NITROGEN CYCLING IN STREAMS: A COMPARISON OF THE ROLES OF DEBRIS DAMS AND MOSSES

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Abstract. The nitrogen (N) saturation theory suggests that long-term increases in atmospheric N deposition will eventually exceed nutrient demand by plants and microbes. As forests become saturated, N is expected to run off into streams via surface runoff and groundwater flow. The microbes associated with debris dams and aquatic plants are expected to play an important role in N cycling and retention. To better understand the role of debris dams in N cycling, we performed streams manipulations that involved removing all debris dams and adding debris dams to three streams. We measured the standing stocks of moss and debris dams and the total amount of N contained in each stream after the manipulations. Debris dams had larger standing stocks in the control (237494.9 g dry mass/100m), addition (580265.4 g dry mass/100m), and removal (18740.13 g dry mass/100m) streams than moss (3063.914 g dry mass/100m, 4178.205 g dry mass/100m, 2335.667 g dry mass/100m). Total microbial N was highest in the addition stream (3.07454 gN/100m), lowest in the removal (0.324219 gN/100m). Moss in the removal, control, and addition streams contained 27.89105 gN/100m, 36.58732 gN/100m, and 49.89347 gN/100m, respectively. Our results indicate that there is a positive correlation between amount of organic material and moss present in a stream and the total amount of N.

INTRODUCTION

Nitrogen (N) is an essential nutrient often limiting plant growth in terrestrial ecosystems in the northeastern United States. Human activities, including fertilizer application, fossil fuel combustion, and human waste disposal, have doubled the rate at which fixed N is supplied to the biosphere (Valett and Schreiber 2005). Increases in the amount of available N are expected to have important effects on the N cycle of receiving ecosystems. Increases in N availability will result in the alleviation of limitations on plant growth and eventually exceed plant demand, a phenomena termed “nitrogen saturation” (Aber et al. 1998, Tietema el al. 1998). A key symptom of N saturation in forested ecosystems is an increased delivery of N to streams through surface runoff and groundwater flow (Stoddard 1994).

Runoff from saturated riparian zones can lead to increased N concentrations in headwater streams, often having significant effects on downstream systems, such as rivers, lakes, and estuaries. It is important to have an understanding of N dynamics in headwater streams where the increased availability of N can lead to eutrophication events and acidification downstream (Aber et al. 1997; Murdoch and Stoddard 1992). Previous studies (Naiman 1983 and Horton 1945) have demonstrated that headwater streams can play a disproportionately large role on the watershed N budget (Peterson et al. 2001). They can comprise up to 85% of total stream length within a watershed and, in turn, collect the most water and nutrients from bordering terrestrial ecosystems (Naiman 1983 and Horton 1945). Understanding the mechanisms by which excess N is cycled in streams is becoming increasingly important given the negative impact increased N loads has on downstream ecosystems.

As N travels through the watershed it goes through multiple cycles of uptake, storage, and release, a process known as “spiraling.” During “spiraling” there are two main processes that contribute to N retention: sedimentation and uptake by photosynthetic organisms. In addition, N can also be removed from a system through denitrification. Nitrate uptake by aquatic macrophytes contributes to the cycling of N in a stream by taking up and storing N in roots and leaves during the growing season (Hill 1986). Yet, previous studies have suggested that aquatic macrophytes serve as a relatively small and temporary N sink compared to other processes, such as denitrification (Nichols 1983; Reddy et al. 1989). In a study by Hill (1979), uptake of N by benthic algae and macrophytes accounted for only 15% of nitrate removal from a small stream ecosystem. Despite small amounts N uptake, macrophytes do indirectly affect N cycling by supplying limiting organic carbon and nitrate to denitrifying bacteria, thus creating ideal conditions for denitrification (Reddy et al., 1989; Weisner et al. 1994). Therefore, although direct N uptake and retention by photosynthetic organisms may not dramatically affect N concentrations in streams, the indirect benefits these organisms supply to denitrifying bacteria makes them important in N cycling in headwater streams.

The process of denitrification permanently removes N from the system, potentially playing a key role in headwater streams with increasing N concentrations as it has generally been assumed to account for the most nitrogen retention in freshwaters (Seitzinger et al. 1998; Jensen et al. 1990; Svendsen & Kronvang 1993). Denitrifying bacteria use nitrate (NO_3^-) or nitrite (NO_2^-) as terminal electron acceptors, releasing N_2 or N_2O gas as a byproduct (Knowles 1982). Microbial denitrification occurs primarily on the biofilm of decaying organic material and in detritus-rich sediments. Common organic material, such as leaves, wood, and sediment, often occur in large accumulations, called debris dams.

