

## Effects of Sediment Deposition on Fine Root Dynamics in Riparian Forests

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### 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. However, few data exist quantifying the impacts of sediment deposition from anthropogenic disturbance on belowground processes within these ecosystems. This study was conducted at Ft. Benning, GA, where disturbance caused by military training has generated a range of sedimentation levels in riparian forests near ephemeral streams. Nine ephemeral streams, exhibiting different levels of sediment deposition, were selected for study. Two paired treatment plots (upper and lower) were established along each catchment to represent potentially disturbed and control conditions, respectively. On highly and moderately disturbed catchments, upper plots had received varying rates of sediment from erosion along unpaved roads. Biomass, turnover, productivity, and nutrient contents of fine roots were compared within and across catchments. Temporal fluctuations in biomass of live and dead fine roots were observed for both treatments in the three disturbance categories, except for upper plots of highly disturbed catchments, where biomass remained fairly low and constant throughout the study. Fine root productivity declined sharply with sediment rates as low as  $0.3 \text{ cm yr}^{-1}$ . Nutrient contents of live and dead fine roots followed a similar trend to that of root biomass. These data suggest that fine root dynamics may be affected by sediment deposition rates commonly occurring in some wetland forests, and the water filtration function performed by these ecosystems may be at risk.

RIPIARIAN FORESTS are among the most diverse, dynamic, and complex biophysical natural systems (Naiman and Décamps, 1997), serving as an interface between aquatic and terrestrial environments (Gregory et al., 1991). The boundary between riparian areas and adjoining uplands may be gradual and not always well defined. However, riparian areas differ from uplands because of levels of soil moisture, frequent flooding, and the unique assemblage of plant and animal communities found there (Gregory et al., 1991; Naiman et al., 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 urban areas through denitrification, sedimentation, or direct root uptake. By filtering sediment in surface runoff, C, N, and P 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). For example, Cooper et al. (1987) estimated that 80 to 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 N and 30% of P from adjacent agricultural areas were retained by riparian forests (Lowrance et al., 1986). Although the sediment-trapping ability of riparian forests is well known (Vought et al., 1995; Phillips, 1989), how susceptible these systems are to degradation by sediment deposition from anthropogenic disturbances remains a key question.

Throughout the USA, the character and vitality of riparian ecosystems have continuously been degraded. Many human activities, including agricultural production, timber harvesting, urban development, and road construction have caused unintended and undesirable increases in nonpoint-source pollution, alterations of hydrological regimes, and degradation of wildlife habitats and populations (Schultz et al., 1995). While some sediment deposition is a natural process in most floodplain forests (Hupp and Morris, 1990), increased sediment accumulation has been observed in forested wetlands as a result of agriculture or urbanization within the surrounding watershed (Hupp and Bazemore, 1993; Kleiss, 1996; Hupp, 2000). The effects of high sediment loads and the sustainable loading of sediments on riverine forests are not well established.

Significant changes in ecosystem structure or function in response to human alterations are not typically noted until the system declines sufficiently so that visual symptoms are evident (Vogt et al., 1993). As a potential measure of physiological condition, 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).

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  $<1$  to  $<5$  mm in diameter. 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 belowground than aboveground. Studies have shown that up to 75% of total forest production may

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**Abbreviations:** HD, highly disturbed; MD, moderately disturbed; NPP, net primary productivity; RF, reference.

be allocated belowground in some ecosystems (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 (Joslin and Henderson, 1987; Fogel, 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, decaying 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. Thus, if there are changes in levels of fine root production and turnover as a result of sediment accumulation from anthropogenic disturbance, this may alter the levels of nutrients in forest soils, and may influence overall forest productivity.

Despite the important role of fine roots in riparian forests (Cooper et al., 1987; Daniels and Gilliam, 1996; Craft and Casey, 2000), we are aware of no data quantifying the effects of excessive sediment accumulation on fine root dynamics in these ecosystems. Within wetland forests, previous fine root studies usually reflect the influence of different flooding regimes on root production, turnover, and nutrient cycling (Powell and Day, 1991; Megonigal and Day, 1992; Baker et al., 2001; Clawson et al., 2001). Discussion of sedimentation in these systems has typically 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 effects similar to flooding, imposing a lack of oxygen on root systems, and anaerobic conditions that may retard root growth and production. If true, roots that are subjected to high levels of sediment deposition might experience a reduction in root biomass and productivity that may seriously degrade forest productivity. To test this, the objective of this study was to examine the relationship of fine root dynamics and sediment deposition in riparian forests near ephemeral streams in the Upper Coastal Plains of the southeast USA, and identify levels beyond which further sediment accumulation becomes a stress, altering patterns of fine root dynamics.

## MATERIALS AND METHODS

### Study Site

This study was conducted at Ft. Benning, GA, a U.S. Army installation, located in southeastern USA, occupying an area of 73 503 ha in Chattahoochee, Muscogee, and Marion Coun-

ties of Georgia and Russell County of Alabama. Two physiographic regions are represented at Ft. Benning: the Piedmont and the Upper Coastal Plain. Disturbance caused by military training activity has generated a range of sediment deposition levels in riparian forests. For the purposes of this study, only riparian forests within the Coastal Plain province 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 forests with *Nyssa sylvatica* Marshall (black gum), *Acer rubrum* L. (red maple), *Liquidambar styraciflua* L. (sweetgum), *Quercus nigra* L. (water oak), *Liriodendron tulipifera* L. (yellow poplar), *Magnolia virginiana* L. (sweetbay), *Cornus florida* L. (flowering dogwood) and *Ilex opaca* Aiton (American holly) being dominant species.

