EFFECTS OF SEDIMENT DEPOSITION ON ABOVEGROUND NET PRIMARY PRODUCTIVITY, VEGETATION COMPOSITION, STRUCTURE, AND FINE ROOT DYNAMICS IN RIPARIAN FORESTS

Except where references is made to the work of others, the work described in this thesis is my own or was done in collaboration with my advisory committee.

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# EFFECTS OF SEDIMENT DEPOSITION IN ABOVEGROUND NET PRIMARY PRODUCTIVITY, VEGETATION COMPOSITION, STRUCTURE, AND FINE ROOT DYNAMICS IN RIPARIAN FORESTS

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THESIS ABSTRACT

EFFECTS OF SEDIMENT DEPOSITION IN ABOVEGROUND NET PRIMARY PRODUCTIVITY, VEGETATION COMPOSITION, STRUCTURE, AND FINE ROOT DYNAMICS IN RIPARIAN FORESTS

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This study examined how increased sediment deposition from anthropogenic disturbance impacts functions performed by riparian forests associated with ephemeral streams. Specifically, this study looked into aboveground net primary productivity, vegetation composition and structure, and fine root dynamics. Across a range of sediment deposition levels, nine ephemeral riparian forests were classified as highly disturbed, moderately disturbed, or reference. Paired circular treatment plots were established in each of the nine areas, with one established in the upper extremities near the stream origin where sediment was most likely to be received and another located farther down, beyond visual evidence of sediment deposition. Comparisons were made between

treatments and among disturbance categories. The features observed by this study included: litterfall, woody increments, aboveground net primary productivity, litterfall nutrient contents, number of seedling and saplings, number of species, shade tolerance, presence/absence of nitrogen fixers, fine root biomass, fine root production, and nutrient contents of fine roots.

Treatment effects (upper vs. lower plots) were not apparent for aboveground parameters, vegetation composition and structure. An exception was the number of seedlings and saplings measured, which was significantly greater in upper plots of highly disturbed areas. However, comparisons of the same variables among disturbance categories at upper plots indicated that litterfall, annual woody increments, and aboveground NPP were significantly lower in highly disturbed areas. No significantly differences were observed between moderately disturbed and reference areas. Vegetation composition and structure were also similar among moderately disturbed and reference areas, where relatively closed canopies, low numbers of seedling and saplings, and dominance of shade tolerant species was observed. In contrast, upper plots of highly disturbed areas exhibited open canopies with very high numbers of seedlings and saplings, dominance of shade intolerant species and presence of nitrogen fixers. Results from this study suggest that sediment deposition has a negative impact upon riparian forests, altering patterns of vegetation composition and structure, and ultimately, decreasing forest productivity.

Fine root dynamics appeared to be most sensitive to high rates of sediment deposition in riparian forests. Fluctuations in fine root standing crop biomass were more pronounced on lower plots and upper plots with fewer disturbances, whereas upper plots

of highly disturbed areas displayed a relatively constant biomass throughout the sample period. Comparisons between upper and lower treatments indicate that fine root productivity was also significantly less in upper plots of highly disturbed areas. No differences were observed between the other two categories. Comparisons across disturbance categories at upper plots followed a similar pattern, with the lowest productivity in highly disturbed areas. Fine root nutrient contents of live and dead roots mirrored changes in fine root biomass and detritus. Lower carbon and nitrogen contents were observed in upper plots of highly disturbed areas. These results suggest that fine roots are good indicators of environmental stress and that high levels of sedimentation may reduce levels of fine root biomass and productivity, which may lead to reductions in forest productivity.

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# I. INTRODUCTION

Riparian forests are one of the most diverse, dynamic, and complex biophysical habitats among natural systems (Naiman and Décamps 1997), serving as an interface between aquatic and terrestrial environments (Gregory et al. 1991). The position of these ecosystems along bodies of water (streams, rivers, lakes) drives their unique vegetation composition and structure. Characteristically, riparian areas have greater diversity of animal and plant species, vegetation structure and are vegetatively more productive than surrounding uplands (Gregory et al. 1991, Naiman et al. 1993).

Many functions performed by riparian systems have great societal value. These functions include: (1) fish and wildlife production; (2) bank erosion protection; (3) flood control; (4) water quality maintenance; (5) timber production; (6) sound absorption; (7) air quality maintenance; (8) recreation; and (9) scenic barriers to upland development (Burns 1984, Johnson et al. 1984, Smith 1984, Bren 1993). However, the character and vitality of riparian systems throughout the United States have been degraded by numerous human activities representing a variety of public and private uses. The result of such uses is the physical alteration of riparian systems and the elimination of some natural functions (Bren 1993). Accelerated streambank and channel erosion, sediment inputs on rivers and streams, large amounts of inundated land, input of polluted water, inappropriate vegetation introduction and loss of native plant species, represent some of the consequence of these uses (Plantico 1984, Smith 1984, Bren, 1993).

One of the most important qualities of riparian zones is their ability to improve water quality by reducing non-point source nutrient loads leaving agricultural fields and other disturbed areas through denitrification, sedimentation, or direct root uptake. By filtering sediment in surface runoff, carbon, nitrogen and phosphorous are sequestered by riparian zones and downstream ecosystem integrity is maintained (Lowrance et al. 1986, Cooper et al. 1987, Daniels and Gilliam 1996, Craft and Casey 2000). Cooper et al. (1987) estimated that 80-90% of the sediments leaving agricultural fields in North Carolina remained in the riparian zone. A study conducted in the Coastal Plain of Georgia found that more than 65% of nitrogen and 30% of phosphorous from adjacent agricultural areas were retained by riparian forests (Lowrance et al. 1986). Although the ability of riparian ecosystems to trap sediment and retain nutrients is well known (Vought et al. 1995), few studies have investigated the impact of sedimentation on riparian forest functions.

Evidence suggests that forest health and productivity may be negatively influenced by high rates of sediment deposition (Kennedy 1970). Mechanisms of tree decline related to sedimentation are not entirely clear, but may be related to restricted oxygen diffusion to roots, decreased respiration, decreased nutrient uptake, and increased root mortality (Broadfoot and Williston 1973). Kozlowski et al. (1991) and Ewing (1996) observed that deposition of sediments on the soil surface might have an effect similar to that of flooding by limiting gas exchange in roots and lenticels. Low oxygen conditions may reduce root metabolism, nutrient uptake and increase root mortality. Therefore, photosynthesis and levels of production by trees may also decrease.

Some community level responses are also evident. Increased levels of disturbance may affect regeneration within riparian forests and may change successional patterns (Loucks 1970, Scott et. al 1985). For example, it has been suggested that high levels of sediment deposition may inhibit recruitment of native plants and reduce the emergence of woody and herbaceous seedlings, and 'functional gaps' may be created (Jurik et al. 1994, Levine and Stromberg 2001). In general, vegetation response to sedimentation appears to be a function of individual plant species and their ability to tolerate sediment. Therefore, more opportunistic individuals and species that are highly tolerant or moderately tolerant to increased burial depth may become dominant over these unoccupied areas (Wardrop and Brooks 1998, Levine and Stromberg 2001). As a result, plant community richness and diversity may decrease, which may cause a forest to revert to an earlier seral stage. A study on the effects of sediment load on recruitment of emergent wetland herbaceous species from the seed bank (Jurik et al. 1994) showed that the number of species and total number of individuals recruited decreased significantly with sediment accretion as low as 0.25 cm. Similar results were found by Levine and Stromberg (2001) in riparian forests in the southwest U.S., where seedling survivorship of three native woody species (*Populus fremontii*, *Salix gooddingii* and *Baccharis salicifolia*) decreased with increasing burial depth.

Changes in successional patterns may also cause changes in litter quality and, therefore, biogeochemical cycling may be affected through alteration of decomposition rates and nutrient cycling (Day 1982, Cote et al. 2000), leading to changes in site productivity. In a study of litter decay in the seasonally flooded Great Dismal Swamp, Day (1982) observed that litter quality was greatly influenced by species composition and was also the prime determining factor of variation in litter decomposition rates. Tupelo (*Nyssa aquatica*) produced the most rapidly decomposing litter, while upland oak species (*Quercus laurifolia* and *Q. alba*) showed the slowest decay rates. In addition to direct effects on succession, sediment deposition may also change biogeochemistry patterns through burial of litter. Herbst (1980) observed that buried leaves of silver maple (*Acer saccharinum*) lost less weight and had higher organic content than leaves deposited on the surface. He observed the same results for buried and unburied leaves of eastern cottonwood (*Populus deltoides*) and suggested that the mechanisms driving such differences in leaves decomposition were: (1) compaction – leaves compacted together have less surface area available for biotic activities; (2) reduced abrasion and mechanical breakage; (3) increased anaerobic conditions and; (4) differences in microbial colonization. In contrast, Mayack et al. (1989) found that even though sediment deposition may alter microbial activity, no significant differences on leaf mass loss were observed for surface and buried leaves of sweetgum (*Liquidambar styraciflua*).

Significant changes in ecosystem structure or function in response to an anthropogenic stress are not typically noted until the system declines sufficiently so that visual symptoms are evident (Vogt et al. 1993). For this reason, fine roots can serve as a sensitive bioindicator of environmental stress. Since they are in direct contact with soil they may provide indications of subtle responses to any anthropogenic stress that results from changes in the physical or chemical characteristics of the soil (Vogt et al. 1993). For example, Brinson (1990) reported that belowground production might be more sensitive to changes in soil oxidation/reduction status than aboveground production.

Total forest productivity is dependent upon acquisition of both above- and belowground resources. Fine roots represent a dynamic portion of the forest community and, in some forests, up to 75% of total net primary production is allocated belowground (Fogel 1985, Nadelhoffer and Raich 1992). However, rates of belowground production have received little attention in studies of riparian forests. Many studies rely only on aboveground parameters to estimate forest productivity including mean annual increment, site index and litterfall (Bray and Gohram 1964, Conner and Day 1992, Conner 1994, Megonigal et al. 1997) and the belowground component is seldom examined due to the many challenges associated with root studies. Therefore, failure to include fine root biomass may underestimate forest productivity and generate misleading conclusions (Day and Megonigal 1993). Fine roots are also an important source and sink for nutrients in terrestrial ecosystems and serve a vital role in fluxes of energy, since root turnover represents a major pathway for nutrient and carbon cycling (Harris et al. 1980, Fogel 1983, Persson 1983, Gordon et al. 2000). According to Vogt et al. (1986), the amount of N added to the soil by fine root turnover was from 18% to 58% greater than that added by aboveground litterfall in some ecosystems. Despite the importance of fine roots in forest dynamics, no studies have been conducted in riparian forests to evaluate the effects of sediment deposition on fine root biomass, production and turnover.

An evaluation of impacts on ecosystem processes depends on the quantification of changes in these processes and their controlling factors. This study examined how increased sediment deposition impacts the functions performed by riparian forests associated with ephemeral streams. The objectives of this study were to quantify aboveground net primary productivity, vegetation composition and structure, and fine root dynamics across a gradient of sediment deposition. Specifically, the following hypotheses were tested to achieve these objectives:

I. Vegetation composition and community structure will be altered by sediment deposition.

    i. Sedimentation will cause vegetation shifts toward early successional species. More opportunistic and stress-tolerant species will dominate.

II. Fine root biomass and productivity will be lower in disturbed areas. Because fine root nutrient content mirror fine root biomass, it will also be lower for disturbed areas.

III. Aboveground net primary productivity will be lowest in sites with high rates of sedimentation.

    i. Changes in stand structure and decreased fine root productivity will affect forest productivity.

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## II. EFFECTS OF SEDIMENT DEPOSITON ON VEGETATION COMPOSITION AND STRUCTURE IN RIPARIAN FORESTS


### ABSTRACT

The importance of riparian forests in water quality improvement through sediment trapping has been well documented. Quantification and identification of sources of sediment deposition has been the focus of many studies. However, how riparian systems respond to high rates of sediment deposition is still unknown. This study was conducted at Fort Benning, GA, where intensive military traffic on sandy roads has generated movement of large amounts of sediment into riparian forests associated with ephemeral streams. The objective of this study was to evaluate how excessive sediment deposition affects riparian forest function, composition and structure. Two paired plots were established in each of nine ephemeral streams, to encompass a wide range of sediment deposition. One treatment plot (upper plot) was established in the upper reaches of each ephemeral stream and another (lower plot) was located farther down, beyond visual evidence of sediment deposition. Comparisons between treatments and among disturbance categories were made in terms of aboveground net primary productivity, litterfall nutrient contents, leaf area index, and changes in vegetation composition and structure. These were assessed by documenting understory vegetation in terms of number

of individuals, number of species, shade tolerance and presence of nitrogen fixers. No significant differences between treatments were observed in any of the aforementioned variables. However, when comparisons were made across disturbance categories, at upper plots, we observed that litterfall, woody increment, aboveground NPP, LAI, and nutrient contents were significant less in highly disturbed areas, whereas the inverse was observed in parameters used to assess changes in vegetation composition and structure. Numbers of individuals in the smallest diameter class (<1.0 cm), numbers of shade intolerants, and numbers of N fixers were significantly greater in highly disturbed areas. Therefore, our results suggest that excessive sediment deposition can have a negative impact on riparian forests, altering patterns of vegetation composition and structure and ultimately compromising forest productivity.

## INTRODUCTION

Riparian forests are complex ecosystems that interact with both terrestrial and aquatic environments (Gregory et al. 1991). The linear position of riparian ecosystems along rivers and streams gives them unique spatial patterns and temporal dynamics. Site conditions (i.e., soil texture, soil moisture, nutrient availability, etc.), surface flow, and disturbance regimes are considered the main factors determining local species composition and forest diversity (Brinson 1990, Perry 1994, Rot et al. 2000). One of the most well known values of riparian forests is that of water quality improvement by retention of sediment loads leaving agricultural fields and associated nutrient removal.

In riparian forests, most sediment studies have focused on large river systems, which transport large quantities of sediments (Hupp et al. 1993). Proportional to their areas, headwater riparian forests may be especially important in sediment removal, but seldom have been studied (Wardrop and Brooks 1998). In one of the few studies addressing ephemeral streams, Cooper et al. (1987) observed that greater than 50% of sediment was trapped in riparian forests. Unfortunately, although riparian systems are largely recognized for sediment removal, the effects of excessive sediment loads on riparian functions are unknown.

Buried stems and presence of adventitious roots are the principal form of botanical evidence of high sediment accumulation (Hupp and Morris 1990). The likelihood of a given species vigorously growing under high rates of sediment deposition appears to be a function of the ability of that species to adjust (i.e. formation of adventitious roots) to sediment depth. For example, in a study relating the effects of fill operations and tree vitality, Clewell and McAninch (1977) observed that loblolly pine (*Pinus taeda*) experienced mortality with as little as 15 cm of burial, sweetgum (*Liquidambar styraciflua*) and water oak (*Quercus nigra*) exhibited mortality at 50 cm burial, while swamp tupelo (*Nyssa sylvatica* var. *biflora*) death occurred following more than 60 cm of burial. In a study of sediment load effects on various life history stages in cattail (*Typha* x *glauca*), a dominant and persistent emergent plant in wetlands, Wang et al. (1994) found that seed germination was reduced to up to 90% when sediment loads of 0.2 – 0.4 cm were applied to the surface of soil.  At the seedling level, these authors observed that increased survivorship was related with increased age and size of seedling, however reductions in survivorship were observed as sediment loads increased from 0.1 to 1.0 cm. Therefore, if sediment deposition has detrimental effects on seed germination and seedling survivorship, then one might expect substantial effects on the composition of riparian vegetation in areas experiencing sediment deposition.

It is not entirely clear how high rates of sediment deposition interact with soil chemical, physical and biological properties. It has been suggested that increased rates of sediment deposition may have effects similar to continuous flooding, which creates an anaerobic rooting zone (Kozlowski 1991, Ewing 1996). Anaerobic respiration within the root system of plants leads to the production of toxic byproducts and limits uptake of nutrients and water, which are critical to forest productivity. In addition, anaerobic conditions may affect decomposition rates of organic matter and thus nutrient incorporation.

Although riparian forests are widely credited with sediment trapping, few studies have quantified changes in riparian forest dynamics as affected by high rates of sediment deposition from anthropogenic disturbance. Even less is known about riparian forests associated with ephemeral streams. Consequently, the main objective of this study was to quantify and compare the components of aboveground net primary productivity in ephemeral riparian forests across a range of sediment deposition levels. To achieve this objective, the following hypotheses were addressed: 1) high rates of sediment deposition will negatively affect litterfall biomass, woody increments, and aboveground net primary production; and 2) high rates of sediment deposition will alter successional patterns.

# MATERIAL AND METHODS

## Study Site

This study was conducted at Fort Benning, GA, a U. S. Army installation, where intensive disturbance by military traffic has generated significant sediment movement into riparian forests. The installation is located in the southeastern United States, occupying an area of 73,503 ha in Chattahoochee, Muscogee, and Marion Counties of Georgia and Russell county of Alabama (Figure 1). Two physiographic regions are encompassed by Fort Benning: the Piedmont and Coastal Plain. For the purposes of this study, only riparian forests within the Coastal Plain were selected. Forest types on the study areas are primarily deciduous and uneven aged, characterized by hardwood or mixed hardwood/pine overstory. Species composition on the study sites reflected an assemblage typical of most southern Coastal Plain wetland forests dominated by: *Nyssa sylvatica* (black gum), *Acer rubrum* (red maple), *Liquidambar styraciflua* (sweetgum), *Quercus nigra* (water oak), *Liriodendrum tulipifera* (yellow poplar), *Magnolia virginiana* (sweetbay), *Cornus* spp. (dogwood) and *Ilex opaca* (american holly), among others.

Soil series found within the study area include Bibb, Troup, Lakeland, Chastain, and Cowarts soils. Bibb soils are coarse-loamy, siliceous, acid, thermic Typic Fluvaquents, and poorly drained. Troup soils are loamy, siliceous, thermic Grossarenic Kandiudults, and somewhat excessivly drained.  The Lakeland soils are coated, thermic Typic Quartzipsamments, and excessively drained. Chastain soils are fine, mixed, acid, thermic Typic Fluvaquents, and poorly drained.  Cowart soils are fine-loamy, siliceous, thermic Typic Kanhapludults, and moderately to well drained (Soil Survey-NCRS).

**Study Design**

Nine ephemeral streams, over a range of sedimentation conditions, were selected and classified as follow: (1) highly disturbed; (2) moderately disturbed; and (3) reference. Widely spreading alluvial fans with exposed, loose, light-colored soil, which was low in organic matter, were an indicator of high sedimentation and were verified by the buried bases of trees. Trunk burial and smaller alluvial fans indicated moderate levels of sedimentation. Reference sites had no trunk burial and lacked active alluvial fans. Sediment sources on highly and moderate disturbed areas were often unimproved (dirt) roads or tracked vehicle corridors, with channels or gullies serving as sediment conduits.

The study was designed using paired plots within catchments. Two permanent 0.04 ha circular treatment plots were established along each of the nine ephemeral streams, based on a vegetation inventory and visual evidence of sedimentation. One plot was established in a topographic position higher in the stream (i.e. nearer to the stream's origin) and another was located farther down stream beyond visual evidence of sediment deposition. On the highly and moderately disturbed areas, the "upper plot" exhibited visual evidence of sedimentation due to the proximity of unpaved roads. Upper plots on highly disturbed areas were located within the alluvial fan, and tended to have a more open canopy and less dense understory vegetation in comparison with lower plots. Both upper and lower plots within moderately disturbed and reference areas displayed an increase in tree species diversity and density, a nearly closed canopy, and a reduction in herbaceous cover compared to highly disturbed areas. In general, lower plots had higher soil moisture contents due to their lower topographic position. Soil texture, soil series and soil chemical properties of each catchment are presented in Table 1.

**Long-term sediment deposition**

Rates of sediment deposition were measured following the dendrogeomorphic approach of Hupp and Morris (1990). In the upper plot of each catchment, trees were excavated to the depth at which primary lateral roots appeared. The depth from the soil surface to the top of these roots was measured and recorded. In addition, a disk from near the base of the tree was removed and sent to the laboratory, where rings were counted and tree age was determined. The sedimentation rate was calculated as the difference between the current soil surface and the depth to primary lateral roots divided by the age of the tree. The following mean rates of sediment deposition were obtained: 2.20 cm $yr^{-1}$ for the highly disturbed areas, 0.66 cm $yr^{-1}$ in the moderately disturbed area, and 0.0 cm $yr^{-1}$ within the reference areas.  Since there was no visual evidence of sediment deposition on lower plots in any catchment, it was assumed to be non-existent.

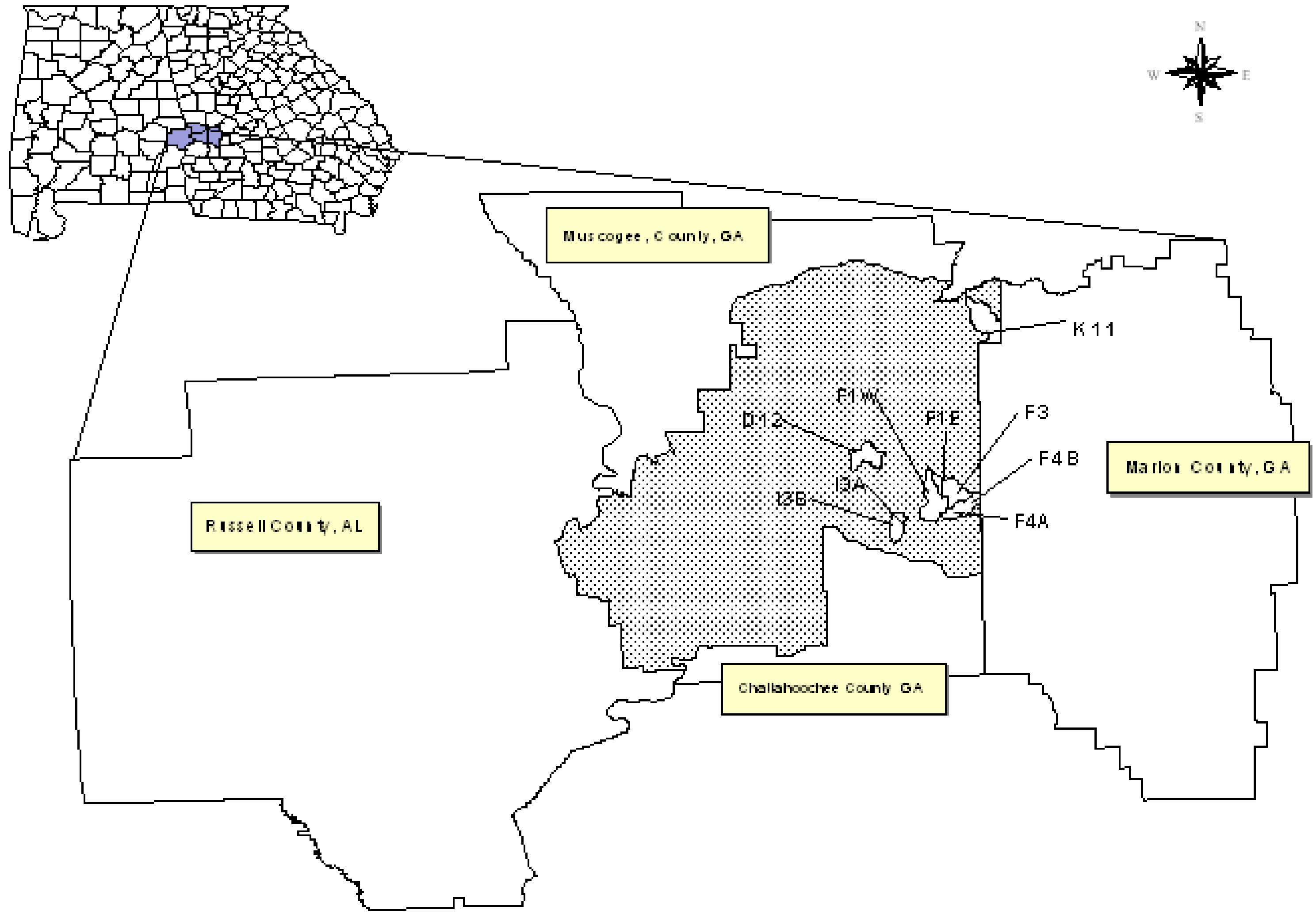


Figure 1. Location of Fort Benning and study sites.

Table 1. Soil texture, soil series and, soil chemical properties of the nine study sites.

| WS | Treatment | Disturbance Category | Soil Texture | Soil Series | pH | P | K | Mg | Ca |
|---|---|---|---|---|---|---|---|---|---|
| D12 | Lower | Highly disturbed | Sandy loam | Bibb, frequently flooded | 5.0 | 2.0 | 46.3 | 26.3 | 135.0 |
| D12 | Upper | Highly disturbed | Fine loamy | Cowarts and Ailey, 12-18% slope | 5.0 | 0.8 | 22.0 | 21.7 | 85.0 |
| F1W | Lower | Highly disturbed | Fine loamy | Cowarts and Ailey, 12-18% slope | 5.2 | 1.8 | 22.2 | 14.3 | 41.7 |
| F1W | Upper | Highly disturbed | Loamy sand | Troup, 12-25% slope | 4.9 | 0.5 | 43.0 | 5.8 | 26.7 |
| F3 | Lower | Highly disturbed | Loamy sand | Troup, 12-25% slope | 5.0 | 1.7 | 48.2 | 23.5 | 81.7 |
| F3 | Upper | Highly disturbed | Loamy sand | Troup, 12-25% slope | 5.4 | 1.0 | 5.0 | 6.5 | 21.7 |
| K11 | Lower | Highly disturbed | Sandy | Lakeland, 5-18% slope | 5.5 | 2.0 | 20.3 | 14.0 | 58.3 |
| K11 | Upper | Highly disturbed | Sandy | Lakeland, 5-18% slope | 5.8 | 1.3 | 15.5 | 9.8 | 36.7 |
| F1E | Lower | Moderately disturbed | Sandy | Lakeland, 5-18% slope | 5.0 | 2.5 | 29.3 | 14.8 | 36.7 |
| F1E | Upper | Moderately disturbed | Sandy | Lakeland, 5-18% slope | 5.2 | 3.0 | 45.8 | 18.5 | 65.0 |
| I3A | Lower | Moderately disturbed | Loamy sand | Troup, 5-12% slope | 4.7 | 0.3 | 35.5 | 32.0 | 63.3 |
| I3A | Upper | Moderately disturbed | Fine loamy | Cowarts and Ailey, 12-18% slope | 5.2 | 0.3 | 14.3 | 19.7 | 140.0 |
| I3B | Lower | Moderately disturbed | Loamy sand | Troup, 12-18% slope | 4.7 | 1.3 | 35.7 | 22.5 | 63.3 |
| I3B | Upper | Moderately disturbed | Loamy sand | Troup, 12-18% slope | 4.8 | 1.2 | 24.8 | 18.5 | 110.0 |
| F4A | Lower | Reference | Loamy sand | Chastain, frequently flooded | 5.3 | 1.8 | 47.8 | 18.8 | 63.3 |
| F4A | Upper | Reference | Loamy sand | Chastain, frequently flooded | 4.4 | 2.0 | 14.7 | 12.5 | 50.0 |
| F4B | Lower | Reference | Loamy sand | Troup, 2-5% slope | 4.9 | 1.0 | 71.3 | 30.3 | 78.3 |
| F4B | Upper | Reference | Loamy sand | Troup, 2-5% slope | 4.7 | 1.0 | 56.0 | 36.3 | 88.3 |

**Aboveground net primary productivity – ANPP**

Determination of aboveground net primary productivity for each site was based on measurements of overstory litter production and tree growth. Overstory litter production was measured with three 0.5 m x 0.5 m litter traps randomly installed in each 0.04 ha circular treatment plot in March of 2002. The bottoms of the traps were covered with 2 mm nylon mesh, and litter was collected monthly from April 2002 through June of 2003. On a plot basis, collected litterfall from the three litter traps was composited and then sorted into components (leaves, twigs, reproductive parts, and others), oven-dried to constant mass (70ºC, 48 hr), and weighed.