Debris dams usually form when a large piece of wood or tree falls into the stream and is held in place against the current by obstructions on the outside edge of the stream (Bilby 1981). Small sticks, leaves, and sediment gradually accumulate behind the wood, forming a natural dam that effectively slows down the flow of water and often creates a pool upstream. Debris dams are associated with greater in-stream retention of N because they provide “hotspots” for microbial activity (Bilby 1981 and Hedin 1990). Several recent studies suggest that small, slow moving streams are sites of maximum N transformation and retention due to high surface to volume ratios, which allows them to process greater amounts of N (Alexander, et al. 2000 and Hall and Tank date). In addition, low velocities and shallow water depths increase contact time between dissolved N and biota in sediment, detritus, and biofilms, promoting N uptake (Bernhardt et al. 2003).

Organic debris dams and mosses are common features of streams in HBEF located in the White Mountains of central New Hampshire. To further investigate and expand on the studies done by Bilby (1981) with debris dams in the Hubbard Brook Experimental Forest (HBEF), we took an experimental approach to explore the importance of moss and debris dams and specifically, the microbes associated with them. We performed debris dam manipulations in two streams; we removed all dams from one stream and added dams to the other. By comparing the amount of total N in both mosses and microbes it is possible to address the following questions: 1) what is the relative importance of microbial N uptake associated with debris dams compared to moss N uptake in these forested headwater streams? and 2) how does the removal or addition of debris dams influence N processing in streams? This project was part of a larger study that looked at overall nutrient uptake lengths and denitrification in streams. We predict that the amount of total N present in a stream is directly related to the amount of debris dam material and moss present. Therefore, our three streams (including a control) should have varying amounts of N based on the manipulations.

METHODS

Study Site

The HBEF is a Long Term Ecological Research (LTER) site located in the White Mountains of central New Hampshire. The streams used in this study are second-order streams located in second growth forest (cut ~1917) dominated by American beech, yellow birch, and sugar maple. Organic debris dams are common features of the channels, and have high microbial activity (Bilby 1981). Bulk deposition of inorganic N averages about 7-8 kg N $ha^{-1}y^{-1}$ in the southwestern White Mountains National Forest (Likens and Bormann 1995; Campbell et al. 2000) and typically increases with elevation (Lovett and Kinsman 1990).

We chose three south facing streams, Crazy Book, Bear Brook, and W-3 as study sites. In the fall of 2005, we removed all debris dams from Crazy Brook in a 100m reach. We added debris dams to a 100m reach immediately below the gauging weir in W-3. A 100m reach approximately 300m from the gauging weir in Bear Brook served as a control. All three streams are of similar size with an average width of ~3-4.5 m and an average depth of 0.3 m.

Sample Collection

To estimate N in biomass of moss and microbes we collected samples of microbe-containing debris dam material and moss, and measured the total amount of N present in each sample. We collected samples from three sites in each 100m reach. We removed moss samples from submerged rocks. They were then rinsed with deionized water, oven dried at 60 degrees Celsius, and weighed.

We sampled microbial biomass from three types of organic material within debris dam habitat, leaves, wood, and coarse benthic organic material (CBOM). We collected leaves from within 5 meters upstream and downstream of each station, placed them into Ziploc bags and kept them moist with stream water until reaching the lab. We collected small pieces of wood from the same areas, including twigs and bark, (<5cm in diameter) and stored as described above. Collection of CBOM was preformed under the same protocol using a large syringe to suction the material from the streambed and transfer it into Ziploc bags.

Standing stocks of microbes and mosses

We measured total standing stocks of moss and microbes to create a scale for comparison of the amount of N present in each. We estimated total standing stocks by using total coverage and average dry mass. We used 25 x 25 cm quadrats to estimate moss coverage in each stream.

We estimated the standing stock of microbes by measuring the debris dam habitat types, including leaves, wood, and CBOM. We used 25 x 25 cm quadrats to estimate leaves, wood, and CBOM coverage throughout the stream independent of debris dams. Quantifying the amount of leaves and wood present in a dam proved difficult without destroying the dam and altering downstream measurements of material. Therefore, we estimated the dimensions of a generic debris dam by averaging the areas of all measured debris dams (2.25m^2) and determined the number of quadrats that would fit into our generic debris dam (36 quadrats). We estimated that leaves covered 100% of each quadrat and wood 50% of each quadrat. Total coverage of debris dam material in each stream was estimated by using Crazy Brook as a base (because it was the stream with no debris dams) and adding the amount of material present in our generic dam multiplied by the number of dams present in each stream. While this is a rough estimate of the amount of material in each stream, it showed the basic trends associated with complete removal and addition of dams.