Soil series found within the study area included poorly drained Bibb and Chastain series (Typic Fluvaquents) and well to excessively drained Troup, Lakeland, and Cowart series (Grossarenic Kandiodults, Typic Quartzipsamments, and Typic Kanhapludults, respectively) (Soil Survey Staff, 2004).

### Study Design

Nine ephemeral streams were selected to encompass a range of sediment conditions. Based on visual evidence of sediment deposition (e.g., alluvial fans, buried stems), catchments were classified as: (i) highly disturbed (HD); (ii) moderately disturbed (MD), and (iii) reference (RF). No evidence of sedimentation was observed on reference catchments. Paired, circular treatment plots (0.04 ha) were established along each catchment. One plot (upper plot) was delineated in a topographic position higher in the catchment (i.e., near stream's origin), where sediment was most likely to be received. Another plot (lower plot) was located farther down catchment, beyond evidence of sediment deposition and it served as a relative control for comparisons with the upper plot (Fig. 1).

On upper plots of disturbed catchments, widely spreading alluvial fans with exposed, loose, light colored soil indicated high sedimentation, which was verified by the presence of buried bases of standing trees. Shallower trunk burial and smaller alluvial fans indicated moderate levels of sediment deposition. Upper plots of HD and MD catchments were located within the alluvial fan, and tended to have overstory canopies ranging from somewhat open to closed, with less dense understory vegetation in relation to lower counterparts. Basal area was as follows: 0.45, 0.85, and 1.23 m<sup>2</sup> within upper plots, and 1.23, 1.46, and 2.30 m<sup>2</sup> within lower plots of HD, MD, and RF, respectively. In general, lower plots tended to have higher soil moisture content probably because of 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, sapling trees (8–10 cm in diameter) 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 sapling tree, rings were counted, and sapling tree age was determined. The average sapling tree age was 25 yr. 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. Since there was no visual evidence of sediment deposition on lower plots in any catchment or on upper plots in RF catchments, it was assumed to be not significant. The mean rates of sediment

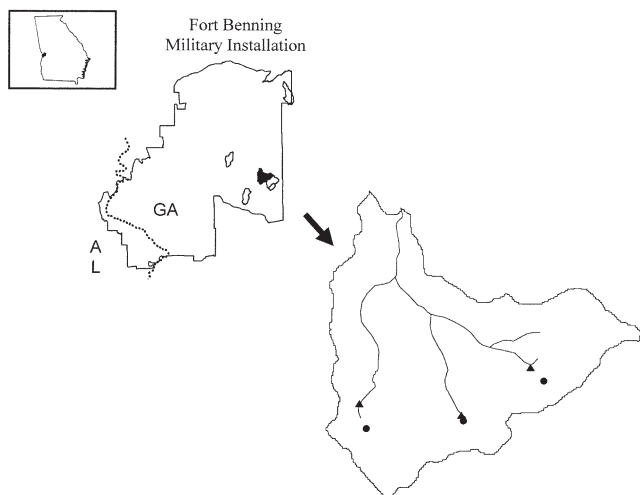


Fig. 1. Location of catchments at Ft. Benning, GA, where ephemeral streams were situated. An expanded view of one catchment shows placement of upper (circle) and lower (triangle) plot pairs within stream drainage.

deposition on upper plots were: 2.20 cm yr<sup>-1</sup> for HD catchments, 0.66 cm yr<sup>-1</sup> in MD catchments, and 0.0 cm yr<sup>-1</sup> within RF catchments.

### Fine Root Standing Crop Biomass and Net Primary Productivity

Starting in February 2002, sequential soil cores (Caldwell and Virginia, 1987; Fahey et al., 1999) were collected in each plot to evaluate fine root biomass and annual productivity for each sample period. Root screens (Melhuish and Lang, 1968; Schilling et al., 1999) were also used to confirm phenological activities. The term *fine root* in this study defines roots having a diameter <3.0 mm. Soil cores were collected approximately every 6 wk during a 74-wk period. A total of 12 soil core samples (one sample per plot, every 6 wk approximately) was collected in each treatment plot within the nine catchments.

Cores were removed from the soil by inserting and extracting a PVC tube (8 cm in diameter) to a depth of 11 cm. 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). Once collected, cores were transported to the laboratory in coolers and stored at 4°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°C until analyzed. Roots were classified into three diameter classes (0.1–1.0, 1.1–2.0, and 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; Bledsoe et al., 1999).

Fine roots were oven-dried to constant mass (70°C, 48 h). Weights were recorded and then converted g m<sup>-2</sup> to an 11-cm depth. Fine root production was calculated as differences in mean fine root biomass between sampling dates. Positive biomass increments were summed across growing seasons (Fogel, 1983). The sequential coring approach does not account for growth and mortality between sampling periods and, consequently, entails some inaccuracy (Fahey et al., 1999). As a result, fine root production estimates are probably conservative to an unknown degree.