Rates of biomass accumulation in the tree stratum were determined using plot inventory and allometric biomass equations. In each 0.04 ha circular treatment plot, all trees $\geq$ 10 cm diameter at breast height (DBH, $\approx$ 1.3 m) were identified according to species, condition (form, live or dead), tagged, and measured for DBH and height. All plots were inventoried in January 2002 and January 2003. Stem biomass production for different hardwood species was calculated from allometric equations developed by the USDA Forest Service for the Gulf Atlantic Coastal Plains (Clark et al. 1985). Pine species stem biomass equations were derived from Ter-Mikaelian and Korzukhin (1997). Stem diameter at breast height was the independent variable for both hardwood and pine biomass equations.

Annual woody biomass production was calculated by subtracting biomass production in 2002 from that of 2003. Annual aboveground net primary productivity

(ANPP) was estimated by adding annual woody biomass production to annual litter fall biomass increments.

**Leaf area index - (LAI)**

Leaf area index was determined based on leaf area and leaf weight. In each treatment plot, combined fresh foliage samples were collected in November and December of 2002. Leaf ares was measured using a Delta T video image system on small fresh samples, and leaves were then dried to constant mass (70ºC, 48 hr). All leaf areas were given as the projection of one side of a leaf. Leaf area index (LAI - $m^2.m^{-2}$ or unit less) was calculated as the product of LA (leaf area) and the leaf litter weight.

**Foliar nutrient analysis**

Oven-dried litterfall samples (70ºC, 48 hr) were ground either by hand (small samples) using a mortar and pestle or in a Wiley mill to pass a 20-mesh screen and analyzed for N, C, and P. Total N and C analyses were determined by thermal combustion using a Perkin Elmer Series II CHNS/O Analyzer 2400 (Perkin Elmer Corp., Norwalk, CT). Litter total P samples were dry-ashed, extracted, and concentration was determined using the vanadomolybdate procedure (Jackson 1958). Total P analyses were read on a Spectronic 501 spectrophotometer (Milton Roy Company, Rochester, NY). Leaf litter N, C, and P concentrations were multiplied by the leaf dry weight at each sample period to determine N, C, and P contents of litter.

## Changes in vegetation composition and structure

To assess possible changes in woody regeneration caused by high rates of sediment deposition, four 1.80-meter radius subplots were installed within each treatment plot. All woody seedlings (< 4cm in root collar diameter) and saplings (> 4.0 – < 11 cm) within the seedling plot boundaries were identified and measured. Herbaceous species were not measured. Species, height, and root collar diameter were recorded. Quantitative evaluation of successional patterns was based on estimates of standing crop biomass of shrubs and small trees. Standing crop biomass was calculated from biomass equations for trees and shrubs from the literature (Clark and Taras 1976, Smith and Brand 1983, Clark et al. 1985, Mader 1990, Hauser 1992). Field sampling was conducted in June 2003. Based on characteristic descriptions (Samuelson and Hogan 2003, Miller and Miller 1999), species were classified as: (1) shade tolerant or intolerant; (2) N fixers; or 3) other. Changes in vegetation composition (early vs. late succession) and structure among disturbance categories were qualitatively estimated based on the shade tolerance of species, presence/absence of N fixers and diameter class distribution (Number of individuals per diameter class). Due to restrict assess in some of the study sites, data for reference areas could be collected only for one of the two areas, and no statistical analyzes could be performed.

## Statistical analysis

Mean comparisons between treatments, within each disturbance category, were performed using T-tests (PROC TTEST, SAS Institute, 1999). Variables compared were:

litterfall, woody increment, ANPP, LAI, litterfall nutrient content, understory standing crop biomass, number of individuals, number of species, and number of nitrogen fixers. Duncan's New Multiple Range procedure was used to test for differences in the same variables among disturbance classes at the upper plots. Unless noted, differences between means were considered statistically significant at $\alpha = 0.05$. In addition, linear regression analyses (PROCREG, SAS Institute, 1999) were conducted to determine whether or not there was a relationship between sediment deposition and aboveground parameters.

## RESULTS

### Aboveground productivity

In the present study, the plant community within the three disturbance categories exhibited two peaks of litter deposition from April 2002 through June 2003. Peaks in October and November correspond to autumn leaf fall, while those in April were probably due the occurrence of storms (Figures 2-4). Reference areas exhibited the highest annual total litterfall for both upper (746 g $m^{-2}$ $yr^{-1}$) and lower (661 g $m^{-2}$ $yr^{-1}$) treatment plots, followed by moderately disturbed (567 g $m^{-2}$ $yr^{-1}$ and 581 g $m^{-2}$ $yr^{-1}$, upper and lower treatment plots, respectively) and highly disturbed areas (554 g $m^{-2}$ $yr^{-1}$ and 306 g $m^{-2}$ $yr^{-1}$, upper and lower treatment plots, respectively). No significant differences were observed between treatments within each disturbance category (Table 2). Comparisons among disturbance categories at the upper plots (Table 4) indicated that reference areas differed significantly from highly disturbed areas. Annual litterfall was greatest in the reference areas, followed by moderately disturbed and highly disturbed areas. Leaves comprised the greatest amount of annual litterfall biomass (64 – 77%) for both treatments on each of the three disturbance categories (Figure 5). Regression analysis of litterfall vs. long-term sedimentation rates was significant at the $P < 0.04$ level, with a $R^2$ of 0.55 (Figure 7a).

Annual woody biomass increments ranged from 158 g $m^{-2}$ $yr^{-1}$ on upper plots of highly disturbed areas to 847 g $m^{-2}$ $yr^{-1}$ on lower plots of reference areas. Comparisons between upper and lower treatment plots within disturbance categories suggested higher woody increments on lower plots of reference areas (Table 2). The high woody increment in lower plots of reference areas was probably due rapid growth by the large pine trees found there. Comparisons of woody biomass increments among disturbance categories at upper plots showed a trend similar to that observed for litterfall. Woody increments exhibited a significant negative regression relationship with long-term sediment deposition rate ($P < 0.04$, $R^2 = 0.53$) (Figure 7b). Tree growth comprised 46%, 36%, 56% and 34%, 38%, 40% of ANPP on lower and upper treatment plots of highly disturbed, moderately disturbed and reference areas, respectively.

The sum of litterfall and wood production was used to approximate aboveground net primary production. Aboveground NPP in this study ranged from 465 g $m^{-2}$ $yr^{-1}$ on upper plots of highly disturbed areas to1507 g $m^{-2}$ $yr^{-1}$ on lower plots of reference areas (Table 2). No statistically significant differences were observed between treatments, however; among disturbance categories, aboveground NPP on upper treatment plots of highly disturbed areas was significantly less ($P < 0.05$) than moderately disturbed and reference areas. Aboveground NPP vs. long-term sedimentation regression trends were similar to those for litterfall biomass and woody increments (Figure 8a). Aboveground NPP decreased significantly with increased sediment deposition ($P<0.03$, $R^2 = 0.54$).

**Leaf area index – LAI**

During the study period, LAI ranged from 3 to 7 (Figure 6). Although LAI was numerically greater in lower plots of highly disturbed areas, no statistically significant difference was observed between treatments. On moderately disturbed areas, LAI was practically the same for both treatments. Highest LAI values for both treatments were obtained for reference areas. Comparisons among disturbance categories at upper treatment plots did not reveal any significant difference, however, LAI exhibited a significant negative relationship with sediment deposition ($P$<0.06, $R^2$ = 0.53) (Figure 8b).

**Foliar nutrient contents**

Comparisons of C, N, and P contents between upper and lower treatment plots within each disturbance category did not indicate any significant difference for moderately disturbed and reference areas (Table 3). However, within highly disturbed areas, C content was significantly less in upper plots. No significant differences between treatments were observed for N and P contents in highly disturbed areas. Consistently, mean carbon, nitrogen, and phosphorus contents were higher in reference areas, followed by moderately disturbed and highly disturbed areas, respectively. Comparisons across disturbance categories at upper treatment plots (Table 4) revealed that carbon content was significant less at highly disturbed areas compared to moderately disturbed and reference areas. Nitrogen content was significantly less in highly disturbed areas in comparison to reference areas, but no significant differences were observed between highly and moderately disturbed areas or moderately disturbed and reference areas. Phosphorous contents were significantly greater in reference areas. In general, nutrient content of litterfall followed the same trend as biomass within each treatment and disturbance category, with higher C, N, and P contents observed in October and November of 2002 and April of 2003. Litterfall N: P ratios in highly disturbed, moderately disturbed and reference areas were 9.0, 9.6 and 9.2 respectively, in lower plots, and 11.1, 8.8, and 7.8 in upper plots.

**Changes in vegetation composition and structure**

Comparisons between treatments in highly disturbed areas indicated that standing crop biomass, number of individuals sampled, and number of individuals that are N fixers were significantly greater in upper plots (Table 6). No significant differences were observed for species richness, and shade tolerance within highly disturbed areas. For moderately disturbed areas, the only significant difference between treatments was observed for number of individuals that are shade intolerants, which was significantly greater in lower plots. Due to missing data, comparisons between treatments in reference areas could not be performed since we had data for only one of the two reference sites. Comparisons across disturbance categories at upper plots (Table 7) indicate that standing crop biomass, number of individuals sampled, number of individuals that are N fixers, and number of shade intolerants were significantly greater in highly disturbed areas. No significant differences were observed between moderately disturbed and reference areas for any of the variables analyzed. No differences were observed in diameter class distribution curves among disturbance categories (Figures 9-11). *Liquidambar styraciflua*, *Acer rubrum,* and *Magnolia virginiana* were the most common species measured in the understory vegetation plots, for both treatments and across disturbance categories (Table 5). In general, both upper and lower treatment plots, in the three disturbance categories, displayed diameter distributions of an inverse J shaped curve, with more individuals within the smallest diameter classes. Even though diameter distributions were similar, the number of individuals within the smallest diameter classes was much higher in upper plots of highly disturbed areas.

## DISCUSSION

### Aboveground productivity

The pattern of litterfall in both upper and lower treatment plots was similar for the three disturbance categories (Figures 2-4). Litterfall reached a peak during October and November of 2002. In the Great Dismal Swamp, Gomes and Day (1982) also observed peaks of litter production occurring in October and November. Conner and Day (1992) documented leaf fall in forested wetlands in Louisiana beginning in September and ending by January.  Similarly, Clawson et al. (2001) reported that litterfall production began in September and continued through December, peaking by November, in the Flint River floodplain, Georgia.

Foliage biomass in the present study constituted 64-77 % of total litterfall production (Figure 5). The leaf fraction was less on upper treatment plots of highly disturbed areas probably due to the lack of tree individuals (Table 2). Gomez and Day

(1982) reported similar total leaf values of 66.9–81.5 % in the Great Dismal Swamp, Virginia. In comparison with Clawson et al.'s (2001) values of 79.5% - 86.5% in the Flint River floodplain, Georgia, the percentage of leaves in litterfall was less on our study. However, it was greater than the 66% reported by Brinson et al. (1980) from a North Carolina alluvial swamp. These variations may be due to differences in species composition and/or density of woody species.

Litterfall values can be useful indicators of minimum levels of net primary production in forests (Bray and Gorham 1964). Annual litterfall is of major importance to nutrient cycles and energy, especially in wetland forests. In the present study, litterfall production decreased as the rates of sediment deposition increased (Table 2). Although comparisons between treatments in each disturbance category did not show statistically significant differences, when comparisons were made for upper treatment plots among disturbance categories, a significant decrease ($P < 0.05$) in litter production was observed for highly disturbed areas (Table 4). Data from our regression analysis (Figure 7a) suggest that a rapid decrease in litterfall biomass occurs with small rates of sediment deposition (0.2 – 0.3 cm $yr^{-1}$), reaching a reduced equilibrium at sediment accumulation above 0.5 cm $yr^{-1}$.

It is not entirely clear how rates of sediment deposition may affect soil physical and chemical properties, but both Kozlowski et al. (1991) and Ewing (1996) suggested that excessive sedimentation on forest soils may have effects similar to those of flooding, causing physiological stress in the forest community imposed by an anaerobic rooting zone. With the exception of upper plots on highly disturbed areas, our litterfall values (554 – 746 g $m^{-2}$ $yr^{-1}$) were consistent with other studies on riparian communities throughout the southeastern United States (Gomes and Day 1982, Megonigal and Day 1988, Megonigal et al. 1997, Clawson et al. 2001). In a study of forest productivity across a hydrologic gradient in South Carolina and Louisiana sites, Megonigal et al. (1997) observed that leaf production on continuously or nearly continuous flooded areas (395 g $m^{-2}$ $yr^{-1}$), was significantly lower than on intermediate or dry sites. Carter et al. (1973) reported similar values (373 g $m^{-2}$ $yr^{-1}$) for an undrained baldcypress (*Taxodium distichum* var. *distichum*) area. Both studies related decreases in litterfall biomass to increased anaerobiosis within the rooting zone. Therefore, assuming that high rates of sediment deposition have the same effects as flooding, our values for litterfall production on the upper plots of highly disturbed areas (306 g $m^{-2}$ $yr^{-1}$) followed similar trends. Clawson et al. (2001) also observed this same trend of decreased litterfall production with increased wetness, however they did not find any significant difference among wetness types. The values reported in their study for poorly drained areas (564 g $m^{-2}$ $yr^{-1}$) were greater than ours. This difference could be explained by a lack of tree individuals in the overstory of our highly disturbed areas (Table 2). Moreover, wet but aerobic conditions at their site may have stimulated productivity (Day 1984).

Woody increments in biomass followed the same pattern as litterfall production, with decreased woody biomass associated with increased rates of sediment deposition (Figure 7b). Apparently, a sediment deposition rate above 0.5 cm $yr^{-1}$ seems to form a threshold beyond which major reductions become evident. Stem biomass ranged from 158 g $m^{-2}$ $yr^{-1}$ on upper plots of highly disturbed areas to 847 g $m^{-2}$ $yr^{-1}$ on lower plots of reference areas (Table 2). The large values for woody biomass in lower plots of reference areas were due to the presence of large pine trees. In contrast, the small values in upper plots of highly disturbed areas were attributed to lack of tree individuals in some of the disturbed catchments. Excluding these two extremes, our values were lower than the values reported by Clawson et al. (2001) in the Flint River floodplain, and also those reported by Megonigal et al. (1997) in the Pearl River, Louisiana. However, values of woody increments in the present study were consistent with those reported by Megonigal et al. (1997) for intermediately flooded sites located on Upper Three Runs Creek, and on Meyers Branch, both of South Carolina. Woody biomass on upper plots of highly disturbed areas in the present study was similar to values reported by Megonigal et al. (1997) on sites with hydrologic perturbations located on the Savannah River, South Carolina (116-213 g $m^{-2}$ $yr^{-1}$), and on the Barataria Basin, Louisiana (92-416 g $m^{-2}$ $yr^{-1}$).

Forest net primary productivity is often used as an index to characterize forest ecosystems, allowing comparisons across systems that have different species composition, structure, and disturbance histories. Comparisons of forest productivity among disturbance categories in the present study suggest that it is negatively affected by high rates of sediment deposition coming from anthropogenic disturbance. Aboveground net primary productivity was lowest (465 g $m^{-2}$ $yr^{-1}$) in upper plots of highly disturbed areas, which were located close to sandy unpaved roads. The heavy military traffic along these roads has generated large amounts of sediment that have accumulated within these forests. Although we do not have physiological data to suggest which mechanisms are driving these decreases in forest productivity, our regression data suggest a close correlation between increased levels of sediment deposition and decreased levels of productivity (Figures 7 and 8). Marked decline in aboveground NPP became apparent with low rates of sediment deposition (0.2 – 0.3 cm $yr^{-1}$), and a low equilibrium seems to be reached with sediment levels near 0.5 cm $yr^{-1}$.

Considering that the effects of high rates of sediment deposition are similar to flooding (Kozlowski et al. 1991, Ewing 1996), our findings are comparable to studies relating forest production and flooding stress. For example, results from Megonigal et al. (1997) showed that aboveground NPP in forests with persistent flooding (mean growing-season water depth > 0 cm) was significantly less than in forests with periodic flooding. In contrast, Clawson et al. (2001) found aboveground productivity to be greater in poorly drained areas than on somewhat poorly drained areas in the Flint River floodplain. However, these authors suggested that the higher ANPP values on poorly drained areas were probably due to the presence of large trees and higher basal area. In our sites, within highly disturbed areas, lower number of trees in upper plots in comparison with lower plots suggests that high rates of mortality may have occurred, and the continuous process of sediment deposition is limiting forest regeneration. Hupp et al. (1988) observed that wetlands upstream from road causeways, where increased sedimentation occurred without substantial increases in hydroperiod, reduced the growth of bottomland hardwood species. However no effect was observed in tupelo gum (*Nyssa aquatica*). This species appears to be very tolerant of sedimentation, whereas several species of riparian woody plants may be highly intolerant (Simon and Hupp 1987). Therefore, any attempt to restore these areas should consider revegetation using species with high tolerance to sediment deposition, like tupelo gum.

For both treatment plots of moderately disturbed and reference areas, and the lower plots of highly disturbed areas, aboveground net primary productivity ranged from

914 to 1507 g m$^{-2}$ yr$^{-1}$. These values were slightly lower than those observed by Megonigal et al. (1997) in bottomland hardwood sites on the Pearl River, Louisiana (974-1608 g m$^{-2}$ yr$^{-1}$) and Clawson et al. (2001) for floodplain forests along the Flint River, Georgia (1392-1672 g m$^{-2}$ yr$^{-1}$). However, values of the present study are closer to those reported by Conner and Day (1976) in a freshwater swamp in Louisiana (1140-1574 g m$^{-2}$ yr$^{-1}$).

**Leaf area index (LAI)**

Leaf area index is broadly defined as the amount of leaf area in a vegetation canopy per unit land area. Leaf area is an important determinant of photosynthetic carbon assimilation, and estimates of LAI are good indicators of growth potential (Barclay 1998). In the present study, LAI ranged from 3 on upper treatment plots of highly disturbed areas to 7 on upper plots of reference areas. Sedimentation levels near 0.2 cm yr$^{-1}$ were associated with major reductions in LAI, and a reduced long-term equilibrium appeared to be reached sediment accumulation above 0.5 cm yr$^{-1}$ (Figure 8b). In a study comparing the structure and primary productivity of cypress ecosystems in Florida, Brown (1981) reported that in cypress domes and scrub cypress forests (where water may be limiting) trees appear to adjust to potential water stress through leaf morphology adaptations and minimum forest development (LAI = 0.5–3.4). However, when limited water is not a potential stress, as in floodplain forests, adaptations to conserve water were lacking (LAI = 8.5). Therefore, in our study, low LAI values (3.1) in upper plots of highly disturbed areas seem to be a morphological response to probable anaerobic rooting zone stress caused by high rates of sediment deposition (Kozlowski 1991), and also are a good indication that the low rates of aboveground productivity were due to stress and not to shifts in root-shoot allocation.

## Foliar nutrient content

Nutrient concentrations in litterfall in the present study were similar among disturbance categories for both upper and lower treatment plots. However, upper plots of highly disturbed areas had significantly less nutrient return to the forest floor due to low litterfall rates, despite relatively similar nutrient concentrations in comparison with the other two areas. In general, moderately disturbed and reference areas, as well as lower plots of highly disturbed areas, exhibited higher litterfall rates and greater litter nutrient contents, possibly indicating greater nutrient availability and uptake than in upper plots of highly disturbed areas. In a decomposition study in the Great Dismal Swamp, VA, Day (1982) observed that lower litter decay in a mixed hardwood forest, in comparison with a maple-gum and a cypress community, possibly resulted in smaller amounts of nutrients available for plant uptake in the mixed hardwood community. In our study, reference and moderately disturbed areas and lower plots of highly disturbed areas apparently cycled greater quantities of nutrients via litterfall, primarily as result of higher litterfall rates.

The N:P ratios in our study were ranked as follows: moderately disturbed > highly disturbed > reference areas in the lower plots and highly disturbed > moderately disturbed > reference areas in the upper plots. Trends in N:P ratios at upper plots in our study were similar to those observed by Clawson et al. (2001) across wetness categories, although our values were slightly greater. Lockaby and Walbridge (1998) suggested that

N:P ratios less than 12 may indicate that a system is N-deficient. Therefore, based on their N: P hypothesis, it would appear that at the upper treatment plots highly disturbed areas are more P-deficient, whereas reference and moderately disturbed areas are more N-deficient (N:P = 11.1, 8.8 and 7.8, highly disturbed, moderately disturbed, and reference areas, respectively).

**Changes in vegetation composition and structure**

In this study we observed two distinct patterns in vegetation composition and structure. The first is found in areas not influenced by sediment deposition (i.e. reference areas and lower plots of highly disturbed and moderately disturbed areas). This pattern is characterized by dominance of overstory trees, with a relatively closed canopy, low seedling and sapling density, a small number of species, and dominance of shade tolerant species. The second pattern is shown by areas receiving high rates of sediment deposition (upper plots of highly disturbed areas), with relatively few tree individuals, a more open canopy, significantly greater numbers of seedlings and saplings individuals (up to five times greater than in other areas), significantly greater understory standing crop biomass, and dominance by shade intolerant species and nitrogen fixers (i.e. *Alnus serrulata* and *Myrica cerifera*).

References have been made to the lower density and reduced species diversity in the understory of riverine forests (Brinson 1990). It has been suggested that limited light availability, due to the relatively complete canopy closure of these systems, may inhibit the development of shrubs, but may also increase competition among overstory trees, resulting in slower increases in basal area (Conner et al. 1981). Therefore, it appears that the lessened understory development of the areas not suffering from sediment deposition is a natural and expected process, caused by limited light availability and competition for nutrients and water with overstory species. Another factor contributing to the lower understory density is the greater degree of litter cover in these forests, which may inhibit germination and seedling emergence (van der Valk 1986) and provide a physical barrier for growing shoots (Nilsson and Grelsson 1990).

In contrast, it has also been demonstrated that when the forest canopy is disturbed, light incidence on the forest floor increases and rapid growth follows (Brinson 1990). As mentioned before, high rates of sediment deposition may create anaerobic soil conditions, which may limit the effective rooting zone and ultimately cause tree death. As discussed in chapter III, root biomass, production and nutrient contents were significantly less in upper plots of highly disturbed areas. Consequently, we suggest that low root production causes tree mortality and the gaps formed in these areas create habitat favorable for seedling growth (e.g. high light intensity, higher water and nutrient availability for plant uptake, among others). The greater number of individuals in the smallest diameter classes, the higher shrub biomass, the dominance of shade intolerant species, and the presence of nitrogen fixers are strong evidence that disturbance caused by heavy sediment deposition is altering vegetation composition and structure. In a study comparing three riparian communities in different successional stages in a South Carolina coastal plain, Giese et al. (2000) observed that herbaceous and shrub biomass were greater in younger forests as a result of low tree biomass, which is similar to the upper plots of highly disturbed areas in our study.

# CONCLUSIONS

Aboveground net primary productivity, vegetation composition and structure appeared to be strongly affected by levels of sediment deposition. Although no significant differences were observed in aboveground parameters between treatments within each of the three disturbance categories, when comparisons were made across disturbance categories at upper treatment plots, we observed that litterfall and woody increments were significantly less in highly disturbed areas. Since we used the sum of litterfall and woody production to approximate aboveground NPP, it was also significantly less in upper plots of highly disturbed areas. No significant differences were observed between reference and moderately disturbed areas, although numerically, litterfall, woody increments and aboveground NPP were greatest for both upper and lower plots of reference areas. Our data suggest that sediment deposition as low as 0.2 cm $yr^{-1}$ greatly reduced levels of litterfall biomass, woody increments and aboveground NPP. Also, it appears that sediment accumulation above 0.2 cm $yr^{-1}$ is a threshold beyond which major reductions in litterfall biomass, woody increments, and aboveground NPP become evident.

It is not entirely clear how sediment deposition may affect tree mortality, but we suspect that the major factor is the creation of an anaerobic rooting zone, which may limit the nutrient and water uptake that are vital for forest productivity. Leaf area index did not significantly differ between treatments or among disturbance categories; however, it was somewhat less in upper plots of highly disturbed areas, which may suggest physiological plant adaptations to stresses caused by sedimentation. Similar to the aboveground parameters, a major reduction in LAI was observed when sediment deposition reached levels near 0.2 cm $yr^{-1}$. Trends in nutrient contents were similar to those of litterfall biomass. Carbon, nitrogen, and phosphorus contents were significantly less in upper plots of highly disturbed areas. No significant differences were observed between reference and moderately disturbed areas for carbon and nitrogen contents. Phosphorous content, however, was significantly greater in reference areas relative to the other disturbance categories.

