonlanthen et al., 2006). Ito et al. (2006) found fewer and more specialized species in areas of frequent sediment deposition. However, there is no previous evidence that suggests that stress from sedimentation may promote greater species richness or diversity.

In experimental studies in wetlands, species richness and abundance have been found to decrease with increased disturbance caused by sedimentation (Welling and

Becker, 1990; Bonis and Lepart, 1994; Dittmar and Neely, 1999; Werner and Zedler, 2002; Barry et al., 2004; Mahaney et al., 2004b; Peterson and Baldwin, 2004). In a study of sedge meadows, Werner and Zedler (2002) calculated that 1.2 species are lost for every 10 cm increment of sediment. They hypothesized that this was due to the smaller proportion of organic matter and greater bulk density of sediment, as well as physical damage by burial and loss of germination sites. In an Alaskan sedge wetland, van der Valk et al. (1983) found decreased shoot density of 35, 72, and 93% with burial depths of 5, 10, and 15 cm, respectively. Peterson and Baldwin (2004) found a decrease in species richness with the addition of 2 cm of sediment, as did Dittmar and Neely (1999). However, Peterson and Baldwin (2004) found no difference with the addition of 0.5 cm.

Species richness in this study was similar to the range reported in other Eastern U.S. riparian forests (Gilliam et al., 1995; Elliot et al., 1997; Howard and Lee, 2003) following disturbance. The quadratic relationship between total *S* and sedimentation rate (Fig. 2) suggests that *S* peaked with increased sedimentation until a threshold was reached but *S* declined at sedimentation rates between 3.9 and 4.3 cm yr^{-1}. This quadratic relationship of species richness along a disturbance gradient has been described by others (Nakamura et al., 1997; Wilson and Tillman, 2002; Cornwell and Grubb, 2003) and is consistent with the intermediate disturbance hypothesis (Grime, 1979).

The quadratic relationship between total *S* and sedimentation may result from the two very different patterns of S_h and S_t. Herbaceous vegetation showed a strong increase in richness with increasing sedimentation, while trees species declined. These patterns may have been driven by increased tree mortality in plots associated with high sedimentation. High mortality likely led to a decline in S_t and created gaps in the overstory. Presumably, these gaps provided higher levels of light, moisture, and nutrients that in turn supported a greater diversity of herbaceous species in the understory (Wilson and Shure, 1993; Gilliam et al., 1995). Greater species richness is often found where disturbance creates gaps in a forest canopy (Halpern and Spies, 1995; Howard and Lee, 2003; Zenner et al., 2006). However, Elliot et al. (1997) reported the greatest S_h in years preceding clearcutting compared with 20 years following the clearcut.

Tolerance to Sedimentation

Species tolerant of disturbance are those that are able to establish, grow, and reproduce in stressful environments (Barbour et al., 1998). The major stress associated with sedimentation is burial of seeds and vegetative structures (Franks and Peterson, 2003; Shi et al., 2004; Kent et al., 2005; Zheng et al., 2005; Perumal and Maun, 2006). Riparian plants, in general, possess adaptations to recover from flooding stress such as root suckering, stem flexibility, and adventitious root development (Naiman and Decamps, 1997). These adaptations also have been associated with plants adapted to dune ecosystems (Franks and Peterson, 2003; Dech and Maun, 2006; Perumal and Maun, 2006). Studies in dune ecosystems have hypothesized that perennials display these traits to a greater extent and may be better adapted to burial than annual species (Kent et al., 2005). However, the present study indicated a decline in perennial species importance and an increase in annual species in HD plots compared with MD and RF plots.

Sedimentation, as with other disturbances, may act as a filter to select for more ruderal species (Dittmar and Neely, 1999; Kent et al., 2005). Grime (1979) suggests that ruderal species are generally small, annual herbs which can reproduce quickly. An increase in exotics, annuals, and upland species at the expense of residual perennial, native, and wetland species in the understory of HD plots may be an indication that ruderal species increase with increased sedimentation. These plots also had a greater density of shrubs and saplings compared with MD and RF plots. Of these shrubs and saplings, there were a greater proportion of shade-intolerant and nitrogen-fixing species in HD plots, suggesting these are early-seral species (Barbour et al., 1998). In forests recovering from disturbance, shade tolerant species generally dominate in later successional stages (Gilliam et al., 1995).

Greenhouse studies have shown that species performance varies greatly with the addition of sedimentation. Some species are very tolerant, others are moderately tolerant, and still others are intolerant to sediment burial (Ewing, 1996; Wardrop and Brooks, 1998; Mahaney et al., 2004a). Mahaney et al. (2004a) found that although fewer species emerged with sediment additions, those that did emerge did not show a reduction in growth. They suggest that the decrease in emergence lowers interspecific competition, allowing more resources for individuals that emerge. In dune succession, early colonizers are often “dune species,” which have stimulated photosynthetic rates and increased above- and belowground biomass following burial (Shi et al., 2004; Kent et al., 2005; Perumal and Maun, 2006). Dech and Maun (2006) found that in a shifting sand dune, woody plants intolerant of burial had lower shoot and adventitious root biomass and eventually died, tolerant species had a neutral response, and ruderal species had enhanced growth following burial. Others have also found that dune-adapted species exhibit stimulation in growth following burial (Kent et al., 2001; Shi et al., 2004; Perumal and Maun, 2006).

Species which had greater growth or abundance in plots with greater sedimentation were considered sediment-tolerant species (Table 5). In the understory layer, species were considered sediment-tolerant if they had significant positive relationships between current sedimentation rates and IV, such as *Acer rubrum*, *Alnus serrulata*, and *Morella cerifera*. In the midstory layer, tolerant species were those which had significant positive relationships between current sedimentation rates and biomass, such as *Acer rubrum*, *Crataegus flava* Ait., *Morella cerifera*, *Nyssa sylvatica*, *Pinus taeda*, and *Q. marilandica*. Most overstory species did not occur in all plots, therefore there were no species with significant regression relationships between current sedimentation rates and mean annual growth measurements. Therefore, species were considered tolerant if they had greater mean annual growth in HD plots compared with MD and RF plots (found using ANOVA), such as *Morella cerifera*, *Pinus echinata* Mill., *Q. hemisphaerica* Bartr. ex Willd, *Prunus serotina* Ehrh., and *Cyrilla racemiflora*. Species were considered intolerant to sediment deposition if growth declined significantly in HD plots. Species that had no significant relationship with current sedimentation rates or did not differ between disturbance classes were considered neutral species.

Acer rubrum showed different responses in the overstory layer than in the understory and midstory layers. *Acer rubrum* showed tolerance in the understory and midstory layers, where a significant positive relationship existed between current sedimentation rates and RI values and biomass. However, in the overstory, *Acer rubrum* annual growth was significantly greater in MD plots compared with HD and RF plots. Therefore it was considered a neutral species in the overstory layer.

Previous studies have reported a shift in species dominance associated with sedimentation (Leendertse et al., 1997; Dittmar and Neely, 1999). In the present study, dominant species in RF and MD plots were *Nyssa sylvatica*, *Acer rubrum*, *Pinus taeda*, *Liquidambar styraciflua*, and *Quercus nigra*. In HD plots, the biomass of *Pinus taeda*, *Liquidambar styraciflua*, and *Quercus nigra* were significantly reduced, leaving two dominant species: *Nyssa sylvatica* and *Acer rubrum*.

Seed Size

Several studies have found a one-time application of 0.5-1.0 cm of sediment can reduce seedling emergence in small-seeded species (Jurik et al., 1994; Gleason et al., 2003; Mahaney et al., 2004b; Peterson and Baldwin, 2004; Petru and Menges, 2004). For larger seeds, a threshold appears to exist around 2 cm (Welling and Becker, 1990; Bonis and Lepart, 1994; Barry et al., 2004; Zheng et al., 2005). From these studies, it appears that sediment differentially affects small and large seeded species. Therefore, sedimentation could potentially cause a shift in community composition in favor of large-seeded species. However, results from this study indicated that species with the largest mean seed size were more frequently found in RF plots compared with MD and HD plots. One explanation for these unexpected results is that smaller seeds may be better suited to the loss of microtopography associated with sedimentation. While large seeds may be more likely to wash away during overland flow events with the decrease in surface roughness, there may be enough microtopography to allow small seeds limited protection. A second explanation may be found in species emergence. It is probable that seed germination was similar across all disturbance types, but the more ruderal species could only emerge in disturbed habitat where there was less competition. Ruderal species generally produce many small seeds that can be dispersed by wind or water and can remain dormant in the seed bank for a very long time (Barbour et al., 1998). Mean seed size in HD and MD plots reflected the greater proportion of ruderal species (annuals and exotics) in those plots.

Species Richness and Productivity

Many studies explored the relationship between plant diversity and productivity, a topic which has undergone much debate in the literature (Rosenzweig and Abramsky, 1993; Giese et al., 2000; Mittelbach et al., 2001; Tilman et al., 2001; Cornwell and Grubb, 2003; Zak et al., 2003; Houseman and Gross, 2006). Some evidence suggests that greater plant diversity promotes greater rates of net primary productivity, though the underlying mechanisms are not well understood (Tilman et al., 2001; Cornwell and Grubb, 2003; Zak et al., 2003). Several studies suggest that N mineralization rates increase with greater species diversity, leading to an increase in litter nutrients and an increase in productivity (Berendse, 1994; Zak et al., 1994; Zak et al., 2003). In the present study, S_t had non-linear relationships with NPP, indicating that diversity peaked and then declined along a gradient of productivity (Fig. 13). This pattern has been described within different biomes in Europe (Cornwell and Grubb, 2003) and in about 30% of the studies reviewed by Waide et al. (1999). There was also a strong positive relationship between overstory H' and N mineralization rates (Fig. 12a) (see Chapter 3).

Ordination

Heterogeneity in forest structure (i.e., differing species among forest layers) often results from differing competitive forces or life-history strategies (Gilliam et al., 1995).

In the understory, greater herbaceous species cover is found in areas of greater light and, as light becomes limited, woody species dominate (Wilson and Shure, 1993; Gilliam et al., 1995). The herb layer also may be more sensitive to edaphic factors and disturbance (Peterson and Rolfe, 1982; Pregitzer and Barnes, 1982; Moore and Vankat, 1986; Gilliam et al., 1995) than overstory layers. Using ordination tools, forest studies comparing environmental gradients among forest layers have found a lack of correlation between species response of tree, herb and shrub layers (McCune and Antos, 1981; Gilliam et al., 1995; Lyon and Gross, 2005), suggesting forest layers respond to different sets of environmental gradients or respond differently to the same gradients.

In the present study, all three vegetation layers showed strongest correlations in axis 1 of DCA ordinations with soil texture, represented by percent sand, with mid- and overstory layers also having significant correlations with soil temperature and soil moisture. These results indicate that, in all three forest layers, changes in species composition are responding to the same gradient, specifically the physical soil attributes of texture, temperature, and moisture. This suggests that changes in the physical structure of soil associated with sedimentation are substantial enough to drive changes in the entire forest community. Surprisingly, light, N-mineralization rate, and soil bulk density were not correlated to any of the ordination axes.

Abiotic Soil Factors

High rates of sediment deposition have been associated with overstory mortality (Cavalcanti, 2004) and loss of microtopography (Werner and Zedler, 2002). It is likely that changes in abiotic soil factors such as moisture and bulk density may lead to increased overstory mortality, which in turn would influence understory light and soil temperatures. Sedimentation has also been associated with greater nutrient availability (Olde Venterink et al., 2006). However, few studies have investigated how sediment affects physical soil properties directly. In a field experiment, Koning (2004) found that the one-time addition of 2 cm of sediment resulted in increased bulk density, decreased organic matter and CEC, and decreased levels of P, Ca, and Mg. However, there was no difference in soil temperature or N availability. In the present study, there was a significant increase in soil bulk density and a decline in CEC with increased sedimentation rates (see Chapter 3). The factor that was most highly correlated to vegetational changes was the change in soil texture and its effect on soil moisture (Fig. 18). Patterns of vegetation distribution are highly influenced by the ability of soils and sediments to hold water (Naiman and Decamps, 1997). An increase in sand and corresponding declines in the proportion of silt and clay may have affected the water-holding capacity of the soil, organic matter, and nutrient associated with clay particles (Fisher and Binkley, 2000).

Conclusions

Response of the plant community to a gradient of sedimentation varied among forest layers. Therefore, the hypothesis that species richness, diversity, and evenness will decline with sedimentation was only supported in the overstory layer. In the herbaceous layer, species richness, diversity, and evenness increased with increasing sedimentation rates. The mid-story, or shrub layer, did not show a significant relationship with increasing sedimentation and the overstory, or tree layer, declined in richness, diversity, and evenness with increasing sedimentation.

Individual species exhibited different levels of tolerance to sedimentation. Within the same species, the levels of tolerance appeared to vary among forest layers. No overstory species responded positively to sedimentation. Contrary to predictions, there was no evidence to suggest that species with larger seed size may be more tolerant of sedimentation. In fact, these data suggest that more tolerant species are those with smaller seeds.

As hypothesized, results indicate that sediment deposition in riparian forests may drive changes in community composition towards more early-seral and opportunistic species. In the understory layer, there was a shift toward annual and exotic species in plots receiving high sedimentation rates. There was an increase in shrub biomass and density, shade intolerant species, and N-fixing species associated with high sedimentation in the mid-story layer. The overstory layer had greater mortality rates in HD plots, which likely allowed for the establishment of opportunistic species in the understory.

The effects of sedimentation drive changes in the physical attributes of soil, such as texture, temperature, and moisture, which may be long-lasting in nature. Soil texture was highly correlated to species composition in all layers of the forests, suggesting that changes in soil texture by sedimentation may have a substantial impact on species diversity in riparian forests. It is likely that the strongest factor driving changes in species composition is the decline in water availability in soils receiving high rates of sediment additions. The lower water holding capacity of sandier soils may affect soil microbes (Zak et al., 1994; Badalucco and Kuikman, 2001), N- mineralization rates (Cassman and Munns, 1980; Pinay et al., 1995), and plant uptake, each of which may drive changes in the plant community.

Riparian forests serve a major function in preserving water quality through filtering and retaining sediments and nutrients. However, results from this study demonstrate that highly sedimented areas may become a source of sediment rather than a sink. The loss of surface roughness through burial of vegetation and litter and high tree mortality may eliminate this critical function of riparian forests, making sediment in surface runoff more likely to reach streams. It it important to note that these rates were found in forests that have been receiving continuous sediment inputs over a long period of time.