To convert total coverage to biomass we found the average dry mass of the samples collected. We used the following equation to estimate the total standing stock (SS_{total}) of moss and microbes based on average dry mass (DM_{avg}) and total coverage (TC):

$$SS_{total} = DM_{avg} * TC$$

We measured total standing stock in g of material/100m of stream.

Microbial nitrogen

We extracted the microbial N present in debris dam material using the chloroform fumigation incubation method (CFIM), originally designed to separate microbial N from total N in soils (Brookes et al. 1985), and adapted for streams (Sanzone et al. 2001). To determine total N after fumigation, we converted N in the K_2SO_4 samples to nitrate using the alkaline persulfate oxidation method (Cabrera & Beare, 1993). We determined nitrate concentrations using automated NO_3 analysis on a Lachat. We used results from both fumigated ($TN_{fumigated}$) and unfumigated ($TN_{unfumigated}$) samples in the following equation (Sanzone, 2001) to determine total N in microbial cells ($TN_{microbial}$):

$$TN_{microbial} = (TN_{fumigated} - TN_{unfumigated}) * 1.85$$

To account for incomplete release of microbial biomass N during the fumigation period we used a correction factor of 1.85 (Brookes et al., 1985).

RESULTS

Standing Stocks of Debris Dam Material and Moss

The amount of organic material and moss correlated with the manipulations made in all three streams. The addition stream contained the largest standing stock of debris dam material, while the removal stream contained the smallest (Table 1). Total debris dam material in the removal stream was ~12 times less than the amount in the control stream. The total amount present in the addition stream was ~2 times the amount in the control (Fig. 1). Moss biomass was ~2 times greater in the addition stream compared to the removal stream (Table 1). Therefore, both the standing stock of moss and debris dam material were greater in the addition stream and less in the removal stream (Fig. 2).

Amount of N in microbial biomass

There is a positive correlation between the amount of debris dam material and the amount of microbial N in the streams. Total microbial N was 2.047973 gN/100m in the control, highest in the addition stream (3.07454 gN/100m), and lowest in the removal (0.324219 gN/100m) (Table 1, Fig. 3). The component of debris dam material containing the most microbial N was correlated with the total amount of that component in the stream (Fig. 4).

Amount of N in Moss

Moss made up a smaller component of stream organic material yet contained more total nitrogen than the three debris dam materials combined (5.446732 gN/100m). The removal, control, and addition streams contained 27.89105 gN/100m, 36.58732 gN/100m, and 49.89347 gN/100m, respectively (Table 1). Compared to the total N contained in debris dam material, moss contained ~84 times the amount of N associated with debris dams in the removal stream, ~18 times the amount in the control stream, and ~16 times the amount in the addition stream (Fig. 5).

DISCUSSION

In this study we found that the amount of organic material and moss in a stream correlates with the total amount of N present. We can discuss the role of microbes and moss in nutrient cycling in streams, as well as the potential fate of N once incorporated into each organism. Our results also allow us to weigh in on watershed scale implications of N retention, including recent decreasing stream N trends across the Northeast. The debris dam manipulations also create an ideal model of the effects that disturbance and forest succession can have on a stream ecosystem.

The role of microbes and mosses in nutrient retention

Differences in uptake and storage between moss and microbes could explain the difference in amount of total N. The standing stocks of moss were smaller than the standing stocks of debris dam material in all study streams, however bryophytes contained more total N. Mack et al. 2004 also found that bryophytes had higher nitrogen stocks (0.64g/m2) than the biofilm layer on organic material (0.24g/m2). As mosses take up N they form compartments for elemental storage in biomass. Uptake and storage will continue to occur as long as the biomass continues to increase. Eventually the moss will reach a point where production is equal to respiration and there will be a cessation of growth and N uptake; therefore, moss uptake and retention is not infinite.

Microbes can retain N in biomass as well as remove N from the stream altogether through the process of denitrification. Laboratory denitrification assays done by Steinhart et al (2001) provided evidence that denitrification within stream sediments in Bear Brook in the HBEF may remove up to 25%-100% of the nitrate measured at upstream weirs. Unlike mosses, microbes are not limited by the extent of their biomass; they can continue to remove N from the stream long after their biomass is saturated.

