PRIMARY RESEARCH PAPER

Effects of wood removal on stream habitat and nitrate uptake in two northeastern US headwater streams

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Abstract Forested headwater streams play an important role in watershed nutrient dynamics, and wood is thought to be a key factor influencing habitat structure and nitrate-nitrogen dynamics in many forested streams. Because wood in streams can promote nitrogen uptake through denitrification, we hypothesized that nitrate uptake velocities would decrease following wood removal. We measured stream characteristics and nitrate uptake velocities before and after wood manipulation experiments conducted at Hubbard Brook Experimental Forest, NH, and the Sleepers River watershed, VT. The mean size of stream substrates and the amount of riffle habitat increased following wood removal. In contrast to our expectations, summer nitrate uptake velocities increased in the wood removal treatments relative to the reference treatments, possibly because wood removal increased the availability of stable substrates for periphyton growth, therefore increasing nitrate demand in these streams. Our results highlight that effects of wood on stream ecosystems occur through multiple pathways and suggest that the relative importance of these pathways may vary seasonally.

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Introduction

The majority of biologically reactive nitrogen (N) exported from headwater streams in the northeastern US occurs as nitrate (Likens & Bormann, 1995). In recent years, increased attention has been paid to the potential role of streams as sinks for excess nitrate (Peterson et al., 2001; Bernhardt et al., 2005a; Mulholland et al., 2008), and it has been suggested that wood in streams from the surrounding forest enhances N retention (Steinhart et al., 2000; Webster et al., 2000; Bernhardt et al., 2003). Wood input to streams has increased in the northeastern US over the past century and wood loading is expected to continue to increase for another century or more (Warren et al., 2009). And, in areas where natural reforestation that promotes wood recruitment is not occurring or where it is occurring slowly, stream restoration efforts increasingly incorporate large wood and other comparable structural elements to mimic large wood function (Bernhardt et al., 2005b). Determining the influence of stream wood on N dynamics in headwater systems is therefore highly relevant to research on stream and whole ecosystem nutrient budgets as well as long-term projections for nutrient biogeochemistry across the region.

Although wood is generally recognized as a stream feature with the potential to influence N dynamics, results from studies evaluating links between large wood or debris dams and nitrogen dynamics have been mixed. A positive relationship between stream wood and nitrogen uptake has been observed in some studies (Webster et al., 2000; Ensign & Doyle, 2005; Roberts et al., 2007b), but others have found no relationship (Aumen et al., 1990; Warren et al., 2007). This result may be due in part to the numerous biological and abiotic stream characteristics that can influence stream N dynamics, including: primary productivity rate (Sabater et al., 2000; Roberts et al., 2007a), availability of labile carbon (Bernhardt & Likens, 2002; Brookshire et al., 2005), stream substrate characteristics (Hoellein et al., 2007), transient storage (Valett et al., 1996; Ensign & Doyle, 2005), and interaction between surface water and the hyporheic zone (Valett

et al., 1996; Brookshire et al., 2005). Large wood and accumulations of wood (debris dams) can influence all of the above stream characteristics to some extent (Bilby & Likens, 1980; Gregory et al., 1991; Montgomery et al., 1995; Gurnell et al., 2002, 2005), however, the degree to which wood influences these characteristics and the degree to which each of the characteristics in turn influences stream N dynamics varies across streams.

Wood increases retention of sediment and organic carbon in headwater streams (Bilby & Likens, 1980; Diez et al., 2000; Gomi et al., 2006). The saturated sediments that develop behind stable large wood and debris dams create anaerobic conditions that promote denitrification (Steinhart et al., 2000), and increased carbon availability promotes nitrate assimilation by heterotrophs (Tank et al., 2000; Bernhardt & Likens, 2002). Wood and other large structural elements in streams can also increase transient storage, and there is evidence that the increased residence time of water associated with wood and other structural elements can increase nutrient uptake velocities (Ensign & Doyle, 2005). Although there are a number of heterotrophic pathways by which inorganic N is removed from the water column, in streams with high autotrophic production algal demand may swamp other N uptake pathways at seasonal or diurnal time scales (Roberts & Mulholland, 2007; Johnson & Tank, 2009) or following restoration efforts that promote primary production (Hoellein et al., 2007).