Riparian forests serve an essential role in maintaining water quality. Anticipated increases in land development will likely lead to greater erosion and sediment deposition in these areas. Results of this study suggest that forests with sedimentation rates greater than 1 cm yr^{-1} had increased annual, exotic, and upland species and a decreased ability to trap and retain incoming sediments. In order to preserve the integrity, biodiversity, and function of these systems, it is essential to prevent the influx of erosional depositions into these areas. The preservation and restoration of intact riparian forest should be a priority for land managers.

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Table 1. Summary of environmental variables associated with each plot (plot codes are listed under each disturbance class) in riparian forests at Ft. Benning, GA, 2004-2006.

Environmental variable	**Disturbance Class**																
	HD					**MD**							**RF**				
	D12B	**F1WAd**	**K11d**	**F3**	**D12A**	**I3Bd**	**F1Wb**	**K11c**	**I3C**	**F1E**	**F4Ac**	**I3Ad**	**F1WAc**	**F4C**	**I3Bc**	**F4Ad**	**I3Ac**
Current sedimentation rate (cm yr^{-1})	5.52	4.38	3.96	1.85	1.39	0.78	0.46	0.43	0.23	0.15	0.14	0.11	0.09	0.01	0.01	0.00	0.00
Historic sedimentation rate (cm yr^{-1})	2.07	1.15	1.71	1.97	4.00	0.32	1.29	0.50	2.06	0.20	0.00	1.48	0.00	0.00	0.00	0.00	0.00
Current sedimentation rate (g m^{-2} yr^{-1})	0.99	0.77	0.70	0.33	0.22	0.11	0.08	0.07	0.04	0.01	0.07	0.02	0.01	<0.01	<0.001	<0.001	<0.001
N mineralization rate (g ha^{-1} day^{-1})	50.2	134	76.2	64.2	107	151	100	77.0	91.8	542	213	233	145	177	192	140	171
Bulk density (Mg m^{-3})	1.80	1.76	1.77	1.80	1.58	1.41	1.62	1.64	1.57	0.99	0.51	1.51	1.02	0.60	1.54	1.31	1.40
Soil texture (% sand)	93.8	96.7	96.7	91.7	80.8	84.8	92.7	91.0	85.8	89.2	76.3	73.3	92.0	87.0	81.6	91.3	60.8
pH	5.80	5.00	5.90	5.20	4.20	4.80	4.70	5.20	4.70	4.70	4.50	4.70	5.30	4.20	4.60	4.40	4.70
Soil moisture (%)	16.4	10.3	6.51	13.4	12.6	11.3	12.8	8.39	28.3	55.7	59.3	16.5	32.2	28.6	11.8	20.1	21.5
Understory light (log lumens m^{-2})	1.60	1.70	1.70	1.50	1.37	1.40	1.30	1.70	1.40	1.40	1.60	1.60	1.60	1.50	1.40	1.60	1.60
Soil temperature (C)	13.5	16.4	17.1	16.8	16.5	18.1	16.9	17.1	16.1	16.9	17.3	17.3	17.3	16.9	18.1	17.4	17.3

Table 2. Comparison of species richness among disturbance classes and growth form in riparian forests at Ft. Benning, GA, 2004-2006. Standard errors are in parentheses. Letters indicate significant differences among disturbance classes by Tukey's HSD (α=0.05).

Mean species richness (species per plot)					
	Disturbance class				
Growth form	HD (N=5)	MD (N=7)	RF (N=5)	F-value	p-value
Trees	11.6 (0.8)	13.9 (1.1)	15.0 (0.9)	2.78	0.10
Shrubs	9.4 (2.0)	9.7 (0.9)	6.6 (1.2)	1.56	0.24
Vines	2.8 (0.4)	2.6 (0.5)	2.3 (0.5)	0.29	0.76
Herbs	10.5 (2.8)^{a}	3.4 (0.7)^{b}	3.5 (0.7)^{b}	7.55	0.008

Table 3. Comparison (by ANOVA) of Shannon's diversity index (*H'*), species richness (*S*), and community evenness (*J'*) among disturbance classes and canopy layers in riparian forests at Ft. Benning GA, 2004-2006. Standard errors are in parentheses. Letters indicate significant differences among disturbance classes by Tukey's HSD (α=0.05).

Canopy Layer	**Variable**	**Disturbance Class**							
		HD		**MD**		**RF**		**F-value**	**p-value**
Understory	H'	2.50	(0.10)	2.30	(0.10)	2.40	(0.10)	2.54	0.09
	S	17.40	(1.00)	15.00	(1.00)	15.00	(1.30)	3.05	0.06
	J'	2.00	(0.20)	1.30	(0.20)	1.50	(0.20)	2.95	0.07
Midstory	H'	1.20	(0.10)	1.30	(0.00)	1.30	(0.10)	1.35	0.26
	S	10.90	(0.70)	11.50	(0.60)	11.80	(0.40)	0.32	0.73
	J'	2.20	(0.20)	2.30	(0.10)	2.30	(0.10)	0.06	0.94
Overstory	H'	1.2^{b}	(0.10)	1.4^{ab}	(0.20)	1.7^{a}	(0.10)	7.24	<0.01
	S	6.10	(0.90)	6.50	(0.70)	8.50	(0.60)	3.05	0.06
	J'	2.0^{b}	(0.20)	2.7^{ab}	(0.50)	3.6^{a}	(0.30)	8.22	<0.01

Table 4. Correlations between environmental variables and DCA axes 1 and 2 ordination scores for each vegetation layer in riparian forests at Ft. Benning, GA, 2004-2006.

			Pearson's correlation coefficient					
Environmental variable	**Mean**	**SE**	**Understory layer**		**Midstory layer**		**Overstory layer**	
			Axis 1	**Axis 2**	**Axis 1**	**Axis 2**	**Axis 1**	**Axis 2**
Current sedimentation rate (cm yr^{-1})	1.1	0.4	-0.5	0.5	-0.3	-0.1	-0.4	-0.4
N mineralization rate (g ha^{-1} day^{-1})	148	20.3	-0.1	-0.3	0.2	0.3	0.1	0.3
Bulk density (Mg m^{-3})	1.4	0.1	-0.05	0.4	0.03	-0.5	0.05	-0.4
Historic sedimentation rate (cm yr^{-1})	1.0	0.3	0.005	0.5	-0.3	-0.5*	-0.07	-0.2
Soil texture (% sand)	86.2	2.3	-0.7*	-0.08	-0.6*	0.2	-0.6*	-0.3
pH	4.9	0.1	-0.3	0.5	-0.06	-0.04	-0.4	-0.2
Soil moisture (%)	16.9	0.3	-0.2	-0.01	-0.3	0.6*	-0.2	0.5
Understory light intensity (log lumens m^{-2})	1.5	0.04	-0.2	0.1	0.1	0.4	0.08	0.05
Soil temperature (C)	16.7	0.6	0.4	-0.6*	0.5*	0.04	0.5	0.2

* $p<0.05$

Table 5. Species tolerance to sedimentation in each canopy layer in riparian forests at Ft. Benning, GA, 2004-2006.

Canopy layer	Tolerant species	Neutral species	Intolerant species
Understory	*Acer rubrum* L. *Alnus serrulata* (Ait.) Willd. *Morella cerifera* (L.) Small *Rubus* spp.	*Aronia arbutifolia* (L.) Ell. *Clethra alnifolia* L. *Ilex glabra* (L.) A. Gray *Ilex opaca* Ait. *Liquidambar styraciflua* L. *Lyonia lucida* (Lam) K. Koch *Nyssa sylvatica* Marsh. *Vaccinium* spp. *Viburnum nudum* L.	*Magnolia virginiana* L. *Pinus taeda* L. *Quercus nigra* L. *Smilax* spp.
Midstory	*Acer rubrum* L. *Cyrilla racemiflora* L. *Morella cerifera* (L.) Small *Nyssa sylvatica* Marsh. *Pinus taeda* L. *Quercus marilandica* Muenchh. *Crataegus flava* Ait.	*Aronia arbutifolia* (L.) Ell. *Clethra alnifolia* L. *Ilex glabra* (L.) A. Gray *Liquidambar styraciflua* L. *Lyonia lucida* (Lam) K. Koch *Magnolia virginiana* L. *Prunus serotina* Ehrh. *Vaccinium* spp. *Viburnum nudum* L. *Quercus falcata* Michx.	*Cornus florida* L. *Callicarpa americana* L. *Diospyros virginiana* L. *Ilex opaca* Ait. *Liriodendron tulipifera* L. *Quercus nigra* L.
Overstory	*Quercus hemisphaerica* Bartr. ex Willd. *Pinus echinata* Mill. *Cyrilla racemiflora* L.	*Acer rubrum* L. *Prunus serotina* Ehrh. *Quercus falcata* Michx. *Liquidambar styraciflua* L.	*Magnolia virginiana* L. *Nyssa sylvatica* Marsh. *Pinus taeda* L. *Quercus nigra* L. *Quercus marilandica* Muenchh.

Table 6. Comparison (ANOVA) of overstory annual mortality rates among disturbance classes in riparian forests at Ft. Benning, GA, 2001-2006. Standard errors are in parentheses. Letters indicate significant differences by Tukey's HSD (α=0.05). NP=not present, NS=not significant

Species	*Annual mortality (% of total trees)*			
	Disturbance class			
	HD	*MD*	*RF*	*p-value*
Acer rubrum L.	1.30 (0.80)	0.06 (0.06)	0.15 (0.09)	0.10
Alnus serrulata (Ait.) Willd.	0	0	NP	NS
Betula nigra L.	NP	NP	0.37 (0.21)	
Carya spp.	NP	0	0	NS
Cornus florida L.	0.14 (0.14)	0	0.36 (0.20)	NS
Crataegus flava Ait.	0.25 (0.25)	NP	NP	
Cyrilla racemiflora L.	1.32 (0)	NP	NP	
Liquidambar styraciflua L.	0.10 (0.05)	0.17 (0.12)	0.12 (0.07)	NS
Magnolia virginiana L.	1.20 (.50)	0.07 (0.07)	0.11 (0.05)	0.10
Morella cerifera (L.) Small	0	0.34 (0.20)	0	0.10
Nyssa sylvatica Marsh.	0.16 (0.07)	0.04 (0.04)	0.02 (0.02)	0.10
Oxydendrum arboretum (L.) DC.	0	NP	0	NS
Pinus echinata Mill.	0.08 (0.08)	NP	0	NS
Pinus palustris Mill.	0.16 (0.10)	NP	NP	
Pinus taeda L.	2.08 (1.36)	0	0.07 (0.05)	0.10
Plantanus occidentalis L.	0	NP	NP	
Prunus serotina Ehrh.	0.13 (0.13)	0	NP	NS
Quercus alba L.	0	0	0	NS
Quercus falcata Michx.	0.16 (0.11)	NP	0.18 (0.18)	NS
Quercus hemisphaerica Bartr. ex Willd.	0	NP	NP	
Quercus laevis Walt.	0	NP	NP	
Quercus marilandica Muenchh.	1.00 (0)^{a}	NP	0^{b}	<0.001
Quercus nigra L.	0.38 (0.19)^{a}	0	0.07 (0.05)^{b}	0.07
Quercus stellata Wang.	1.00 (0.58)	NP	NP	
Salix nigra L.	0.29 (0.17)	NP	NP	
Mean species mortality	**0.43 (0.12)^{a}**	**0.06 (0.02)^{c}**	**0.08 (0.02)^{b}**	**<0.01**

Figure 1. Location of study area and 17 plots in riparian forest at Ft. Benning, GA.

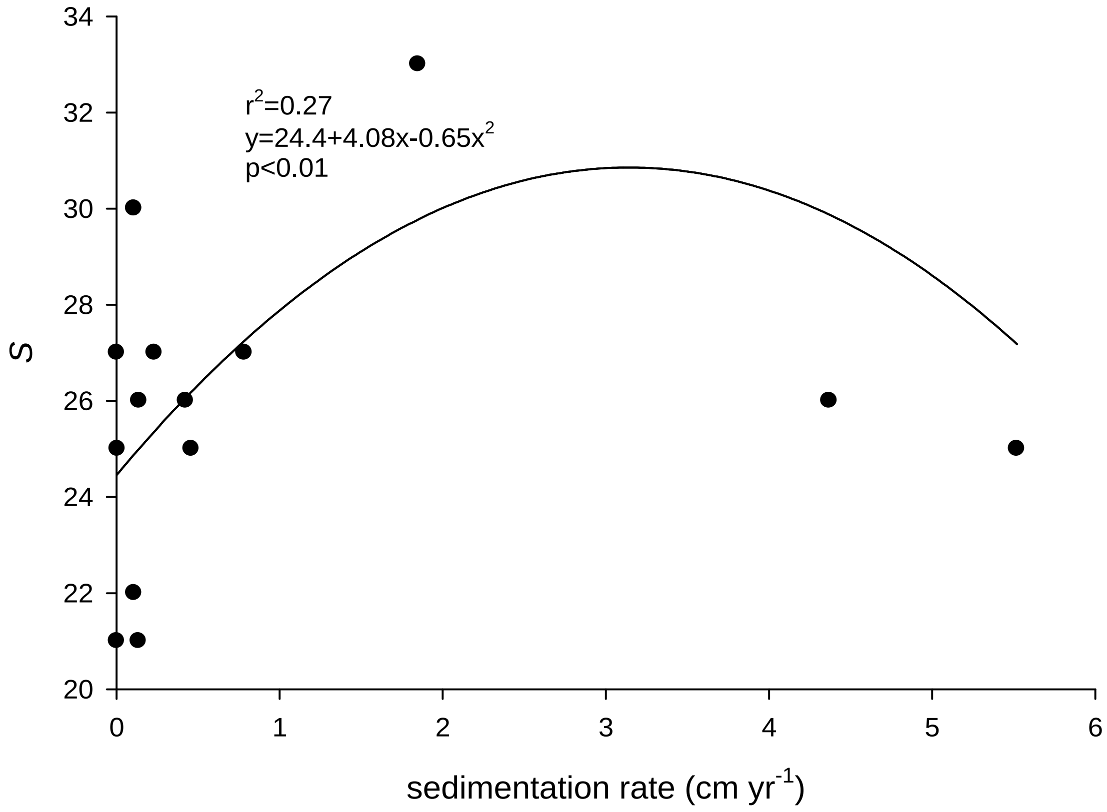

Figure 2. Non-linear regression relationship between total species richness (*S*) and current sedimentation rates in riparian forests at Ft. Benning, GA, 2004-2006.