Vegetation composition and structure were similar among disturbance categories, except for upper plots of highly disturbed areas. In general, these areas were occupied by large trees with a relative closed canopy and the occurrence of seedlings and saplings was relatively low, probably due to limitations in light availability. On average 66% of the individuals sampled in these areas were classified as other than shade intolerants (i.e. either shade tolerant or moderately tolerant). In contrast, upper plots of highly disturbed areas were dominated by shrubs. Standing crop biomass of shrubs in these areas was up to three times greater than that observed in moderately disturbed and reference areas. More than 70% of the individuals sampled in upper plots of highly disturbed areas were classified as shade intolerants, and nitrogen fixers were very common in these areas. Therefore, our results suggest that rates of sediment deposition as low as 0.2 cm $yr^{-1}$ negatively impact riparian forests, altering patterns of vegetation composition and structure, ultimately compromising forest productivity.

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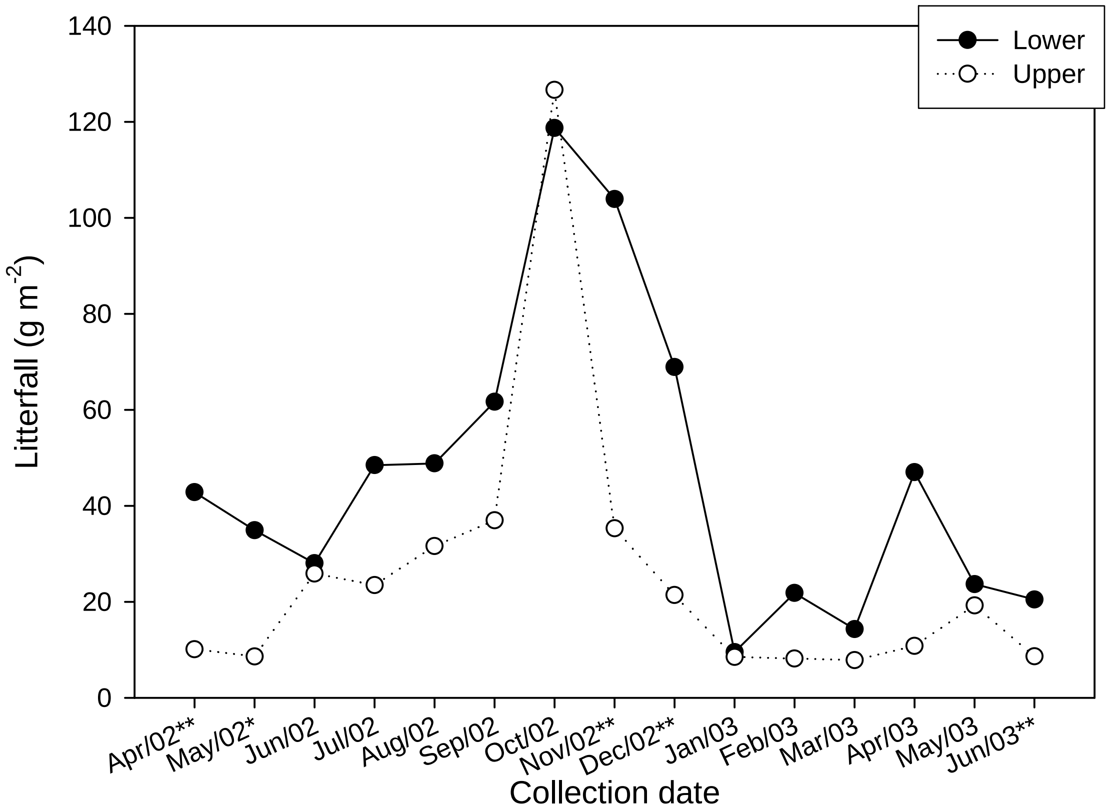



**Figure 2.** **Monthly comparisons of mean litterfall biomass between treatments in highly disturbed areas.** ***Asterisks indicate significant differences between treatment pairs (T-test, *$\alpha$= 0.10, **$\alpha$=0.05).***

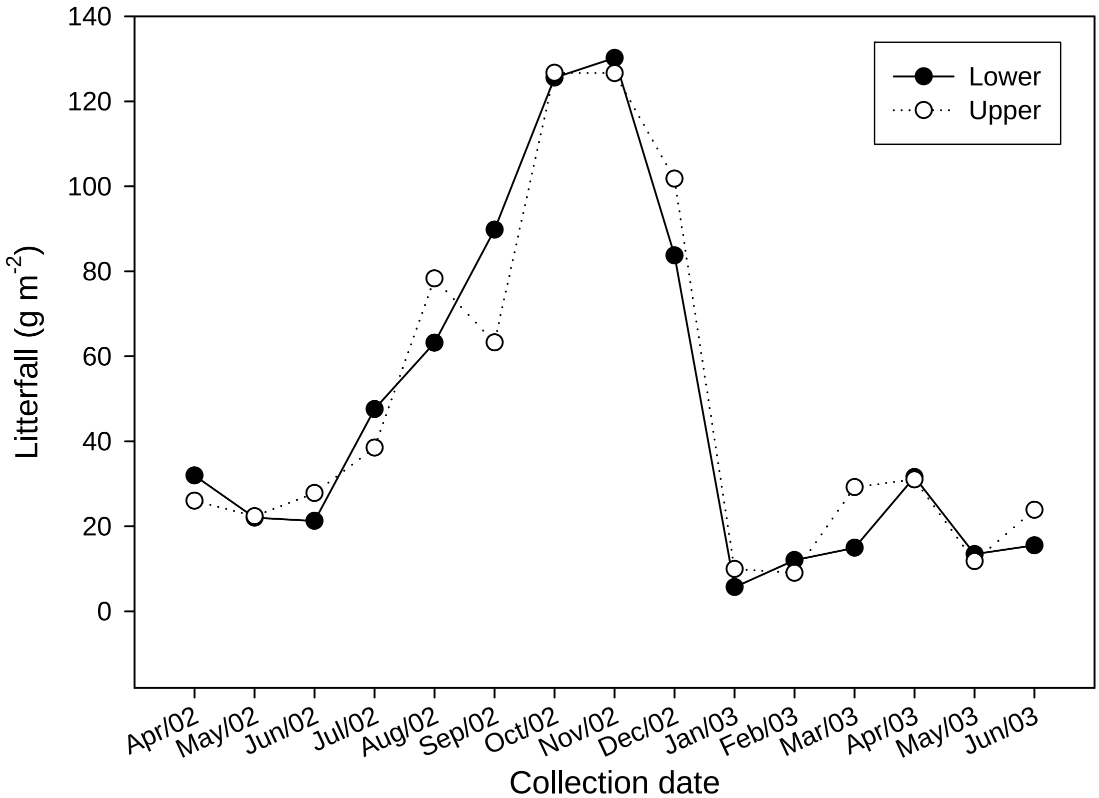



**Figure 3.** **Monthly comparisons of mean litterfall biomass between treatments in moderately disturbed areas. No significant differences between treatments were observed.**

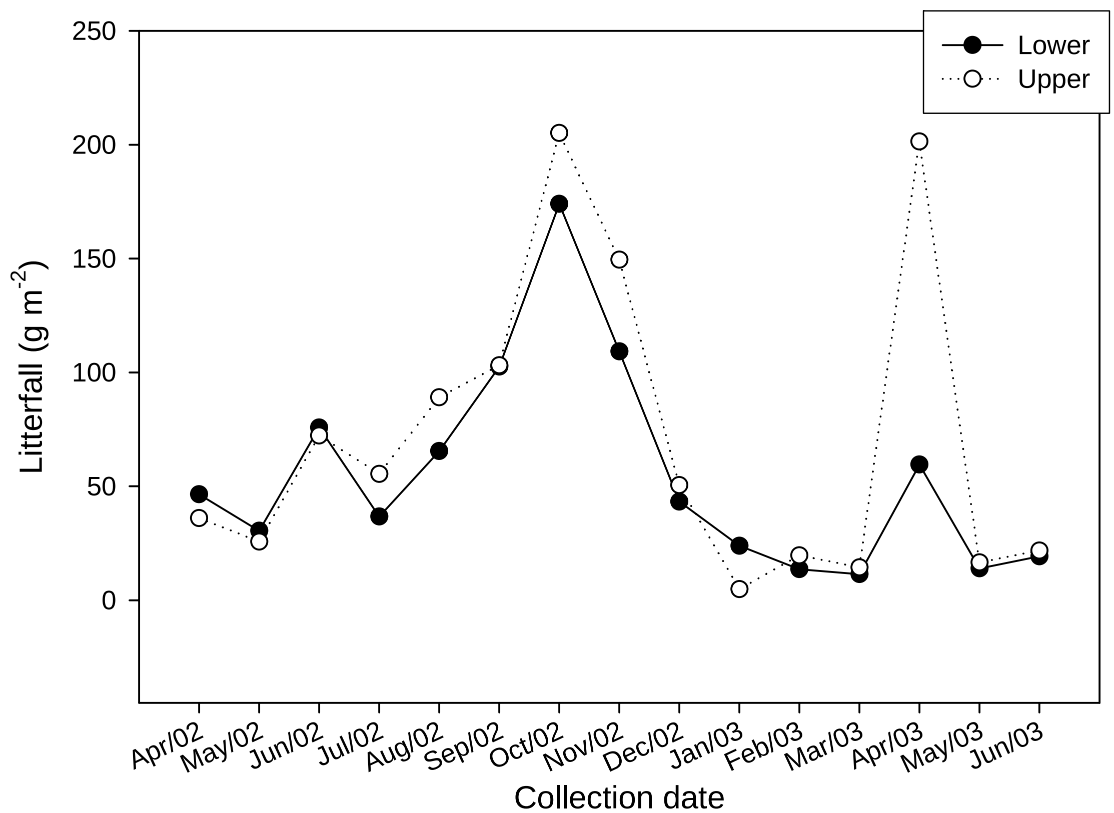



**Figure 4.** **Monthly comparisons of mean litterfall biomass between treatments in reference areas. No significant differences between treatments were observed.**

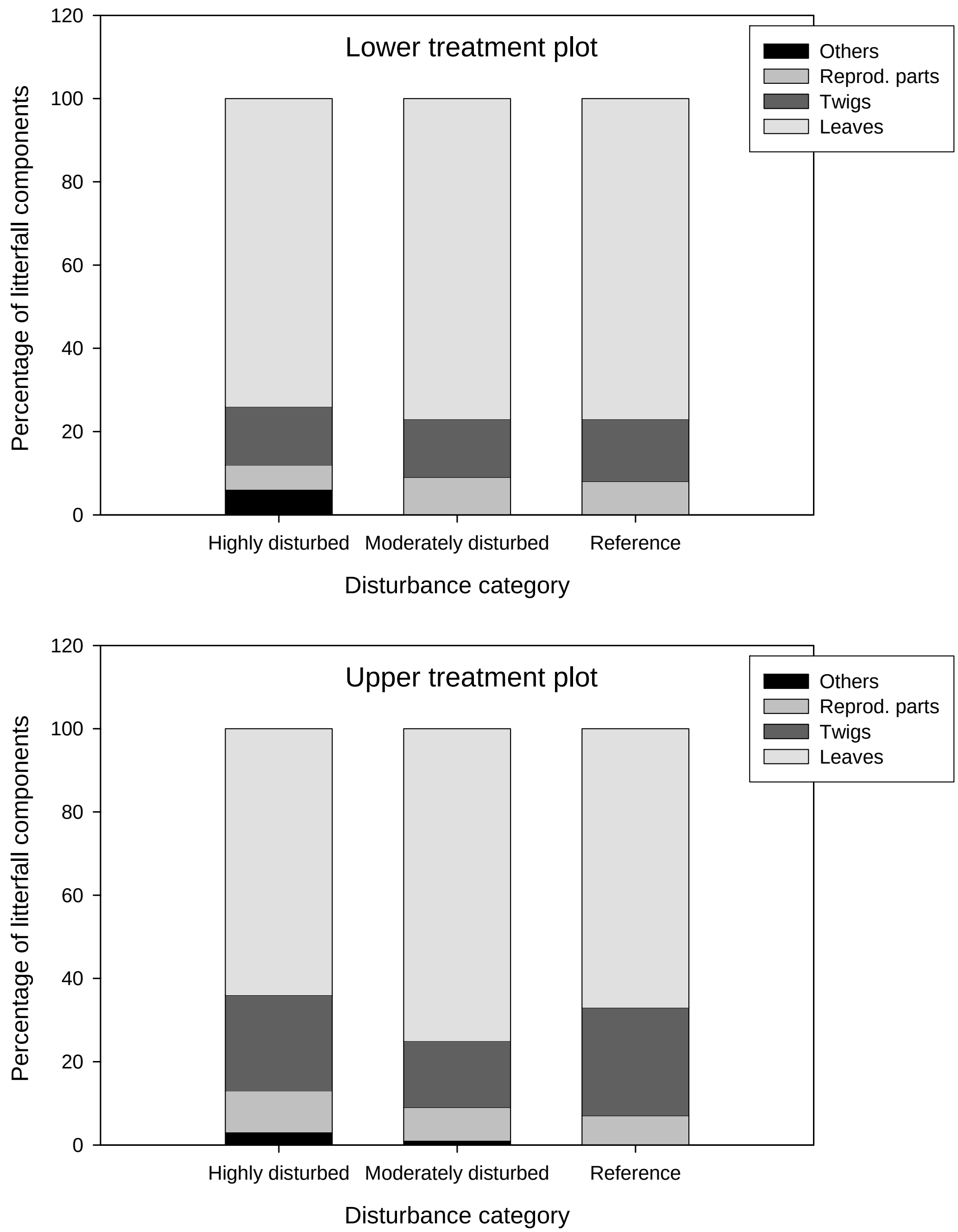



**Figure 5.** **Percentage of litterfall components (leaves, twigs, reproductive parts, others) among disturbance categories.**

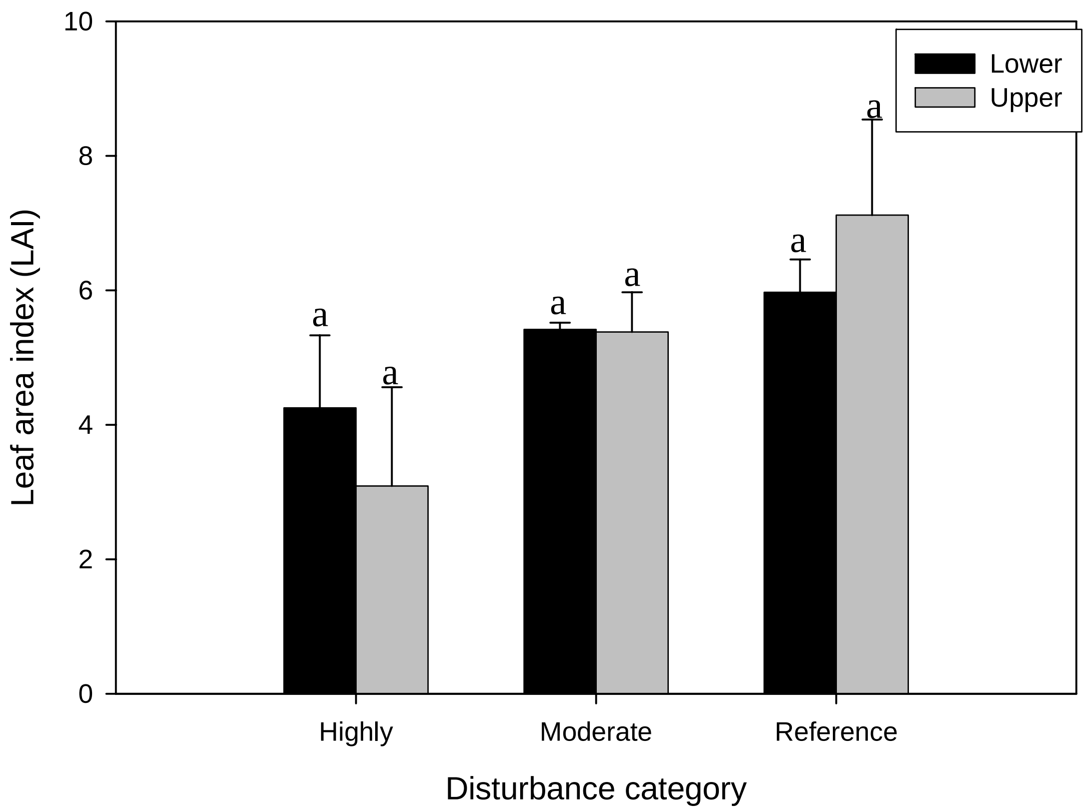
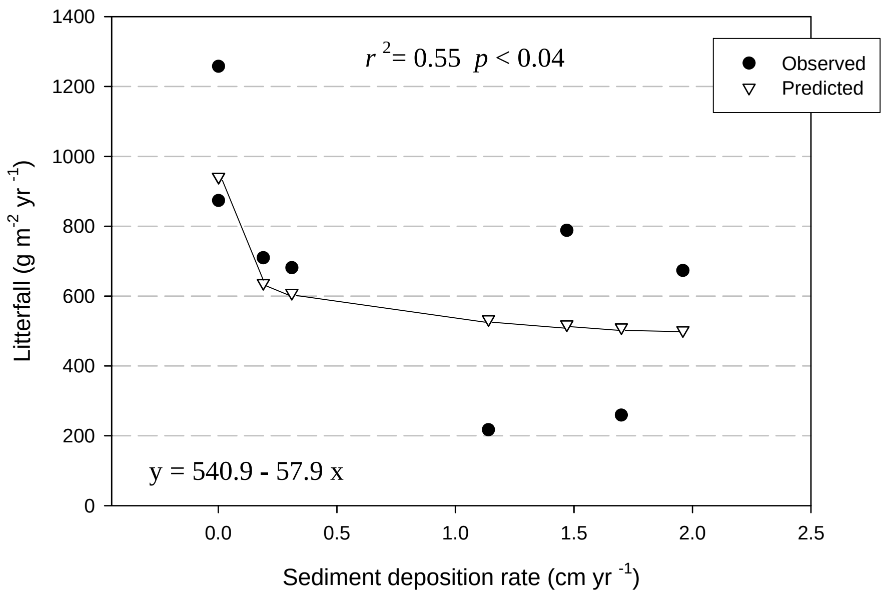



**Figure 6.** **Comparison of leaf area index (expressed as $m^2.m^{-2}$) between treatments in the three disturbance categories. Different lowercase letters denotes significant difference between treatments (T-test, $\alpha$=0.05).**

a)




b)

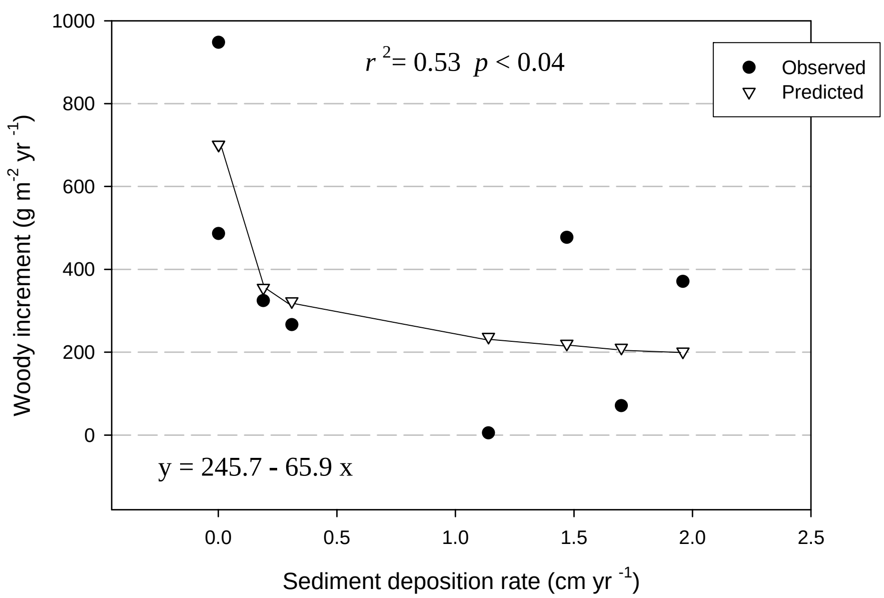
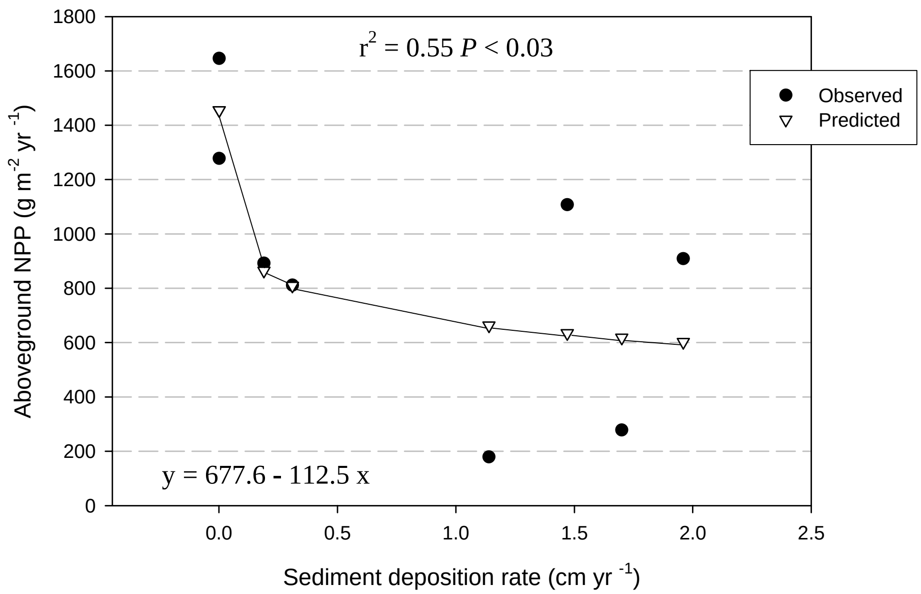



**Figure 7. The relationship of litterfall (a) and woody increments (b) across a range of sediment deposition.**

a)




b)

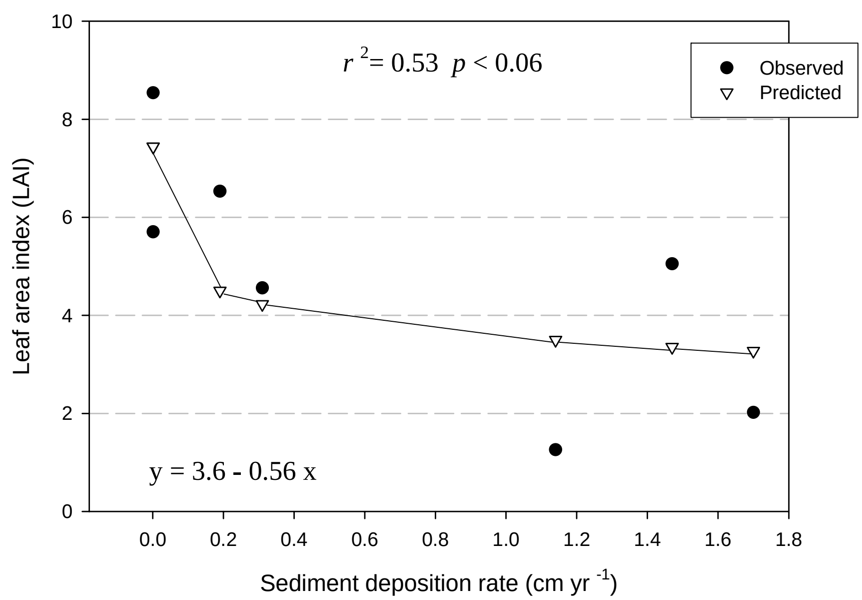



**Figure 8.** **The relationship of aboveground productivity (a) and leaf area index (b) across a range of sediment deposition.**

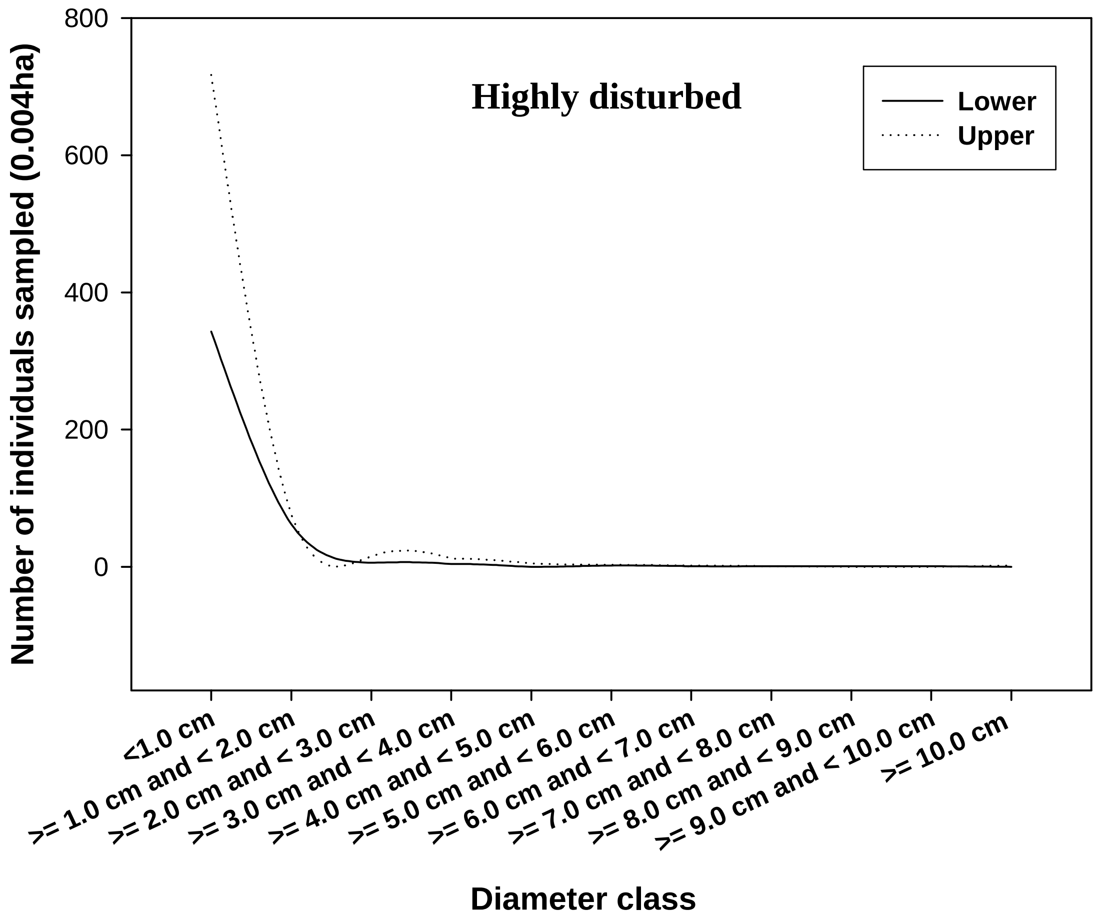



**Figure 9.** **Diameter distribution of seedlings and saplings at lower and upper treatment plots of highly disturbed areas.**