The goal of this study was to determine whether nitrate nitrogen (NO_3^--N) uptake changes in response to wood removal. We focused specifically on NO_3^--N (rather than N as ammonium, for example) because this is the form in which most inorganic N is exported from forested streams in this region. We used reach-scale wood removal experiments, and measured summer NO_3^- uptake in two northeastern US headwater stream systems draining second-growth northern hardwood riparian forests, one in New Hampshire, and one in Vermont, before and after wood removal. Pre-treatment data on nitrate uptake velocities were collected in summer 2005 using ^{15}N-NO_3^- releases (three releases in each of two streams in Vermont and one in the stream in New Hampshire). Wood was removed from one of the two streams in Vermont and from the stream in New Hampshire in Fall of 2005 and post-treatment uptake velocities were quantified in

summer 2006 (two releases in the Vermont streams and one release in the stream in New Hampshire). We expected wood removal to reduce carbon storage, increase solute transport (reduce water residence time), and eliminate pools with saturated sediment where denitrification is likely to occur. Given the predominantly heterotrophic nature of forested headwater streams in this region (Fisher & Likens, 1972; Wallace et al., 1997), we expected these collective impacts of wood removal to reduce the relative demand for nitrate as measured by NO_3^--N uptake velocities.

Study site

Study reaches of approximately 100 m in length were established in three streams within the Hubbard Brook Experimental Forest (HBEF) and Sleepers River with well-characterized hydrology and nutrient export (Likens & Bormann, 1995; Hornbeck et al., 1997). At the Sleepers River watershed (SRW) in northeastern Vermont, we studied a pair of first-order streams directly adjacent to each other and in close proximity to the USGS study watershed, W9 (Fig. 1). Nutrient releases were conducted on both streams three times in
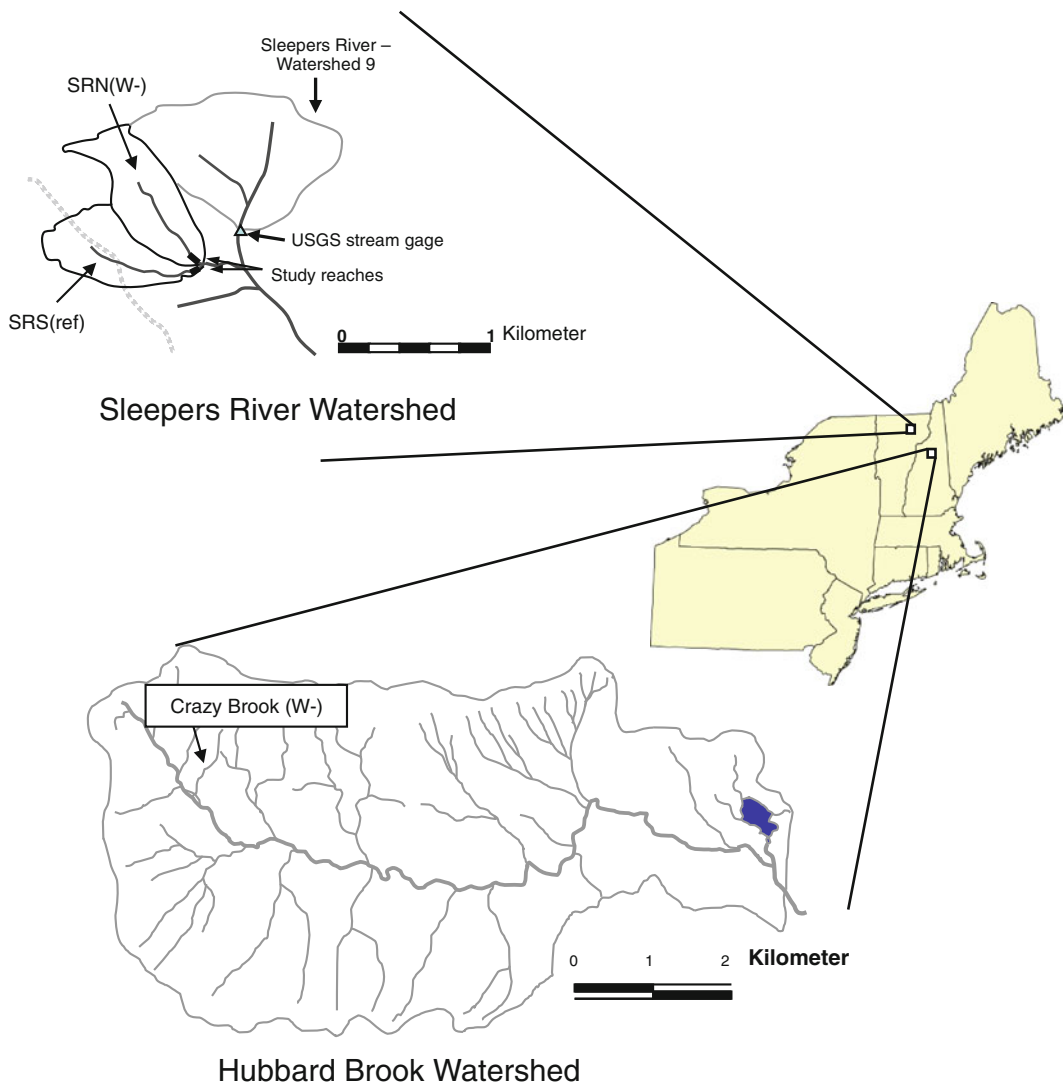
Fig. 1 Study site locations in the northeastern US and stream locations within each larger watershed (HBEF: Crazy Brook = wood removal; SR: North = wood removal, South = reference)