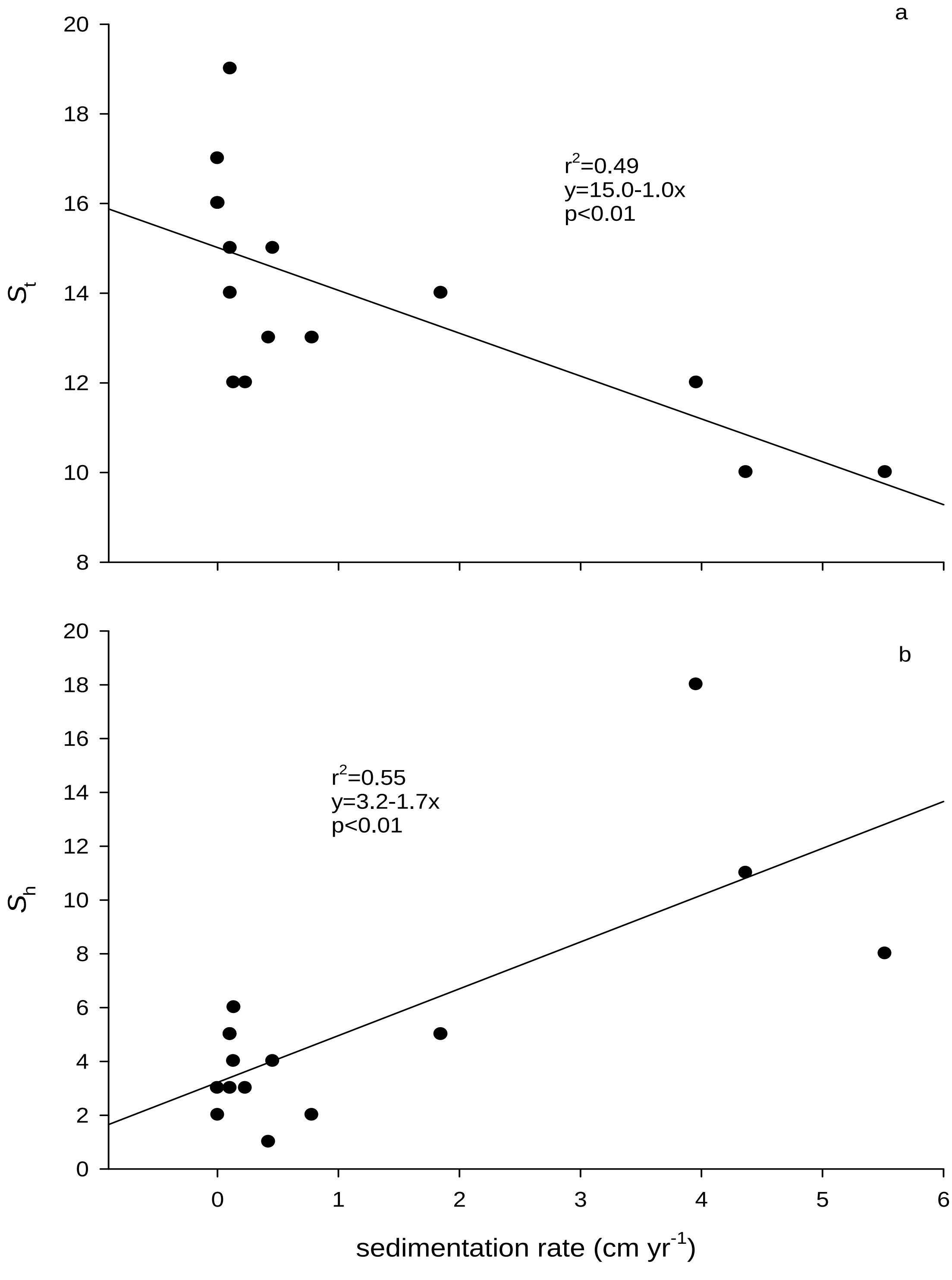

Figure 3. Regression relationship between current sedimentation rates and a) species richness of trees (S_t) and b) species richness of herbs and grasses (S_h) in riparian forests at Ft. Benning, GA, 2004-2006.

Figure 4. Comparison of relative importance values of exotic and native species among disturbance classes in riparian forests at Ft. Benning, GA, 2004-2006. Vertical bars indicate standard error. Uppercase letters indicate significant differences among disturbance classes in exotic species and lowercase letters indicate significant differences among disturbance classes in native species, using Tukey’s HSD ($\alpha=0.05$).

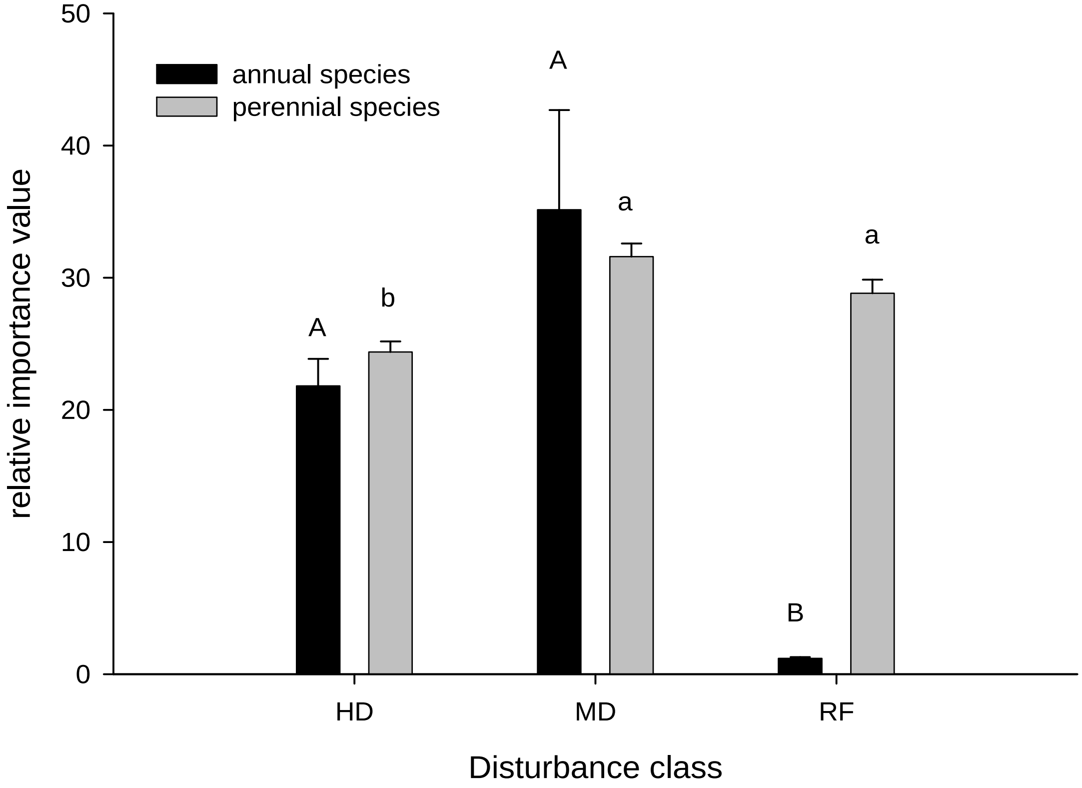

Figure 5. Comparison of relative importance values of annual and perennial species among disturbance classes in riparian forests at Ft. Benning, GA, 2004-2006. Vertical bars indicate standard error. Uppercase letters indicate significant differences among disturbance classes in annual species and lowercase letters indicate significant differences among disturbance classes in perennial species, using Tukey's HSD (α=0.05).

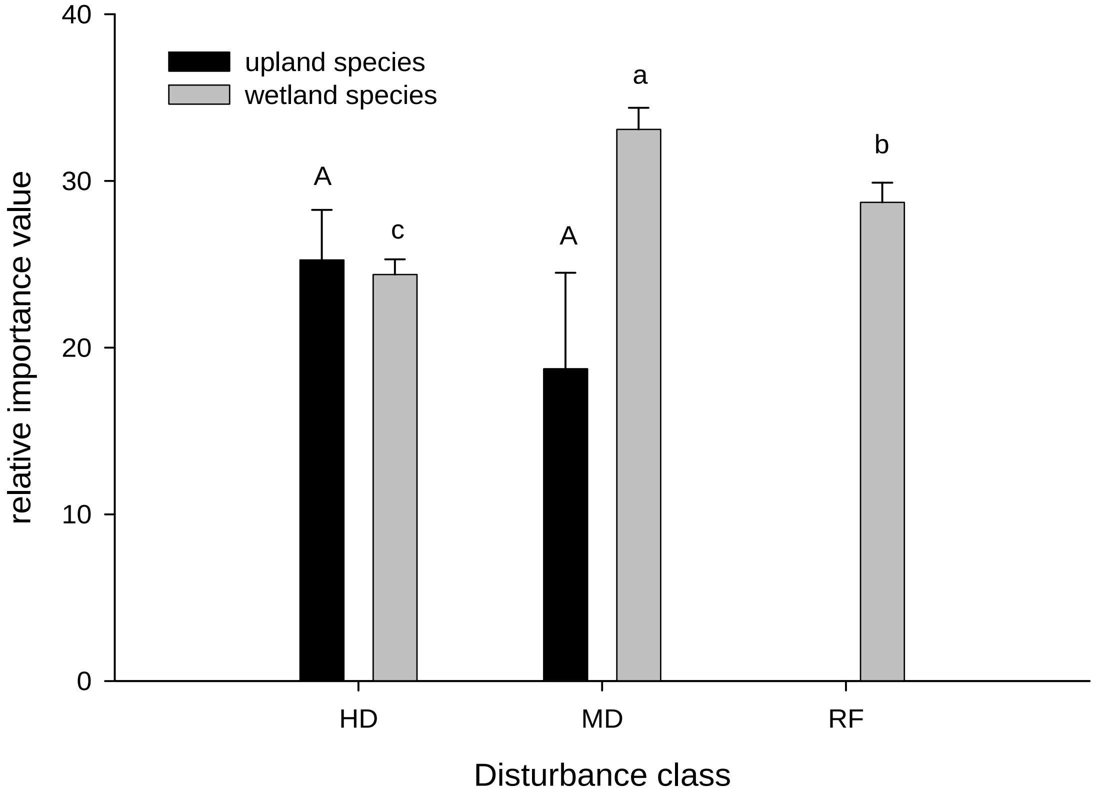

Figure 6. Comparison of relative importance values for wetland and upland species among disturbance classes in riparian forests at Ft. Benning, GA, 2004-2006. Vertical bars indicate standard error. Uppercase letters indicate significant differences among disturbance classes in upland species and lowercase letters indicate significant differences among disturbance classes in wetland species, using Tukey’s HSD ($\alpha=0.05$).

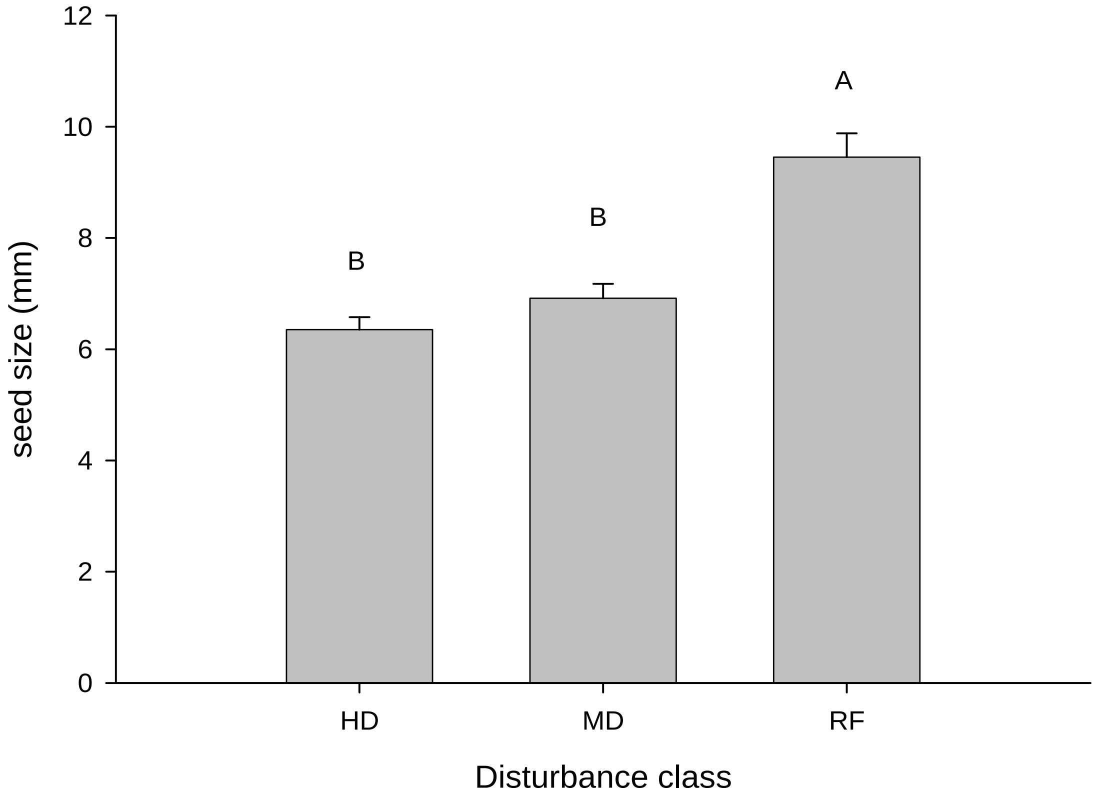

Figure 7. Comparison of species mean seed size among disturbance classes in riparian forests at Ft. Benning, GA, 2004-2006. Vertical bars indicate standard error. Letters indicate significant differences by Tukey's HSD (α=0.05).