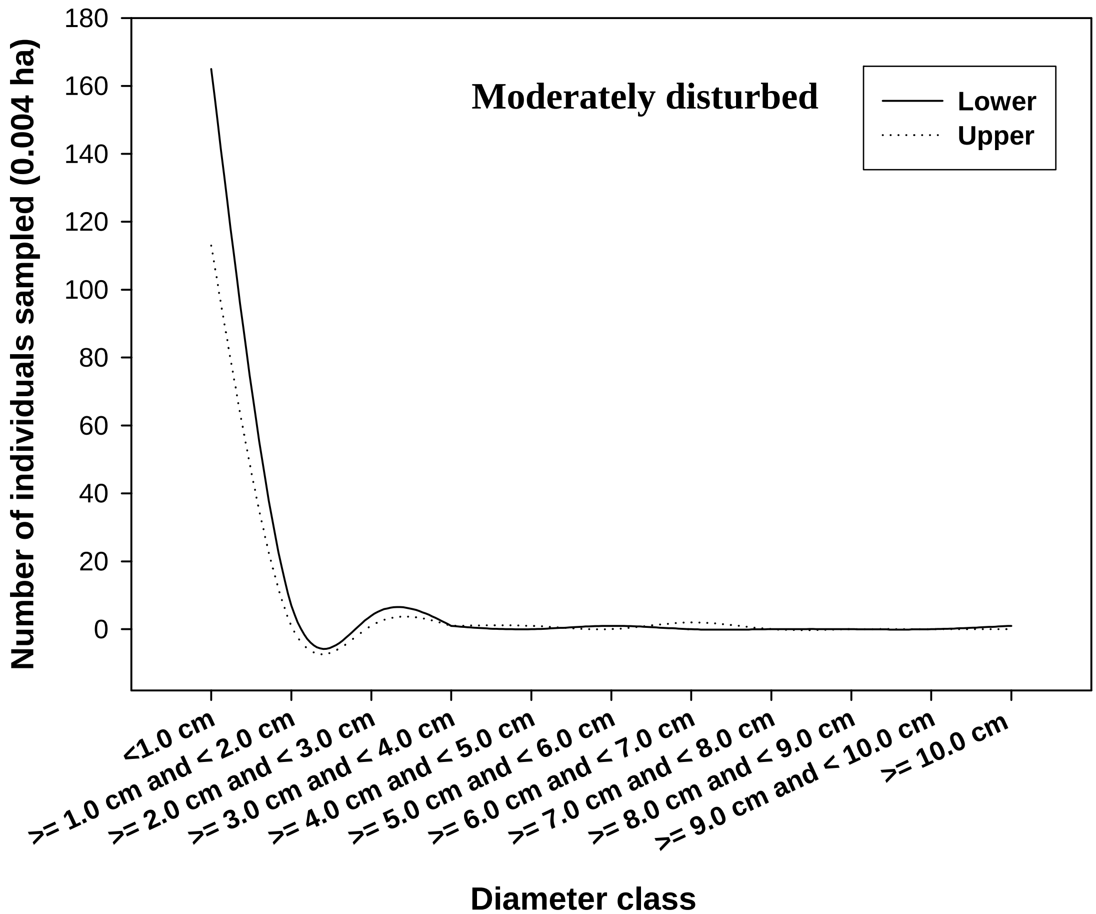



**Figure 10.** **Diameter distribution of seedlings and saplings at lower and upper treatment plots of moderately disturbed areas.**

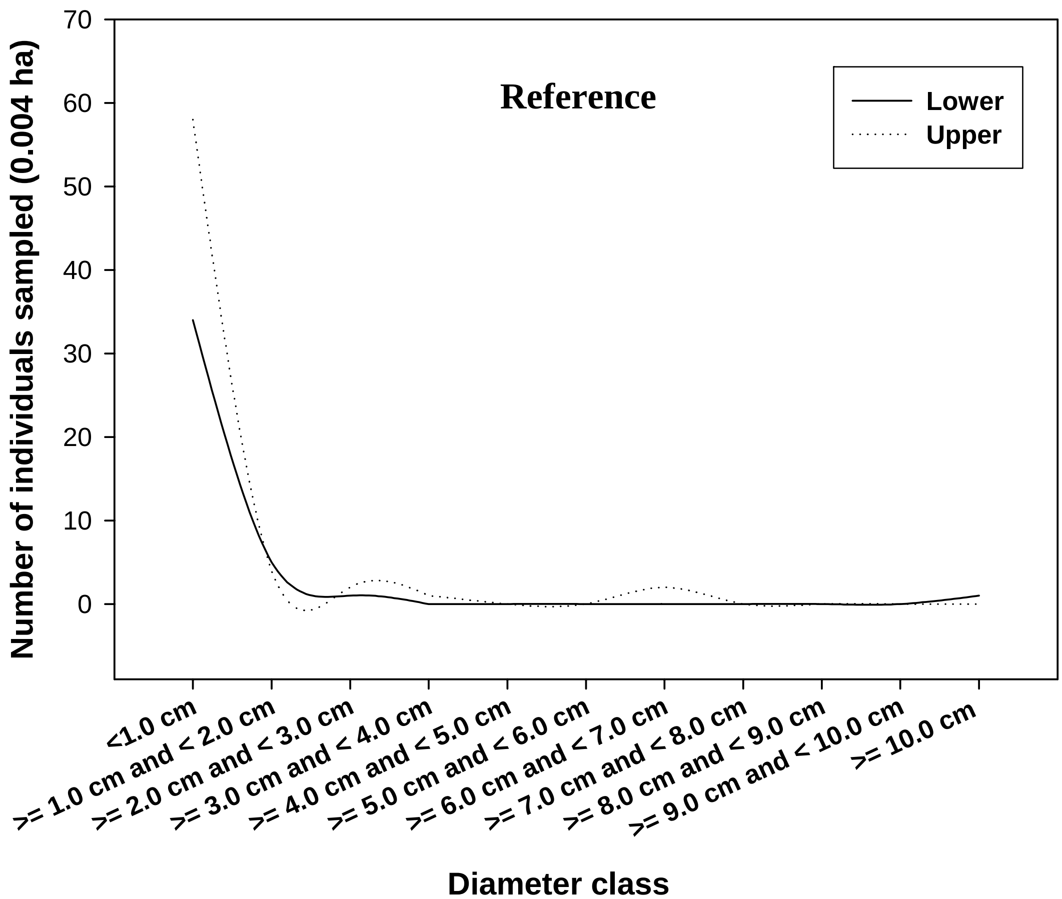



**Figure 11. Diameter distribution of seedlings and saplings at lower and upper treatment plots of reference areas.**

**Table 2. Mean annual rates[1] of litterfall, woody increments and aboveground net primary production for both upper and lower treatments in each disturbance category (expressed as g $m^{-2}$ $yr^{-1}$).**

| | | | |
|---|---|---|---|
| **Litterfall (g $m^{-2}$ $yr^{-1}$)** | | | |
| | Highly disturbed | Moderately disturbed | Reference |
| Lower treatment | 554 a (36) | 567 a (51) | 661 a (106) |
| Upper treatment | 306 a (116) | 581 s (26) | 746 a (47) |
| **Woody increment(g $m^{-2}$ $yr^{-1}$)** | | | |
| | Highly disturbed | Moderately disturbed | Reference |
| Lower treatment | 465 a (117) | 348 a (21) | 847 a (70) |
| Upper treatment | 158 a (107) | 356 a (63) | 488 b (1.8) |
| **Aboveground primary productivity (g $m^{-2}$ $yr^{-1}$)** | | | |
| | Highly disturbed | Moderately disturbed | Reference |
| Lower treatment | 1019 a (145) | 914 a (31) | 1507 a (176) |
| Upper treatment | 465 a (223) | 937 a (88) | 1234 a (45) |

[1] Different lowercase letters in columns indicate significant difference between treatments within each disturbance category (T-test, $\alpha$=0.05). Numbers in parentheses are SE.

**Table 3. Mean annual C, N, and P contents[1] of litterfall, for both upper and lower treatments in each disturbance category (expressed as g m$^{-2}$ yr$^{-1}$).**

| | Highly disturbed | Moderately disturbed | Reference |
|---|---|---|---|
| **Carbon content (g m$^{-2}$ yr$^{-1}$)** | | | |
| Lower treatment | 217.1 a (13.6) | 219.9 a (20.9) | 259.1 a (45.4) |
| Upper treatment | 116.6 b (44.3) | 227.0 a (9.7) | 292.2 a (16.3) |
| **Nitrogen content (g m$^{-2}$ yr$^{-1}$)** | | | |
| Lower treatment | 3.3a (0.61) | 4.6 a (0.16) | 5.0 a (0.03) |
| Upper treatment | 2.2 a (0.96) | 4.2 a (0.22) | 5.1 a (0.71) |
| **Phosphorous content (g m$^{-2}$ yr$^{-1}$)** | | | |
| Lower treatment | 0.3 a (0.04) | 0.4 a (0.04) | 0.5 a (0.01) |
| Upper treatment | 0.2 a (0.14) | 0.4 a (0.03) | 0.6 a (0.02) |

[1] Different lowercase letters in columns indicate significant difference between treatments within each disturbance category (T-test, $\alpha$=0.10). Numbers in parentheses are SE.

**Table 4. Comparisons of mean[1] annual litterfall, woody increment, aboveground NPP, leaf area index, and nutrient content of litterfall, among disturbance categories at upper treatment plots.**

| | Highly disturbed | Moderately disturbed | Reference |
|---|---|---|---|
| Litterfall (g $m^{-2}$ $yr^{-1}$) | 306 b (116) | 581 ab (26) | 746 a (47) |
| C in litterfall (g $m^{-2}$ $yr^{-1}$) | 116.6 b (44.3) | 227.0 a (9.7) | 292.2 a (16.3) |
| N in litterfall (g $m^{-2}$ $yr^{-1}$) | 2.2 b (0.96) | 4.2 a (0.22) | 5.1 a (0.71) |
| P in litterfall (g $m^{-2}$ $yr^{-1}$) | 0.2 b (0.14) | 0.4 b (0.03) | 0.6 a (0.02) |
| Woody (g $m^{-2}$ $yr^{-1}$) | 158 b (107) | 356 ab (63) | 488 a (1.8) |
| ANPP (g $m^{-}2$ $yr^{-1}$) | 465 b (223) | 934 ab (88) | 1234 a (45) |
| LAI ($m^2.m^{-2}$) | 3.0 a (1.5) | 5.3 a (0.6) | 7.1 a (1.4) |

[1] Row mean followed by different lowercase letters indicates significant difference among disturbance categories (Duncan's procedure, $\alpha$=0.05). Numbers in parentheses are SE.

**Table 5. List of most common species measured in lower and upper treatments plots within each disturbance category.**

| Disturbance category | Treatment | Most common species |
|---|---|---|
| Highly disturbed | Lower | tupelo (*Nyssa syvlatica*), red maple (*Acer rubrum*), hazel alder (*Alnus serrulata*), galberry (*Ilex glabra*) |
| | Upper | sweetgum (*Liquidambar styraciflua*), hazel alder, red maple, tupelo, wax myrtle (*Myrica cerifera*) |
| Moderately disturbed | Lower | sweetbay (*Magnolia virginiana*), dogwood (*Cornus* spp.), southern red oak (*Quercus falcata*) |
| | Upper | southern red oak, sweetgum, white oak (*Quercus alba*) |
| Reference | Lower | sweetgum, sweetbay |
| | Upper | red maple, American holly (*Ilex opaca*), sweetbay, sweetgum |

**Table 6. Comparisons of means[1] per plot of biomass, species richness (S), number of individuals sampled (N), number of individuals that are nitrogen fixers (NF), shade intolerants (SI), other shade tolerance (other). Comparisons were made between treatments for each disturbance category.**

| Disturbance category | Treatment | Biomass (g $m^{-2}$) | S | N | NF | SI | Other |
|---|---|---|---|---|---|---|---|
| Highly | lower | 1344.8 b* (209) | 9.5 a | 112 b** | 10.0 b** | 66 a | 46 a |
| disturbed | upper | 2537.3 a (243) | 10.5 a | 353 a | 69.5 a | 237.5 a | 115.5 a |
| Moderately | lower | 802.6 a (406) | 11.0 a | 114 a | 9.0 a | 17.0 a | 97.0 a |
| disturbed | upper | 933.4 a (45) | 10.5 a | 36 a | 10.0 a | 12.5 a | 23.5 b*** |
| Reference | lower | 184.9 | 7 | 41 | * | 21 | 20 |
| | upper | 759.4 | 7 | 67 | * | 6 | 51 |

[1] Different lowercase letters in columns indicate significant differences between treatments within each disturbance category (T-test, * $\alpha < 0.10$, * *$\alpha = 0.05$, * ** $\alpha = 0.001$). Numbers in parentheses are SE.

**Table 7. Comparisons of means[1] per plot of biomass, species richness (S), number of individuals sampled (N), number of individuals that are nitrogen fixers (NF), shade intolerants (SI), other shade tolerance (other). Comparisons were made at upper plots, among disturbance category.**

| Disturbance category | Biomass (g m-2) | S | N | NF | SI | Other |
|---|---|---|---|---|---|---|
| Highly disturbed | 2537.3 a | 10.5 a | 353 a | 69.5 a | 237.5 a | 115.5 a |
| Moderately disturbed | 933.4 b | 10.5 a | 36 b | 10.0 b | 12.5 b | 23.5 a |
| Reference | 759.4 b | 7.0 a | 67 b | * | 6 b | 51 a |

[1] Different lowercase letters in columns indicate significant differences among disturbance categories (Duncan's procedure, $\alpha = 0.05$).

# III. EFFECTS OF SEDIMENT DEPOSITON ON FINE ROOT DYNAMICS IN RIPARIAN FORESTS

## ABSTRACT

One of the most important functions of riparian zones is their ability to improve water quality by trapping sediment leaving agricultural fields and other disturbed areas. Many studies have quantified sediment deposition and identified sources of sediments in riparian ecosystems. However, little information exists regarding the impacts of sediment deposition from anthropogenic disturbance on belowground processes within these ecosystems. This study was conducted at Fort Benning, GA, where intense disturbance caused by military traffic has generated significant sediment movement into riparian forests associated with ephemeral streams. Two paired treatment plots were established along each of nine ephemeral streams exhibiting different levels of sediment deposition and classified as highly disturbed, moderately disturbed, or reference. The two treatments were: an upper plot located in a topographic position higher in the drain (i.e. nearer to stream origins) and a lower plot located farther down stream beyond visual evidence of sediment deposition. On highly disturbed and moderately disturbed areas, the upper plot exhibited visual evidence of sediment deposition due the proximity of unpaved roads. Fine root (≤ 3.0 mm diameter) estimates were compared between treatments within each disturbance category in terms of fine root biomass, turnover, productivity, and nutrient

contents (C and N). Comparisons of the aforementioned variables were also made among disturbance categories at upper plots. Within highly disturbed areas, fine root biomass, detritus, and production were significantly decreased in upper plots, whereas no differences between treatments were observed for the other two disturbance categories. Ranking of root biomass, detritus, and production among disturbance categories at upper plots were as follows: reference = moderately disturbed > highly disturbed. Live fine root nutrient contents followed the same trends as root biomass; however, no significant differences between treatments were observed for N contents within highly disturbed areas, even though values were greatest for lower plots. No significant differences in dead root nutrient contents of were observed.

## INTRODUCTION

Fine root dynamics (production and turnover) represent a pathway of significant energy and nutrient flux through forest ecosystems. They are an important component influencing the effectiveness of riparian systems in immobilizing and processing soil water pollutants and improving soil quality (Groffman et al. 1992). Generally, fine roots are defined as nonwoody, small diameter roots with mycorrhizae (Nadelhoffer and Raich 1992), and fine root size maxima typically fall within the range of less than 1 mm to less than 5 mm. The definition of fine roots in terms of diameter varies greatly among published studies; however, all point out that fine roots represent a dynamic portion of belowground biomass and a significant part of net primary production (NPP) in forest ecosystems (Fahey and Hughes 1994, Gordon and Jackson 2000). Across a range of ecosystems, NPP can be greater below- than aboveground. Studies have shown that up to 75% of total forest production may be allocated belowground in some ecosystems (Grier et al. 1981, Vogt et al. 1982, Fogel 1983, Santantonio and Hermann 1985). However, due to methodological difficulties associated with root studies, many authors still rely only on aboveground parameters to estimate forest productivity.

Fine roots are also an important sink and source of N and P, and their turnover can represent a substantial C and nutrient input into soil each year (Cox et al. 1978, Joslin and Henderson 1987, Harris et al 1980, Fogel 1983, Persson 1983, Santantonio and Hermann 1985). In forests, the amount of C and nutrients released to the soil from root detritus may equal or exceed that from leaf litter (Joslin and Henderson 1987, Raich and Nadelhoffer 1989). Megonigal and Day (1988) observed that in some flooded communities of the Great Dismal Swamp, roots contributed approximately 60% of annual soil organic inputs, whereas leaf litter contributions ranged from 6 to 28%, and woody debris 5 to 15%, of annual soil organic inputs. Joslin and Henderson (1987) reported that mortality and decomposition of fine roots contributed about 30% of the total organic detritus mass in a mature white oak forest in USA. Thus, changes in levels of fine root production and turnover as a result of sediment accumulation from anthropogenic disturbance may alter the levels of nutrients in forest soils, and may influence overall forest productivity.

Despite the important role of fine roots in trapping nutrients from sediment deposition in riparian zones (Cooper et al. 1987, Daniels and Gilliam 1996, Craft and Casey 2000), we are aware of no information regarding the effects of excessive sediment accumulation on fine root dynamics in these ecosystems. Within wetland forests, fine root studies usually reflect the influence of different flooding regimes on root production, turnover, and nutrient cycling (Montague and Day 1980, Powell and Day 1991, Megonigal and Day 1992, Baker et al. 2001,Clawson et al. 2001). In relation to sediment deposition in these systems, most research has focused on quantification of sediment deposition (Lowrance et al 1986, Hupp and Morris 1990, McIntyre and Naney 1991, Heimann and Roell 2000).

Kozlowski et al. (1991) suggested that the burial of trunks by alluvial deposits produces the same effect as flooding, by imposing a lack of oxygen upon root systems, and anaerobic conditions may retard root growth and production (Montague and Day 1980). Therefore, as a result of high levels of sediment deposition, one might expect a reduction in root biomass and productivity that may seriously degrade forest productivity.

This study examined the impacts of sediment deposition from military traffic in riparian forests of ephemeral streams. Across a range of sediment deposition, sampling was stratified among three levels of disturbance. Comparisons between treatments and among disturbance categories were made in terms of belowground processes, specifically fine root biomass, production, turnover, and nutrient contents. A study of community root systems, together with aboveground data, is essential to evaluate the nutrient and energy dynamics of riparian forests under excessive sediment deposition from anthropogenic disturbance.

# MATERIAL AND METHODS

## Study Site

This study was conducted at Fort Benning, GA, a U.S. Army installation, where intensive disturbance caused by heavy military traffic has generated significant sediment movement into riparian forests. The installation is located in the southeastern United States, occupying an area of 73,503 ha in Chattahoochee, Muscogee, and Marion Counties of Georgia and Russell County of Alabama (Figure 1). Two physiographic regions are represented at Fort Benning: the Piedmont and the Upper Coastal Plain. For the purposes of this study, only riparian forests within the Coastal Plain were selected. Forest types on the study areas are primarily deciduous and uneven aged, characterized by hardwoods and mixed hardwood/pine overstories. Species composition is typical of most southern Coastal Plain wetland forest, dominated by: *Nyssa sylvatica* (black gum), *Acer rubrum* (red maple), *Liquidambar styraciflua* (sweetgum), *Quercus nigra* (water oak), *Liriodendrum tulipifera* (yellow poplar), *Magnolia virginiana* (sweetbay), *Cornus* spp. (dogwood) and *Ilex opaca* (American holly), among others.

The soil series found within the study area include Bibb, Troup, Lakeland, Chastain, and Cowarts soils. Bibb soils are coarse-loamy, siliceous, acid, thermic Typic Fluvaquents, and poorly drained. Troup soils are loamy, siliceous, thermic Grossarenic Kandiudults, and somewhat excessively drained.  The Lakeland soils are coated, thermic Typic Quartzipsamments, and excessively drained. Chastain soils are fine, mixed, acid, thermic Typic Fluvaquents, and poorly drained.  Cowart soils are fine-loamy, siliceous, thermic Typic Kanhapludults, and moderately to well drained (Soil Survey-NCRS).

## Study Design

Nine ephemeral streams were selected to encompass a range of sedimentation conditions, and classified as follows: (1) highly disturbed; (2) moderately disturbed; and (3) reference. Widely spreading alluvial fans with exposed, loose, light-colored soil, low in organic matter, were an indicator of high sedimentation and were verified by the presence of buried bases of trees. Trunk burial and smaller alluvial fans indicated moderate levels of sedimentation.  Reference sites had no trunk burial and no active alluvial fans. Sediment sources, on highly and moderately disturbed areas, were often unimproved (dirt) roads or tracked vehicle corridors, with channels or gullies serving as sediment conduits.

The study was designed using paired plots within catchments. Two permanent 0.04 ha circular treatment plots were established along each of the nine ephemeral streams, based on a vegetation inventory and visual evidence of sedimentation. One plot was established in a topographic position higher in the drain (i.e. nearer to the stream's origin), and another was located farther down stream beyond visual evidence of sediment deposition. On highly and moderately disturbed areas, the "upper plot" exhibited visual evidence of sedimentation due to the proximity of unpaved roads. Upper plots on highly disturbed areas were located within the alluvial fan, and tended to have more open canopy and less dense understory vegetation in comparison with lower plots. Both upper and lower plots within moderately disturbed and reference areas displayed an increase in trees species and coverage, a nearly closed canopy, and a reduction in herbaceous cover compared to those of the highly disturbed areas. In general, lower plots had higher soil moisture content due to their lower topographic position.

### Long-term sediment deposition

Rates of sediment deposition were measured following the dendrogeomorphic approach of Hupp and Morris (1990). In the upper plot of each catchment, trees were excavated to the depth at which primary lateral roots appeared. Soil depth from the surface to the top of these roots was measured and recorded. In addition, a disk was cut from near the base of the tree, rings were counted and tree age was determined in laboratory. The sedimentation rate was calculated as the difference between the current soil surface and the depth to primary lateral roots, divided by the age of the tree. The following mean rates of sediment deposition were obtained: 2.20 cm $yr^{-1}$for the highly disturbed areas, 0.66 cm $yr^{-1}$ in the moderately disturbed area, and 0.0 cm $yr^{-1}$ within the reference areas.  Since there was no visual evidence of sediment deposition on lower plots in any catchment, it was assumed to be non-existent.

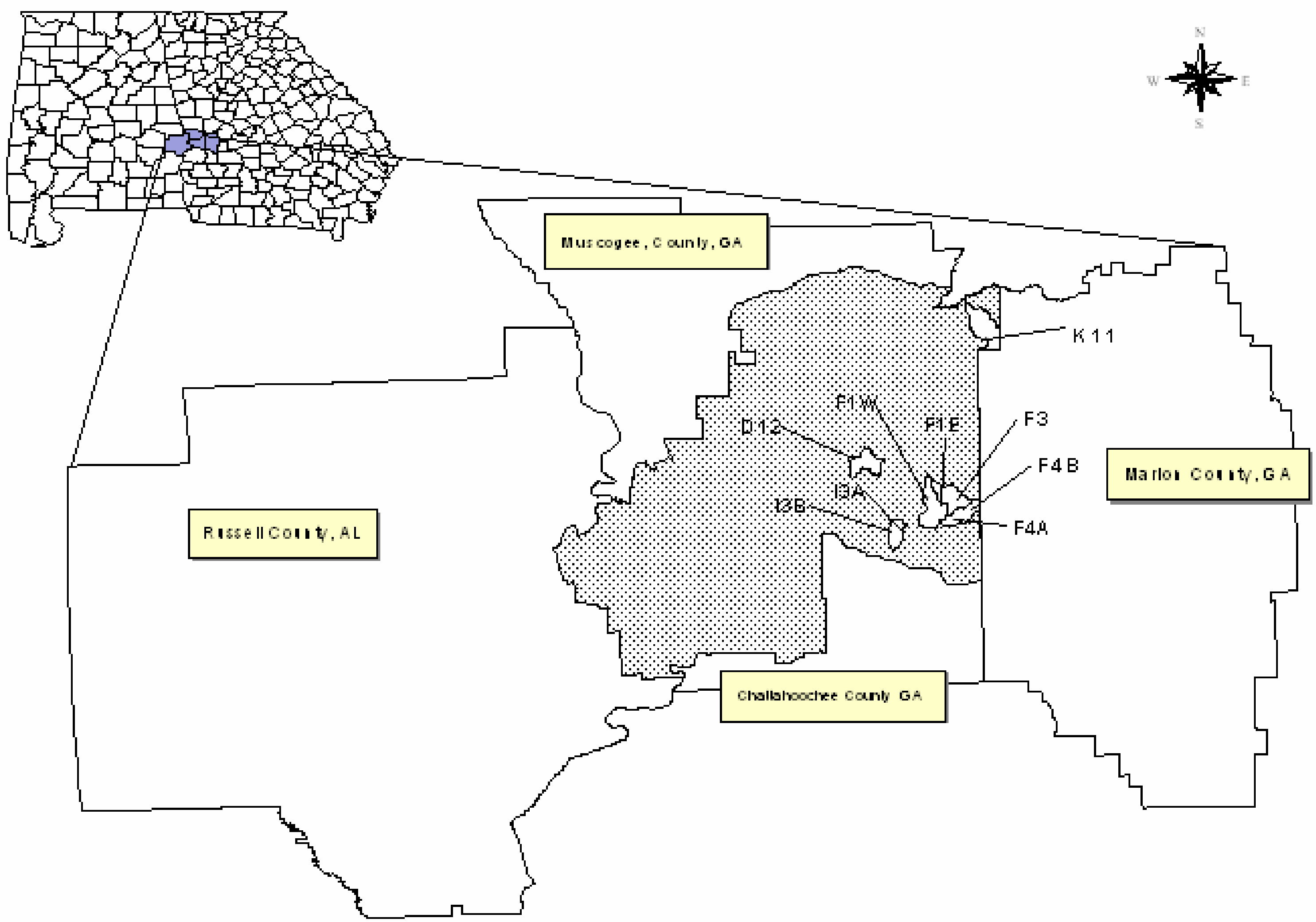



Figure 1. Location of Fort Benning and study sites.