Table 1. Standing crop biomass (g m<sup>-2</sup>) of live and dead fine roots by diameter classes within highly disturbed areas.

Time	0.1–1.0 mm		1.1–2.0 mm		2.1–3.0 mm	
	Lower	Upper	Lower	Upper	Lower	Upper
<b>Live fine roots</b>						
Feb/02	92.46a†	17.55a	57.59a	2.57b	86.17a	2.68a
Apr/02	133.80a	10.81a	53.57a	2.53a	68.44a	0.00a
May/02	136.68a	9.79a	54.55a	0.00a	51.10a	0.00a
Jul/02	171.90a	4.17a	93.54a	4.59a	145.50a	0.00a
Sep/02	87.32a	10.09a	55.84a	0.00a	63.64a	0.00a
Nov/02	155.74a	6.97a	42.86a	0.00a	113.85a	0.00a
Jan/03	129.85a	10.14a	92.25a	0.00a	148.66a	0.00a
Feb/03	110.95a	4.86a	90.35a	0.00b	21.33a	0.00a
Apr/03	132.29a	3.49b	88.44a	0.00b	140.55a	0.00a
May/03	68.47a	11.25a	36.72a	1.19a	48.58a	0.00a
Jun/03	186.06a	7.88a	105.59a	3.81a	109.61a	0.00a
Jul/03	176.06a	38.41a	74.62a	0.00b	187.26a	44.01a
<b>Dead fine roots</b>						
Feb/02	2.29a	0.63a	4.41a	0.00a	8.30a	0.00a
Apr/02	1.12a	0.00a	2.56a	0.00a	0.00	0.00
May/02	1.47a	0.00a	0.00	0.00	0.00	0.00
Jul/02	9.72a	1.86a	0.00	0.00	0.00	0.00
Sep/02	5.61a	0.12a	13.63a	0.00a	6.49a	0.00a
Nov/02	25.44a	0.00a	4.03a	0.00a	8.06a	0.00a
Jan/03	2.89a	0.75a	4.89a	0.00a	4.65a	0.00a
Feb/03	10.17a	0.00a	2.42a	0.00a	0.00	0.00
Apr/03	11.38a	0.27a	4.74a	0.00a	0.00	0.00
May/03	6.84a	0.54a	0.00	0.00	0.00	0.00
Jun/03	2.67a	0.45a	0.00	0.00	8.14a	0.00a
Jul/03	0.00	0.00	0.00	0.00	0.00	0.00

† Row mean followed by different lowercase letters indicates significant difference between treatments at the 0.05 level.

### Fine Root Nutrient Analysis

Samples were ground either by hand (small samples) or in a Wiley mill to pass a 20-mesh screen after oven-drying to constant weight (70°C, 48 h). Total C and N analyses were conducted using a PerkinElmer Series II CHNS/O Analyzer 2400 (PerkinElmer Corp., Norwalk, CT). Total nutrient content was calculated as the product of root dry weight and nutrient concentration in the roots.

### Statistical Analysis

All analyses were performed using the Statistical Analysis System (SAS Institute, Inc., 1999–2001). One-way analysis of variance (ANOVA) was used with the General Linear Model Procedures (GLM) to evaluate differences in mean fine root response variables (standing crop biomass, production, and nutrient contents) between treatments (i.e., upper vs. lower plots) within each disturbance category and diameter class. Tukey's mean comparison test was performed to evaluate differences in fine root production among the three disturbance categories at upper plots. In addition, linear regression analyses were conducted to determine whether or not there was a relationship between sediment deposition and fine root production. All differences between treatments and across disturbance categories were considered significant at the 0.05 level.

## RESULTS

### Standing Crop Biomass

#### Highly Disturbed Catchments

Standing crop biomass of live and dead fine roots for various size classes (0.1–1.0, 1.1–2.0, and 2.1–3.0 mm) and total biomass (0.1–3.0 mm) for both lower and upper treatments in HD catchments are given in Table 1 and