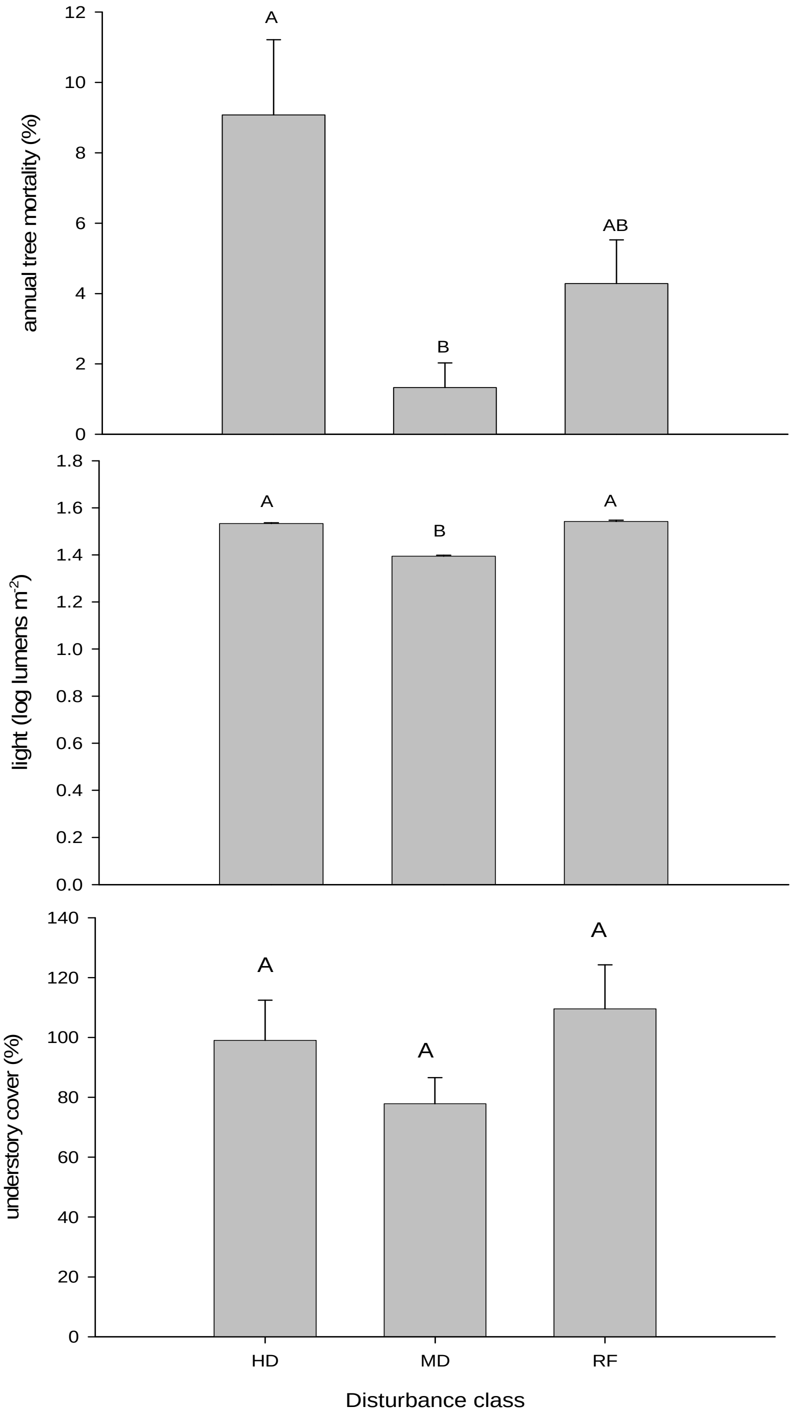

Figure 8. Comparison of means among disturbance classes by a) tree mortality from 2001-2006, b) understory light from 2004-2006, and c) understory vegetation cover from 2004-2006 in riparian forests at Ft. Benning, GA.

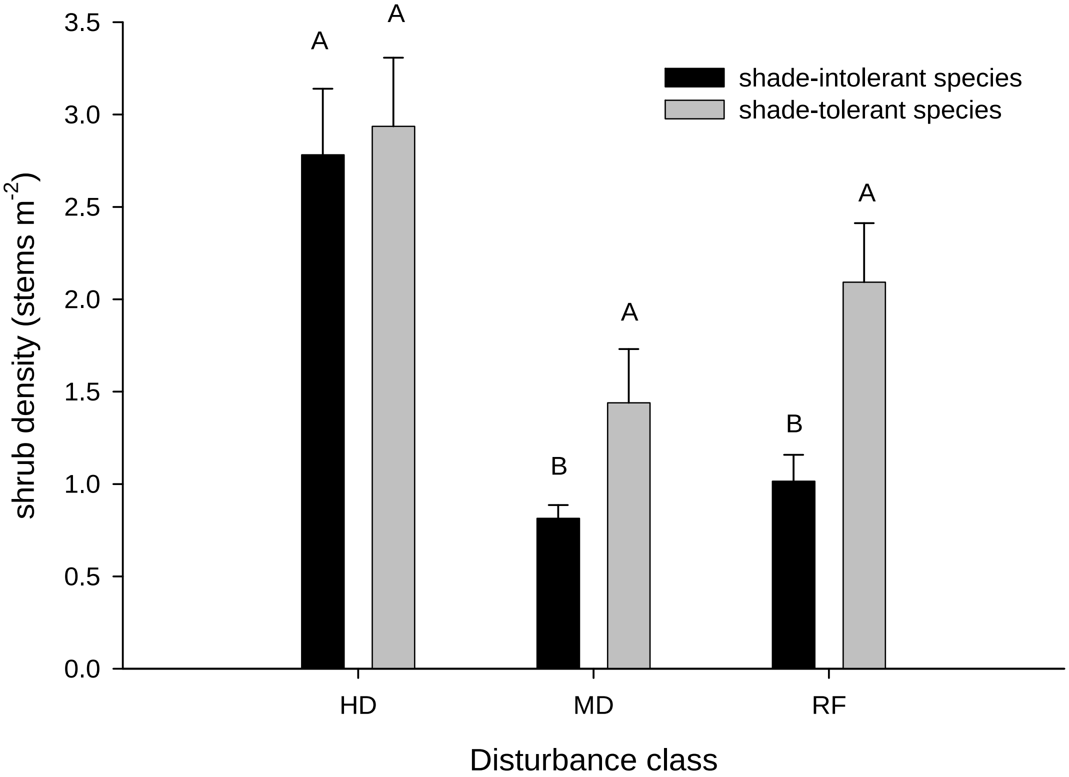

Figure 9. Comparison of shrub density (subdivided into shade tolerant and intolerant species) among disturbance classes in riparian forests at Ft. Benning, GA, 2003-2006. Vertical bars indicate standard error. Letters indicate significant differences by Tukey's HSD (α=0.05).

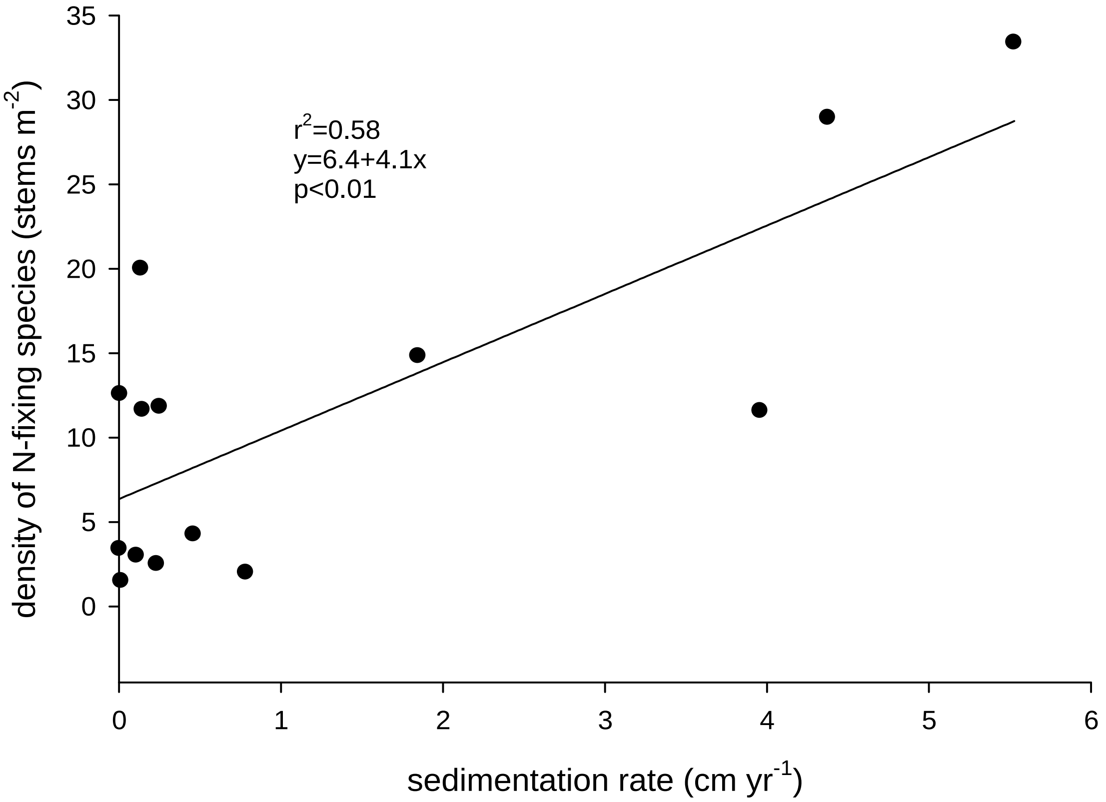

Figure 10. Regression relationship between density of N-fixing species and current sedimentation rate in riparian forests at Ft. Benning, GA, 2003-2006.

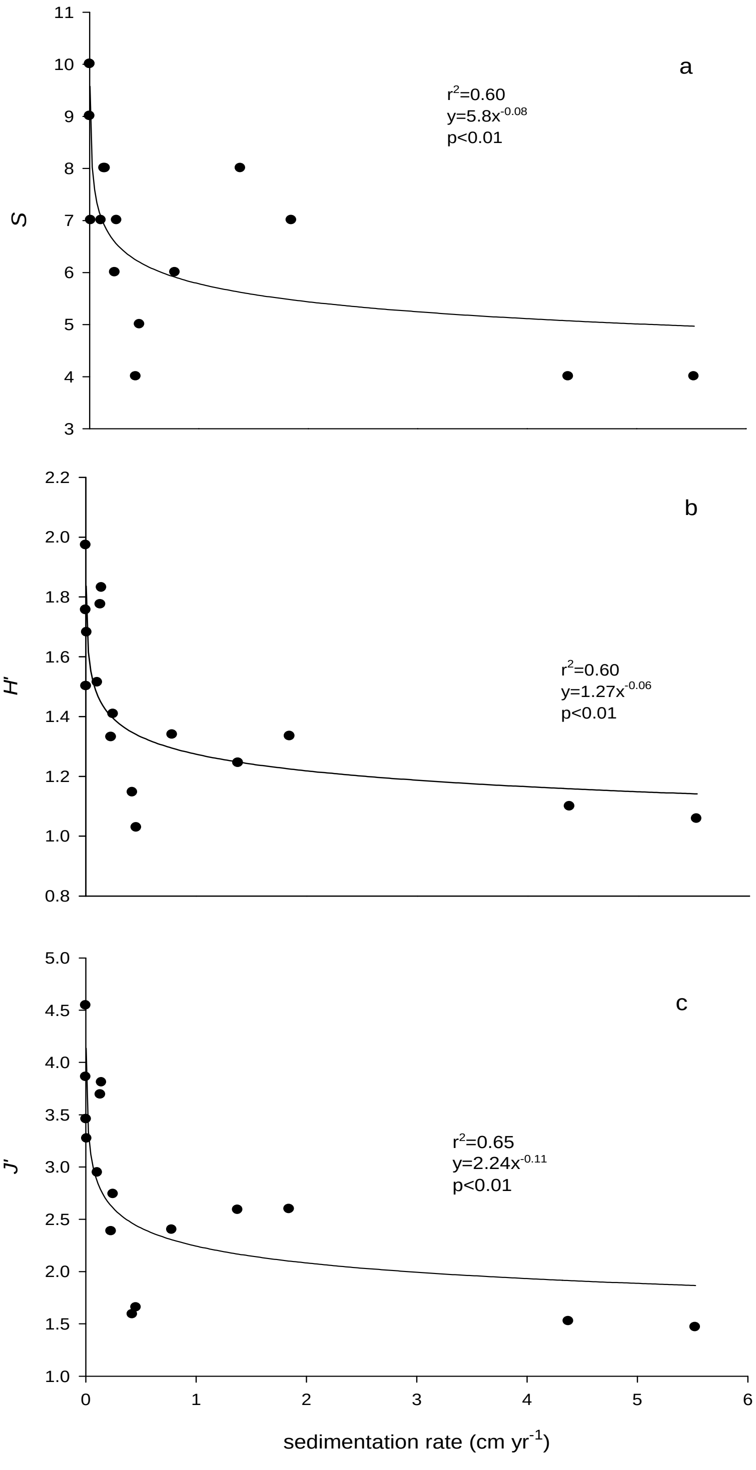

Figure 11. Regression relationship between current sedimentation rate and a) species richness (*S*), b) Shannon's species diversity (*H'*), and c) Pielou's evenness (*J'*) in the overstory of riparian forests at Ft. Benning, GA, 2004-2006.

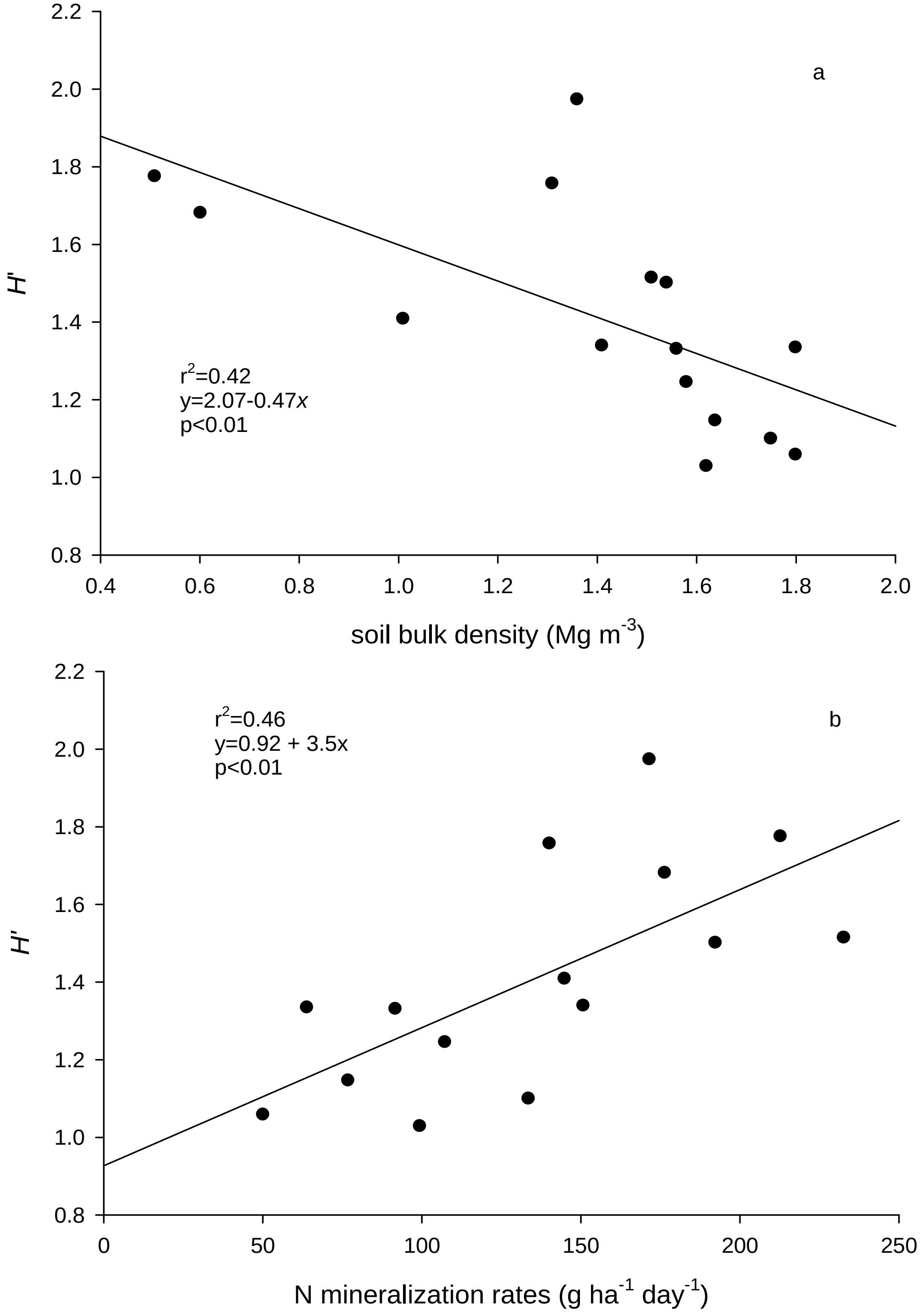

Figure 12. Regression relationship between overstory species diversity (*H'*) and a) soil bulk density and b) N-mineralization rate in riparian forests at Ft. Benning, GA, 2004-2006.