Table 1. Soil texture, soil series and, soil chemical properties of the nine study sites.

| WS | Treatment | Disturbance Category | Soil Texture | Soil Series | pH | P | K | Mg | Ca |
|---|---|---|---|---|---|---|---|---|---|
| D12 | Lower | Highly disturbed | Sandy loam | Bibb, frequently flooded | 5.0 | 2.0 | 46.3 | 26.3 | 135.0 |
| D12 | Upper | Highly disturbed | Fine loamy | Cowarts and Ailey, 12-18% slope | 5.0 | 0.8 | 22.0 | 21.7 | 85.0 |
| F1W | Lower | Highly disturbed | Fine loamy | Cowarts and Ailey, 12-18% slope | 5.2 | 1.8 | 22.2 | 14.3 | 41.7 |
| F1W | Upper | Highly disturbed | Loamy sand | Troup, 12-25% slope | 4.9 | 0.5 | 43.0 | 5.8 | 26.7 |
| F3 | Lower | Highly disturbed | Loamy sand | Troup, 12-25% slope | 5.0 | 1.7 | 48.2 | 23.5 | 81.7 |
| F3 | Upper | Highly disturbed | Loamy sand | Troup, 12-25% slope | 5.4 | 1.0 | 5.0 | 6.5 | 21.7 |
| K11 | Lower | Highly disturbed | Sandy | Lakeland, 5-18% slope | 5.5 | 2.0 | 20.3 | 14.0 | 58.3 |
| K11 | Upper | Highly disturbed | Sandy | Lakeland, 5-18% slope | 5.8 | 1.3 | 15.5 | 9.8 | 36.7 |
| F1E | Lower | Moderately disturbed | Sandy | Lakeland, 5-18% slope | 5.0 | 2.5 | 29.3 | 14.8 | 36.7 |
| F1E | Upper | Moderately disturbed | Sandy | Lakeland, 5-18% slope | 5.2 | 3.0 | 45.8 | 18.5 | 65.0 |
| I3A | Lower | Moderately disturbed | Loamy sand | Troup, 5-12% slope | 4.7 | 0.3 | 35.5 | 32.0 | 63.3 |
| I3A | Upper | Moderately disturbed | Fine loamy | Cowarts and Ailey, 12-18% slope | 5.2 | 0.3 | 14.3 | 19.7 | 140.0 |
| I3B | Lower | Moderately disturbed | Loamy sand | Troup, 12-18% slope | 4.7 | 1.3 | 35.7 | 22.5 | 63.3 |
| I3B | Upper | Moderately disturbed | Loamy sand | Troup, 12-18% slope | 4.8 | 1.2 | 24.8 | 18.5 | 110.0 |
| F4A | Lower | Reference | Loamy sand | Chastain, frequently flooded | 5.3 | 1.8 | 47.8 | 18.8 | 63.3 |
| F4A | Upper | Reference | Loamy sand | Chastain, frequently flooded | 4.4 | 2.0 | 14.7 | 12.5 | 50.0 |
| F4B | Lower | Reference | Loamy sand | Troup, 2-5% slope | 4.9 | 1.0 | 71.3 | 30.3 | 78.3 |
| F4B | Upper | Reference | Loamy sand | Troup, 2-5% slope | 4.7 | 1.0 | 56.0 | 36.3 | 88.3 |

**Fine Root Net Primary Productivity – *In-situ* screens**

Fine root productivity was estimated using the screen method (Melhuish and Lang 1968, 1971) as adapted by Schilling et al. (1999). Melhuish and Lang (1968) have demonstrated a relationship between estimated fine root length and number of growing fine roots that intersect a plane of known area through the expression: $L_T = 2 * n$. For this equation, $L_T$ is equal to the probable fine root length per unit volume soil (root length per $cm^3$ of soil), while $n$ is equal to the number of fine root intersections per screen (Number of intersections $cm^{-2}$ screen). In January 2002, eighteen screens, 1 m apart, were inserted into the soil of each site using a sharpshooter shovel. Rectangular screens were made of clear fiberglass (Phifer Wire Products, Inc, Tuscaloosa, AL) with 15 holes per $cm^{-2}$ (15.2 cm length, 7.6 cm width). Melhuish and Lang (1971) recommended a combination of horizontal and vertical planes to correct for non-random root angles when planes are used to estimate root density. To compensate for isotropism, screens were placed at an angle of $45^o$ to a vertical depth of 11 cm (Melhuish and Lang, 1968; 1971; Schilling 1999; Jones et al., 2000). This depth is based on previous studies that found a very high proportion of fine and small root biomass in the top 15 cm of soil (Powell and Day 1991, Baker et al.2001, Clawson *et al*. 2001).

Starting in February 2002, one screen was randomly selected and removed from each plot approximately every six weeks over a period of 74 weeks, totaling 12 screens per treatment in each plot. An intact block of soil (about 20 cm in diameter, 30 cm in depth) was excavated around each screen. Immediately afterward, the soil surrounding each screen was gently removed by hand and the number of roots crossing all intersections for each diameter class (0.1 – 1.0 mm, 1.1 – 2.0 mm, 2.1 – 3.0 mm) were counted and recorded. Probable fine root length was calculated based on the equation of Melhuish and Lang (1968). To express root length (cm $m^{-2}$) on a weight basis (g $m^{-2}$), a conversion rate following Schilling (1999) was used. Within each diameter class three 1-cm long root pieces were cut, dried to a constant weight (70ºC, 48 hr) and weighed. Mean weight per centimeter piece was recorded and then multiplied by the calculated root length (cm $m^{-2}$) for the corresponding class. Fine root net primary productivity was calculated by differencing biomass production between subsequent sample periods (i.e. April 2002 – February 2002, May 2002 – April 2002, etc. until July 2003 – June 2003) and by adding the sum of all positive differences to the biomass of the first sample date of February 2002 (Fogel 1983).

**Fine Root Standing Crop Biomass and Net Primary Productivity – Soil Cores**

Starting in February 2002, sequential soil cores (Caldwell and Virginia 1987) were collected in each plot, beside the sampled screen, in order to evaluate fine root biomass and annual productivity for each sample period and compare the last with those estimated by the screen method. The term *fine root* in this study defines roots having a diameter < 3.0 mm. Soil cores were collected approximately every six weeks, during 74 weeks. A total of 12 soil core samples were collected in each treatment plot within the nine catchments.

Cores were removed from soil by inserting and extracting a PVC tube (8 cm in diameter) to a depth of 11 cm. Once collected, cores were transported to the Auburn laboratory in coolers and stored at 4$^{o}$C to preserve live roots until they could be washed. Fine roots were manually removed from soil in the laboratory using a low-pressure water wash to minimize nutrient and fine root loss. Washed root samples were stored in water at 4$^{o}$C until analyzed. Roots were classified into three diameter classes (0.1 – 1.0 mm, 1.1 –2.0 mm, 2.1-3.0 mm) and classified as live or dead by visual criteria. Live roots are firm, flexible, and either white or brown with succulent white tips, whereas dead roots often show signs of decay, are soft, either gray or black, and lack white tips (Powell and Day 1991). Fine roots were oven-dried to constant mass (70ºC, 48 hr) and weight recorded. An expansion factor was used to express actual weight in g m$^{-2}$ to an 11 cm depth. Estimated root length (for each diameter class and status) was calculated following the line-intercept method as described by Böhm (1979). Estimated root length was multiplied by an expansion factor to obtain root length in a 1 m$^{-2}$ plot to a depth of 11 cm. Conversion of root length (cm m$^{-2}$) to a weight basis (g m$^{-2}$) followed the same procedures as described above for the in-situ screen method. Fine root production, for both actual and estimated weights, was calculated as differences in means of fine root biomass between sampling dates. Positive biomass increments were summed across growing seasons (Fogel 1983).

**Fine Root Nutrient Analysis**

Samples were ground either by hand (small samples) or in a Wiley mill to pass a 20-mesh screen after being oven-dried to constant weight (70ºC, 48 hr). Total C and N analyses were conducted using a Perkin Elmer Series II CHNS/O Analyzer 2400 (Perkin

Elmer Corp., Norwalk, CT). Total P was not analyzed because of insufficient sample weights. The total nutrient content was defined as the product of root dry weight and nutrient concentration in the roots.

### Statistical analysis

Differences in mean fine root response variables (standing crop biomass, production, nutrient contents) between treatments within each disturbance category and diameter class were identified using T-tests (PROC TTEST, SAS Institute, 1999). Duncan's New Multiple Range procedure was used to test for methodological differences in estimates of fine root production and to test differences in fine root production among the three disturbance categories for the upper plots. Differences between means were considered statistically significant at $\alpha = 0.10$. In addition, linear regression analyses (PROCREG, SAS Institute, 1999) were conducted to determine whether or not there was a relationship between sediment deposition and fine root production and nutrient contents. The less conservative 90% level of significance was chosen due to the highly variable nature of fine root data.

## RESULTS

#### *Highly disturbed areas*

Live fine root standing crop biomass for various size classes (0.1 –1.0 mm, 1.1-2.0 mm, 2.1-3.0 mm, and total – 0.1 – 3.0 mm) for both lower and upper treatments are given in Figures 2 and 3. Generally, standing crop biomass of live roots was much greater at lower plots for all root diameter classes during the sample period; however, significant differences ($P < 0.10$) were observed for only a few collection dates. At lower plots, total root biomass varied from 178.0 to 530.5 g $m^{-2}$ and for upper plots, total fine root biomass ranged from 9.8 to 170.4 g $m^{-2}$. Seasonal fluctuations in standing crop biomass of fine roots were observed in lower plots for all diameter classes, whereas upper plots maintained a relatively stable and low standing crop throughout the sample period. Lower plots peaked during the summer of 2002 (July) and 2003 (July), and also in the winter 2003 (January/February) for all diameter classes, while a few isolated peaks were observed in upper plots: May 2002 (intermediate and large diameter classes), January 2003 (intermediate diameter class) and July 2003 (large diameter class).

During the study period, total fine root necromass varied from 5.4 to 48.3 g $m^{-2}$ on lower plots and 0.4 to 12.0 g $m^{-2}$ on the upper counterparts. Similarly to live fine roots, standing crop biomass of dead fine roots remained somewhat stable over the sample period in upper plots, whereas seasonal variation was observed on lower plots for all diameter classes, with autumn 2002 (September and November) and winter 2003 (January and February) peaks (Figures 4 and 5). For upper plots, dead fine roots mostly occurred in the smallest diameter class. With the exception of May 2002, no dead root biomass was observed for the intermediate and large diameter classes. Comparisons between upper and lower plots were significant ($P < 0.10$) only for the smallest diameter class.

*Moderately Disturbed Areas*

Live fine root standing crop biomass within the moderately disturbed areas are presented in Figures 6 and 7. With the single exception of the intermediate diameter class, no significant difference was observed between upper and lower plots. On lower plots, total fine root biomass varied from 281.12 to 466.36 g $m^{-2}$ while upper plots, ranged from 244.10 to 596.39 g $m^{-2}$. Both lower and upper plots showed a seasonal fluctuation in root biomass. Maximum live fine root biomass within lower plots occurred in spring 2002 (April and May) and late spring/summer 2003 (May and July) for all diameter classes, whereas the peaks for upper plots were similar to those for lower plots on highly disturbed areas: summer of 2002 and 2003 (July), and winter of 2003 (January/February).

For most of the sample collections, dead biomass was somewhat higher in upper plots, with the exception of the intermediate diameter class; yet, only very few statistical differences were observed. Total necromass ranged from 12.3 to 68.9 g $m^{-2}$ and 1.7 to 96.6 g $m^{-2}$, on lower and upper plots, respectively. Dead fine roots also showed a seasonal trend for standing crop biomass (Figure 8 and 9). Lower plots exhibited peaks of dead biomass in late spring/summer of 2002 (May and July), winter 2003 (January) and spring 2003 (April). Within the largest diameter class, no detritus was observed during the autumn/winter season, from September 2002 to February 2003. Peaks of dead root biomass for upper plots were similar to those found for lower plots: summer of 2002 (July), followed by peaks in autumn of 2002 (November) and spring of 2003. (April).

*Reference areas*

Standing crop biomass of live fine roots within reference areas is presented in Figures 10 and 11. In general, root biomass was greater in lower plots, and with the exceptions of November 2002 and April 2003 within the intermediate diameter class (Figure 10), no other significant differences were observed. Total standing crop biomass of fine roots ranged from 265.5 to 820.0 g $m^{-2}$ on lower plots and, for upper plots, fine root biomass varied from 153.6 to 437.1 g $m^{-2}$. Temporal variation was observed in both treatments for live roots. Peaks of biomass in the lower plots occurred in the late spring of 2002 (May), winter of 2003 (January) and spring of 2003 (April). In upper plots, temporal fluctuation in root biomass among diameter classes varied more than in lower plots but, in general, a decline in root biomass of all classes was observed in April 2002 and 2003, followed by peaks of biomass in May of the same years.

Standing crop root necromass (Figures 12 and 13) was higher within the lower plots for all diameter classes, with only few significant differences between treatments. Total necromass varied from 13.6 to 119.8 g $m^{-2}$ and 5.0 to 41.1 on lower and upper plots, respectively. Seasonal fluctuation was observed only for lower plots, whereas upper plots remained fairly stable over the sample period, especially in the intermediate and largest diameter classes, where little or no dead biomass was observed. For lower plots, peaks of necromass varied among diameter class, but in general, autumn 2002 (September) and spring 2003 (April) peaks were observed for each.

**Fine root net primary production**

Annual belowground primary productivity of various diameter classes within each disturbance category and treatment are presented in Figure 14. Net primary productivity of fine roots was significantly greater in lower plots (803.1 g $m^{-2}$) of highly disturbed areas compared to upper plots (82.7 g $m^{-2}$). At moderately disturbed areas, net primary productivity was relatively similar in both treatments (843.6 and 873.2 g $m^{-2}$, lower and upper plots, respectively). On reference areas, even though belowground net primary productivity was greater at lower plots (1300.8 g $m^{-2}$) compared to upper plots (746.5 g $m^{-2}$), no significant difference between treatments was observed. On upper plots, belowground productivity on highly disturbed areas was significantly less than on upper plots within the other two categories.

Comparisons of fine root production determined using the three methods (in-situ screen, core-estimated weight, and core-actual weight) for each diameter class, disturbance category and treatment are presented in Table 2. Highly disturbed areas appear to be the least sensitive of the three disturbance categories, since no significant differences among methods were observed for any diameter class in any treatment. On moderately disturbed areas, within the small diameter class fine root NPP was significantly less using the screen method. Similar pattern was observed for the large diameter class. Within intermediate diameter class, fine root NPP from the core estimated method was significantly less. No differences were observed for the large diameter class. For reference areas, fine root NPP estimates using the screen method was significantly less in upper plots in comparison to core estimated method. No differences were observed in lower plots for the small diameter class and both treatments in intermediate diameter class. Within the large diameter class, in lower plots fine root NP estimated from the screen method was significantly less than that of core estimated method. No differences were observed within upper plots. Total fine root NPP estimates was significantly less using the screen method for both treatments in reference areas. In general, within the smallest size class, the in situ method tended to be less useful than the core method (both estimated and actual weight), especially on lower plots, where the wetter soil and high number of large roots made it more difficult extract the screen from the soil. Consequently, counting the roots growing through the screens was more difficult and less precise. Thus, further discussion concerning fine root production will pertain to those estimates determined using actual fine root weights only.

Seasonal variations in productivity of total fine root for lower and upper treatments across the three disturbance categories are given in Table 3. Within all diameter classes and disturbance categories, fine root production was significantly greater during the spring and summer of 2002 and 2003, which coincides with periods of heavy rain (Figure 15) during the sample period. For highly disturbed areas, production was significantly greater on the lower plots.

In the other two disturbance categories, no significant differences between treatments were observed. Fine root productivity was lower during autumn/winter season (September-February) for all diameter classes and disturbance categories.

**Fine root nutrient contents – Carbon and Nitrogen**

Live fine carbon and nitrogen contents for total roots (<3.0 mm in diameter) are presented in Table 4. Carbon and nitrogen contents of live roots in highly disturbed areas showed a clear trend during the sample period, where lower plots consistently had greater carbon and nitrogen contents than the upper plot. Mean values for C and N contents of total fine roots within highly disturbed areas were 474.9 g C $m^{-2}$ and 8.8 g N $m^{-2}$ for lower plots, and 57.1 g C $m^{-2}$ and 0.9 g N $m^{-2}$ for upper ones. For the other two disturbance categories, no clear trend between treatments was observed. When comparisons were made among disturbance categories at upper plots (Table 5), carbon contents for highly disturbed areas were significantly less than for the other two disturbance categories, whereas only few significant differences were observed among disturbance categories for nitrogen. Pool sizes for both nutrients mirrored changes in live fine root biomass during the study period.

Dead fine carbon and nitrogen contents for total roots (<3.0 mm in diameter) are presented in Table 6. Nutrient contents for dead roots a followed similar trend as that for live roots. However, even though carbon and nitrogen contents of lower plots within highly disturbed areas were greater than their upper plot counterparts, no significant differences were observed. Comparisons of nutrient content among the three disturbance categories at upper plots are presented in Table 7 and followed similar trends as live roots. Dead root nutrient pools tracked changes in dead root mass for each sample period.

# DISCUSSION

## Fine root standing crop biomass

Seasonal variations in standing crop biomass of live and dead roots in forest ecosystems have been documented (Fahey and Hughes 1994, Schilling et al. 1999, Baker et al. 2001, Clawson et. al 2001). In the present study, fluctuations in fine root biomass were observed for all diameter classes, treatments, and disturbance categories, with the exception of upper plots of highly disturbed areas, where standing crop biomass of roots remained relatively constant throughout the sample period (Figure 2-7). A substantial decline in fine root biomass during the autumn was observed in this study for all treatments, disturbance categories and diameter classes. Joslin and Henderson (1987) and McClaugherty et al. (1982) also observed a substantial autumn decline in fine root biomass. Hendrick and Pregitzer (1993) reported considerable loss of root length during late summer and autumn. Schilling et al. (1999) found fine root biomass to be lowest during the winter.

Examination of fine root standing crop estimates for each sample collection revealed three distinct peaks of biomass. The first was a spring peak (April and May of 2002/03) within lower plots of moderately disturbed areas and upper plots of reference areas. A second trend was spring (April and May of 2002/03) and winter (January 2003) peaks within lower plots of reference areas, and finally, the third was summer (July 2002/03) and winter (January and February 2003) peaks in biomass for lower plots of highly disturbed areas and upper plots of moderately disturbed areas. Powell and Day (1991) also observed this summer/winter peak of production in mixed hardwood and cedar stands, whereas Schilling et al. (1999) noted a spring/autumn peak of fine root biomass on a Mississippi floodplain, which reflects the bimodal belowground growth curve proposed by Symbula and Day (1988). Clawson et al. (2001) also observed different peaks in root biomass in their Flint River floodplain study, with a somewhat poorly drained community peaking in April, September, and January. Intermediate drained community showed continuous biomass accumulation until reaching a September peak, and finally, a poorly drained community maintaining a relatively constant standing crop biomass, as did upper plots of highly disturbed areas in the present study.

Some species such as baldcypress (*Taxodium distichum* var *distichum*) and water tupelo (*Nyssa aquatica*) are capable of obtaining oxygen and growing in saturated soils, however, roots of most tree species will not survive long under such conditions (Broadfoot and Williston 1973). In our upper plots of highly disturbed areas, sediment deposition is a continuous process. Therefore it appears that this relative constancy in standing crop biomass in both our study and Clawson et al.'s (2001) could be related to frequent anaerobic conditions: in our study due sediment deposition and, in Clawson et al. (2001) due to standing water.

The seasonality of dead fine root biomass was opposite that of live fine root biomass. Maximum dead fine root biomass for most diameter classes, disturbance categories and treatments occurred during autumn (September 2002), when live fine root biomass was at a minimum. Hendrick and Pregitzer (1993) reported an annual necromass peak in late summer or autumn, while Joslin and Henderson (1987) observed peaks of dead fine root biomass in late spring /early summer and late summer or autumn in a white oak stand.

Fine root growth and production depends largely on environmental conditions and forest community structure. It has been demonstrated that following natural (Silver and Vogt 1993) and anthropogenic disturbances (Jones et al. 1996), fine root biomass may decrease and recovery to pre-disturbance levels may take years (Vogt et al. 1981, Fahey and Hughes 1994). In the present study, our data suggest that sediment accumulation greatly reduced fine root biomass in these riparian forests. No data are available regarding on how fine root biomass may recover if sediment deposition is controlled or reduced, and this should be the focus of further studies.

**Fine root net primary production**

Fine root production estimates determined using both actual and estimated root weights (Table 2) were found to be significantly different for moderately disturbed and reference areas, and the in situ screens appeared to be the most sensitive method, especially within the smallest root diameter class. Our findings correspond to those of Fahey and Hughes (1994), who reported that estimates of fine root production using the screen method might be 20 – 30% less than that of coring methods. Also, usage of the screen method presented a number of technical difficulties associated with the removal of screens from the soil and counting the number of roots growing through the screen intersections. This was especially true on lower plots, where the presence of large roots, and the wetter nature of the soils, made it difficult to extract screens.

Thus, for this study, the fine root production estimates calculated using the in situ screens did not appear to provide a realistic measure of root production. The use of the core method has been questioned (Nadelhoffer and Raich 1992) because it is highly sensitive to sampling errors and can lead to over-estimates when fine root biomass is large. However, for this study, this method seems to be the most feasible and further discussion were based on the actual weight of roots.

In the present study, examination of fine root productivity along a gradient of sediment deposition revealed a drastic reduction of root production in areas receiving high rates of sediment deposition (upper plots of highly disturbed areas). Production was 82.7, 873.2, and 746.5 g $m^{-2}$ $yr^{-1}$ on upper plots, and 803.1, 843.6, and 1300.8 g $m^{-2}$ $yr^{-1}$ on lower plots of highly disturbed, moderately disturbed, and reference areas, respectively. Even though production tended to be greater lower plots of reference areas, significant differences between treatments were observed only for highly disturbed areas.

Our data indicate a strong relationship between increased levels of sediment deposition and reductions in fine root production ($P < 0.005$, $R^2 = 0.82$) (Figure 15). A long-term sediment accumulation rate near 0.3 cm $yr^{-1}$ appeared to be an approximate threshold beyond which major reductions in fine root production become evident. However, we have no physiological data to suggest a causal link between the two processes, and further studies on the effects of sedimentation on soil oxygen would be necessary. Kozlowski et al. (1991) suggested that sediment deposition might produce the same effect as flooding by imposing a lack of oxygen on root systems, which impedes root respiration and restricts the development of fine roots. In a study comparing three deciduous communities across a wetness gradient within a floodplain forest, Clawson et al. (2001) found that annual fine root production decreased as wetness increased. This trend was also observed by Baker et al. (2001) in their floodplain forests. Megonigal and

Day (1988) reported that annual fine root production on flooded stands was lower than on the unflooded stand.

Levels of root production in this study are within the ranges found by Powell and Day (1991) within a rarely flooded mixed hardwood community (354 - 989 g $m^{-2}$ $yr^{-1}$), and a cypress community (68 – 308 g $m^{-2}$ $yr^{-1}$), which experienced the longest duration of winter flooding in the Great Dismal Swamp. However, the values reported by Clawson et al. (2001) were much lower in comparison with our findings: 211.1 g $m^{-2}$ $yr^{-1}$in the somewhat drained site, 130.5 g $m^{-2}$ $yr^{-1}$ in the intermediate site, and 56.2 g $m^{-2}$ $yr^{-1}$ in the poorly drained area. It is important to note that in the Clawson et al. (2001) study only roots < 2.0 mm in diameter were examined. Therefore, our greater values may be due the inclusion of larger diameter roots. The production estimates from this study were also within the range of that estimated by Sundarapandian and Swamy (1996) in moist deciduous forests of South India (630.19 – 936.62 g $m^{-2}$ $yr^{-1}$).

**Fine root nutrient content**

Some authors have observed that the loss of nutrients such as P, N, and C in fine roots mirror losses of biomass (Silver and Vogt 1993, Schilling et al. 1999). In the present study, no significant differences between treatments within the three disturbance categories were observed in terms of nutrient (C and N) concentrations of live and dead fine roots. However, in terms of nutrient content, some differences were observed and they were driven by changes in fine root biomass. At upper plots of highly disturbed areas, carbon content of live fine roots significantly decreased as root biomass decreased.

The same trend was observed for nitrogen content in upper plots of highly disturbed areas. For the other two disturbance categories, no significant difference between treatments was observed either for root biomass or root nutrient concentration and, therefore, fine root nutrient content did not show significant differences. Thus, the findings from this study appear to be in agreement with those observed by the aforementioned authors. Comparisons of fine root nutrient content among disturbance categories across upper plots followed similar trends (reference=moderately disturbed > highly disturbed). Clawson et al. (2001) found a similar trend in fine root nutrient content in their Flint River floodplain study, where nutrient content in poorly drained areas was significantly lower than for intermediate and somewhat drained areas. For dead fine roots, no statistical difference was observed in the present study.

## CONCLUSIONS

The use of in situ screens did not appear to be useful in this study. The presence of large roots, especially in the lower treatment plots, made the removal of screens, and counting the number of roots growing through screens difficult. In addition, actual weight of roots seemed to be the most feasible for this study. Levels of fine root biomass and production were significantly reduced in areas under high rates of sediment deposition (upper plots of highly disturbed areas). It is still not entirely clear what mechanisms are driving such reductions. The growth of roots depends upon many factors such as soil nutrients and moisture supply, temperature, and aeration. Usually, roots do not persist in zones of permanent saturation, and we believe that the dominant growth-limiting factor in this study could be reduced oxygen to roots. Since we did not assess anaerobiosis in this study, further studies on the effects of sediment deposition on soil oxygen would be necessary to clarify this point.