summer 2005 and two times in summer 2006. Between sampling in 2005 and 2006 (during late-summer 2005), wood was removed from one of the streams (indicated as "w−"), while the other stream was left unaltered as a reference site (indicated as "ref"). The two Sleepers River streams are comparable in size and gradient (Table 1). Prior to wood manipulation, the substrate in Sleepers River—South (SRS(ref)) had 34% less total wood volume than Sleepers River—North (SRN(w−)), the wood removal site (Table 1). Stream discharge in the SRW peaks in spring during snowmelt and is lowest in mid-summer. The adjacent riparian zone and watershed are dominated by early-mature second-growth northern hardwood forests. Sleepers River streams are well-buffered relative to other systems in the northeastern US due to the underlying glacial till of calcareous granulite and quartz mica phyllite. Summer nitrate concentrations at Sleepers River were consistently higher in SRN(w−) than in SRS(ref) during both years. Mean NO_3^--N concentrations in SRN(w−) during nutrient releases ranged from a low of 46 µg l^{-1} in late June 2006 to 125 µg l^{-1} in mid-August 2005. Mean NO_3^--N concentrations in SRS(ref) during this period ranged from 13 to 69 µg l^{-1}.

At the HBEF, we evaluated only before–after data from a wood removal stream (no reference). Crazy Brook is a first-order stream at the western end of the larger Hubbard Brook Valley with a mean bankfull width of about 2.9 m and gradient of approximately 10% (Fig. 1). As with Sleepers River, peak discharge occurs in the spring during snowmelt and baseflow predominated in mid-summer. The watershed contains large glacial till and stream substrate is dominated by boulders, cobble, and gravel. Forests in the Hubbard Brook Valley are second-growth northern hardwood forests generally between 80 and 100 years of age with a few older remnant trees. Streams in this region are generally poorly buffered and are subject to chronic or episodic acidification (Likens & Buso, 2006). Mean NO_3^--N concentrations over the two summers at Crazy Brook ranged from 2 µg l^{-1} (detection limit) to 14 µg l^{-1}.

Methods

Study design

We used a Before–After Control-Impact (BACI) study design at Sleepers River sites (Stewart-Oaten et al.,

Table 1 Study reach and stream characteristics in 2005 and 2006, before and after wood manipulations

Stream	Years	Reach length (m)	Mean bankfull width (m)	# Cross sections at pools	# Cross sections at riffles	LW volume (m³)	# LW	# Debris dams	% Organic substrate	% Substrate >5 cm	Overall % points with moss
Sleepers River—North: wood removal	2005 (before)	116	2.1	4	8	3.63	56	13	8	28	8
	2006 (after)	116	1.9	1	11	0.38	4	0	16	39	5
Sleepers River—South: no treatment	2005 (before)	100	2.5	2	9	1.05	37	9	20	47	11
	2006 (after)	100	2.2	1	10	1.04	28	14	8	50	10
Crazy Brook: wood removal	2005 (before)	100	2.96	6	5	1.65	33	7	15	43	30
	2006 (after)	100	2.87	2	9	0.11	1	0	15	47	24

LW refers to wood >10 cm diameter and >1 m length

1986) and a simple before–after comparison at Crazy Brook (CB(w−)). We measured nitrate uptake three times between June 21 and August 18 in each of the two Sleepers River streams in summer 2005 prior to wood removal from SRN(w−). Stream habitat (large wood, substrates, and habitat units—see Table 1) was measured once in summer 2005. Wood was removed from SRN(w−) in late August 2005, and post-treatment nutrient uptake and habitat measurements were conducted in July and September of 2006. Although we include a reference site, with limited replication, we focused on differences only within comparable seasonal conditions to remove potential seasonal variability. The 10-month period between the removal and the first-post-treatment sampling allowed redistribution of the stream substrates. At HBEF, stream habitat assessments and pre-treatment nitrate uptake measurement were conducted in CB(w−) in June 2005. In September 2005, wood was removed from the 100-m study reach. Post-treatment habitat data and nutrient uptake measurement data were collected 1 year later.