The differences in the fate of N in moss and microbes must be taken into account when determining the importance of both components. The time scale of retention is different between the two as moss store N in biomass long term, while microbes continuously cycle what they consume. Our results only represent a moment in time and do not reflect the rate of uptake or denitrification in microbes or moss.

Moss and microbial N retention: an explanation for regional N trends?

An unusual trend of decreasing N concentrations in streams across the Northeast has been observed since the mid-1970's despite increased inputs of atmospheric nitrogen (Likens and Bormann 1995). Therefore, potential N sinks that could explain these trends include an increase in the amount of debris dams and the N uptake and removal associated with microbes living in them and/or an increase in the amount of moss present in streams.

The decline in NO_3^- concentrations in streams across the entire northeast suggests a regional controller, such as climate change or changes in atmospheric chemistry (Goodale 2003). Atmospheric carbon dioxide (CO_2) concentration increased by 10% from 330 to 3664 ppm between 1973-74 to 1996-97 (Keeling and Whorf, 2000). This change in carbon availability could potentially increase vegetation growth and N uptake, thereby reducing stream nitrate export (Vitousek et al. 1997). The results from our moss survey indicate that there has been very little change in the standing stocks of moss in streams at HBEF over the past 30 years (Fisher and Likens 1973). Therefore, an increase in moss and incorporation of N in biomass cannot account for decreased N export.

Increasing the number of debris dams in a stream increased total N in our experimental addition stream. An increase in dams and the subsequent microbial activity associated with them is a possible explanation for decreased N export from streams. The true importance of microbes in N retention and removal is possibly being underrepresented in our results, as our measurements do not account for rates of denitrification. However, the results from other studies associated with this project, including denitrification rates may be able to provide a complete picture of the role of microbes and mosses in N cycling.

The role of disturbance and succession on stream ecosystems

Disturbances to the forested ecosystem surrounding a stream, caused by events such as storms, often increase the stream's capacity to retain more N (Bernhardt el al. 2003). Mechanisms for the increase in N retention include decreased canopy cover and the subsequent stimulation of primary production in aquatic plants, as well as an increase in the amount of woody debris entering streams (Hall & Tank 2003; Valett et al. 2002). As stands age, the wood volume in streams increases about one m3/ha/yr (Warren et al.). The stands in HBEF are ~20-86 years

old and are potentially contributing to an increase in the number of debris dams in neighboring streams (Warren et al. in press).
Our manipulations serve as a model to demonstrate the affect disturbances and increasing stand age have on N retention in streams based on differences between sites with and without debris dams. Our results indicate that streams with more organic material contain more total N due, in part, to an increase in the amount of suitable habitat for microbes. Debris dams have also shown to be important in modifying stream channel morphology, creating pools upstream and slowing down the flow of water (Zimmerman et al 1967, Bilby and Likens 1980). A decreased flow rate maximizes the contact time between dissolved N and biota, including microbes and mosses. Therefore, the increase in organic material entering streams caused by disturbances and factors associated with aging stands may play an important role in N cycling and retention in small headwater streams.

Based on the preliminary data from this debris dam manipulation study, it can be concluded that the amount of organic material and moss in a stream influences the total amount of N present. Further study into the fate of N once consumed by moss and microbes is needed to gain a better understanding of N cycling in streams, especially in the presence of increased anthropogenic-caused N deposition and the predicted health and environmental effects it will have.

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APPENDIX

TABLE 1. Standing stock of organic matter (Dry Mass, g/100m) and nitrogen (N, g/100m) of sampled stream compartments. We removed all debris dams from a 100m reach in Crazy Brook, added debris dams to W-3, and left Bear Brook as a control. Values represent the averages of three samples taken from each stream.