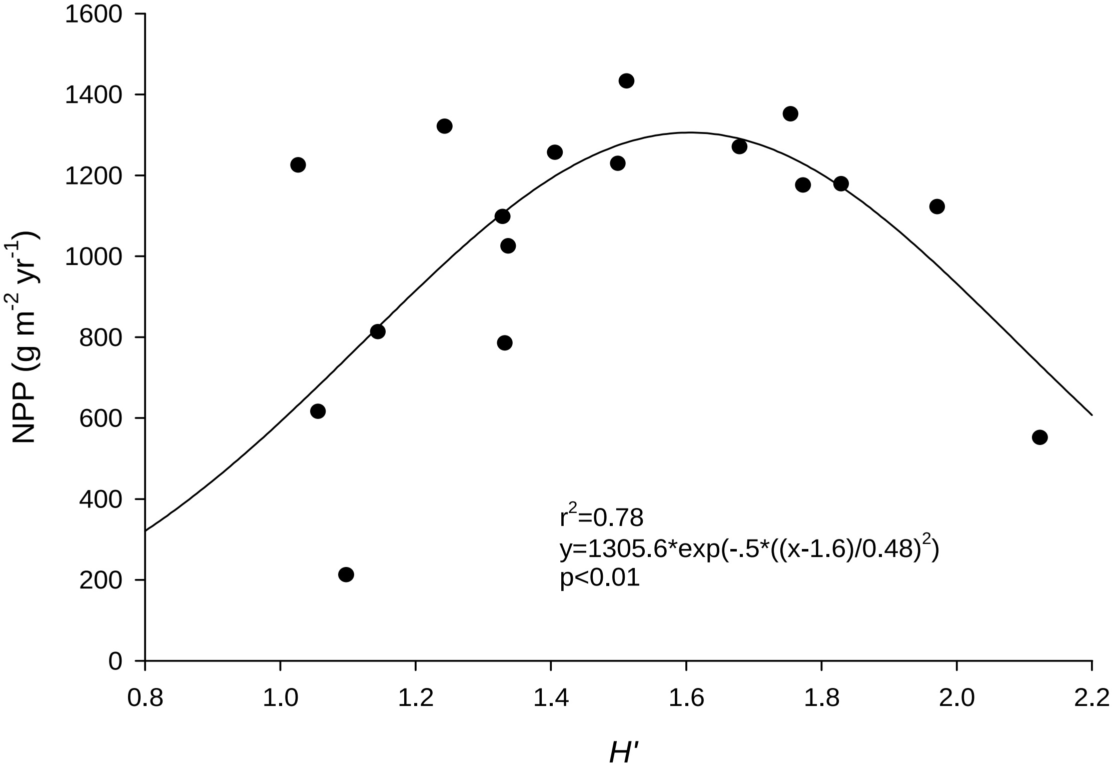

Figure 13. Relationship between net primary productivity (NPP) and species diversity (*H'*) in the overstory of riparian forests at Ft. Benning, GA, 2004-2006.

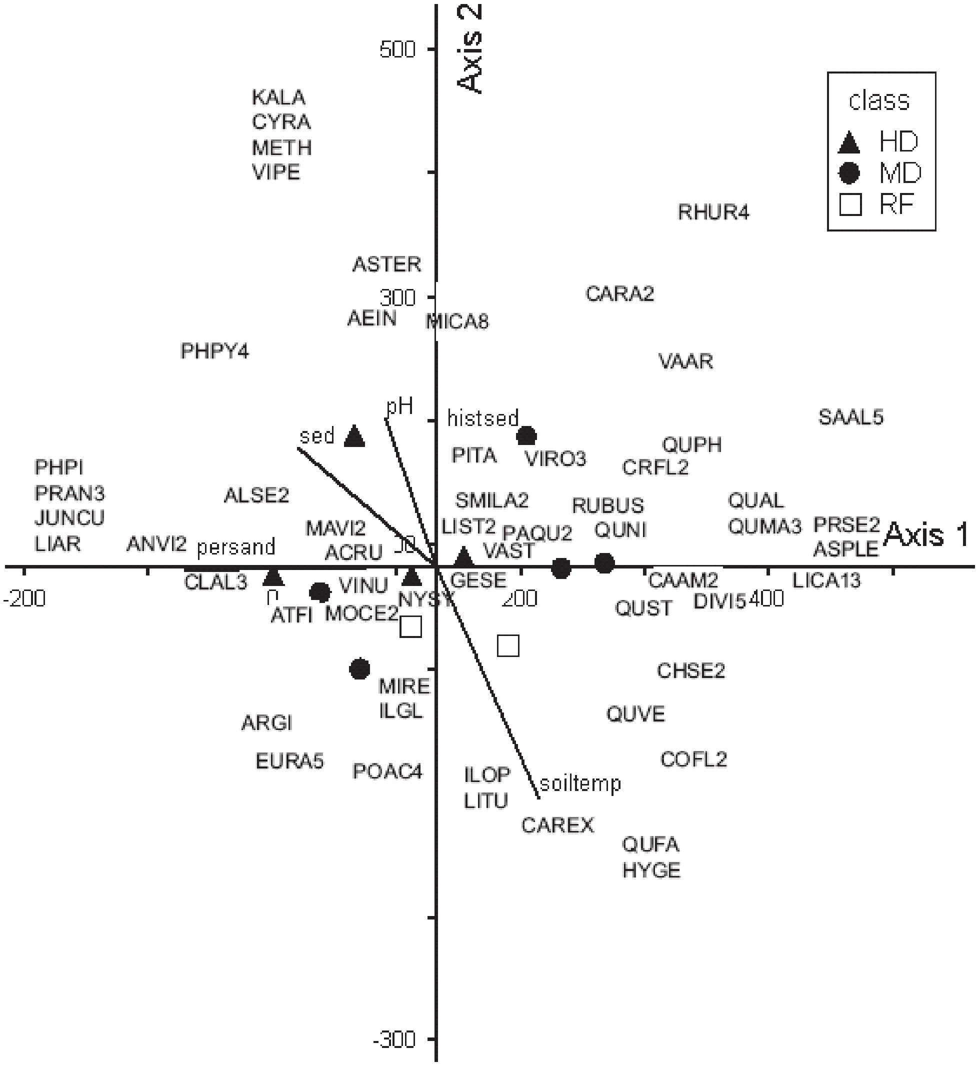

Figure 14. DCA ordination of the understory vegetation layer in riparian forests at Ft. Benning, GA, 2004-2006. Eigenvalues for the first two axes were 0.41 and 0.20, respectively. Biplot vectors shown represent the major explanatory variables. Longer vector lines represent stronger correlations. Species codes follow USDA PLANTS database (USDA, 2005).

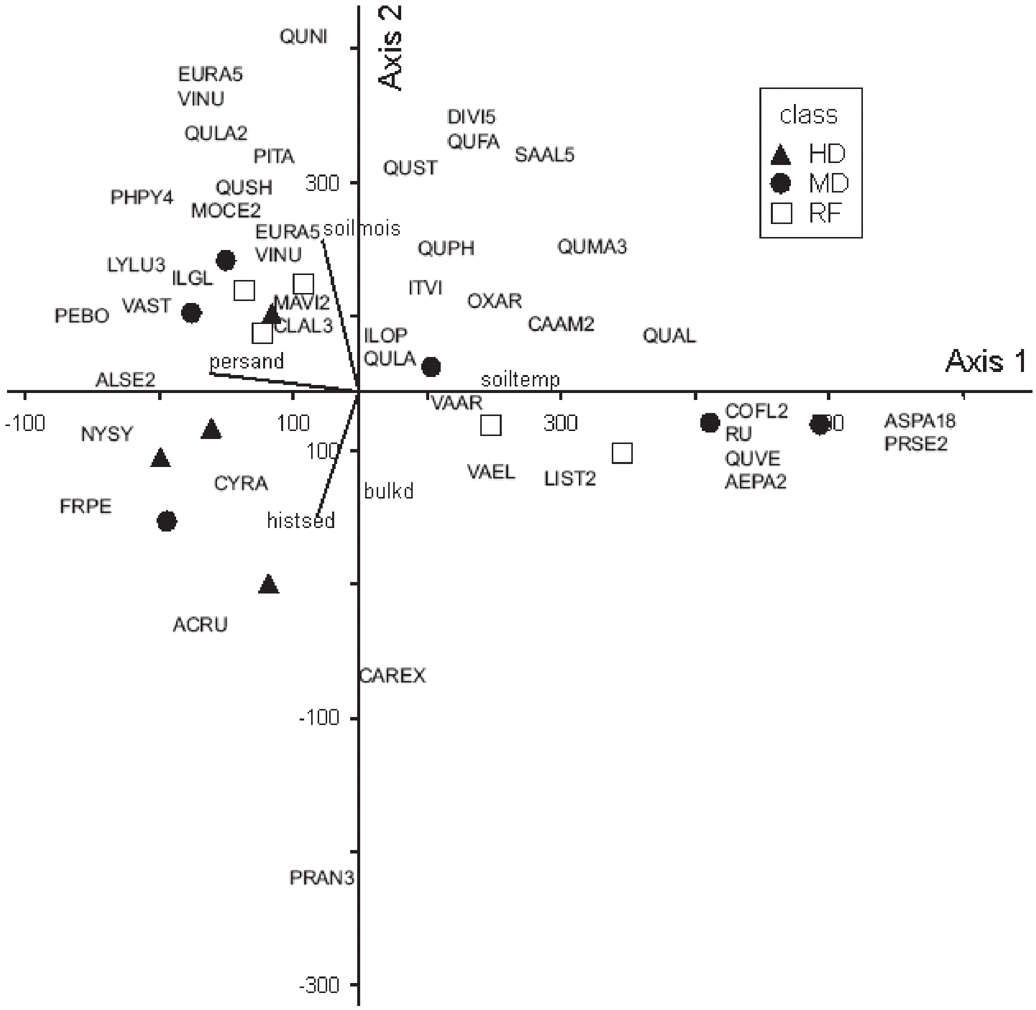

Figure 15. DCA ordination of the midstory vegetation layer in riparian forests at Ft. Benning, GA, 2004-2006. Eigenvalues for axes 1 and 3 were 0.90 and 0.35, respectively. Biplot vectors shown represent the major explanatory variables. Longer vector lines represent stronger correlations. Species codes are according to PLANTS database (USDA, 2005).

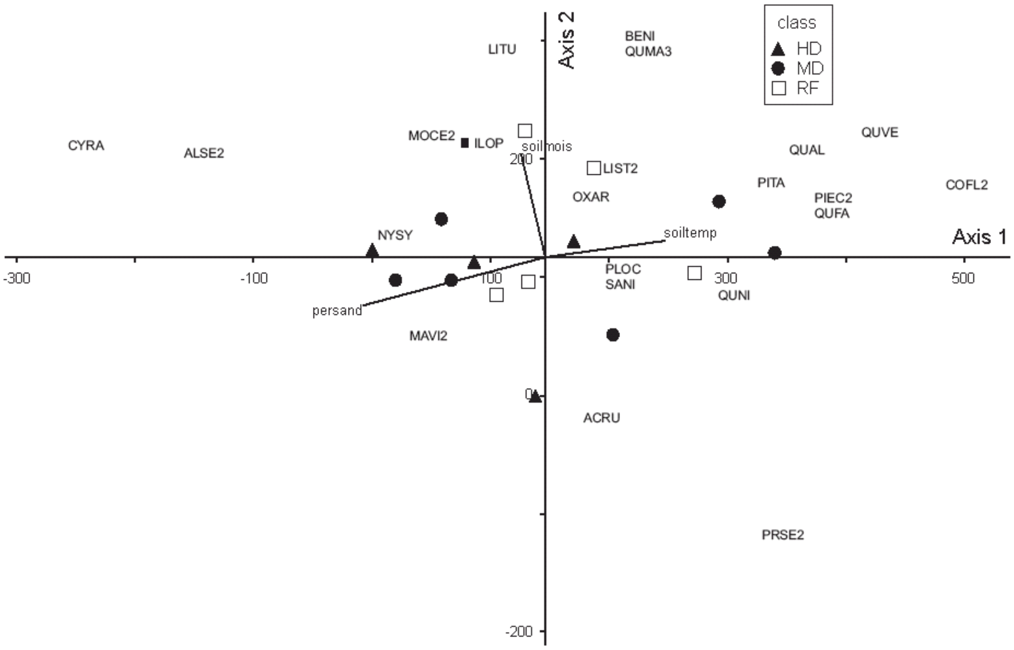

Figure 16. CCA ordination of the overstory vegetation layer in riparian forests at Ft. Benning, GA, 2004-2006. Eigenvalues for axes 1 and 2 were 0.53 and 0.24, respectively. Biplot vectors shown represent the major explanatory variables. Longer vector lines represent stronger correlations. Species codes follow USDA PLANTS database (USDA, 2005).