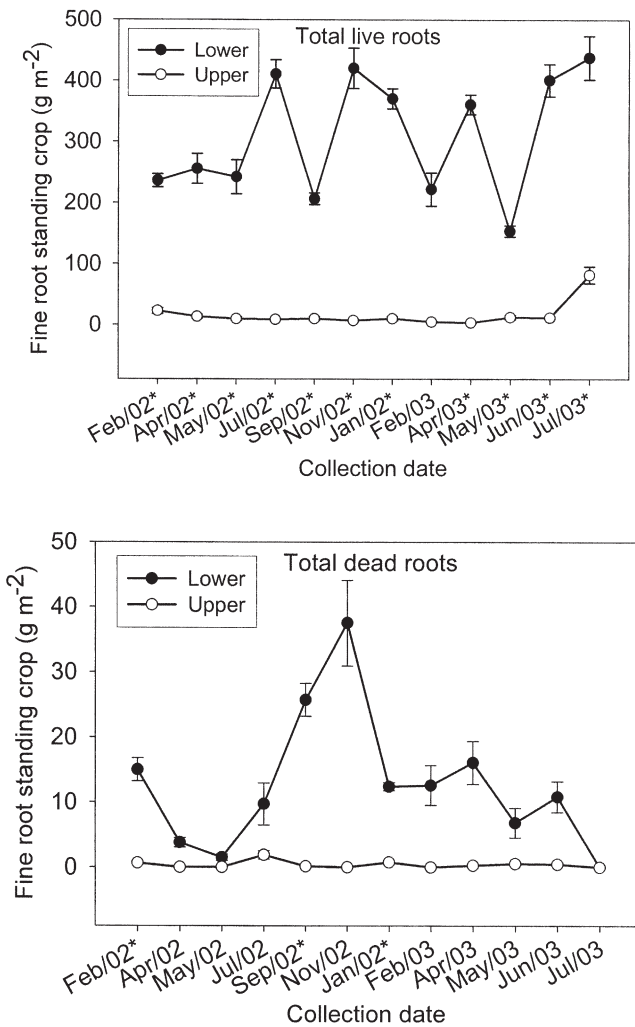


Fig. 2. Total live and dead fine root standing crop biomass (0.1–3.0 mm) to a depth of 11 cm on highly disturbed (HD) areas. Error bars represent one standard error; \* represents significant at the 0.05 level.

Fig. 2. Generally, standing crop biomass of live roots was numerically greater at lower plots for all root diameter classes during the sample period, with significant differences ( $P < 0.05$ ) observed. Total root biomass varied from 153.8 to 437.9  $\text{g m}^{-2}$  and 3.5 to 82.4  $\text{g m}^{-2}$  for lower and upper plots, respectively. Temporal 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 and 2003 (July), and also in the winter of 2003 (January/February) for all diameter classes, while a single peak was observed in upper plots in July 2003.

During the study period, total fine root necromass in HD catchments varied from 1.5 to 37.5  $\text{g m}^{-2}$  on lower plots and 0.1 to 1.9  $\text{g m}^{-2}$  on the upper counterparts. As was the case with live fine roots, standing crop biomass of dead fine roots remained somewhat stable over the sample period in upper plots, whereas temporal variation was observed on lower plots for all diameter classes, with autumn 2002 (September and November)

Table 2. Standing crop biomass ( $\text{g m}^{-2}$ ) of live and dead fine roots by diameter classes within moderately disturbed areas.

Time	0.1–1.0 mm		1.1–2.0 mm		2.1–3.0 mm	
	Lower	Upper	Lower	Upper	Lower	Upper
<b>Live fine roots</b>						
Feb/02	112.06a†	171.26a	49.36a	61.5a	95.88a	59.25a
Apr/02	222.49a	214.57a	76.12a	65.26a	160.19a	130.47a
May/02	218.54a	224.75a	59.68a	63.65a	125.43a	102.89a
Jul/02	267.57a	276.08a	73.74a	103.95a	65.09a	36.87a
Sep/02	234.93a	178.78a	82.89a	29.08a	106.76a	7.24b
Nov/02	200.26a	139.50a	80.00a	45.16a	132.73a	57.42a
Jan/03	141.12a	212.63a	55.99a	90.20a	145.73a	91.01a
Feb/03	138.60a	220.57a	50.47a	95.79a	62.35a	94.91a
Apr/03	211.59a	244.37a	25.75a	56.97a	121.46a	29.06a
May/03	249.62a	192.24a	78.42a	42.69a	134.43a	20.55a
Jun/03	171.49a	142.58a	43.59a	38.29a	66.03a	74.90a
Jul/03	233.53a	246.09a	61.00a	93.66a	86.35a	256.65a
<b>Dead fine roots</b>						
Feb/02	3.71a	5.07a	6.33a	4.63a	0.76a	6.39a
Apr/02	3.82a	2.43a	6.40a	6.79a	1.67a	1.20a
May/02	8.01a	7.31a	3.25a	2.21a	0.00	0.00
Jul/02	6.81a	10.88a	2.29a	5.37a	0.00a	4.71a
Sep/02	6.13a	6.74a	5.64a	4.89a	0.00a	3.10a
Nov/02	5.82a	14.34a	2.35a	1.64a	0.00a	9.77a
Jan/03	6.74a	1.73a	4.93a	0.00a	0.00	0.00
Feb/03	4.71a	6.46a	3.90a	0.00a	0.00a	4.81a
Apr/03	7.09a	17.43a	3.82a	5.69a	0.00a	20.71a
May/03	7.55a	20.46a	3.81a	2.24a	0.00a	9.36a
Jun/03	5.51a	6.99a	2.59a	8.43a	0.00a	9.54a
Jul/03	8.78a	6.24a	0.00a	9.35a	8.04a	7.47a