In the other categories (moderately disturbed and reference areas), no significant differences were observed between upper and lower plots, for both standing crop biomass and production. Comparisons among disturbance categories across upper plots also did not show any significant difference between these two areas (873.2 and 746.5 g $m^{-2}$ $yr^{-1}$, moderately disturbed and reference, respectively). However, the regression relationship between fine root production and long-term sediment deposition rates indicates that major reductions in fine root production become apparent with rates of sediment accumulation near 0.3 cm $yr^{-1}$, and average sediment deposition rate in moderately disturbed areas was 0.6 cm $yr^{-1}$.

Fine root carbon and nitrogen concentrations did not differ between upper and lower plots or among disturbance categories. However, when comparisons were made in terms of nutrient content, they followed the same trends as root production, where significant reductions were observed in upper plots of highly disturbed areas. Again, no differences were observed between moderately disturbed and reference areas. These results suggest that high rates of sediment deposition negatively affect levels of belowground production and nutrient allocation, which should also be reflected in levels of forest productivity as a whole.

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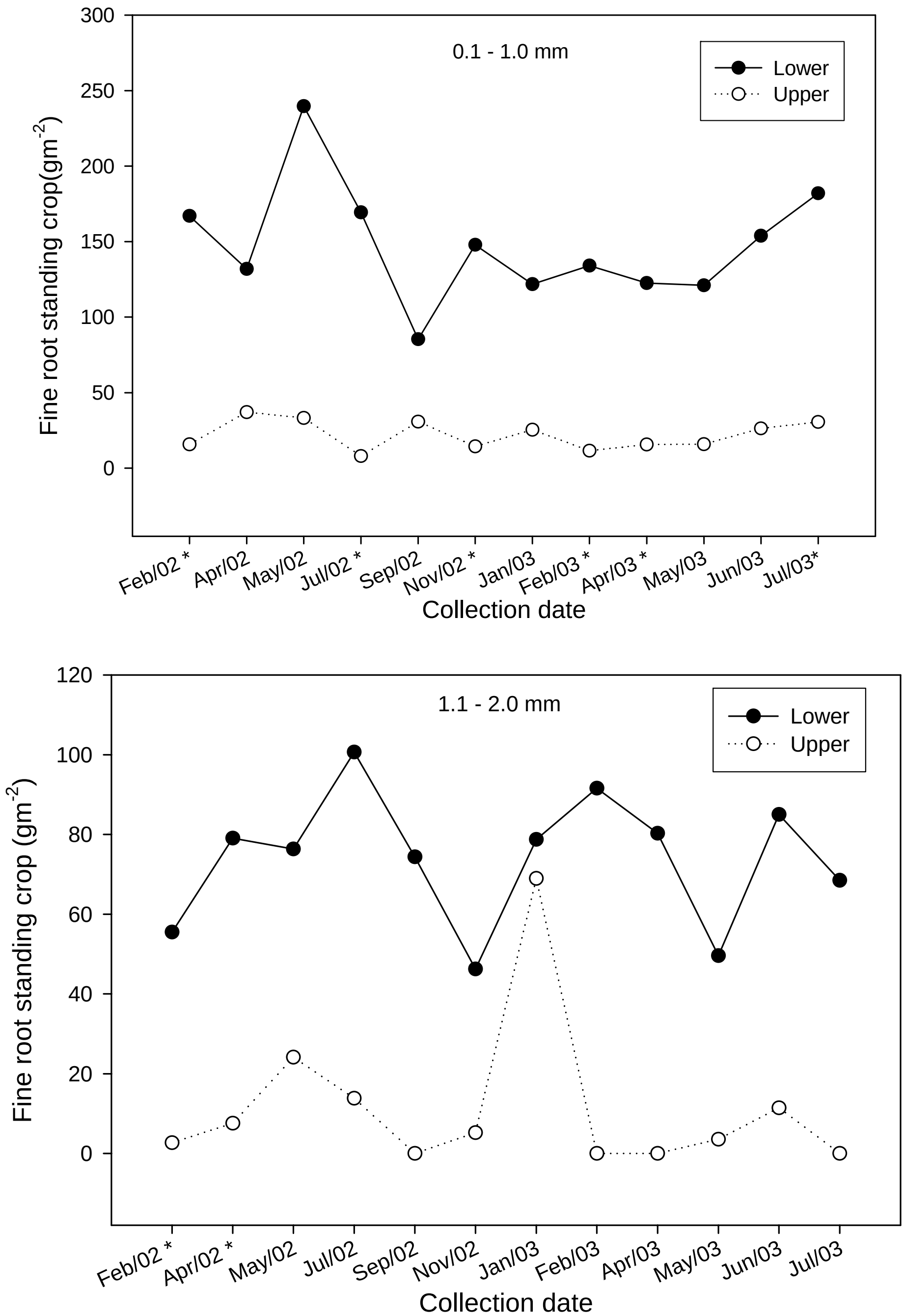



**Figure 2.** **Live fine root standing crop biomass by diameter class to a depth of 11 cm on highly disturbed areas, determined using actual root weights.** ***Asterisks indicate significant differences between treatment pairs. (T-test, $\alpha$= 0.10).***

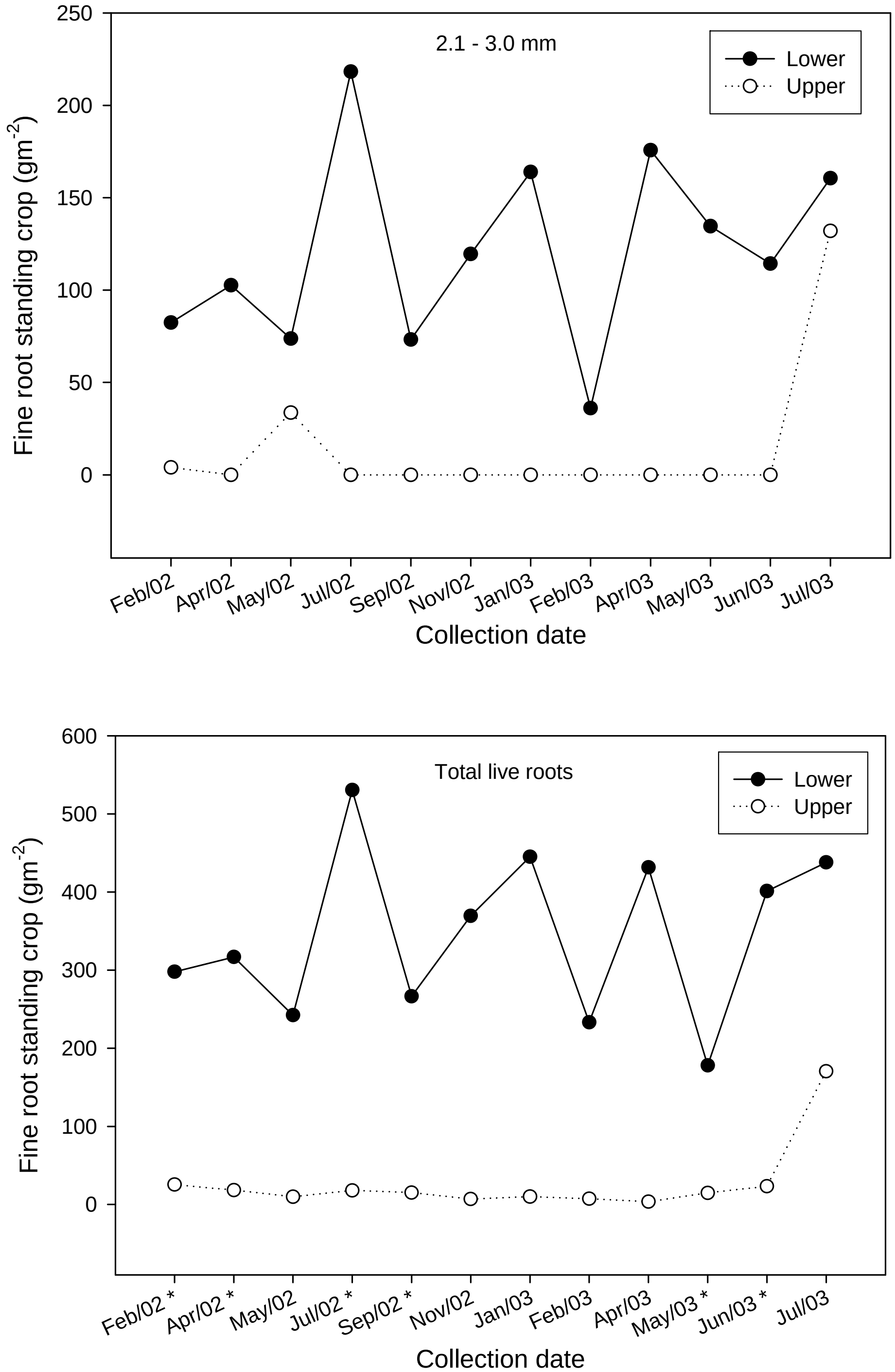
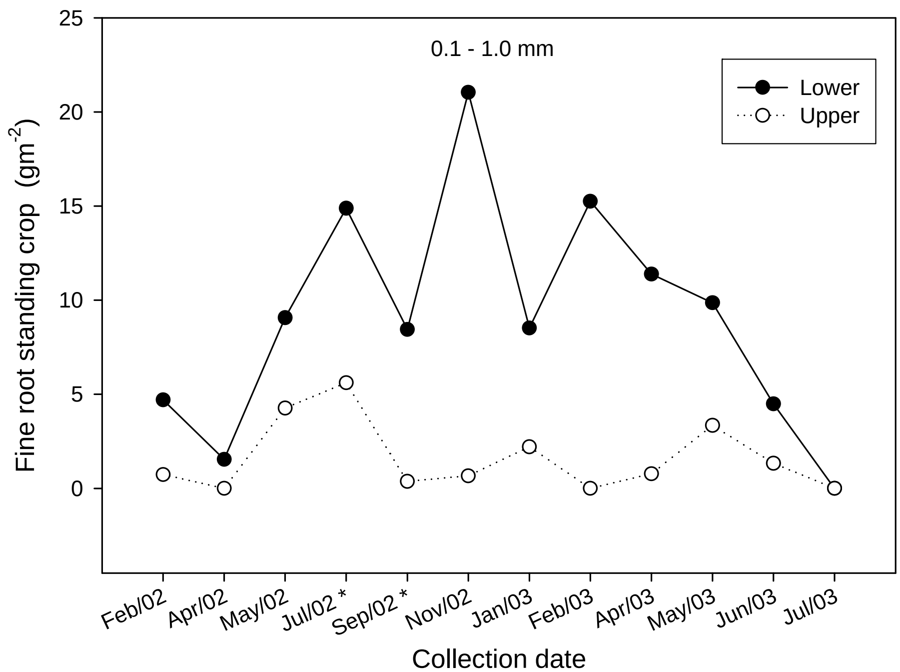



**Figure 3.** **Live fine root standing crop biomass by diameter class to a depth of 11 cm on highly disturbed areas, determined using actual root weights.** ***Asterisks indicate significant differences between treatment pairs. (T-test, $\alpha$= 0.10).***



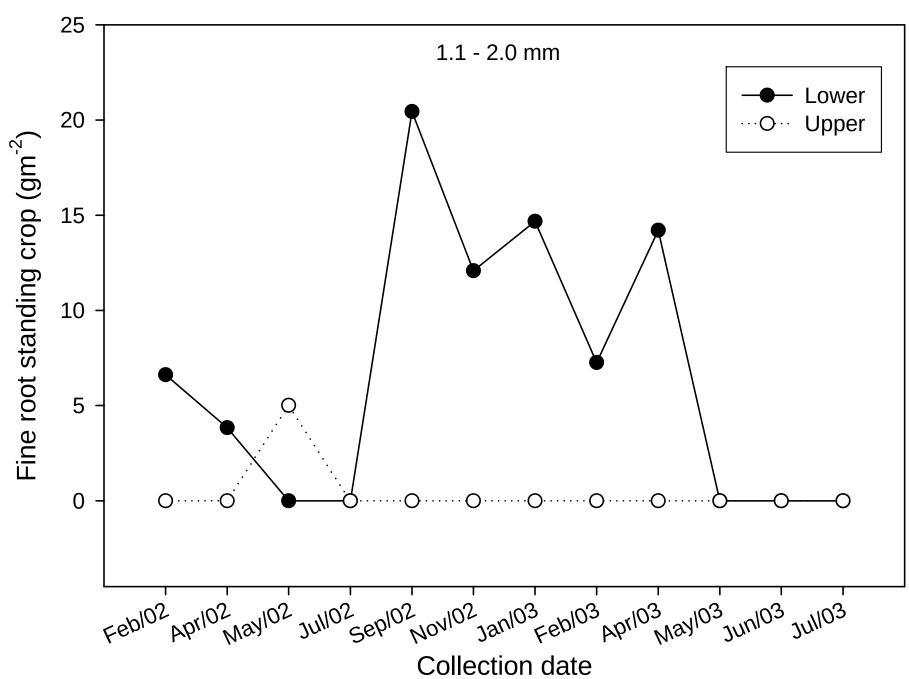
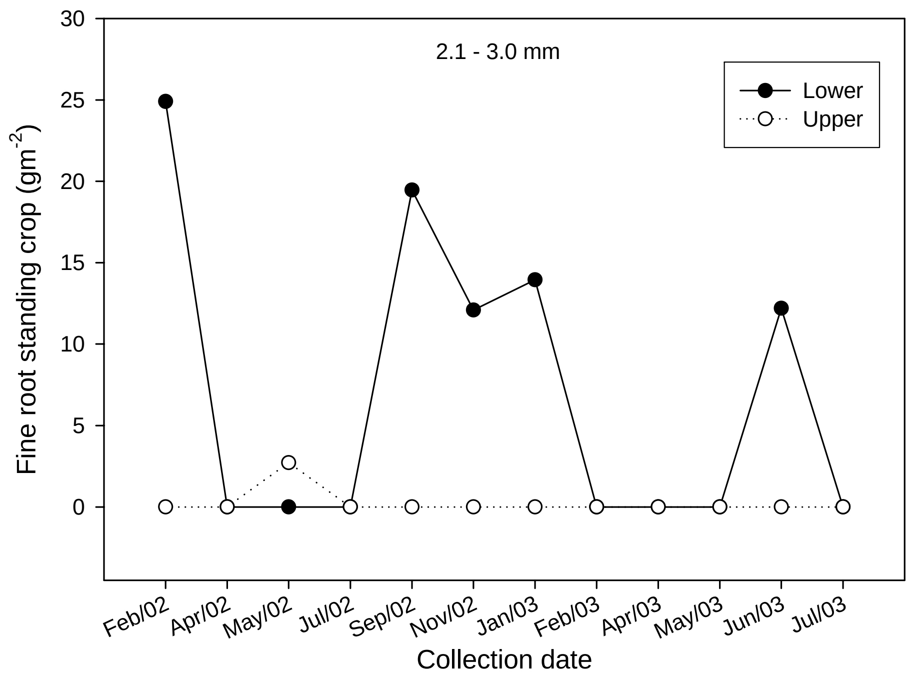




**Figure 4.** **Dead fine root standing crop biomass by diameter class to a depth of 11 cm on highly disturbed areas, determined using actual root weights.** ***Asterisks indicate significant differences between treatment pairs. (T-test, $\alpha$= 0.10).***



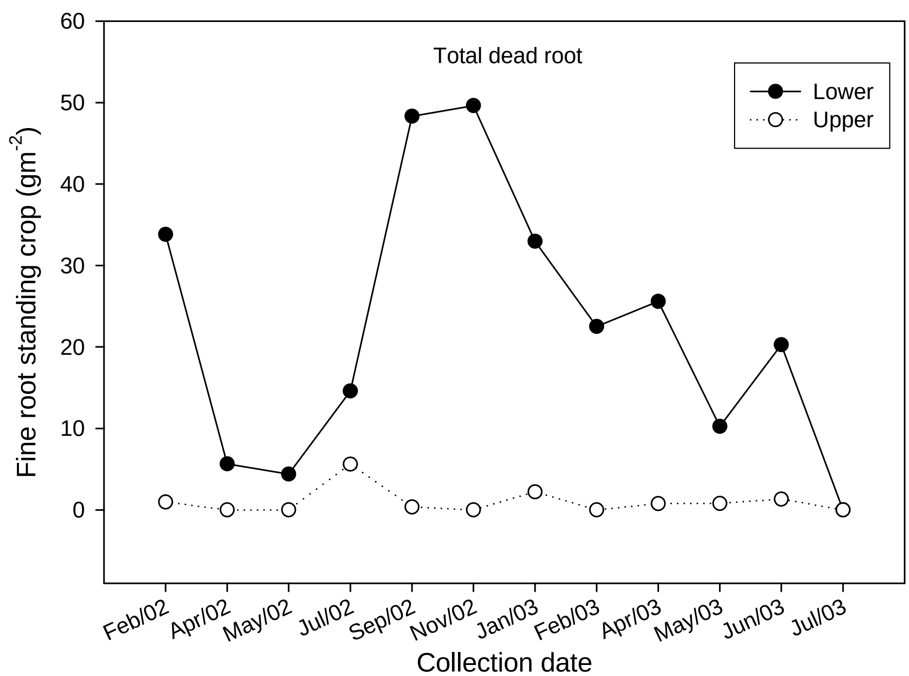
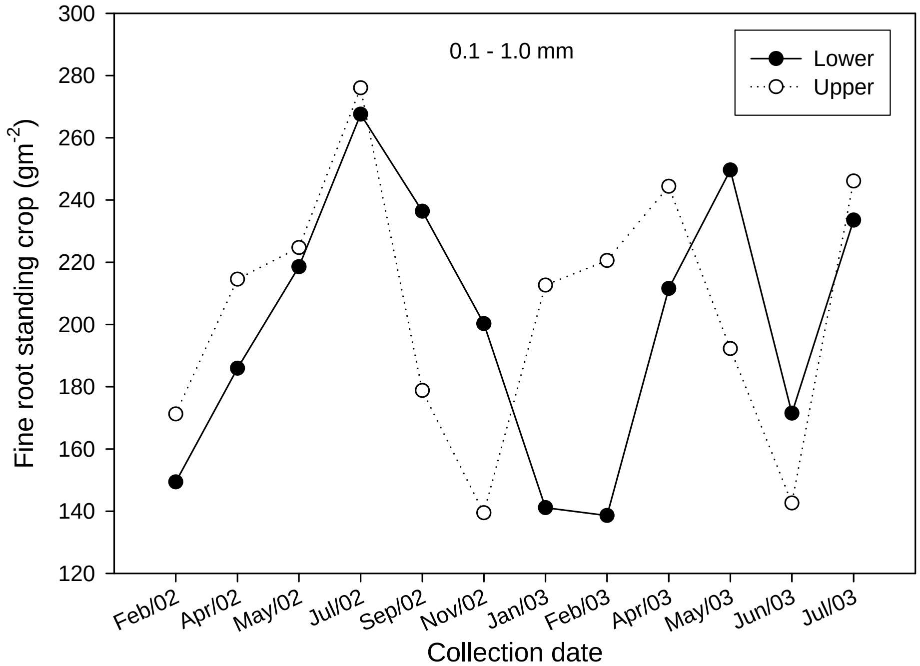




**Figure 5.** **Dead fine root standing crop biomass by diameter class to a depth of 11 cm on highly disturbed areas, determined using actual root weights.** ***Asterisks indicate significant differences between treatment pairs. (T-test, $\alpha$= 0.10)***



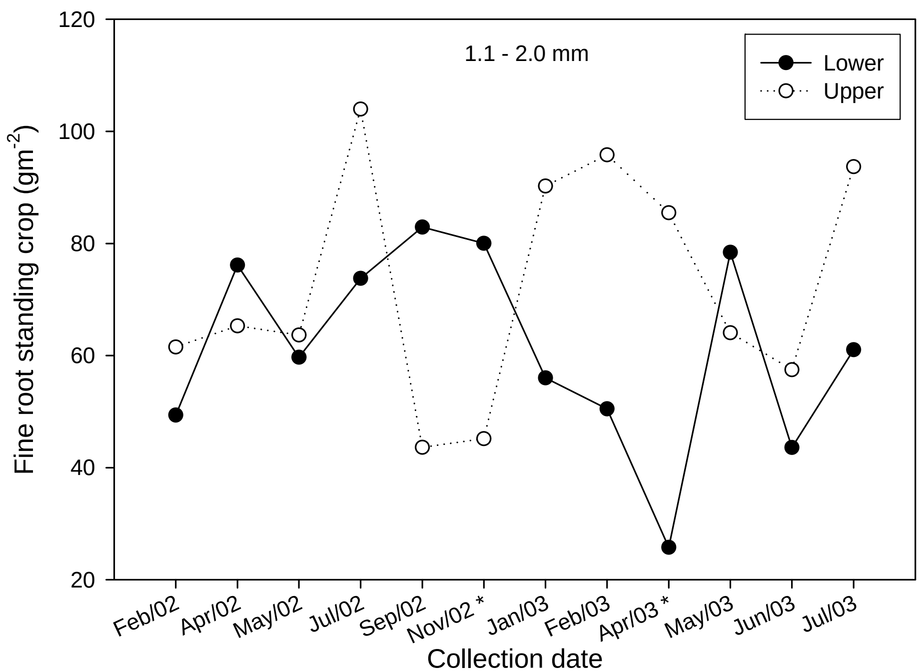
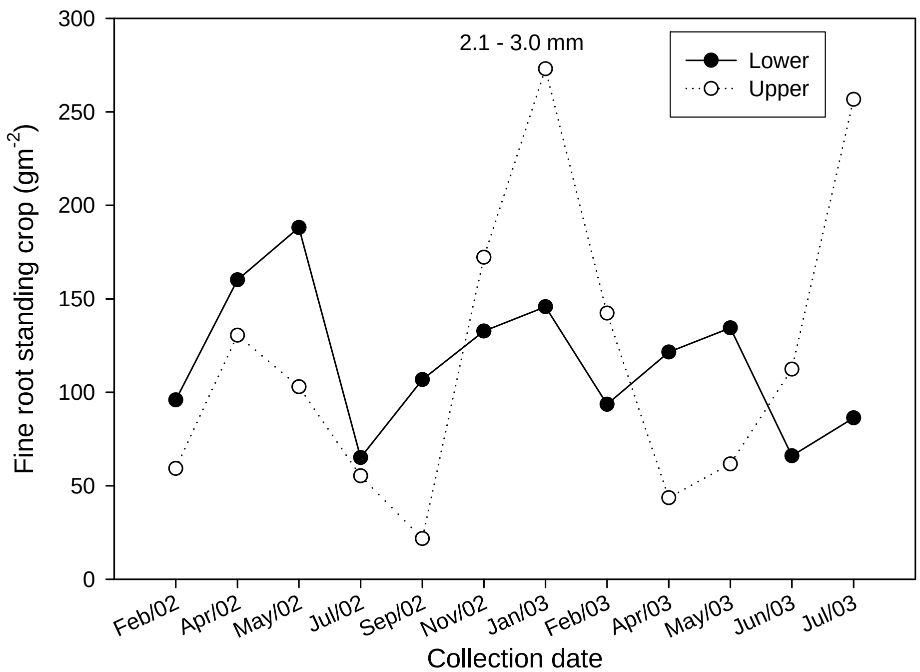




**Figure 6.** **Live fine root standing crop biomass by diameter class to a depth of 11 cm on moderately disturbed areas, determined using actual root weights.** ***Asterisks indicate significant differences between treatment pairs. (T-test, $\alpha$= 0.10).***



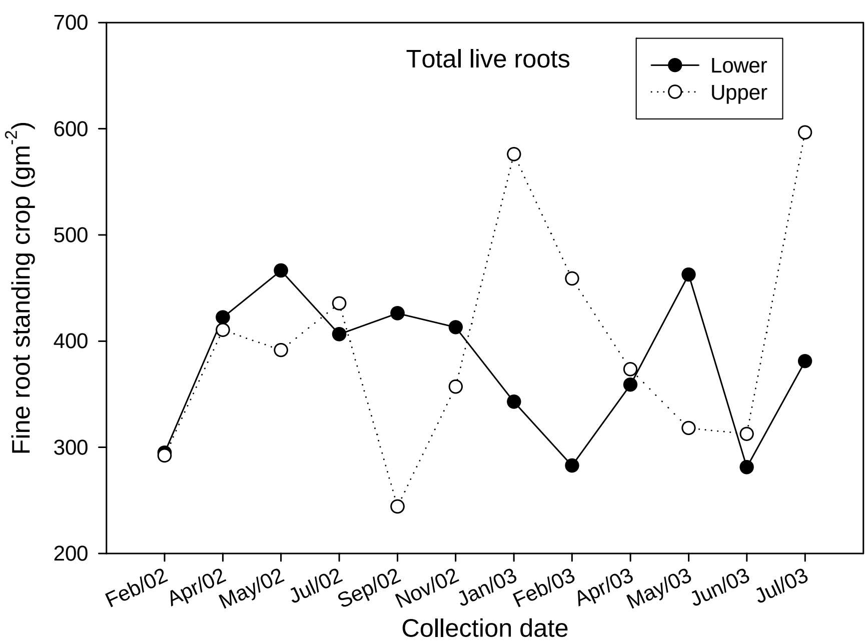
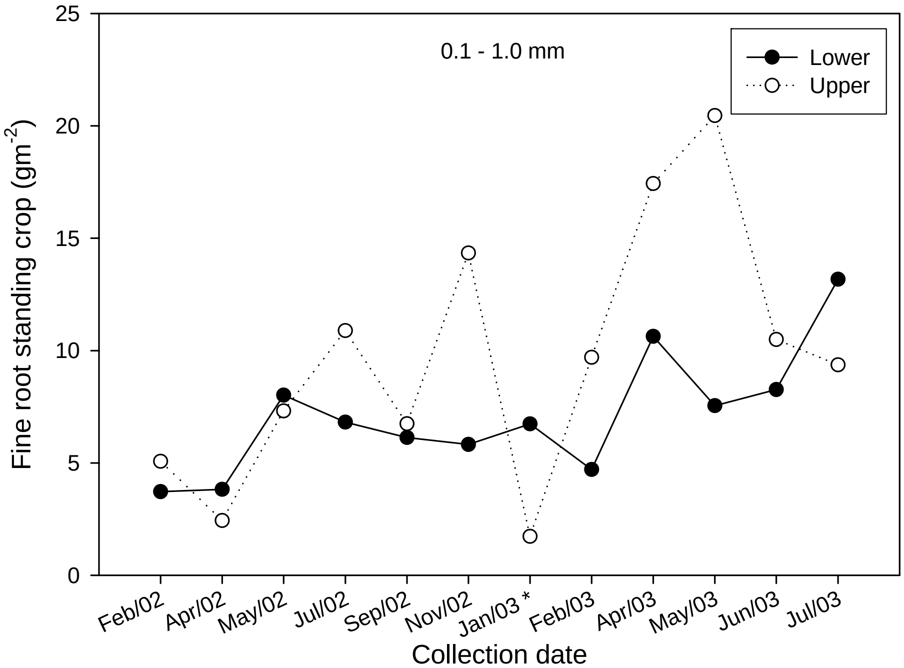