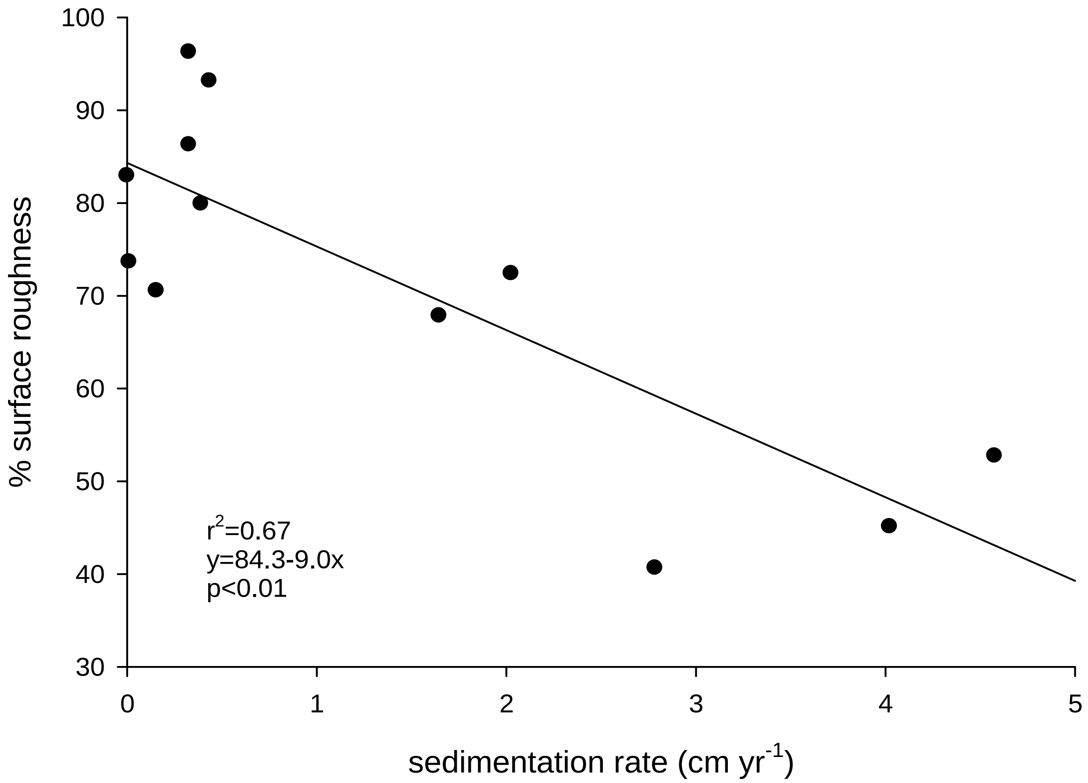

Figure 17. Regression relationship between surface roughness and current sedimentation rate in riparian forests at Ft. Benning, GA, 2004-2006.

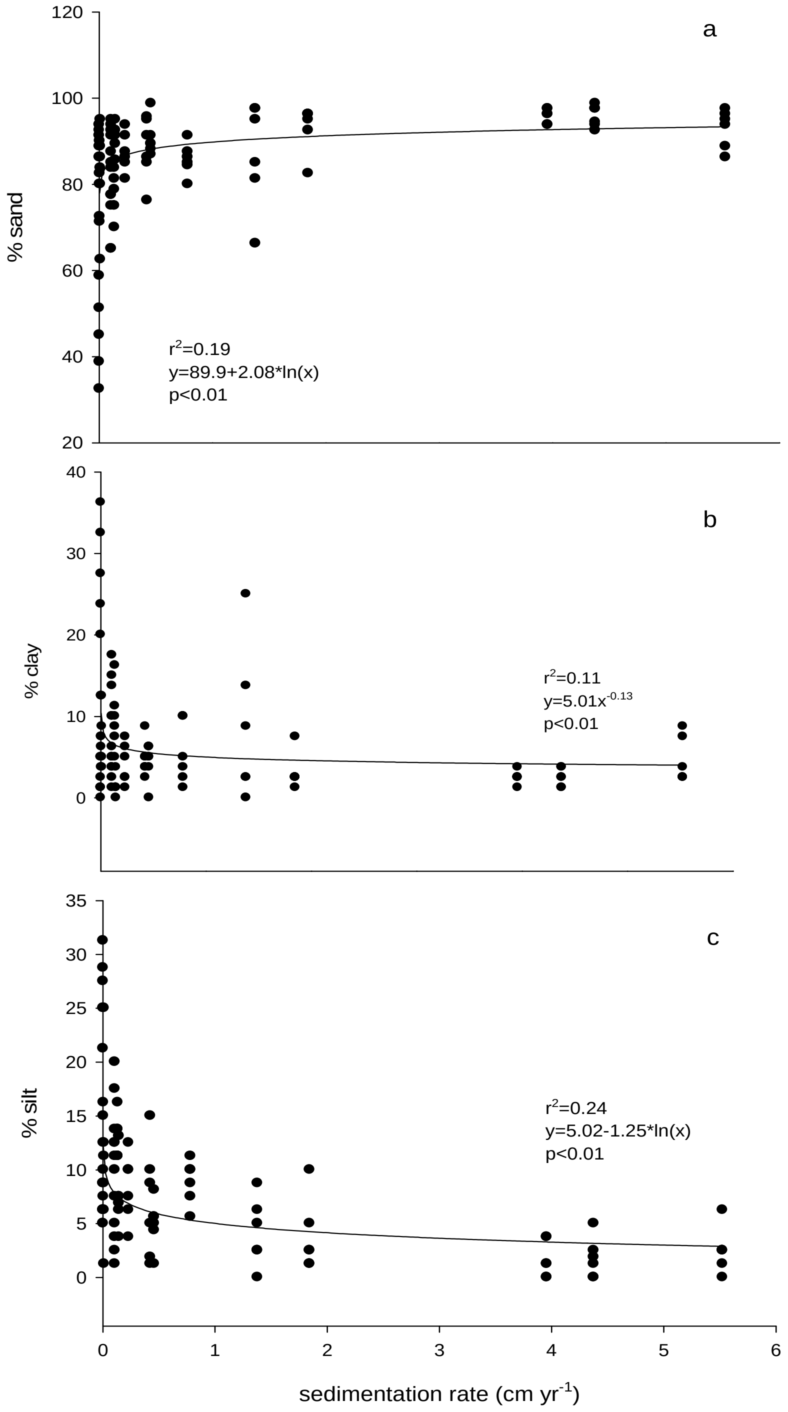

Figure 18. Regression relationships between current sedimentation rates and soil texture as measured by percent a) sand, b) clay, and c) silt in riparian forests at Ft. Benning, GA, 2002-2006.

CHAPTER V

SUMMARY AND CONCLUSIONS

Study Findings

The goal of this research was to understand how sediment deposition affected the function and structure of riparian forests, specifically above- and belowground productivity, nutrient cycling, and the vegetative community composition. Study objectives were to: 1) quantify how above- and belowground forest productivity changes along a gradient of sedimentation rates; 2) determine how biogeochemical processes and nutrient circulation in riparian forests are affected by sediment deposition; and 3) examine how differing rates of sedimentation result in changes to understory, midstory, and overstory canopy layers in riparian forests.

Productivity

Total NPP, ANPP (litterfall and woody biomass increments), and BNPP (fine root productivity) decreased with increasing sedimentation rate. A dramatic decline in NPP was observed in plots with current sedimentation rates greater than 0.1-0.4 cm yr^{-1}. Aboveground and belowground standing crop biomass also decreased with increasing sedimentation rate, and showed a similar threshold for sedimentation rates greater than 0.1-0.4 cm yr^{-1}. Shrub biomass and stem density increased with increasing sedimentation rate. Leaf-area index (LAI) also showed a marked declined with as little sedimentation as 0.1-0.4 cm yr^{-1}.

Nutrient cycling

Changes in forest floor biomass and decomposition studies indicated that RF plots had greater decomposition and nutrient release compared with highly disturbed (HD) and moderately disturbed (MD) plots. Net immobilization of both N and P during decomposition were increased in plots receiving high sediment deposition (HD) compared with reference (RF) plots. Net N mineralization rates declined with sedimentation rates as low as 0.1-0.4 cm yr^{-1}. There was also a significant decline in net N mineralization rate with soil bulk densities above 1.5 Mg m^{-3}, values associated with high sedimentation rates. Microbial N and C showed a similar decline with sedimentation rates greater than 0.1-0.4 cm yr^{-1}.

Differences in nutrient concentrations and content in plant tissues among disturbance classes suggested changes in nutrient-use efficiencies with differing rates of sedimentation. Foliar C concentrations declined along a gradient of increasing sedimentation rates. However, foliar N increased in plots with greater sediment deposition, probably due to the high proportion of N-fixing species in those plots. Increased P use efficiency in HD plots suggested that P became more limiting with increased sedimentation rates. Nutrient resorption efficiency and proficiency for both N and P were greatest in HD plots, suggesting greater N and P limitations with increased sedimentation rates. Fine root N concentration was greatest in HD plots, corresponding to a greater proportion of N-fixers in those plots.

The major driving factor in nutrient cycling was likely changes in soil texture. Soil texture changed dramatically with sedimentation rates around 0.1-0.4 cm yr^{-1}, with an increase in percent sand and a corresponding decrease in percent silt and clay. Increased sand in plots with greater sedimentation rates likely caused the decline in soil moisture found in these plots. Plots with sedimentation rates above 0.1-0.4 cm yr^{-1} also declined in soil macronutrients, such as Mg, Al, K, B, and Fe.

Community composition

Changes in species composition in all three forest layers were most strongly associated with physical soil characteristics such as soil texture, bulk density, moisture, and temperature. Species most tolerant to sedimentation across all forest layers were *Morella cerifera*, *Crataegus flava*, *Cyrilla racemiflora*, *Pinus echinata*, and *Quercus hemisphaerica*. Total species richness increased with sedimentation rates up to 4 cm yr^{-1}, but beyond this richness declined.

Community response in each canopy layer (i.e., understory, mid-story, and overstory) showed different responses to increased sedimentation rate. Understory species had greater species richness, diversity, and evenness in HD plots compared to RF and MD plots. There were also a greater proportion of annuals, exotics, and upland species in the understory layer of HD plots compared with MD and RF plots. The mid-story layer had greater densities of N-fixing species and shade-intolerant species in HD plots compared with MD and RF plots. Changes in the overstory tree community over the 5-year study period indicated that HD plots had the greatest mortality rates, compared to MD and RF plots.

The function of riparian forests in trapping and retaining sediments decreased with increased sedimentation. Plots receiving the greatest sediment deposition also showed the greatest export of sediments. Net sediment export increased with the decline in surface roughness associated with greater sedimentation rates.

Synthesis

This study demonstrated that sedimentation is linked to declines in forest productivity, nutrient circulation, and changes in the community composition of riparian forests. The driving factor is suggested to be decreased moisture availability due to sandier surface soils. The ramifications of these changes in riparian forests are far reaching. These parameters are all intimately linked to the critical function these riparian forests play in maintaining water quality and providing areas high in biodiversity (Naiman and Decamps, 1997). A decline in forest productivity with increasing sedimentation rates has significant ramifications for the ‘kidney’ function, or the filtration of nutrients and pollutants, of riparian forests (Lockaby et al., 2005). The ability of riparian forests to take up nutrients is largely dependent on forest productivity (Brinson et al., 1981a; Naiman and Decamps, 1997). A decline in productivity will result in decreased uptake of nutrients by vegetation. Thus, nutrients entering riparian forests have a greater potential to continue downstream.

In this study, sedimentation did not provide any apparent subsidy for productivity in riparian forests. Instead, sedimentation appeared to be a chronic stress to the system. High rates of sedimentation created an additional layer of sandy soil which had lower water holding capacity. Declines in nutrient circulation and biogeochemical processes in plots receiving high rates of sedimentation may result in less nutrients available for plant uptake and growth. This may have been a driver for lower productivity rates.

Changes in species composition across a gradient of sedimentation may have also been a result of and/or a driver of observed biogeochemical changes. Different species have different nutrient requirements and will contribute litter of differing quality. Changes in forest communities due to sedimentation may have long-lasting and far-reaching effects. Riparian forests function as biodiversity corridors (Naiman et al., 1993) due to their connectivity with aquatic systems, which often play a major role in transporting seeds and propagules. Therefore, the decline in native species and the increase in exotic species associated with sedimentation may result in the spread of invasive species along these corridors and impact areas further downstream.

With the decline in the number of riparian forests (Brinson et al., 1981b; Abernethy and Turner, 1987), it is essential that those remaining be intact and functioning. Increases in land development will likely lead to greater erosion and greater sedimentation rates in riparian forests. This study indicates that sedimentation decreases sediment retention in riparian forests and thus increases the potential for degradation of water quality.

Future directions

In this study, a decline in many parameters was observed with sedimentation rates between 0.1-0.4 cm yr^{-1}. This ‘threshold’ sedimentation rate corresponded to abrupt changes in sediment texture, which also had significant correlations to species composition in all three forest layers. Unlike disturbances such as fire, harvesting, or storms, sedimentation results in a layer of “new” soil that may have very different nutrient composition and texture from the underlying soils. Changes in the physical characteristics of soils may be long-lasting, posing a chronic stress to forest system. It is well known that soil texture can influence soil moisture, organic matter, and cation exchange capacity (CEC). It has also been suggested that the textural composition of sediment may influence N supplies in soils (Cassman and Munns, 1980). Therefore, it is likely that secondary succession in riparian forests disturbed by high sedimentation rates will follow a different trajectory than those forests disturbed by fire, harvesting, or storms. Future research comparing and contrasting secondary succession among these disturbance types may provide insight into the long-term effects of these soil changes.

This study examined only effects of sedimentation on riparian forests in the upper coastal plain of Ft. Benning, GA, where sediments were largely coarse-sand. In order to fully understand the impact of sedimentation on riparian forests, it is necessary to compare these results with those of forests receiving fine-textured sediments. Perhaps sedimentation that is greater in silt or clay may prove to be subsidy to riparian forests in low levels. Similar studies in different soil types would be useful in isolating the impacts of sedimentation rate from those of changes in soil texture.