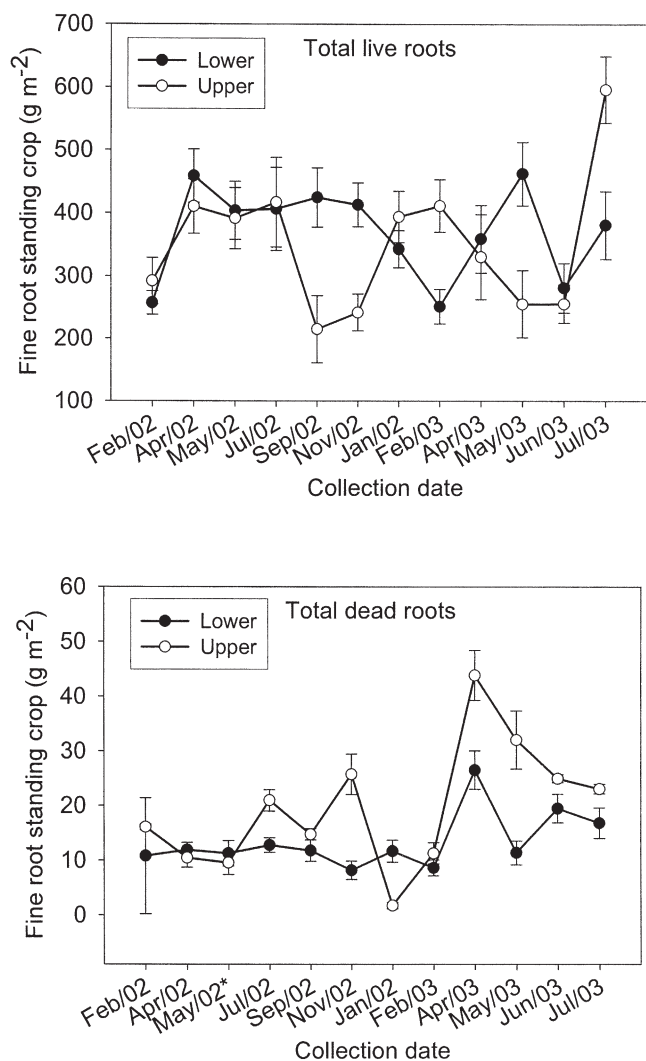
† Row mean followed by different lowercase letters indicates significant difference between treatments at the 0.05 level.

and spring 2003 (April) peaks. For upper plots, dead fine roots occurred only in the smallest diameter class. Comparisons between upper and lower plots were significant ( $P < 0.05$ ) for a few collection dates.

### Moderately Disturbed Catchments

Live and dead fine roots standing crop biomass within MD catchments are presented in Table 2 and Fig. 3. With the single exception of September 2002, for the large diameter class, no significant difference was observed between upper and lower plots in MD catchments. On lower plots, total fine root biomass varied from 251.4 to 462.5  $\text{g m}^{-2}$ , while upper plots ranged from 215.1 to 596.4  $\text{g m}^{-2}$ . Both lower and upper plots showed temporal fluctuations in root biomass. Maximum live fine root biomass within lower plots occurred in spring 2002 (April) 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 catchments: summer of 2002 and 2003 (July), and winter of 2003 (January/February).

For most of the sample collections, dead biomass was somewhat higher numerically in upper plots, with the exception of the intermediate diameter class. Few significant differences were observed in the smallest and intermediate diameter classes. Total necromass ranged from 8.6 to 26.5  $\text{g m}^{-2}$  and 1.7 to 43.8  $\text{g m}^{-2}$  on lower and upper plots, respectively. Dead fine roots also showed a temporal trend for standing crop biomass. Lower plots exhibited peaks of dead biomass in late spring/summer of 2002 (May and July), winter 2003 (January), and spring 2003 (May). Within lower plots in the largest diameter class, detritus was observed only in February and April 2002,



**Fig. 3.** Total live and dead fine root standing crop biomass (0.1–3.0 mm) to a depth of 11 cm on moderately disturbed (MD) areas. Error bars represent one standard error; \* represents significant at the 0.05 level.

and July 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 Catchments

Standing crop biomass and necromass of fine roots within RF catchments for various diameter classes are presented in Table 3 and Fig. 4. In general, root biomass was numerically greater in lower plots, however only a few significant differences were observed (Table 3). Total standing crop biomass of fine roots ranged from 265.5 to 820.0 g m<sup>-2</sup> on lower plots and 138.1 to 393.9 g m<sup>-2</sup> in upper plots. 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 counterparts but, there was a general decline in root biomass of all

**Table 3.** Standing crop biomass (g m<sup>-2</sup>) of live and dead fine roots by diameter classes within reference areas.

Time	0.1–1.0 mm		1.1–2.0 mm		2.1–3.0 mm	
	Lower	Upper	Lower	Upper	Lower	Upper
<b>Live fine roots</b>						
Feb/02	159.72a†	168.17a	72.39a	100.43a	61.92a	116.43a
Apr/02	294.30a	154.39a	94.76a	29.64a	138.04a	26.55a
May/02	391.00a	249.89a	131.05a	68.64a	297.93a	47.06b
Jul/02	183.00a	182.27a	86.72a	133.65a	176.10a	43.59a
Sep/02	161.68a	162.88a	131.80a	44.46b	74.41a	186.59a
Nov/02	250.25a	182.31a	100.21a	55.58	112.19a	79.52a
Jan/03	206.05a	153.29a	145.34a	63.95a	186.93a	60.82b
Feb/03	185.26a	111.10a	103.29a	25.57a	139.36a	20.00a
Apr/03	273.71a	103.24a	74.06a	19.31b	240.42a	15.56b
May/03	188.34a	199.92a	79.09a	82.00a	189.00a	77.60a
Jun/03	124.36a	177.59a	42.86a	43.14a	98.25a	79.41a
Jul/03	311.03a	129.01b	122.16a	82.85a	238.35a	57.50a
<b>Dead fine roots</b>						
Feb/02	3.38a	1.62a	7.43a	3.38a	1.38a	0.00a
Apr/02	7.56a	4.06a	4.24a	2.85a	6.71a	0.00a
May/02	9.80a	15.07a	4.55a	0.00a	5.24a	0.00a
Jul/02	7.18a	16.27a	9.29a	2.40a	3.56a	0.00a
Sep/02	51.31a	8.29a	40.12a	0.00b	28.37a	0.00a
Nov/02	18.47a	5.04b	21.57a	0.00a	8.44a	0.00b
Jan/03	14.27a	7.45a	0.00a	2.57a	5.40a	0.00a
Feb/03	1.27a	0.00a	17.31a	0.00a	3.72a	0.00a
Apr/03	3.33a	15.52a	12.26a	0.00a	39.71a	5.00a
May/03	12.13a	6.01a	14.20a	0.00b	14.09a	0.00a
Jun/03	9.39a	4.08a	1.97a	0.00a	1.32a	2.91a
Jul/03	7.52a	5.23a	5.61a	1.07a	5.99a	3.35a