Stream habitat

Stream habitat measurements were collected following the methods in the Lotic Intersite Nitrogen eXperiment II (LINX II) protocols (http://www.biol.vt.edu/faculty/webster/linx/linx2proto-rev5.pdf). Cross sections were established every 10 m on each approximately 100 m reach. At each cross section, we measured substrate size and type, wetted and bankfull widths, and categorized the stream habitat as a pool or a riffle. Substrate that was too small to be measured directly was classified as sand (<2 mm diameter, primarily inorganic) or fine organic material (<1 mm diameter, primarily organic material). When the sample point occurred on a piece of stable wood that was buried in the stream and functioning as substrate, we classified the substrate as wood. For analysis, wood and particulate organic material were combined into a single "organic" substrate category. At each sampling point in a cross section, we noted whether or not moss was present on the substrate at that location. Stream depths at each cross section were measured at regular intervals across the wetted width. Transect locations were established and well marked in 2005 so post-treatment assessments could be conducted at the same location in 2006.

Surveys of large wood and debris dams were conducted following the methods described in Warren et al. (2007). Briefly, for all wood greater than 10-cm diameter and 1-m length within the bankfull channel of the stream ("large wood"), we estimated length within the stream channel to the nearest 0.5 m and diameter at a central point of the piece to the nearest 0.01 m. From these measurements, we estimated wood volume for each piece as a cylinder and total wood volume was calculated by summing the volume of all large wood pieces within the study reach. Large wood frequency was measured as the number of pieces encountered in a 100-m stream reach. We defined debris dams as accumulations of smaller wood, leaves, and organic matter in association with one or more pieces of large wood that provide geomorphic functions, including retaining bedload or stream sediment, altering stream flow, or constraining the stream channel. For each debris dam we estimated length, width, and height from which we calculated an estimate of debris dam volume.

We used a single-factor ANOVA to compare mean bankfull width, mean wetted width, and mean inorganic substrate size at cross sections for each of the streams before and after wood manipulations. We were able to make simple comparisons of pre-treatment versus post-treatment values relative to changes in the treatment versus the reference stream but for some components (large wood volume, stream habitat units at cross sections, and the proportion of substrates at cross sections) a statistical comparison could not be done due to a single measurement before and after the wood manipulation.

Nutrient releases

Nitrate uptake length was determined following the (LINX II) protocols for releases of ^{15}N-NO$_3$ labeled KNO$_3$ (Mulholland et al., 2008). All releases were conducted during baseflow conditions and consisted of an 8- to 20-h drip of a solution containing ^{15}N-NO$_3^-$. We calculated the amount of ^{15}N-NO$_3^-$ to add using estimates of stream discharge and stream NO$_3^-$ concentrations. We sought to achieve a target δ^{15}N of 20,000‰ at CB and a target δ^{15}N of 20,000 or 10,000‰ at the Sleepers River sites. We had a high target enrichment rate because we also intended to quantify stream denitrification rates, however, due to logistical and budgetary constraints; this component

of the project was not completed. A target enrichment of this magnitude does present the possibility of an increase in concentration and therefore a small fertilization effect. We used sodium chloride (NaCl) as our non-reactive tracer and measured stream conductivity as a proxy for chloride concentration (background conductivity was below 160 µS on all three streams and increases associated with the release were quite clear). The NaCl tracer was used to determine discharge, groundwater flux, and to assess when the reach had achieved hydrologic steady state (plateau). Four sampling stations were established along each study reach (about 100 m long). Background water chemistry were collected at each site prior to initiating the drip. Sampling at each station consisted of three replicate 1-l samples for $^{15}N\text{-}NO_3^-$ analysis and three 50-ml water samples for measuring total nitrate concentration. Stream nitrate and $^{15}N\text{-}NO_3^-$ background and plateau samples were filtered during collection (Whatman GFF filters) and subsequently refrigerated at 4°C for 4–8 weeks until processing and analysis. All $^{15}N\text{-}NO_3$ samples were processed according to Sigman et al. (1997). Filter analysis for $^{15}N\text{-}NO_3^-$ was conducted by the Cornell University Stable Isotope Laboratory (COIL) and nutrient concentrations were measured by the Water Quality Analysis Lab at the University of New Hampshire. Due to the high ^{15}N enrichment the samples were diluted with known amounts of $^{14}N\text{-}NO_3^-$ prior to the processing in order to avoid contamination of the mass spectrometer and to achieve delta $^{15}N\text{-}NO_3^-$ values within the range of greatest accuracy for the COIL facility. The $^{14}N\text{-}NO_3^-$ spike and the amount of nitrogen in the Devarda's Alloy used in the diffusion process (and its delta value) were included in the back calculation of stream delta $^{15}N\text{-}NO_3$ values at each sampling transect.