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APPENDICES

Appendix A: Annual mast crop comparison

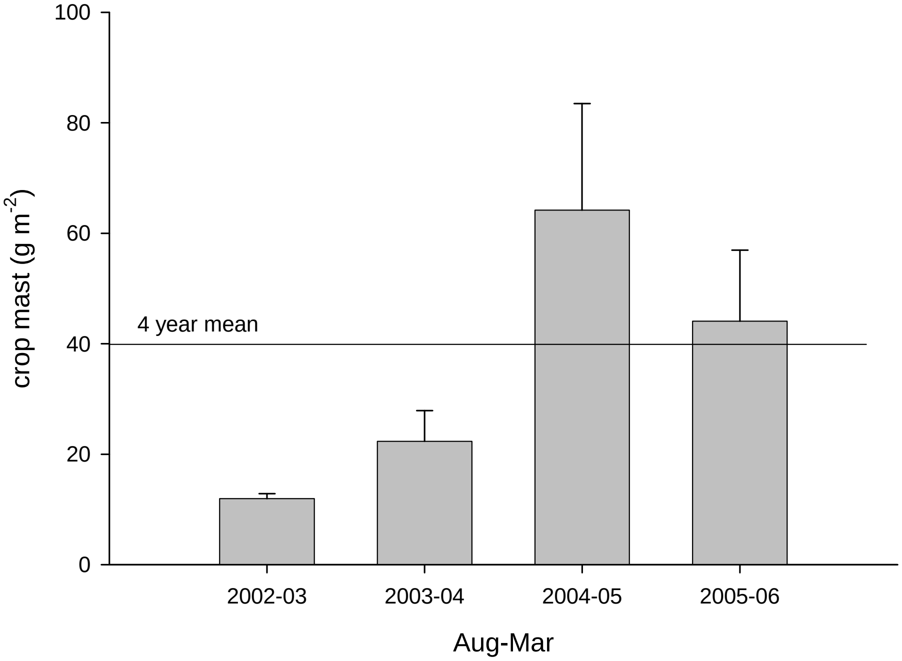

Figure A1. Comparison of annual mast crop of plots dominated by oak (*Quercus*) species in riparian forests at Ft. Benning, GA, 2002-2006. Vertical bars indicate standard error, line indicates 4-year mean.

Appendix B: Species inventory of 17 riparian forests at Ft. Benning, GA, 2004-2006

Plot: D12A
Disturbance class: High
Current sedimentation rate: 1.38 cm yr^{-1}
H'=*1.24*
S=*18*
J'=2.58
Species:

Acer rubrum L.
Carya spp.
Leucothoe racemosa (L.) Gray
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Magnolia virginiana L.
Nyssa sylvatica Marsh.
Parthenocissus quinquefolia (L.) Planch.
Plantanus occidentalis L.
Prunus angustifolia Marsh.
Prunus serotina Ehrh.
Quercus alba L.
Quercus nigra L.
Quercus phellos L.
Rubus spp.
Salix nigra L.
Smilax spp.
Vitis rotundifolia Michx.

Plot: D12B
Disturbance class: High
Current sedimentation rate: 5.52 cm yr^{-1}
H'=*1.06*
S=*25*
J'=*1.47*
Species:

Acer rubrum L.
Aeschynomene indica L.
Alnus serrulata (Ait.) Willd.
Arenaria caroliniana Walter
Aronia arbutifolia (L.) Ell.
Bromus spp.
Campsis radicans (L.) Seem. ex Bureau
*Car*ex spp.
Clethra alnifolia L.
Cyrilla racemiflora L.
Fraxinus pennsylvanica Marsh.
*I*lex *glabra* (L.) A. Gray
Itea virginica L.
Kalmia latifolia L.
Liquidambar styraciflua L.
Lonicera japonica Thunb.
Magnolia virginiana L.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Pinus taeda L.
Prunus serotina Ehrh.
Quercus nigra L.
Smilax spp.
Viburnum nudum L.
Viola pedata L.

Plot: F1E
Disturbance class: Moderate
Current sedimentation rate: 0.14 cm yr^{-1}
H'=*1.83*
S=*26*
J'=*3.81*
Species:

Acer rubrum L.
Alnus serrulata (Ait.) Willd.
Andropogon spp.
Aronia arbutifolia (L.) Ell.
Arundinaria gigantea (Walter) MuhL.
Athyrium filix-femina (L.) Roth
Clethra alnifolia L.
*I*lex *glabra* (L.) A. Gray
*I*lex *opaca* Ait.
Leucothoe racemosa (L.) Gray
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Lyonia lucida (Lam.) K. Koch
Magnolia virginiana L.
Muhlenbergia spp.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Parthenocissus quinquefolia (L.) Planch.
Pinus taeda L.
Polystichum acrostichoides (Michx.) Schott
Quercus nigra L.
Quercus phellos L.
Smilax spp.
Vaccinium arboreum Marsh.
Viburnum nudum L.
Vitis rotundifolia Michx.

Plot: F1WAc
Disturbance class: Reference
Current sedimentation rate: 0.10 cm yr^{-1}
H'=*1.41*
S=*22*
J'=*2.74*
Species:

Acer rubrum L.
Callicarpa americana L.
Clethra alnifolia L.
Ilex opaca Ait.
Juncus spp.
Leucothoe racemosa (L.) Gray
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Magnolia virginiana L.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Oxydendrum arboreum (L.) DC.
Pinus taeda L.
Polystichum acrostichoides (Michx.) Schott
Quercus falcata Michx.
Quercus hemisphaerica Bartr. ex Willd.
Quercus nigra L.
Quercus phellos L.
Quercus stellata Wang.
Vaccinium stamineum L.
Viburnum nudum L.
Vitis rotundifolia Michx.

Plot: F1WAd
Disturbance class: High
Current sedimentation rate: 4.38 cm yr^{-1}
H'=*1.10*
S=*26*
J'=*1.52*
Species:

Acer rubrum L.
Alnus serrulata (Ait.) Willd.
Ambrosia artemisiifolia L.
Andropogon spp.
Arenaria caroliniana Walter
Aronia arbutifolia (L.) Ell.
Arundinaria gigantea (Walter) Muhl.
Clethra alnifolia L.
Cornus florida L.
Eupatoria spp.
Gelsemium sepervirens (L.) Jaume St. Hil.
Hypericum gentianoides (L.) B.S.P.
*I*lex *glabra* (L.) A. Gray
*I*lex *opaca* Ait.
Itea virginica L.
Juncus spp.
Leucothoe racemosa (L.) Gray
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Lyonia lucida (Lam.) K. Koch
Magnolia virginiana L.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Pinus taeda L.
Prunus angustifolia Marsh.
Smilax spp.

Plot: F1WB

Disturbance class: Moderate

Current sedimentation rate: 0.46 cm yr^{-1}

H'=*1.03*

S=*25*

J'=*1.65*

Species:

Acer rubrum L.
Alnus serrulata (Ait.) Willd.
Arundinaria gigantea (Walter) Muhl.
Athyrium filix-femina (L.) Roth
Carya spp.
Clethra alnifolia L.
Cornus florida L.
Fraxinus pennsylvanica Marsh.
Gelsemium sepervirens (L.) Jaume St. Hil.
Ilex glabra (L.) A. Gray
Ilex opaca Ait.
Itea virginica L.
Leucothoe racemosa (L.) Gray
Liquidambar styraciflua L.
Lyonia lucida (Lam.) K. Koch
Magnolia virginiana L.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Pinus taeda L.
Polystichum acrostichoides (Michx.) Schott
Quercus nigra L.
Smilax spp.
Vaccinium elliottii Champ.
Viburnum nudum L.
Vitis rotundifolia Michx.

Plot: F3
Disturbance class: High
Current sedimentation rate: 1.84 cm yr^{-1}
H’*=1.33*
S*=33*
J’=2.60
Species:

Acer rubrum L.
Aeschynomene indica L.
Alnus serrulata (Ait.) Willd.
Arenaria caroliniana Walter
Aronia arbutifolia (L.) Ell.
Arundinaria gigantea (Walter) Muhl.
Callicarpa americana L.
Chasmanthium sessiliflorum (Poir.) Yates
Cornus florida L.
Crataegus flava Ait.
Cyrilla racemiflora L.
Desmodium spp.
Fraxinus pennsylvanica Marsh.
Ilex glabra (L.) A. Gray
Ilex opaca Ait.
Itea virginica L.
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Lyonia lucida (Lam.) K. Koch
Magnolia virginiana L.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Oxydendrum arboreum (L.) DC.
Persea borbonia (L.) Spreng.
Pinus taeda L.
Prunus serotina Ehrh.
Quercus nigra L.
Rhus copallina L.
Smilax spp.
Vaccinium arboreum Marsh.
Vaccinium stamineum L.
Viburnum nudum L.
Vitis rotundifolia Michx.

Plot: F4Ac
Disturbance class: Reference
Current sedimentation rate: 0.10 cm yr^{-1}
H'=*1.77*
S=*21*
J'=*3.69*
Species:

Acer rubrum L.
Aronia arbutifolia (L.) Ell.
Carya spp.
Festuca spp.
Ilex glabra (L.) A. Gray
Ilex opaca Ait.
Juncus spp.
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Lyonia lucida (Lam.) K. Koch
Magnolia virginiana L.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Pinus taeda L.
Polystichum acrostichoides (Michx.) Schott
Quercus nigra L.
Quercus phellos L.
Quercus shumardii Buckl.
Quercus stellata Wang.
Vaccinium stamineum L.
Viburnum nudum L.

Plot: F4Ad ***Disturbance class: Reference*** ***Current sedimentation rate: 0.003 cm yr^{-1}*** **H'=*1.76*** **S=*27*** ***J'=3.86*** ***Species:***
Acer rubrum L.
Betula nigra L.
Callicarpa americana L.
*Car*ex spp.
Carya spp.
Chasmanthium sessiliflorum (Poir.) Yates
Diospyros virginiana L.
Hypericum gentianoides (L.) B.S.P.
*I*lex *glabra* (L.) A. Gray
*I*lex *opaca* Ait.
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Magnolia virginiana L.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Pinus taeda L.
Quercus falcata Michx.
Quercus marilandica Muenchh.
Quercus nigra L.
Quercus phellos L.
Quercus stellata Wang.
Quercus velutina Lam.
Smilax spp.
Vaccinium arboreum Marsh.
Vaccinium stamineum L.
Viburnum nudum L.
Vitis rotundifolia Michx.

Plot: F4C
Disturbance class: Reference
Current sedimentation rate: 0.01 cm yr^{-1}
H'*=1.68*
S*=30*
J'*=3.27*
Species:

Acer rubrum L.
Aronia arbutifolia (L.) Ell.
Arundinaria gigantea (Walter) MuhL.
Athyrium filix-femina (L.) Roth
Carya spp.
Chasmanthium sessiliflorum (Poir.) Yates
Diospyros virginiana L.
Hypericum gentianoides (L.) B.S.P.
Ilex glabra (L.) A. Gray
Ilex opaca Ait.
Itea virginica L.
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Lyonia lucida (Lam.) K. Koch
Magnolia virginiana L.
Mitchella repens L.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Pinus taeda L.
Polystichum acrostichoides (Michx.) Schott
Quercus alba L.
Quercus falcata Michx.
Quercus nigra L.
Quercus stellata Wang.
Quercus velutina Lam.
Sassafras albidum (Nutt.) Nees
Smilax spp.
Vaccinium stamineum L.
Viburnum nudum L.
Vitis rotundifolia Michx.

Plot: I3Ac
Disturbance class: Reference
Current sedimentation rate: 0.003 cm yr^{-1}
H'=*1.97*
S=*21*
J'=*4.54*
Species:

Acer rubrum L.
Campsis radicans (L.) Seem. ex Bureau
Cornus florida L.
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Magnolia virginiana L.
Nyssa sylvatica Marsh.
Oxydendrum arboreum (L.) DC.
Pinus echinata Mill.
Pinus taeda L.
Prunus serotina Ehrh.
Quercus alba L.
Quercus falcata Michx.
Quercus marilandica Muenchh.
Quercus nigra L.
Quercus stellata Wang.
Quercus velutina Lam.
Sassafras albidum (Nutt.) Nees
Smilax spp.
Vaccinium arboreum Marsh.
Vitis rotundifolia Michx.

Plot: I3Ad
Disturbance class: Moderate
Current sedimentation rate: 0.11 cm yr^{-1}
H’=*1.51*
S=*30*
J’=*2.94*
Species:

Aesculus parviflora Walt.
Arenaria caroliniana Walter
Callicarpa americana L.
Campsis radicans (L.) Seem. ex Bureau
Carya spp.
Chasmanthium sessiliflorum (Poir.) Yates
Cornus florida L.
Diospyros virginiana L.
Gelsemium sempervirens (L.) Jaume St. Hil.
Heliotropium amplexicaule Vahl.
Ilex opaca Ait.
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Lithospermum caroliniense (Walt. ex J.F. Gmel.) MacM.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Pinus taeda L.
Polystichum acrostichoides (Michx.) Schott
Prunus serotina Ehrh.
Quercus alba L.
Quercus falcata Michx.
Quercus marilandica Muenchh.
Quercus nigra L.
Quercus stellata Wang.
Quercus velutina Lam.
Rubus spp.
Sassafras albidum (Nutt.) Nees
Smilax spp.
Vaccinium arboreum Marsh.
Vitis rotundifolia Michx.

Plot: I3Bc
Disturbance class: Reference
Current sedimentation rate: 0.007 cm yr^{-1}
H’*=1.50*
S*=25*
J’*=3.45*
Species:

Acer rubrum L.
Callicarpa americana L.
Carya spp.
Chasmanthium sessiliflorum (Poir.) Yates
Cornus florida L.
Diospyros virginiana L.
Ilex opaca Ait.
Itea virginica L.
Liquidambar styraciflua L.
Liriodendron tulipifera L.
Magnolia virginiana L.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Pinus taeda L.
Prunus serotina Ehrh.
Quercus alba L.
Quercus falcata Michx.
Quercus nigra L.
Quercus nigra L.
Quercus phellos L.
Quercus stellata Wang.
Smilax spp.
Vaccinium arboreum Marsh.
Vaccinium stamineum L.
Vitis rotundifolia Michx.

Plot: I3Bd
Disturbance class: Moderate
Current sedimentation rate: 0.78 cm yr^{-1}
H'=*1.34*
S=*27*
J'=*2.40*
Species:

Acer rubrum L.
Aesculus parviflora Walt.
Asimina parviflora (Michx.) Dunal.
Asplenium spp.
Callicarpa americana L.
Chasmanthium sessiliflorum (Poir.) Yates
Cornus florida L.
Cornus florida L.
Crataegus spp.
Diospyros virginiana L.
*I*lex *glabra* (L.) A. Gray
*I*lex *opaca* Ait.
Liquidambar styraciflua L.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Parthenocissus quinquefolia (L.) Planch.
Pinus taeda L.
Prunus serotina Ehrh.
Quercus falcata Michx.
Quercus nigra L.
Quercus phellos L.
Quercus stellata Wang.
Sassafras albidum (Nutt.) Nees
Smilax spp.
Vaccinium arboreum Marsh.
Vaccinium stamineum L.
Vitis rotundifolia Michx.