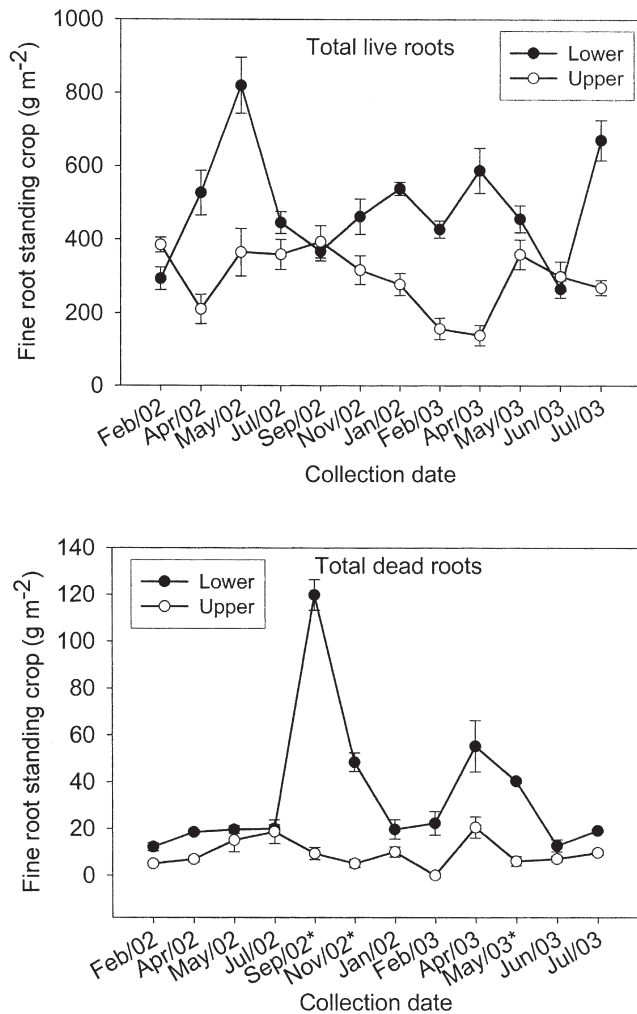
† Row mean followed by different lowercase letters indicates significant difference between treatments at the 0.05 level.

classes observed in April 2002 and 2003, followed by peaks of biomass in May of the same years.

Standing crop root necromass was numerically higher within the lower plots for all diameter classes, with only few significant differences between treatments. Total necromass varied from 12.2 to 119.8 and 5.0 to 20.5 g m<sup>-2</sup> on lower and upper plots, respectively. Temporal 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 generally occurred in autumn 2002 (September) and spring 2003 (April).

### Fine Root Net Primary Production

Annual belowground primary productivity within each disturbance category and treatment are presented in Fig. 5. Net primary productivity of fine roots was significantly greater in lower plots (803.4 g m<sup>-2</sup>) of HD catchments compared with upper counterparts (82.7 g m<sup>-2</sup>). At MD catchments, NPP was relatively similar in both treatments (843.7 and 873.2 g m<sup>-2</sup>, lower and upper plots, respectively). On RF catchments, belowground net primary productivity was significantly greater at lower plots (1261.5 g m<sup>-2</sup>) compared with upper plots (746.5 g m<sup>-2</sup>). Comparisons across disturbance categories at upper plots suggested that in catchments receiving higher sedimentation rates, fine root productivity were significantly reduced. The regression relationship between fine root productivity and long-term sediment deposition rates was significant at the  $P < 0.005$  level, with an  $R^2$  of 0.82 (Fig. 6). Apparently, a rapid decrease



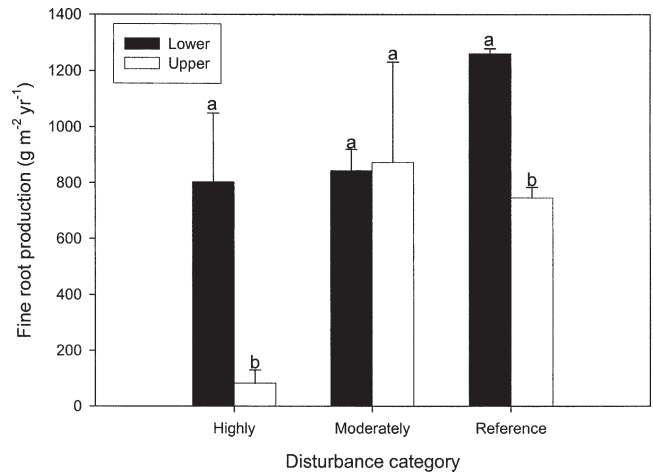
**Fig. 4.** Total live and dead fine root standing crop biomass (0.1–3.0 mm) to a depth of 11 cm on reference (RF) areas. Error bars represent one standard error; \* represents significant at the 0.05 level.

in fine root productivity occurred with rates of sedimentation as low as 0.3 cm yr<sup>-1</sup>.