Nitrate uptake lengths were calculated from the longitudinal decline in the ratio of $^{15}N\text{-}NO_3$ to stream conductivity using a negative exponential model (Newbold et al., 1981), correcting for subsurface input using the conservative tracer. The negative inverse of the slope of that line is the uptake length, the mean distance traveled by $^{15}N\text{-}NO_3$ before it is taken up within the stream. The uptake length was used to calculate nitrate uptake velocity (V_f), a measurement of the average rate at which a nutrient (or particle) moves from the water column to the stream benthos (Stream Solute Workshop, 1990). The uptake velocity is the most commonly used metric to compare nutrient uptake among streams because it corrects for stream velocity and stream width, two features with strong influence on the uptake length itself (Newbold et al., 1981; Stream Solute Workshop, 1990; Peterson et al., 2001).

A single-factor ANOVA was run to compare the mean difference in uptake velocities between the Sleepers River reference and treatment reaches before versus after wood removal, based on the three releases prior to wood removal and the two releases after wood removal. Before/after was the single factor in the ANOVA and differences in uptake velocity between SRN(w−) and SRS(ref) were the independent variables. Statistical analyses could not be conducted on nitrate uptake results from Crazy Brook at HBEF due to the single sampling period in summer prior to wood manipulation and the single sampling period after wood manipulation. Nevertheless, error around the uptake velocity estimate was estimated using the standard error values in the slope of the line fit to the negative log-linear decline in $^{15}N\text{-}NO_3$ (that was used to calculate uptake length). Using this approach we calculated the upper and lower 95% confidence intervals of uptake length during each release. The upper and lower bounds on the uptake length were then used to calculate the upper and lower 95% confidence intervals for each uptake velocity estimate with all other stream metrics remaining unchanged in the calculations. We then determined whether or not the 95% confidence intervals of uptake velocity before versus after manipulations overlapped in order to assess significance at an α of 0.05.

Solute transport

In order to evaluate changes in solute transport, we compared the rate at which the non-reactive tracer (sodium chloride) reached plateau in the two Sleepers River streams before and after wood removal from SRN(w−). Discharge in the two streams were similar to each other in 2005 (4.5 and 4.1 l s^{-1} for SRN(w−) and SRS(ref), respectively) and 2006 (6.2 and 6.1 l s^{-1} for SRN(w−) and SRS(ref), respectively) when solute transport was documented. So, although discharge can clearly influence the shape of breakthrough curves, the matched discharge values allowed us to conduct a comparison of the two streams before versus after wood removal. We conducted a two-

sample Kolmogorov–Smirnov test to compare the cumulative distribution functions of conductivity from the point in time at which the solute reached the most downstream station (T4) until it reached plateau (a constant concentration) at that site. Because background and plateau conductivities differed between streams and between sampling date, we normalized the cumulative increase in conductivity relative to plateau conductivities at each site. We compared distributions between SRN(w−) and SRS(ref) before and after wood removal. Without data on the tail of the solute release curve, we were unable to fully quantify transient storage. Fortunately, the curve for increases in the concentration of a non-reactive tracer is commonly correlated with transient storage and can therefore provide a point of comparison, if not a specific measure of the magnitude of a given change (Roberts et al., 2007b).

Results

Changes in stream habitat

Overall, wood removal resulted in a 90% decrease in large wood volume in SRN(w−) (Table 1). A total of 13 debris dams were removed and no dams remained immediately following wood removal (Table 1). The frequency and volume of large wood and debris dams changed somewhat from 2005 to 2006 in SRS(ref) but, these natural fluctuations were small relative to changes due to the wood manipulation (Table 1). As in SRN(w−), the volume of wood in CB(w−) was reduced by over 90% through the experimental manipulation (Table 1).

Riffle habitat increased in all three study reaches from 2005 to 2006 as judged by the number of transects that intersected riffles. In SRN(w−), where wood was removed, three of the cross sections initially classified as intersecting pool habitat were reclassified as intersecting riffle habitat. In the SRS(ref), only one site was reclassified from a pool to a riffle. At CB(w−) in the HBEF watershed, four transects shifted from intersecting pools to intersecting riffles (Table 1). Although discharge was slightly greater during the 2006 post-removal habitat assessments than in 2005 during the pre-treatment habitat assessments, the average of the maximum depth decreased in SRN(w−) following wood removal while remaining largely unchanged in SRS(ref) ($P < 0.01$ and $P = 0.25$ for SRN(w−) and SRS(ref), respectively, Table 2).