	Removal (Crazy Brook)		***Control (Bear Brook)***		***Addition (W-3)***	
	Dry Mass	N	Dry Mass	N	Dry Mass	N
Leaves	2163.738	0.039946	127510.7	0.691822	301389	1.318404
Wood	1494.218	0.040677	108249.5	1.313162	255862.5	1.724613
CBOM	15082.17	0.243596	1734.688	0.042989	23013.88	0.031522
Total Debris Dam	18740.13	0.324219	237494.9	2.047973	580265.4	3.07454
Total Moss	2335.667	27.89105	3063.914	36.58732	4178.205	49.89347

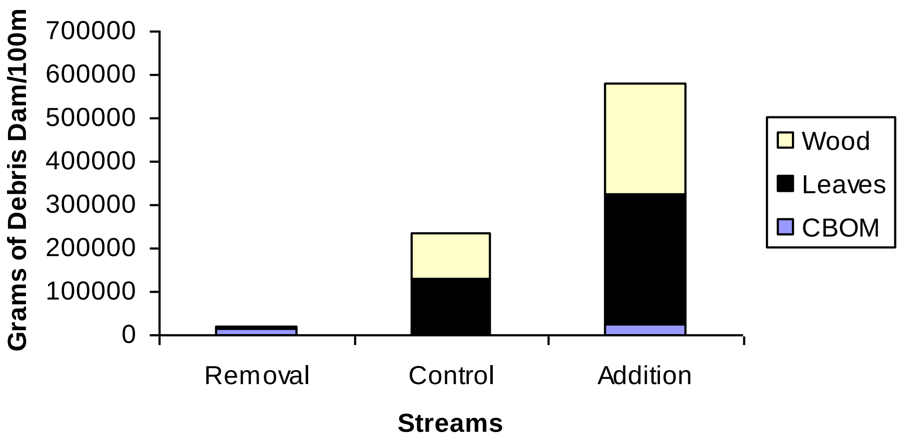

FIGURE 1. Total standing stock of debris dam material was greatest in the addition stream and least in removal streams**.** We removed all debris dams from a 100m reach in Crazy Brook, added debris dams to W-3, and left Bear Brook as a control. We calculated the standing stock of debris dam material by estimating the total coverage and average biomass of three main components of dams, wood, leaves, and coarse benthic organic material (CBOM).

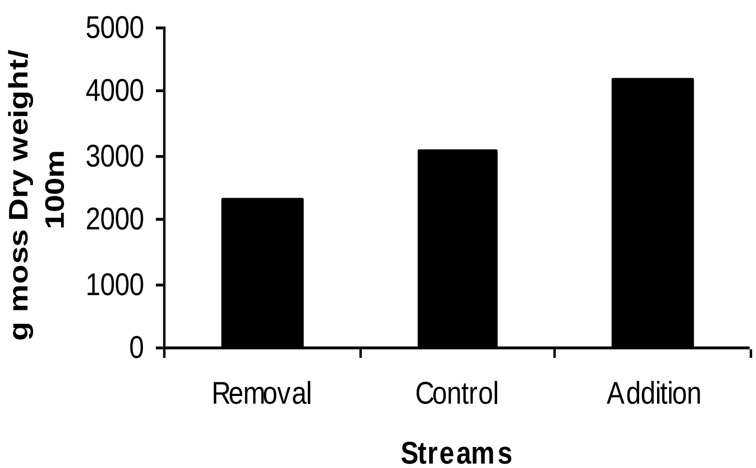

FIGURE 2. Total standing stock of moss material was greatest in the addition stream and least in removal streams. We removed all debris dams from a 100m reach in Crazy Brook, added debris dams to W-3, and left Bear Brook as a control. We calculated the standing stock of moss by estimating the total coverage and average biomass of moss in each stream.

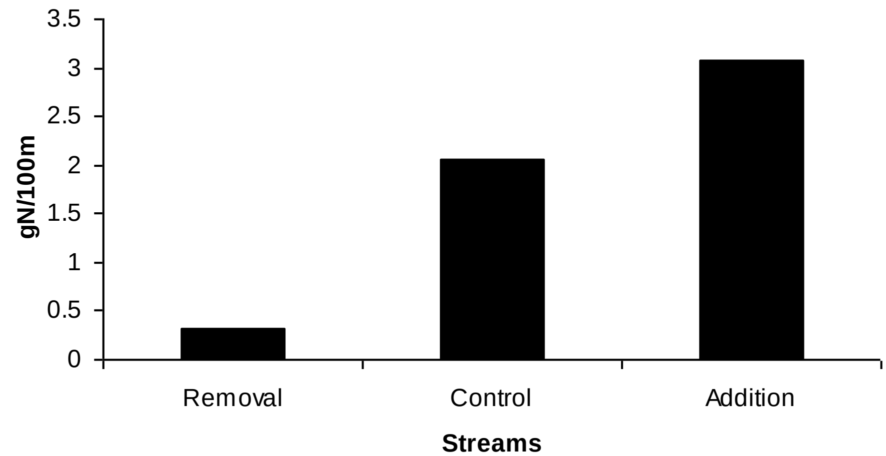

FIGURE 3. Total microbial N in debris dam material was greatest in the addition stream, least in the removal stream. We removed all debris dams from a 100m reach in Crazy Brook, added debris dams to W-3, and left Bear Brook as a control. We measured total N in the three main components of debris dams, wood, leaves, and coarse benthic organic material. The values here represent the averages of total N found in these three components in each stream.