### Fine Root Nutrient Contents—Carbon and Nitrogen

Carbon and N contents of live roots in HD catchments showed a clear trend during the sample period, where lower plots consistently had numerically greater C and N contents than the upper plot. Significant differences were observed at the  $P < 0.05$  level. There were no clear trends between treatments in MD and RF plots. When comparisons were made among disturbance categories at upper plots (Table 4), C contents for HD catchments were significantly less than for the other two disturbance categories, with the single exception of February 2003. Fewer significant differences were observed among disturbance categories for N. Pool sizes for both nutrients mirrored changes in live fine root biomass during the study period.

Nutrient contents for dead roots followed a trend



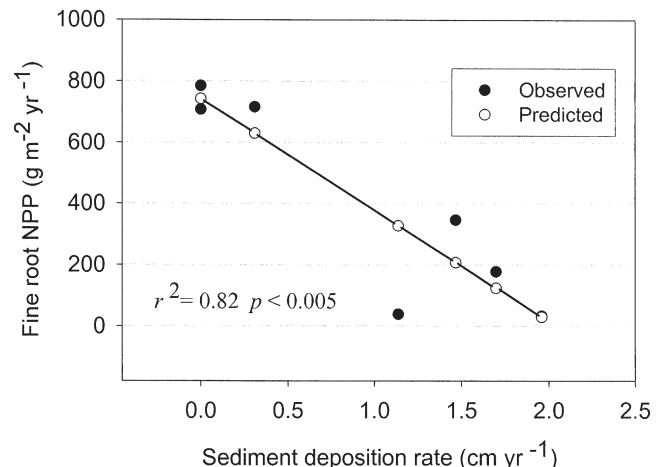
**Fig. 5.** Comparison of fine root production estimates (g m<sup>-2</sup> yr<sup>-1</sup>) between treatments in the three disturbance categories. Error bars represent one standard error of each treatment. Different lowercase letters denote significant difference between treatments at the 0.05 level.

similar to that for live roots. However, even though C and N contents of lower plots within HD catchments were numerically greater than their upper counterparts, no significant differences were observed. Comparisons of nutrient content among the three disturbance categories at upper plots are presented in Table 5 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

Fluctuations in fine root biomass were observed for all diameter classes, treatments, and disturbance categories, with the exception of upper plots of HD catchments, where standing crop biomass of roots remained relatively constant throughout the sample period. A substantial decline in fine root biomass during the autumn was observed for all treatments, disturbance categories, and root diameter classes. Joslin and Henderson



**Fig. 6.** Relationship between fine root net primary productivity (NPP) and rates of sediment deposition.

**Table 4. Monthly comparisons of live fine root C and N contents ( $\text{g m}^{-2}$ ) across disturbance categories at upper plots.†**

Time	C content, $\text{g m}^{-2}$			N content, $\text{g m}^{-2}$		
	HD	MD	RF	HD	MD	RF
Feb/02	2.61b‡	44.14a	60.60a	0.06b	0.93ab	1.38a
Apr/02	1.95b	62.05a	33.23ab	0.04b	1.58a	0.78ab
May/02	0.90b	58.08a	56.08a	0.03b	1.09ab	1.3a
Jul/02	1.28b	62.34a	54.58a	0.03a	1.21a	1.06a
Sep/02	1.40b	33.36ab	63.42a	0.03a	0.69a	0.85a
Nov/02	1.02b	37.79a	54.17a	0.03a	0.84a	0.86a
Jan/03	1.59b	64.89a	46.72ab	0.03a	0.75a	0.75a
Feb/03	0.75a	67.14a	25.72ab	0.02b	1.16a	0.50ab
Apr/03	0.44b	50.54a	22.67a	0.01a	1.13a	0.48a
May/03	1.61b	40.90ab	57.06a	0.04a	0.78a	1.27a
Jun/03	1.84b	38.20a	49.74a	0.02b	0.68ab	1.10a
Jul/03	11.82b	95.61a	41.51ab	0.06b	1.56a	0.67ab

† HD, highly disturbed; MD, moderately disturbed; RF, reference.

‡ Row mean followed by different lowercase letters indicates significant difference among disturbance categories at the 0.05 level.