Mean size of inorganic substrates increased by about 50% in SRN(w−) less than 1 year after wood removal from a mean of 6.3 cm to a mean of 9.5 cm ($P = 0.03$; Fig. 2). In contrast, mean substrate size in SRS(ref) did not change significantly (means of 15.2 and 16.7 cm for 2005 and 2006, respectively; $P = 0.53$; Fig. 2). At CB(w−), mean substrate size also increased after wood removal (by about 30%), but the difference was not significant ($P = 0.25$; Fig. 2). Overall, while statistical comparisons could not be conducted, an evaluation of the proportion of sample points with substrate sizes greater than 5 cm in median diameter increased in all three reaches. We selected 5 cm as a substrate size that is relatively stable in these streams during summer and as such could support summer periphyton growth (hereafter "stable summer substrate"). The Sleepers River wood removal site, SRN(w−), had a much larger increase in stable

Table 2 Stream substrate and depths in 2005 and 2006, before and after wood manipulations

Stream	Years	Discharge during measurements (L/s)	Mean wetted width (m)	Mean of max depth (cm)	Overall mean depth (cm)
Sleepers River—North: wood removal	2005 (before)	4.7	1.5 (0.1)	15.2 (2.1)	6.9 (0.5)
	2006 (after)	6.5	1.1 (0.1)	10.4 (0.8)	4.8 (0.3)
Sleepers River—South: Reference (no removal)	2005 (before)	4.3	1.3 (0.2)	13.3 (1.2)	5.5 (0.4)
	2006 (after)	6.2	1.2 (0.1)	13.0 (0.9)	6.1 (0.4)
Crazy Brook: wood removal	2005 (before)	4.4	1.8 (0.2)	22.1 (3.3)	10.5 (0.8)
	2006 (after)	6.6	1.7 (0.1)	19.4 (3.4)	7.3 (0.7)

Values in parentheses indicate one standard error
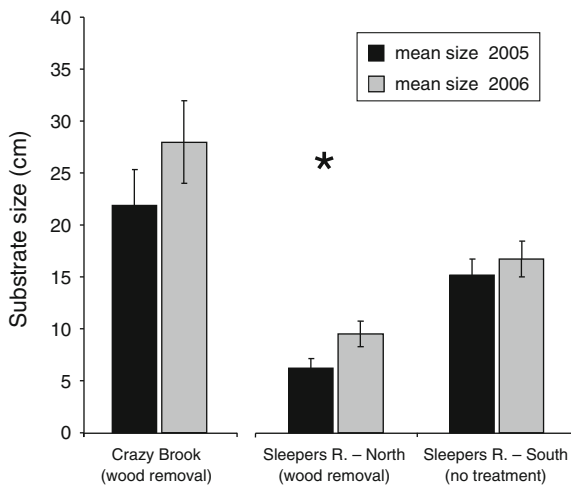
Fig. 2 Mean substrate size in each study stream before (*dark bars*) and after (*light bars*) wood manipulations. The reference site at Sleepers River was unaltered. *Error bars* represent one standard error. The *asterisk* represents a significant difference ($\alpha = 0.05$) in mean substrate size before versus after wood manipulation

summer substrates (11% increase) than SRS(ref) (3% increase; Table 1). The change in % stable summer substrate in CB(w−) was moderate (4%; Table 1).

Nitrate uptake

We documented clear and significant uptake of the ^{15}N-NO$_3$ in 10 of the 12 releases in this study (Appendix—Electronic supplementary material). In one of the two releases the relationship between the change ^{15}N-NO$_3$ relative to the change in conductivity over the length of the stream exhibited a clear decline but variability was higher than in the other releases. In the final release, there was a trend toward an overall decline in ^{15}N-NO$_3$ relative to the change in conductivity but the fit of the line was very poor and we concluded that there was "no measurable uptake" over the study reach for that release (Appendix— Electronic supplementary material). Overall, Stream nitrate uptake velocities at the Sleepers River sites ranged from "no measurable uptake" to 2.83 mm s^{-1}. Seasonal changes in uptake velocities for the monthly releases were comparable between the two streams in this first year (Fig. 3), indicating that SRS(ref) was a reasonable reference for SRN(w−). In contrast to our expectations, nitrate uptake velocities increased in SRN(w−) after wood removal relative to the

unmanipulated SRS(ref) ($P = 0.06$, $n = 5$ releases). There was also an increase in uptake rates following wood removal, however, the before versus after responses were muted relative to the uptake velocity results ($P = 0.6$ for ANOVA for Sleepers River comparison of differences before versus after wood removal in SRN(w−)). Consistent with results from Sleepers River, but in contrast to our expectations, nitrate uptake velocity in the HBEF wood removal stream (CB(w−)) was substantially greater in June 2006, following wood removal, than it was in the same period of 2005 (with no overlap in the 95% confidence intervals around the uptake estimates; Fig. 4).