**Figure 7.** **Live fine root standing crop biomass by diameter class to a depth of 11 cm on moderately disturbed areas, determined using actual root weights.** ***Asterisks indicate significant difference between treatment pairs. (T-test, $\alpha$= 0.10).***



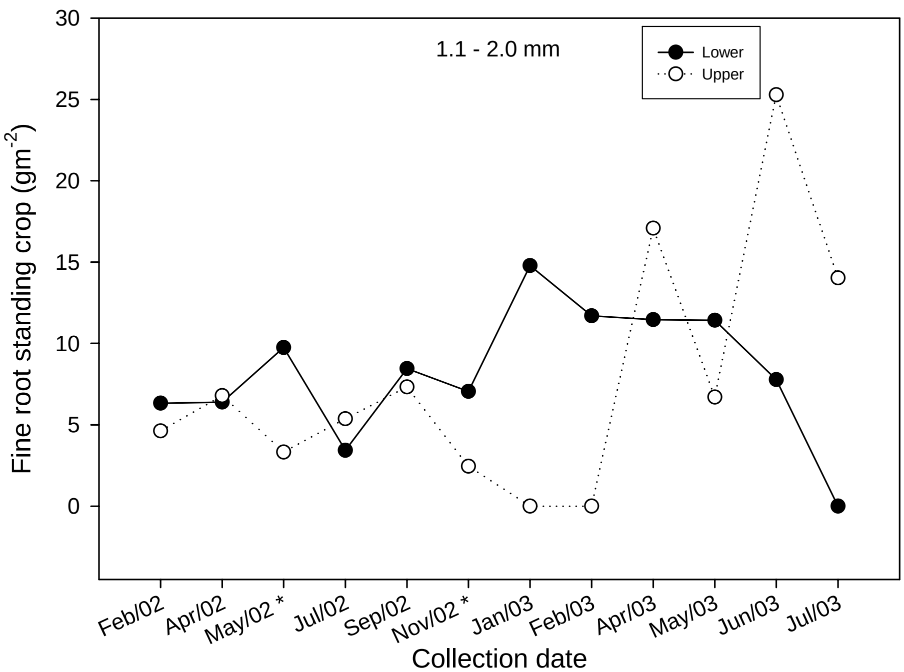
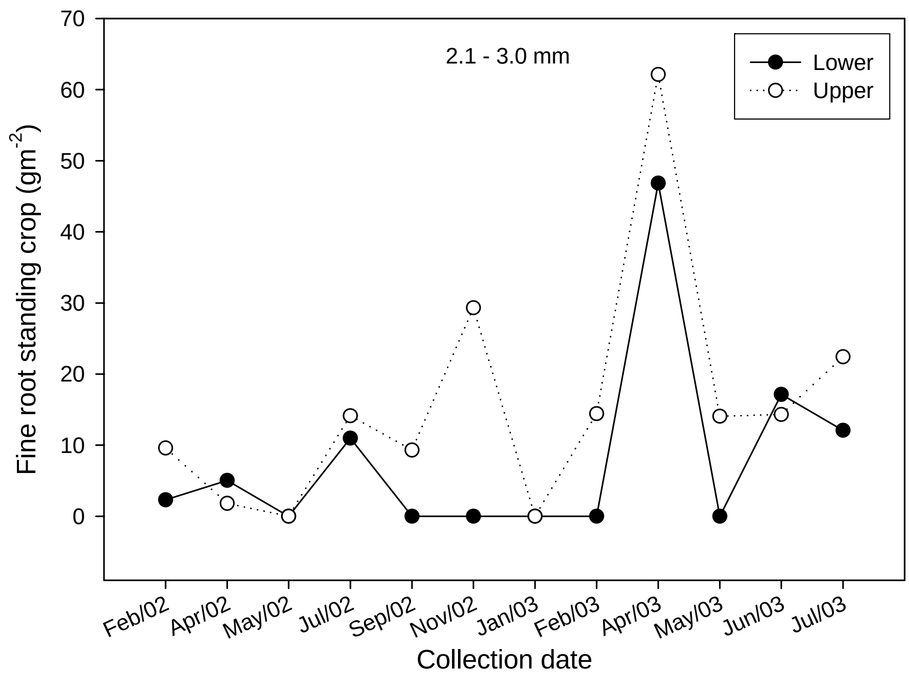




**Figure 8.** **Dead fine root standing crop biomass by diameter class to a depth of 11 cm on moderately disturbed areas, determined using actual root weights.** ***Asterisks indicate significant differences between treatment pairs. (T-test, $\alpha$= 0.10).***



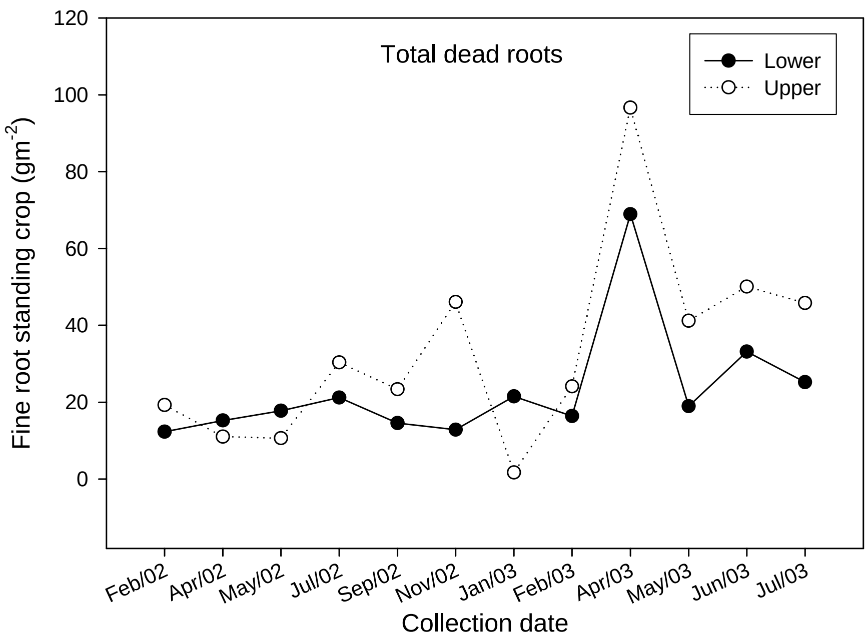




**Figure 9.** **Dead fine root standing crop biomass by diameter class to a depth of 11 cm on moderately disturbed areas, determined using actual root weights.** ***Asterisks indicate significant differences between treatment pairs. (T-test, $\alpha$= 0.10).***

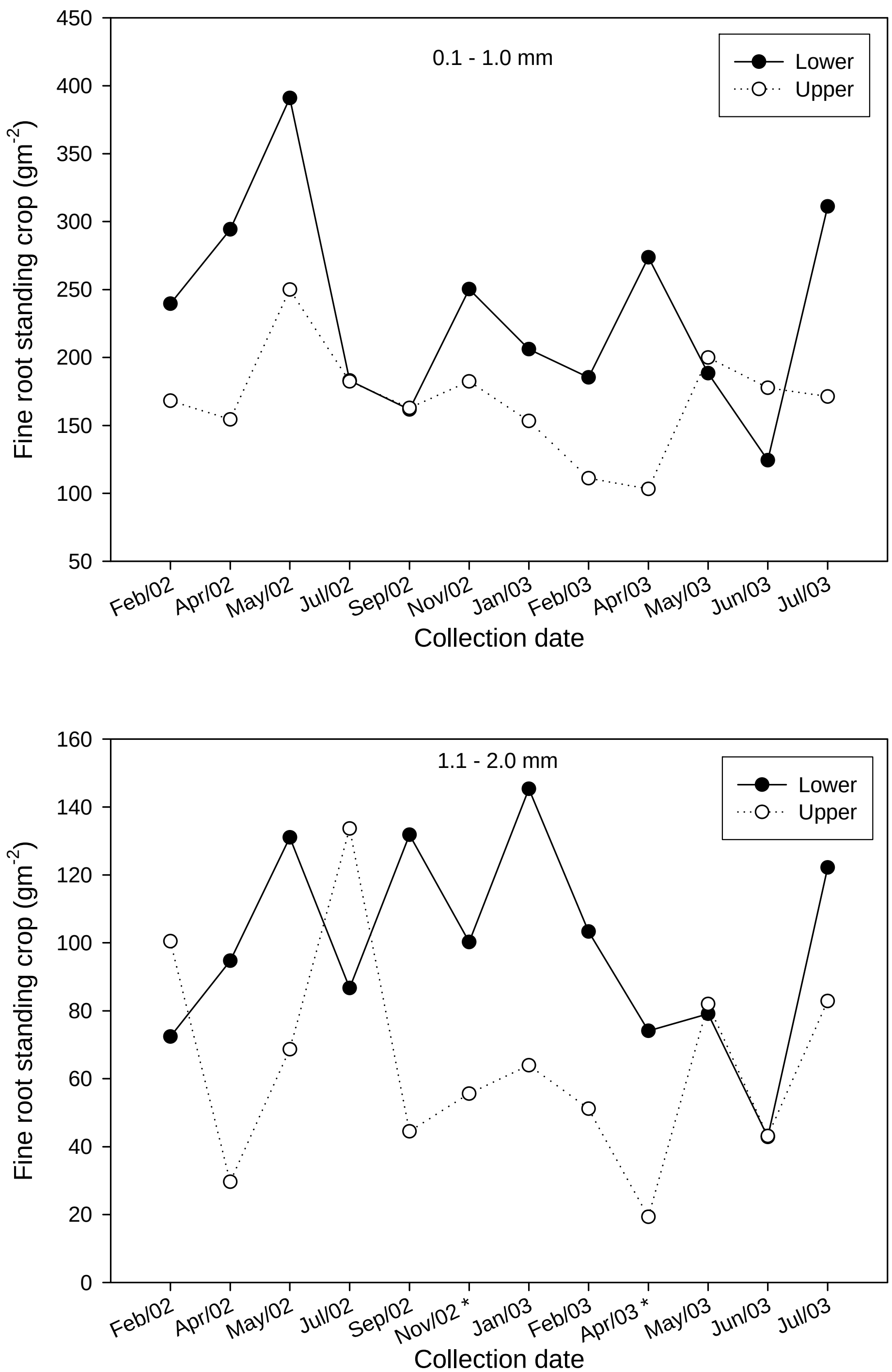
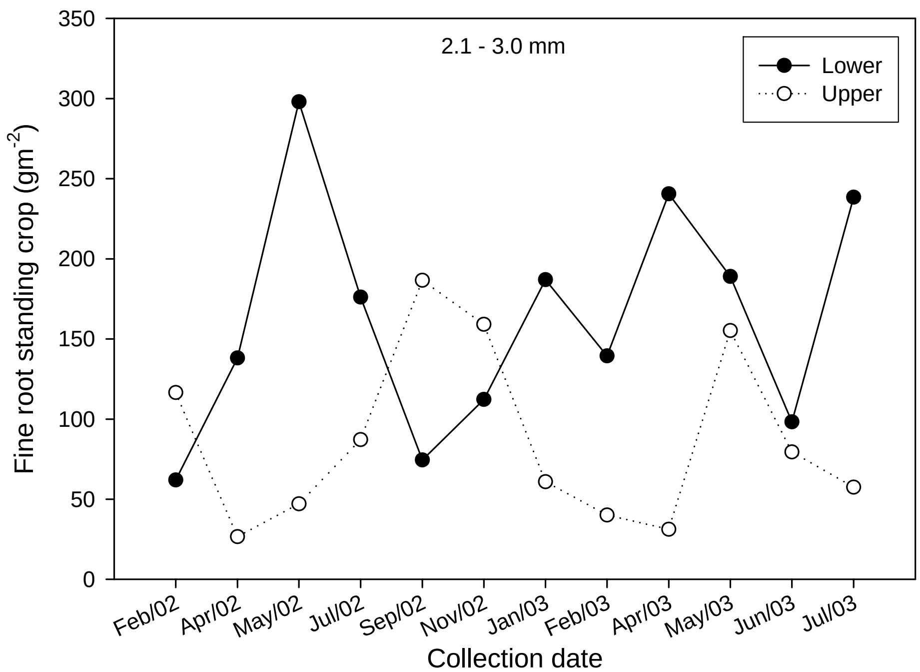



**Figure 10.** **Live fine root standing crop biomass by diameter class to a depth of 11 cm on reference areas, determined using actual root weights.** ***Asterisks indicate significant differences between treatment pairs. (T-test, $\alpha$= 0.10).***



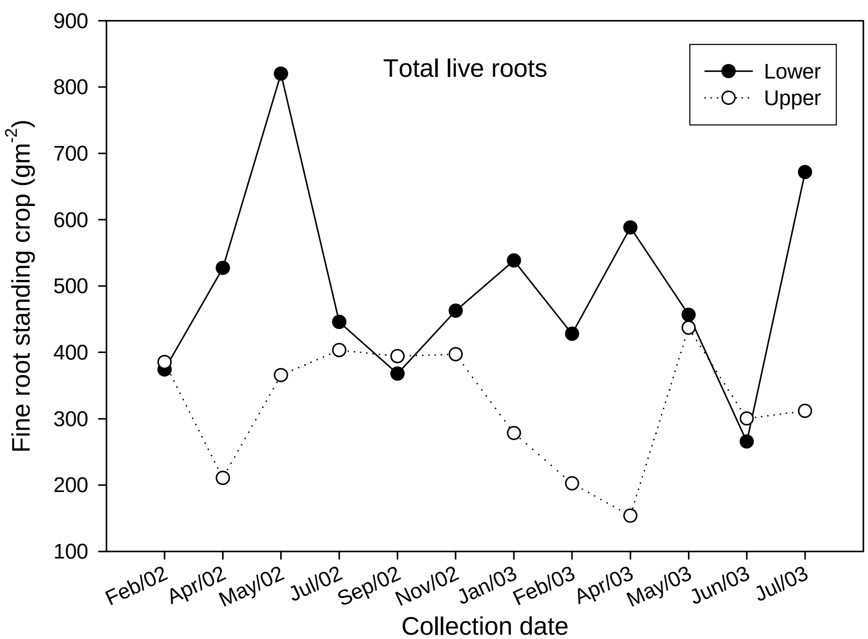
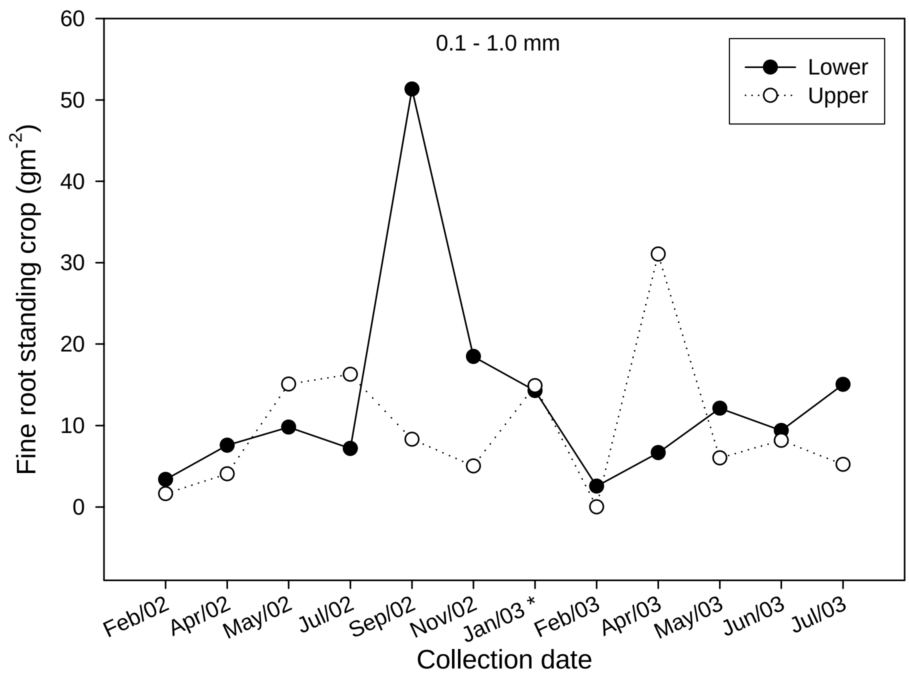




**Figure 11.** **Live fine root standing crop biomass by diameter class to a depth of 11 cm on reference areas, determined using actual root weights.** ***Asterisks indicate significant differences between treatment pairs. (T-test, $\alpha$= 0.10).***



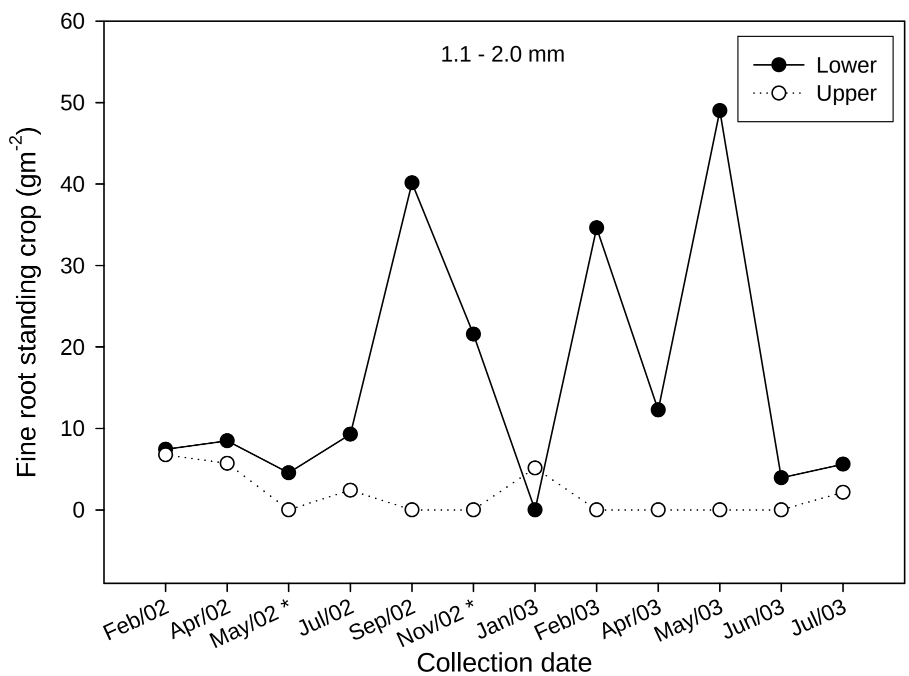
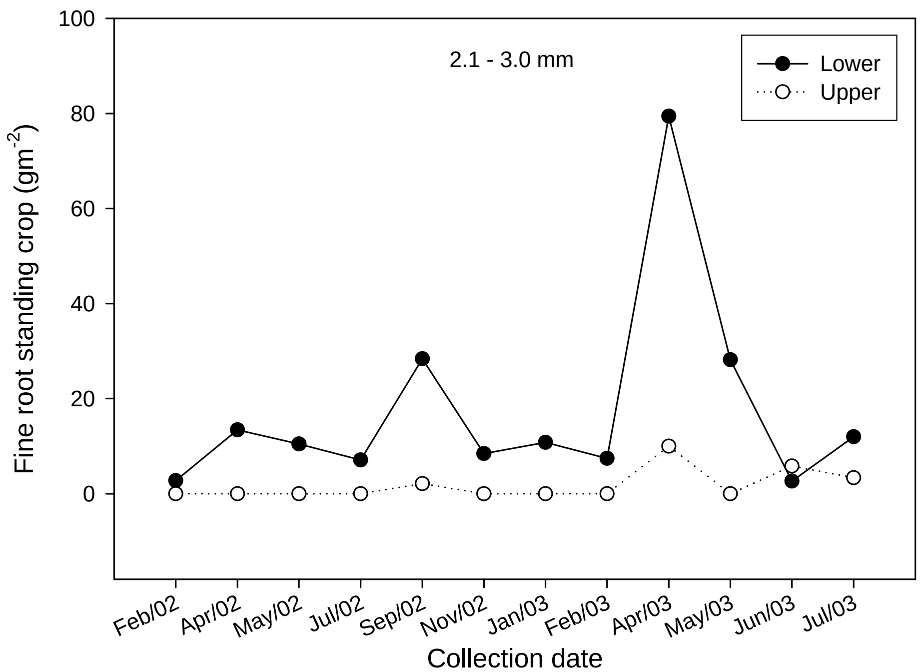




**Figure 12.** **Dead fine root standing crop biomass by diameter class to a depth of 11 cm on reference areas, determined using actual root weights.** ***Asterisks indicate significant differences between treatment pairs. (T-test, $\alpha$= 0.10).***



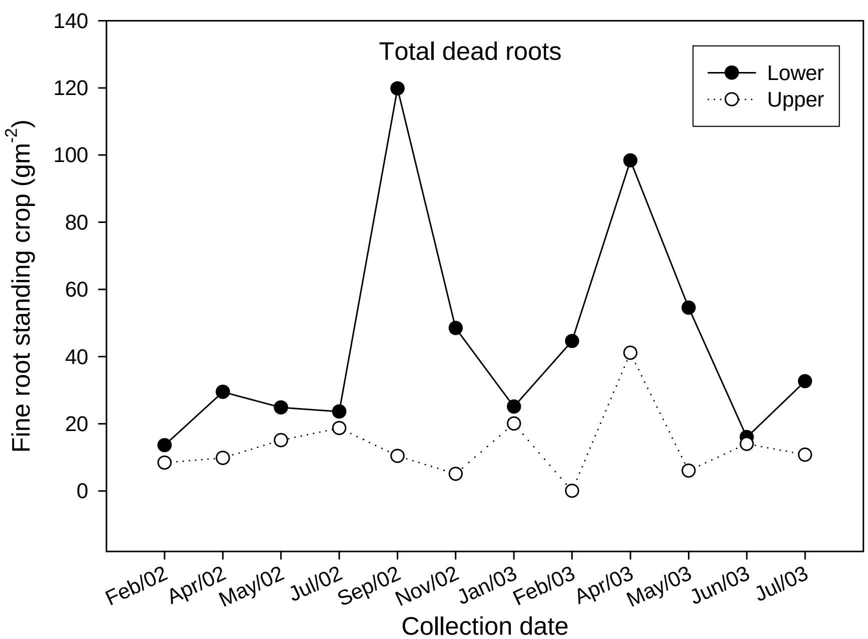




**Figure 13.** **Dead fine root standing crop biomass by diameter class to a depth of 11 cm on reference areas, determined using actual root weights.** ***Asterisks indicate significant differences between treatment pairs. (T-test, $\alpha$= 0.10).***

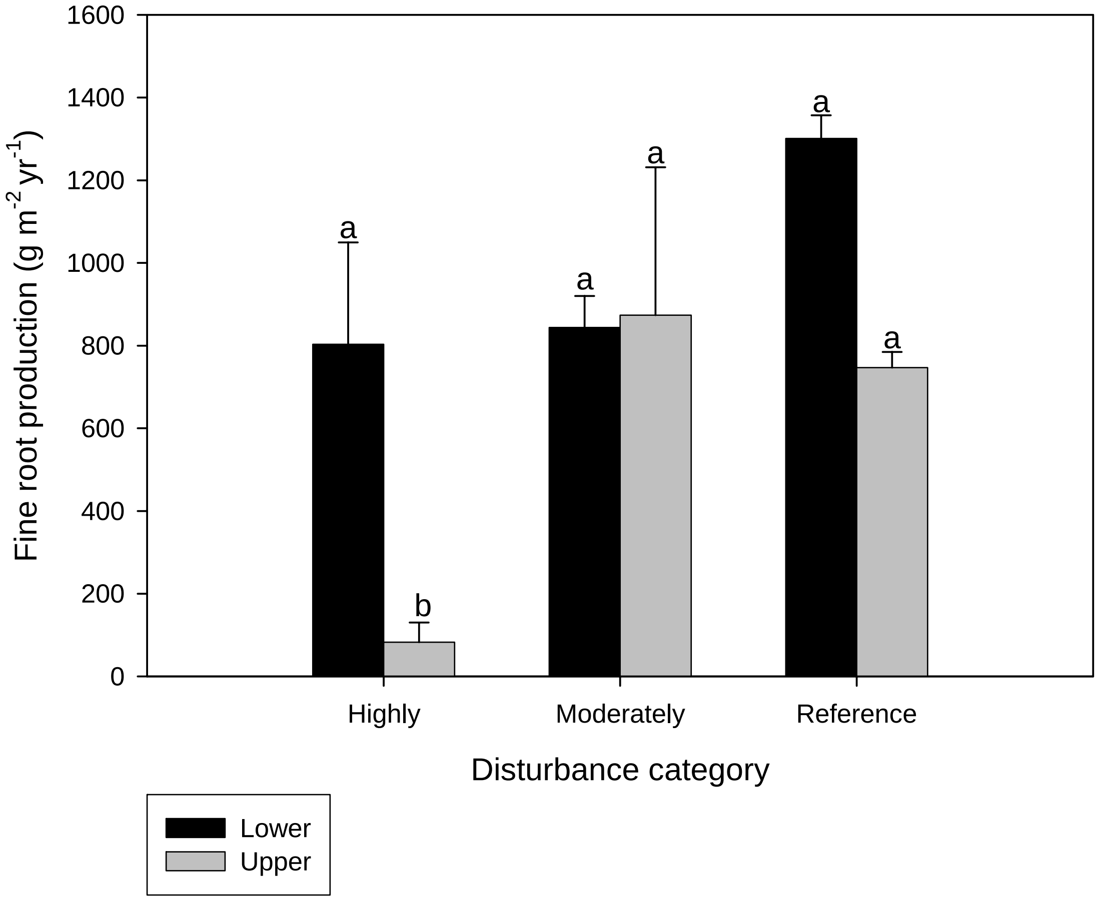



**Figure 14.** **Comparison of fine root production estimates (expressed as g $m^{-2}$ $yr^{-1}$ to a depth of 11 cm, actual weight) between treatments in the three disturbance categories.** ***Different lowercase letters denote significant difference between treatments (T-test, $\alpha$=0.05).***