(1987) 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 in spring, spring/winter, and summer/winter. 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. An intermediately drained community showed continuous biomass accumulation until reaching a September peak, while a poorly drained community maintained a relatively constant standing crop biomass, similar to upper plots of HD catchments in the present study. Some species such as baldcypress (*Taxodium distichum* var. *distichum*) and water tupelo (*Nyssa aquatica* L.) are capable of obtaining oxygen and growing in saturated soils. However, roots of most tree species will

**Table 5. Monthly comparisons of dead fine root carbon and nitrogen contents ( $\text{g m}^{-2}$ ) across disturbance categories at upper plots.†**

Time	C content, $\text{g m}^{-2}$			N content, $\text{g m}^{-2}$		
	HD	MD	RF	HD	MD	RF
Feb/02	0.09b‡	2.32a	0.65ab	0.001b	0.06a	0.02ab
Apr/02	–	1.57a	1.01a	–	0.04a	0.03a
May/02	–	1.45a	2.28a	–	0.04a	0.07a
Jul/02	0.29a	3.16a	2.69a	0.005a	0.06a	0.07a
Sep/02	0.02a	2.06a	1.42a	–	0.04a	0.03a
Nov/02	–	4.01a	0.86a	–	0.09a	0.02a
Jan/03	0.11a	0.28a	1.67a	0.001a	0.01a	0.04a
Feb/03	–	1.86	–	–	0.03	–
Apr/03	0.04a	5.81a	3.32a	0.001a	0.15a	0.07a
May/03	0.07b	4.65a	0.98ab	0.003b	0.11a	0.02a
Jun/03	0.06a	3.89a	1.16a	0.001a	0.01a	0.03a
Jul/03	–	3.21a	1.57a	–	0.19a	0.03a

† HD, highly disturbed; MD, moderately disturbed; RF, reference.

‡ Row mean followed by different lowercase letters indicates significant difference among disturbance categories at the 0.05 level.

not survive long under such conditions (Broadfoot and Williston, 1973). In our upper plots of HD catchments, sediment deposition is a continuous process. Therefore, it appears that the 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 to sediment deposition and in Clawson et al. (2001) due to flooded conditions.

The temporal variation of dead fine root biomass was opposite to that of live fine root biomass as might be expected. 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 predisturbance levels may take years (Fahay and Hughes, 1994). Our data suggest that sediment accumulation greatly reduced fine root biomass in these riparian forests. No data are available regarding 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

Our data indicate a strong relationship between levels of sediment deposition and reductions in fine root production ( $P < 0.005$ ,  $R^2 = 0.82$ ) (Fig. 6). A long-term sediment accumulation rate at or above  $0.3 \text{ cm yr}^{-1}$  appeared to be an approximate threshold beyond which major reductions in fine root production become evident. Many studies have shown that rates of sediment deposition in this range are common in some floodplains. For example, sedimentation rates have been estimated at  $0.18$  to  $0.75 \text{ cm yr}^{-1}$  along wetlands of West Tennessee (Hupp et al., 1988), and  $0.02$  to  $0.20$  and  $0.20$  to  $0.36 \text{ cm yr}^{-1}$  within floodplain forests at the Coosa-whatchie River–SC, and Cache River–AR, respectively (Hupp, 2000). 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 floodplain forests. Similarly, Megonigal and Day (1988) reported that annual fine root production on flooded stands was lower than in unflooded stands.

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<sup>-2</sup> yr<sup>-1</sup>), and a cypress community (68–308 g m<sup>-2</sup> yr<sup>-1</sup>), which experienced extensive 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<sup>-2</sup> yr<sup>-1</sup> in the somewhat drained site, 130.5 g m<sup>-2</sup> yr<sup>-1</sup> in the intermediate site, and 56.2 g m<sup>-2</sup> yr<sup>-1</sup> 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 to 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<sup>-2</sup> yr<sup>-1</sup>). The significant difference between treatments observed within reference areas may be related to higher soil moisture and basal area in lower plots.

### Fine Root Nutrient Content

Some authors have observed that the loss of nutrients such as C, N, and P 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 C and N concentrations of live and dead fine roots. However, in terms of nutrient content, some differences were observed and were driven by changes in fine root biomass. At upper plots of HD catchments, C content of live fine roots significantly decreased as root biomass decreased. The same trend was observed for N content in upper plots of HD catchments. For the other two disturbance categories, no significant difference between treatments was observed either for root biomass or root nutrient concentration; therefore, fine root nutrient content did not show significant differences. Thus, the findings from this study appear to be in agreement with those of the authors cited above. Comparisons of fine root nutrient content among disturbance categories across upper plots followed similar trends (RF = MD > HD). Clawson et al. (2001) found the same 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

Sediment deposition rates at or above 0.3 cm yr<sup>-1</sup> were associated with sharp declines in fine root biomass and production. Carbon and N content of fine roots mirrored changes in fine root biomass, which was significantly less at higher sediment deposition rates. However, it is not clear what mechanisms are driving reductions in biomass as sedimentation rates approach 0.3 cm yr<sup>-1</sup>. The growth of roots depends on many factors such as soil nutrients and moisture supply, temperature, and aeration. Usually, roots do not persist in zones of permanent saturation, and we speculate that the dominant growth-limiting factor in this study could be reduced

oxygen to roots imposed by increased sediment deposition.

Rates of sediment accumulation near 0.3 cm yr<sup>-1</sup> are common in floodplain forests (Hupp, 2000), especially in areas where the catchments are subject to disturbance such as agriculture and urbanization. Consequently, data from this study suggest that to preserve the sustainability of water filtration functions in riparian forests, road maintenance practices in military installations and other areas subject to erosion should be implemented, and the impacts of sedimentation on these ecosystems should be fully considered.

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