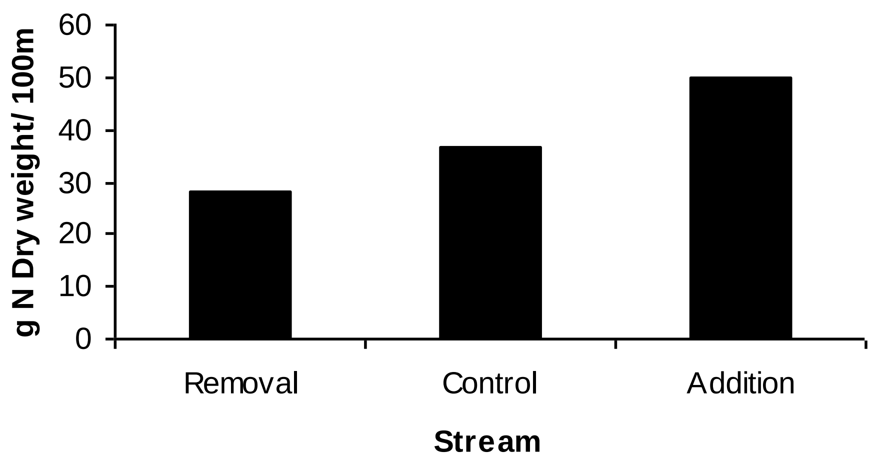

FIGURE 4. Total N in moss was greatest in the addition stream, least in the removal stream. We removed all debris dams from a 100m reach in Crazy Brook, added debris dams to W-3, and left Bear Brook as a control. The values here represent the averages of total N from three samples of moss in each stream.

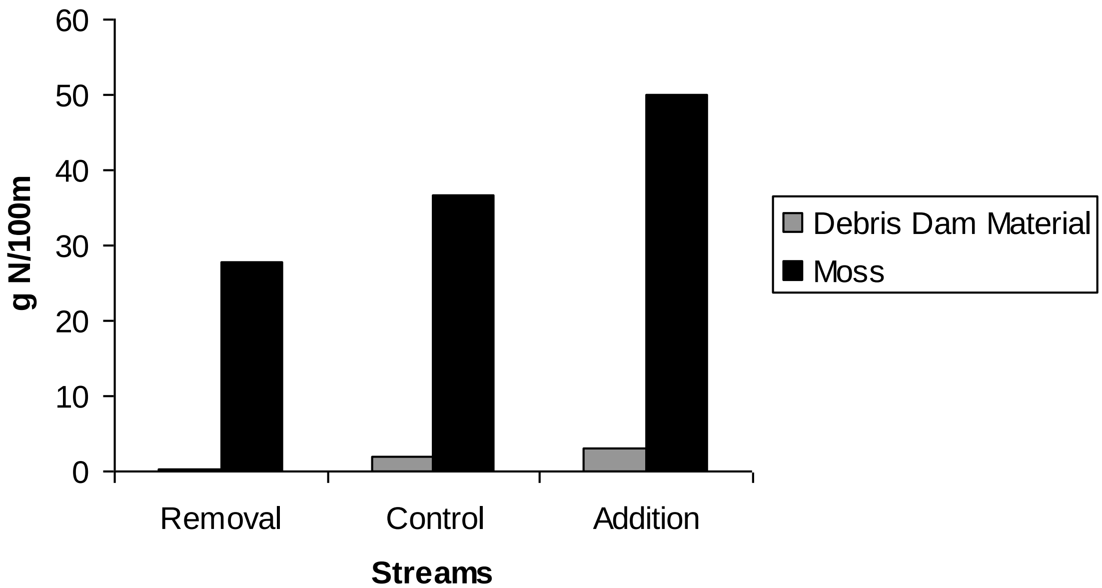

FIGURE 5. The amount of total N is greater in moss than microbes. We removed all debris dams from a 100m reach in Crazy Brook, added debris dams to W-3, and left Bear Brook as a control. The values here represent the averages of total N from three samples of both moss and debris dam material in each stream. The average N in debris dam material is comprised of three samples of leaves, wood, and coarse benthic organic material.