Solute transport

Prior to wood removal, the Kolmogorov–Smirnov two-sample test indicated significant differences between SRN(w−) and SRS(ref) in their cumulative distribution curves for solute transport prior to wood removal, with time to plateau occurring much later in SRN(w−) than in SRS(ref) ($P = 0.05$; Fig. 5a). After wood removal the time to plateau was not significantly different in the two streams. Based on the change from significantly different solute transport curves before wood removal to nearly identical solute transport curves after wood removal, we can conclude that solute transport capacity was increased in SRN(w−) following wood removal.

Discussion

Our wood removal manipulations reduced the retention of fine organic and inorganic material and increased downstream solute transport rates, which we expected would lead to a decline in in-stream demand for nitrate. Somewhat surprisingly, however, summer nitrate uptake velocities increased following wood removal in this study. So in contrast to our initial hypothesis, these results suggest that in-stream wood loading would be unlikely to promote nitrate uptake in summer. Therefore long-term declines in total summer nitrate export from headwaters are unlikely to be attributable directly to increased wood loading to these streams.

In the year following wood removal, mean substrates size in SRN(w−) increased significantly while the mean substrates size in the reference stream
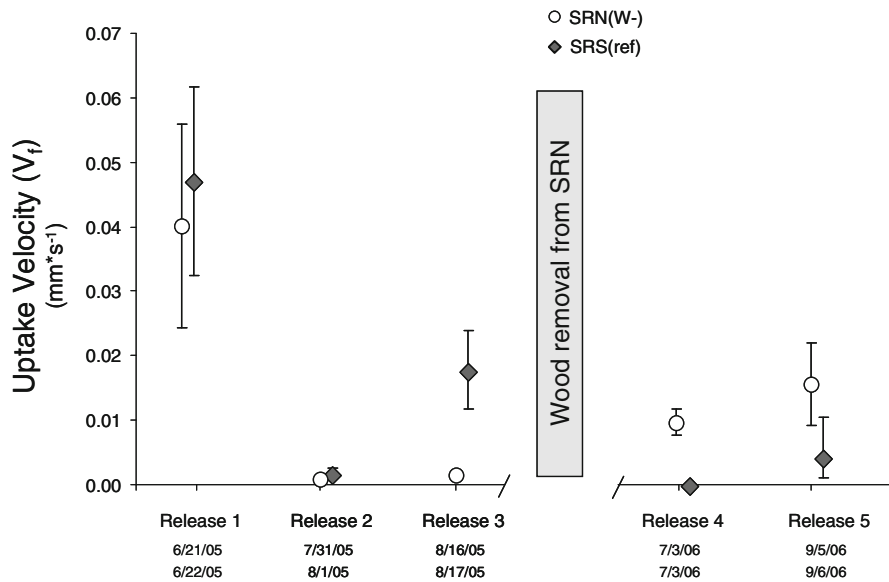
Fig. 3 Uptake velocities in Sleepers River streams before and after wood manipulation to Sleepers River—North. *Circles* represent values from Sleepers River—South (SRS) and *triangles* represent values from Sleepers River—North (SRN). The *upper and lower bounds* of the *error bars* represent uptake velocities calculated using the upper and lower 95% confidence interval values around the slope of the line fit to the log-linear loss of labels nitrate along a stream. The zero value for SRS during release four indicates no documented uptake of nitrate in our study reach
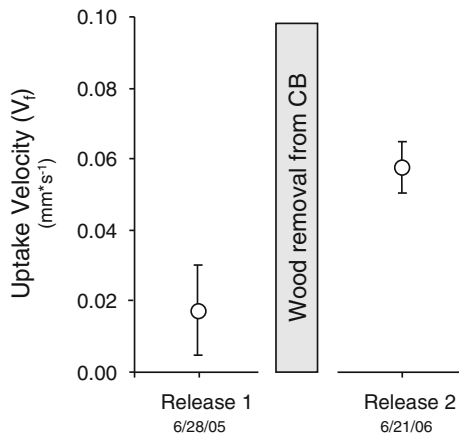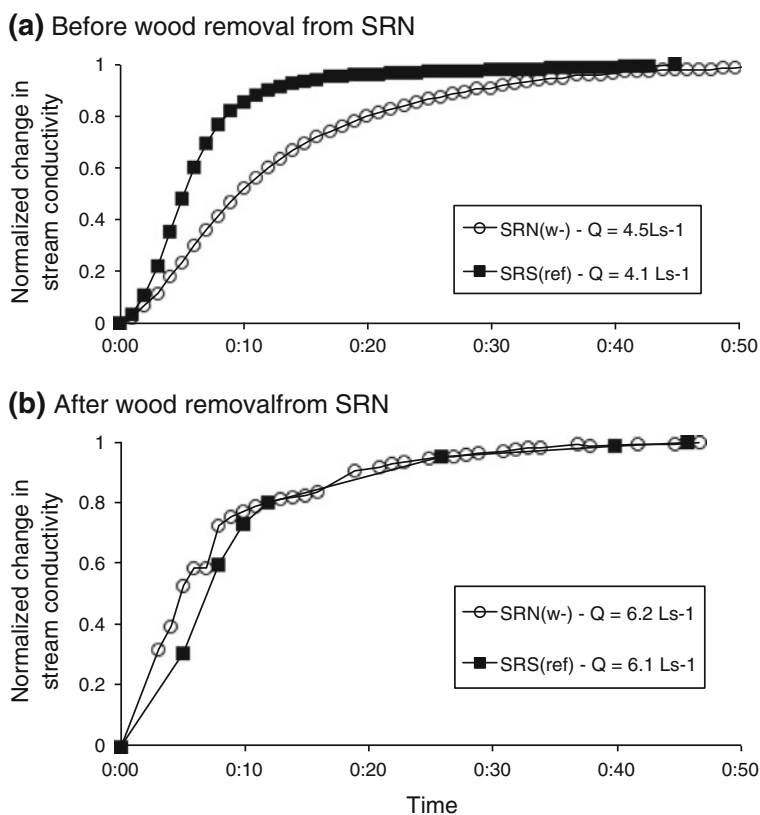