Plot: I3C
Disturbance class: Moderate
Current sedimentation rate: 0.23 cm yr^{-1}
H'*=1.33*
S*=27*
J'*=2.38*
Species:

Acer rubrum L.
Arenaria caroliniana Walter
Aster spp.
Callicarpa americana L.
Campsis radicans (L.) Seem. ex Bureau
Chasmanthium sessiliflorum (Poir.) Yates
Cornus florida L.
Diospyros virginiana L.
Gelsemium sempervirens (L.) Jaume St. Hil.
Liquidambar styraciflua L.
Morella cerifera (L.) Small
Nyssa sylvatica Marsh.
Pinus taeda L.
Prunus serotina Ehrh.
Quercus alba L.
Quercus falcata Michx.
Quercus laevis Walt.
Quercus marilandica Muenchh.
Quercus nigra L.
Quercus phellos L.
Rhus aromatica Ait.
Sassafras albidum (Nutt.) Nees
Sassafras albidum (Nutt.) Nees
Smilax spp.
Vaccinium arboreum Marsh.
Vaccinium stamineum L.
Vitis rotundifolia Michx.

Plot: K11c
Disturbance class: Moderate
Current sedimentation rate: 0.43 cm yr^{-1}
H'=*1.15*
S=*26*
J'=*1.60*
Species:

Albizia julibrissin Durazz.
Ceanothus americanus L.
Crataegus flava Ait.
Diospyros virginiana L.
Ilex glabra (L.) A. Gray
Nyssa sylvatica Marsh.
Panicum virgatum L.
Pinus echinata Mill.
Pinus palustris Mill.
Pinus taeda L.
Prunus serotina Ehrh.
Quercus falcata Michx.
Quercus falcata Michx.
Quercus hemisphaerica Bartr. ex Willd.
Quercus incana Bartr.
Quercus laevis Walt.
Quercus marilandica Muenchh.
Quercus phellos L.
Rhus copallina L.
Sassafras albidum (Nutt.) Nees
Smilax spp.
Toxicodendron radicans (L.) Kuntze
Toxicodendron toxicarium (Salisb.) Gillis
Vaccinium arboreum Marsh.
Vaccinium elliottii Champ.
Vaccinium stamineum L.

Plot: K11d
Disturbance class: High
Current sedimentation rate: 3.96 cm yr^{-1}
H'*=2.12*
S*=40*
J'*=4.89*
Species:

Acer rubrum L.
Aeschynomene indica L.
Albizia julibrissin Durazz.
Ambrosia artemisiifolia L.
Ambrosia spp.
Andropogon spp.
annual grass
Arenaria caroliniana Walter
Conyza spp.
Crataegus flava Ait.
Diospyros virginiana L.
Festuca spp.
Gallium spp.
Gelsemium sempervirens (L.) Jaume St. Hil.
Helianthus spp.
Lespedeza bicolor Turcz.
Lespedeza cuneata (Dum.-Cours.) G. Don
Morella cerifera (L.) Small
Panicum virgatum L.
Pinus palustris Mill.
Prunus serotina Ehrh.
Quercus falcata Michx.
Quercus hemisphaerica Bartr. ex Willd.
Quercus incana Bartr.
Quercus laevis Walt.
Quercus margaretta Ashe
Quercus marilandica Muenchh.
Quercus nigra L.
Quercus stellata Wang.
Rhus copallina L.
Sassafras albidum (Nutt.) Nees
Smilax spp.
Sporobolus spp.
Toxicodendron radicans (L.) Kuntze
Toxicodendron toxicarium (Salisb.) Gillis
Vaccinium arboreum Marsh.
Vaccinium elliottii Chapm.

Vaccinium stamineum L.
Vitis rotundifolia Michx.
Wahlenbergia marginata (Thunb.) A. DC.

Appendix C: Species response to sedimentation

Table C1. Comparison of mean annual growth of overstory species among disturbance classes. Significant differences Among disturbance classes (found by ANOVA) are indicated by p-values in bold.

Species	**class**										
	HD			**MD**			**RF**				
	N	**gm^2**	**stderr**	**N**	**gm^2**	**stderr**	**N**	**gm^2**	**stderr**	**F-VALUE**	**P**
Acer rubrum	23	2.09	0.45	31	**12.19**	2.88	26	7.95	1.67	5.39	**<0.01**
Alnus serrulata	1	0.75	.	5	1.87	0.40	.	.	.	1.33	0.30
Betula nigra	.	.	.	.	.	.	4	12.48	4.40	.	.
Carya spp.	.	.	.	1	6.66	.	2	21.14	7.75	1.17	0.48
Cornus florida	.	.	.	24	2.02	0.29	4	1.43	0.31	0.67	0.42
Crataegus flava	5	1.55	1.03	.	.	.	.	.	.	.	.
Cyrilla racemiflora	27	2.14	0.27	.	.	.	.	.	.	.	.
Ilex opaca	.	.	.	3	4.94	3.06	6	3.83	1.19	0.18	0.69
Liquidambar styraciflua	24	3.55	0.58	42	10.45	2.24	43	11.30	2.38	2.76	0.07
Liriodendron tulipifera	.	.	.	9	8.22	2.19	16	11.63	2.22	1.01	0.33
Magnolia virginiana	12	1.58	0.51	42	**7.55**	1.51	49	3.82	0.73	4.67	**<0.01**
Morella cerifera	1	2.67	.	5	0.84	0.26	1	0.00	.	5.73	0.07
Nyssa sylvatica	90	4.25	0.55	96	6.71	0.81	46	**8.03**	1.68	4.16	**0.02**
Oxydendrum arboreum	1	4.18	.	.	.	.	1	8.38	.	.	.
Pinus echinata	1	18.62	.	20	5.90	2.23	1	5.65	.	0.78	0.48
P. palustris	2	14.60	0.00	7	9.61	3.81	.	.	.	0.44	0.53
P. taeda	1	4.00	.	9	22.70	5.72	3	39.88	19.19	1.26	0.33
Prunus serotina	3	2.56	1.13	7	1.17	0.39	.	.	.	2.32	0.17
Quercus alba	.	.	.	3	3.88	1.88	3	9.67	4.20	1.59	0.28
Q. falcata	1	4.47	.	9	4.41	1.59	1	5.05	.	0.01	0.99
Q. hemisphaerica	3	15.49	10.91	2	5.83	4.02	.	.	.	0.45	0.56
Q. laevis	1	0.46	.	.	.	.	.	.	.	.	.
Q. marilandica	5	-0.76	1.46	.	.	.	1	**23.14**	.	44.70	**<0.01**
Q. nigra	1	1.06	.	18	14.96	3.83	16	14.93	4.41	0.33	0.73
Q. stellata	1	4.90	.	.	.	.	.	.	.	.	.
Q. velutinus	.	.	.	2	22.98	2.80	.	.	.	.	.

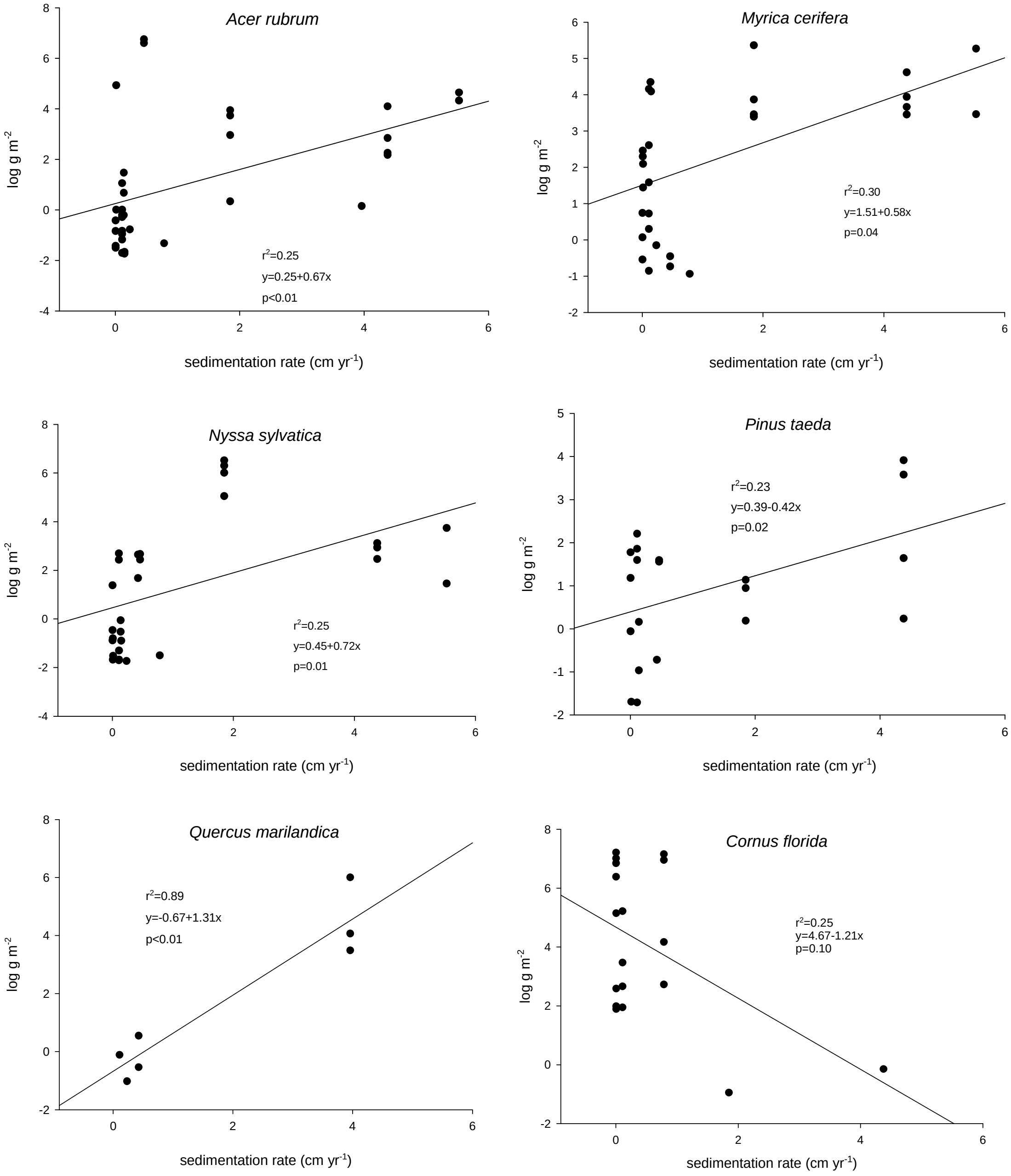

Figure C1. Significant (p<0.01) linear regression relationships between midstory species biomass and current sedimentation rates. Species shown are those which were determined to have significant linear regression relationships using PROC REG.

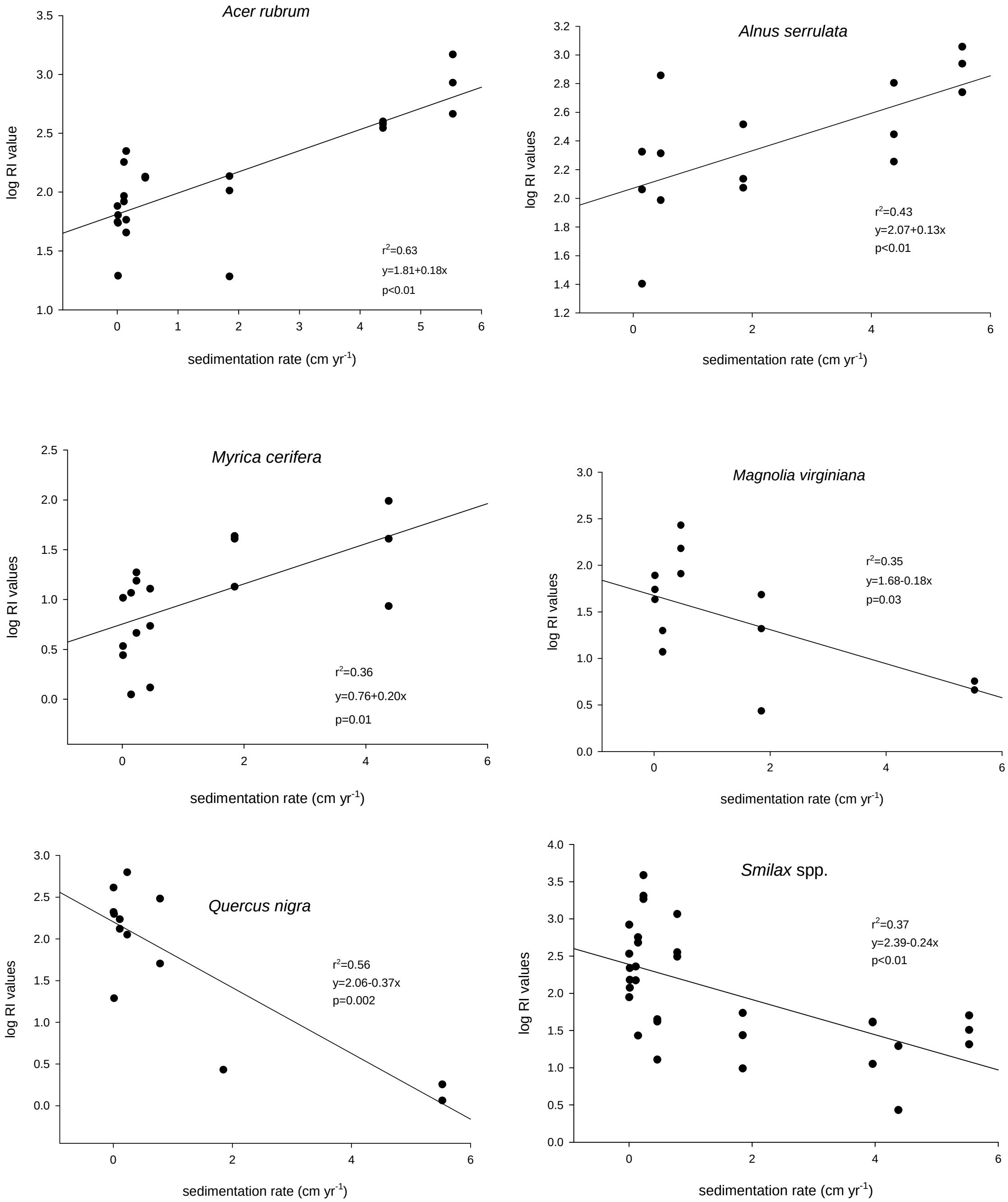

Figure C2. Significant ($p<0.01$) regression relationships between understory species relative importance values and current sedimentation rates.