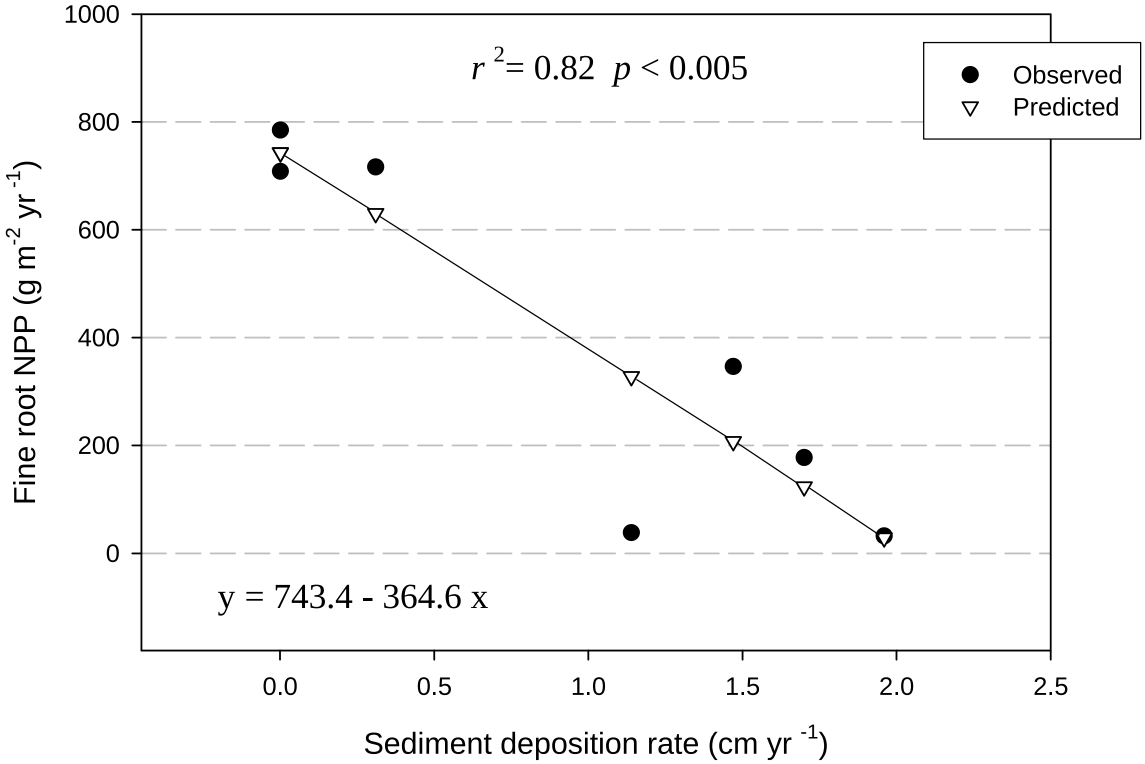



**Figure 15. The relationship between fine root net primary productivity and rates of sediment deposition.**

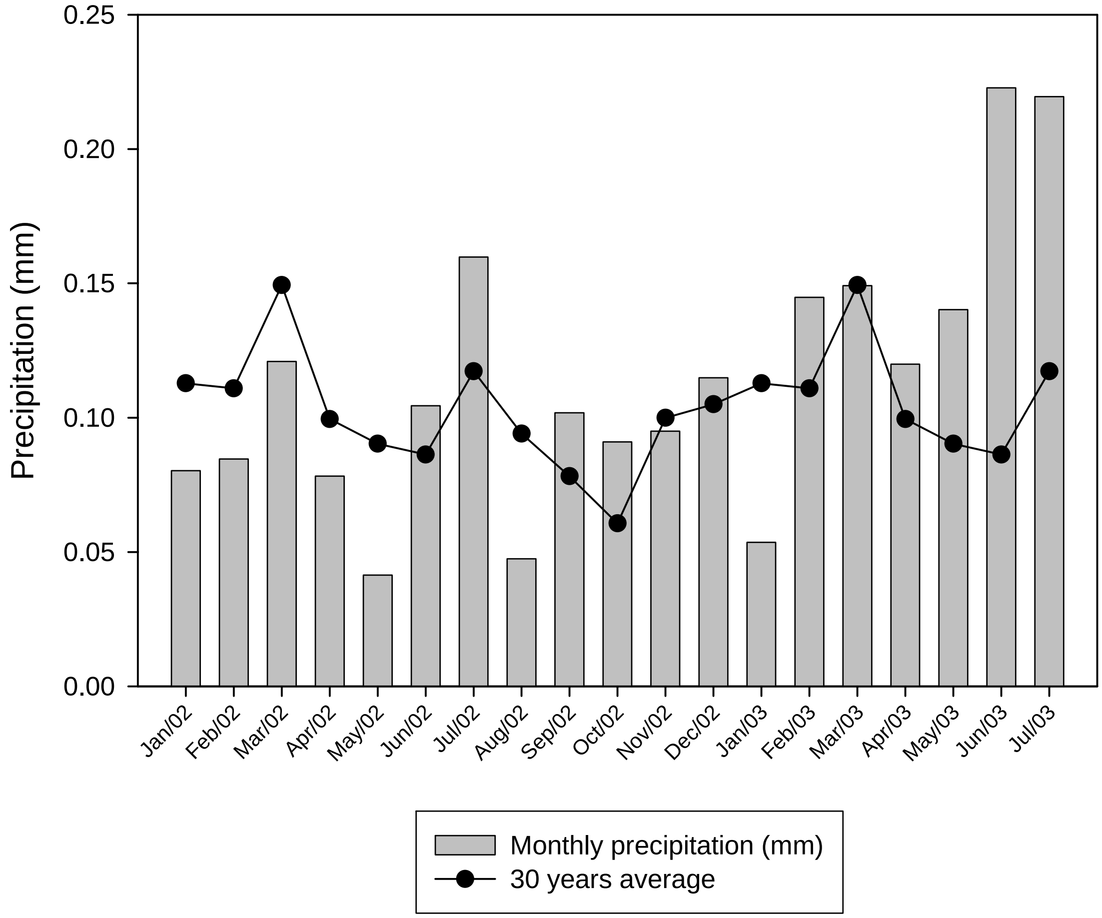



**Figure 16.** **Monthly precipitation* during the study period for the Columbus Metropolitan Airport, GA. * *Source: U.S department of Commerce – National Oceanic & Atmospheric Administration***

**Table 2. Comparison of three methods used to estimate fine root production[1] by diameter class, disturbance category and treatment. Estimates are for the twelve collection periods on annual basis, with means expressed as g m$^{-2}$ to a depth of 11 cm.**

**…0.1 - 1.0 mm…**

| | Highly Disturbed | | Moderately Disturbed | | Reference | |
|---|---|---|---|---|---|---|
| Method | Lower | Upper | Lower | Upper | Lower | Upper |
| In situ screen | 137.5 a | 108.7 a | 110.6 b | 140.7b | 135.7 a | 147.1 b |
| Core-estimated | 333.5 a | 61.2 a | 458.3 a | 480.6 a | 756.6 a | 423.4 a |
| Core-actual | 237.8 a | 45.6a | 355.6 a | 379.0 ab | 551.7 a | 321.7 ab |

**…1.1 - 2.0 mm…**

| | Highly Disturbed | | Moderately Disturbed | | Reference | |
|---|---|---|---|---|---|---|
| Method | Lower | Upper | Lower | Upper | Lower | Upper |
| In situ screen | 357.5 a | 56.6 a | 198.2 a | 109.9 a | 292.0 a | 236.8 a |
| Core-estimated | 251.7 a | 53.6 a | 109.8b | 243.3 a | 270.4 a | 188.8 a |
| Core-actual | 170.1 a | 6.1 a | 134.9 ab | 208.8 a | 228.2 a | 166.7 a |

**…2.1 -3.0 mm…**

| | Highly Disturbed | | Moderately Disturbed | | Reference | |
|---|---|---|---|---|---|---|
| Method | Lower | Upper | Lower | Upper | Lower | Upper |
| In situ screen | 309.7 a | 94.3 a | 198.9 a | 190.5 a | 399.5 b | 267.5 a |
| Core-estimated | 380.2 a | 120.8 a | 328.4 a | 364.1 a | 462.7 ab | 209.9 a |
| Core-actual | 395.5 a | 93.2 a | 353.2 a | 285.4 a | 520.9 a | 258.1a |

**…Total (0.1 -3.0 mm)…**

| | Highly Disturbed | | Moderately Disturbed | | Reference | |
|---|---|---|---|---|---|---|
| Method | Lower | Upper | Lower | Upper | Lower | Upper |
| In situ screen | 804.7 a | 158.9 a | 387.5 b | 210.9 b | 827.2 b | 651.4 b |
| Core-estimated | 967.1 a | 137.2 a | 896.5 a | 1087.9 a | 1489.7 a | 822.1 a |
| Core-actual | 803.2 a | 82.7 a | 843.6 a | 873.2 ab | 1300.8 ab | 746.5 ab |

[1] Column mean followed by different lowercase letters indicates significant difference among methods within each treatment. (Duncan's procedure, $\alpha$=0.10).

**Table 3. Monthly total fine root production (g m$^{-2}$) for lower and upper treatments at a highly disturbed, moderately disturbed, and reference areas.**

| | **Total (0.1 - 3.0 mm)** | | | | | |
|---|---|---|---|---|---|---|
| | Highly disturbed | | Moderately disturbed | | Reference | |
| | Lower | Upper | Lower | Upper | Lower | Upper |
| Feb-02 | . | . | . | . | . | . |
| Apr-02 | 18.96 | -7.03 | 127.58 | 118.29 | 153.22 | -174.45 |
| May-02 | -74.49 | -8.60 | 44.13 | -19.00 | 292.88 | 155.02 |
| Jul-02 | 288.14 | 8.14 | -59.96 | 44.03 | -374.17 | 37.51 |
| Sep-02 | -263.93 | -2.79 | 19.61 | -191.23 | -77.93 | -9.15 |
| Nov-02 | 102.84 | -8.17 | -13.01 | 112.82 | 94.77 | 2.97 |
| Jan-03 | 75.72 | 3.17 | -70.17 | 218.96 | 75.67 | -118.87 |
| Feb-03 | -211.79 | -2.85 | -60.23 | -117.16 | -110.41 | -75.81 |
| Apr-03 | 198.26 | -3.80 | 76.21 | -85.32 | 160.28 | -48.60 |
| May-03 | -253.51 | 11.31 | 103.66 | -55.48 | -131.77 | 283.47 |
| Jun-03 | 223.20 | 8.45 | -181.35 | -5.55 | -190.95 | -136.98 |
| Jul-03 | 36.68 | 147.19 | 99.77 | 284.02 | 406.06 | 11.36 |

**Table 4. Monthly mean carbon and nitrogen contents[1] for total live fine roots (0.1 – 3.0 mm in diameter) for each disturbance category and treatment.**

| | Carbon content (g m$^{-2}$) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Highly disturbed | | | | Moderately disturbed | | | | Reference | | | |
| Time | Lower | | Upper | | Lower | | Upper | | Lower | | Upper | |
| Feb/02 | 41.2 | a | 6.0 | b** | 44.1 | a | 44.4 | a | 56.1 | a | 60.6 | a |
| Apr/02 | 42.9 | a | 5.8 | b** | 61.0 | a | 62.1 | a | 83.8 | a | 33.2 | a |
| May/02 | 33.4 | a | 4.1 | a | 48.4 | a | 58.1 | a | 120.9 | a | 56.1 | b** |
| Jul/02 | 76.1 | a | 1.8 | a | 58.8 | a | 70.1 | a | 63.4 | a | 65.5 | a |
| Sep/02 | 40.7 | a | 6.3 | b* | 64.1 | a | 50.0 | a | 50.5 | a | 63.4 | a |
| Nov/02 | 54.7 | a | 3.1 | a | 66.5 | a | 48.6 | a | 76.4 | a | 65.0 | a |
| Jan/03 | 76.8 | a | 4.8 | b** | 56.5 | a | 83.4 | a | 85.8 | a | 46.7 | b** |
| Feb/03 | 40.3 | a | 3.4 | b | 36.6 | a | 75.5 | a | 69.4 | a | 38.6 | a |
| Apr/03 | 61.7 | a | 1.3 | b** | 50.1 | a | 65.0 | a | 95.2 | a | 27.2 | b** |
| May/03 | 27.5 | a | 4.8 | a | 65.9 | a | 61.4 | a | 58.2 | a | 68.5 | a |
| Jun/03 | 57.5 | a | 5.5 | b* | 41.7 | a | 41.6 | a | 41.6 | a | 49.7 | a |
| Jul/03 | 67.7 | a | 26.6 | a | 50.5 | a | 95.6 | a | 106.9 | a | 41.5 | a |

| | Nitrogen content (g m$^{-2}$) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Highly disturbed | | | | Moderately disturbed | | | | Reference | | | |
| Time | Lower | | Upper | | Lower | | Upper | | Lower | | Upper | |
| Feb/02 | 0.9 | a | 0.1 | a | 0.8 | a | 0.9 | a | 1.4 | a | 1.4 | a |
| Apr/02 | 1.1 | a | 0.1 | b* | 1.2 | a | 1.6 | a | 1.8 | a | 0.8 | a |
| May/02 | 0.7 | a | 0.1 | a | 1.7 | a | 1.1 | a | 2.2 | a | 1.3 | a |
| Jul/02 | 1.4 | a | 0.1 | a | 1.4 | a | 1.4 | a | 1.2 | a | 1.3 | a |
| Sep/02 | 0.1 | a | 0.1 | a | 1.2 | a | 1.0 | a | 1.1 | a | 0.9 | a |
| Nov/02 | 1.2 | a | 0.8 | a | 1.3 | a | 1.1 | a | 1.5 | a | 1.0 | a |
| Jan/03 | 0.8 | a | 0.1 | a | 0.6 | a | 1.0 | a | 1.2 | a | 0.8 | a |
| Feb/03 | 0.9 | a | 0.1 | a | 1.0 | a | 1.3 | a | 1.5 | a | 0.8 | a |
| Apr/03 | 1.1 | a | 0.0 | a | 1.2 | a | 1.5 | a | 1.7 | a | 0.6 | a |
| May/03 | 0.6 | a | 0.1 | a | 1.5 | a | 1.2 | a | 1.5 | a | 1.5 | a |
| Jun/03 | 1.1 | a | 0.1 | a | 0.9 | a | 0.9 | a | 0.9 | a | 1.1 | a |
| Jul/03 | 1.1 | a | 0.1 | a | 1.1 | a | 1.2 | a | 1.7 | a | 0.7 | a |

[1] Row mean followed by different lowercase letters indicates significant difference between treatments within each disturbance category (T-test, *$\alpha$=0.10, **$\alpha$=0.05).

**Table 5. Monthly comparisons of live fine root carbon and nitrogen contents[1] (expressed as g $m^{-2}$) among the three disturbance categories at upper plots.**

| | Carbon content (g $m^{-2}$) | | | | | | Nitrogen content (g $m^{-2}$) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Time | Highly disturbed | | Moderately disturbed | | Reference | | Highly disturbed | | Moderately disturbed | | Reference | |
| Feb/02 | 6.0 | b | 44.4 | a | 60.6 | ab | 0.1 | b | 0.9 | ab | 1.4 | a |
| Apr/02 | 5.8 | b | 62.1 | a | 33.2 | a | 0.1 | b | 1.6 | a | 0.8 | ab |
| May/02 | 4.1 | a | 58.1 | a | 56.1 | a | 0.1 | a | 1.1 | a | 1.3 | a |
| Jul/02 | 1.8 | b | 70.1 | a | 65.5 | a | 0.1 | a | 1.4 | a | 1.3 | a |
| Sep/02 | 6.3 | a | 50.0 | a | 63.4 | a | 0.1 | a | 1.0 | a | 0.9 | a |
| Nov/02 | 3.1 | b | 48.6 | a | 65.0 | a | 0.8 | a | 1.1 | a | 1.0 | a |
| Jan/03 | 4.8 | b | 83.4 | a | 46.7 | a | 0.1 | a | 1.0 | a | 0.8 | a |
| Feb/03 | 3.4 | a | 75.5 | a | 38.6 | a | 0.1 | a | 1.3 | a | 0.8 | a |
| Apr/03 | 1.3 | a | 65.0 | a | 27.2 | a | 0.0 | a | 1.5 | a | 0.6 | a |
| May/03 | 4.8 | a | 61.4 | a | 68.5 | a | 0.1 | a | 1.2 | a | 1.5 | a |
| Jun/03 | 5.5 | b | 41.6 | ab | 49.7 | a | 0.1 | a | 0.9 | a | 1.1 | a |
| Jul/03 | 26.6 | b | 95.6 | a | 41.5 | ab | 0.1 | b | 1.2 | a | 0.7 | ab |

[1] Row mean followed by different lowercase letters indicates significant difference among disturbance category (Duncan's procedure, $\alpha$=0.10).

**Table 6. Monthly mean carbon and nitrogen contents[1] for total dead fine roots (0.1 – 3.0 mm in diameter) for each disturbance category and treatment.**

| | Carbon content (g m$^{-2}$) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Highly disturbed | | | | Moderately disturbed | | | | Reference | | | |
| Time | Lower | | Upper | | Lower | | Upper | | Lower | | Upper | |
| Feb/02 | 3.4 | a | 0.4 | a | 2.0 | a | 3.0 | a | 2.1 | a | 2.0 | a |
| Apr/02 | 1.2 | | . | | 2.2 | a | 1.8 | a | 4.1 | a | 2.1 | a |
| May/02 | 2.0 | | . | | 2.9 | a | 2.6 | a | 4.3 | a | 13.7 | a |
| Jul/02 | 3.1 | a | 2.6 | a | 2.9 | a | 4.1 | a | 3.8 | a | 4.2 | a |
| Sep/02 | 6.9 | a | 0.1 | a | 3.0 | a | 3.1 | a | 19.1 | a | 2.8 | a |
| Nov/02 | 8.6 | | . | | 2.1 | a | 6.0 | a | 8.2 | a | 2.6 | a |
| Jan/03 | 4.5 | a | 1.0 | a | 4.4 | a | 0.8 | b** | 6.0 | a | 5.0 | a |
| Feb/03 | 6.1 | | . | | 3.1 | a | 3.2 | a | 7.3 | a | . | |
| Apr/03 | 4.6 | a | 0.3 | a | 7.7 | a | 9.4 | a | 13.6 | a | 10.0 | a |
| May/03 | 5.0 | a | 0.3 | a | 2.6 | a | 7.0 | a | 7.3 | | 3.0 | a |
| Jun/03 | 5.0 | a | 0.6 | a | 5.0 | a | 7.0 | a | 2.9 | a | 3.5 | a |
| Jul/03 | . | | . | | 4.9 | a | 5.8 | a | 4.6 | a | 1.1 | b** |

| | Nitrogen content (g m$^{-2}$) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Highly disturbed | | | | Moderately disturbed | | | | Reference | | | |
| Time | Lower | | Upper | | Lower | | Upper | | Lower | | Upper | |
| Feb/02 | 0.06 | a | 0.01 | a | 0.01 | a | 0.07 | a | 0.06 | a | 0.06 | a |
| Apr/02 | 0.03 | | . | | 0.06 | a | 0.05 | a | 0.12 | a | 0.06 | a |
| May/02 | 0.05 | | . | | 0.09 | a | 0.07 | a | 0.11 | a | 0.39 | a |
| Jul/02 | 0.12 | a | 0.05 | a | 0.11 | a | 0.08 | a | 0.10 | a | 0.11 | a |
| Sep/02 | 0.19 | | . | | 0.06 | a | 0.06 | a | 0.40 | a | 0.06 | a |
| Nov/02 | 0.21 | | . | | 0.06 | a | 0.13 | a | 0.14 | a | 0.05 | a |
| Jan/03 | 0.05 | a | 0.01 | a | 0.08 | a | 0.02 | b* | 0.09 | a | 0.12 | a |
| Feb/03 | 0.12 | | . | | 0.07 | a | 0.11 | a | 0.18 | | . | |
| Apr/03 | 0.10 | a | 0.01 | a | 0.17 | a | 0.29 | a | 0.31 | a | 0.20 | a |
| May/03 | 0.10 | a | 0.01 | a | 0.12 | a | 0.16 | a | 0.22 | a | 0.07 | a |
| Jun/03 | 0.10 | a | 0.01 | a | 0.13 | a | 0.18 | a | 0.10 | a | 0.10 | a |
| Jul/03 | . | | . | | 0.14 | a | 0.35 | a | 0.12 | a | 0.03 | b** |

[1] Row mean followed by different lowercase letters indicates significant difference between treatments within each disturbance category (T-test, *$\alpha$=0.10, **$\alpha$=0.05).

**Table 7. Monthly comparisons of dead fine root carbon and nitrogen contents[1] (expressed as g $m^{-2}$) among the three disturbance categories at upper plots.**

| | Carbon content (g $m^{-2}$) | | | | | | Nitrogen content (g $m^{-2}$) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Time | Highly disturbed | | Moderately disturbed | | Reference | | Highly disturbed | | Moderately disturbed | | Reference | |
| Feb/02 | 0.4 | a | 3.0 | a | 2.0 | a | 0.01 | b | 0.07 | ab | 0.06 | a |
| Apr/02 | . | | 1.8 | a | 2.1 | a | . | | 0.05 | a | 0.06 | ab |
| May/02 | . | | 2.6 | a | 13.7 | a | . | | 0.07 | a | 0.39 | a |
| Jul/02 | 2.6 | a | 4.1 | a | 4.2 | a | 0.05 | a | 0.08 | a | 0.11 | a |
| Sep/02 | 0.1 | a | 3.1 | a | 2.8 | a | . | | 0.06 | a | 0.06 | a |
| Nov/02 | . | | 6.0 | a | 2.6 | a | . | | 0.13 | a | 0.05 | a |
| Jan/03 | 1.0 | a | 0.8 | ab | 5.0 | a | 0.01 | b | 0.02 | b | 0.12 | a |
| Feb/03 | . | | 3.2 | | . | | . | | 0.11 | | . | |
| Apr/03 | 0.3 | a | 9.4 | a | 10.0 | a | 0.01 | a | 0.29 | a | 0.20 | a |
| May/03 | 0.3 | a | 7.0 | a | 3.0 | a | 0.01 | a | 0.16 | a | 0.07 | a |
| Jun/03 | 0.6 | a | 7.0 | a | 3.5 | a | 0.01 | a | 0.18 | a | 0.10 | a |
| Jul/03 | . | | 5.8 | a | 1.1 | b | . | | 0.35 | a | 0.03 | a |

[1] Row mean followed by different lowercase letters indicates significant difference among disturbance category (Duncan's procedure, $\alpha$=0.10).

# IV. SUMMARY

We had hypothesized that sediment deposition would cause changes in vegetation composition and structure, where more opportunistic and stress tolerant species would dominate. This hypothesis was accepted. Undisturbed areas (i.e. not affected by sediment deposition) displayed a nearly closed canopy, with reduced incidence of seedlings and saplings, whereas areas receiving high rates of sediment deposition had lower tree density, high incidence of seedlings and saplings of pioneer species (shade intolerants) and, nitrogen fixing species. The latter, in general, have traits associated with invasive species, such as rapid growth, short juvenile period, prolific seed production and tolerance to a wide range of soil conditions (Miller and Miller 1999, Samuelson and Hogan 2003).

Secondly, we hypothesized that as rates of sediment deposition increased, fine root biomass and production would decline. Because fine root nutrient contents mirror changes in fine root biomass, they also would be lowest in highly disturbed areas. This hypothesis was also accepted. Fine root biomass was least and fairly constant over the sample period in upper plots of highly disturbed areas, probably as a result of constant anaerobic conditions in the rooting zone resulting from constant sediment deposition. Fine root production and nutrient contents were least in upper plots of highly disturbed areas as well. No differences were observed between moderately disturbed and reference areas. These findings support previous studies that have reported decreased levels of fine root biomass following natural and anthropogenic disturbances.

Finally, we had hypothesized that aboveground net primary productivity (aboveground NPP = litterfall + woody increment) would be less in disturbed sites due changes in vegetation structure and reduced fine root productivity. This hypothesis was also supported. Aboveground NPP was significantly less in upper plots of highly disturbed areas (reference 1233.7 g $m^{-2}$ $yr^{-1}$> moderately disturbed 934.0 g $m^{-2}$ $yr^{-1}$ > highly disturbed 464.8 g $m^{-2}$ $yr^{-1}$). Litterfall and woody components were also significantly less in highly disturbed areas, probably due decreased tree density as a result of reduced fine root production. Foliar nutrient contents were also least in upper plots of highly disturbed areas, primarily as a result of the smallest litterfall rates. These results support the conclusions of Ewing (1996) and van der Valk et al. (1982) that plant growth and productivity can be depressed as a result of increased sediment burial. The rationale for this is that sediment placed on the soil surface may have effects similar to flooding, thereby limiting gas exchange by roots, which in turn limits nutrient and water uptake.

In summary, the results of this study suggest that sedimentation rates near 0.2 cm $yr^{-1}$ negatively affect above- and belowground productivity in riparian forests, possibly by changes in forest composition and structure. The aboveground parameters (litterfall biomass, woody increments, ANPP, and LAI) appeared to attain a reduced equilibrium when sediment accumulation reached levels between 0.3 and 0.5 cm $yr^{-1}$, whereas fine root production seemed to decrease linearly with increased rates of sediment deposition.

Therefore, the functions performed by these riparian forests, such as improvement of water quality, may be negatively affected as well. These findings are applicable to other wetland forests subjected to sediment deposition from other sources, such as urbanization and conversion of forested uplands to agriculture. Consequently, it is critical to the sustainability of water filtration functions that the impacts of sedimentation are understood and riparian vegetation be maintained in spite of anthropogenic stresses.

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