Fig. 4 Uptake velocities in Crazy Brook in the HBEF before and after wood manipulation. The *upper and lower bounds* of the *error bars* represent uptake velocities calculated using the upper and lower 95% confidence interval values around the slope of the line fit to the log-linear loss of labels nitrate along a stream

remained similar between 2005 and 2006. We hypothesize that the relative increase in nitrate uptake velocities observed in SRN(w−) in 2006 was related to this disproportionate shift in substrate size. Specifically, we speculate that an increase in the amount of

stable substrate in SRN as a result of wood removal allowed for an increase in summer periphyton biomass. This conclusion is based on a number of studies that have found positive relationships between availability of stable substrates, periphyton, and nutrient uptake (e.g., Munn & Meyer, 1990; Marti & Sabater, 1996; Hoellein et al., 2007). In a year-long assessment of nutrient uptake in streams in the upper peninsula of Michigan, Hoellein et al. (2007) found a strong positive correlation between an increase in large inorganic substrates and an increase in mean nutrient uptake velocities for nitrate, ammonium, and phosphate. The authors of this study noted that large stable substrates were key for periphyton and bryophyte growth and they suggest greater uptake by periphyton and moss as the primary mechanism for this response. Munn & Meyer (1990) and Marti & Sabater (1996) also found greater ammonium uptake in forested streams where large substrates were more abundant. And, in a study on similar headwater streams the HBEF, nutrient availability was been linked to periphyton biomass associated with cobble in streams (Bernhardt & Likens, 2004).

Forested streams in the northeastern US are widely recognized as net heterotrophic systems (Fisher &

Fig. 5 Cumulative distribution curves of the normalized change in conductivity over time at the downstream sampling station (T4) in each of the two Sleepers River streams starting from the time at which the salt reached the sampling station until conductivity values reached a plateau. The normalized change in conductivity divides the increase in conductivity above background at time *t* by the total change in conductivity at plateau. Discharge values were comparable in two streams both before and after wood removal from SRN(w−). A Kolmogorov–Smirnov analysis indicated significantly slower time to plateau in SRN(w−) than in SRS(ref) before wood removal but comparable times to plateau after wood removal

(a) Before wood removal from SRN

SRN(w-) - Q = 4.5Ls-1
SRS(ref) - Q = 4.1 Ls-1

(b) After wood removalfrom SRN

SRN(w-) - Q = 6.2 Ls-1
SRS(ref) - Q = 6.1 Ls-1

Time

Likens, 1973), but primary productivity occurs throughout the summer in these streams (Bernhardt et al., 2003, 2005a; Bernhardt & Likens, 2004), and anecdotal observations at long-term research sites in the region suggest that stream algae are becoming more common, particularly during the spring gap between earlier snowmelt and the leafing out of the canopy (D.C. Buso, personal communication). Greater primary production has been linked to greater uptake velocities of nitrate and ammonium in the Rocky Mountains of Wyoming (Hall & Tank, 2003) and greater uptake velocities of ammonium in the Catskill Mountains of New York (Newbold et al., 2006).

While we speculate that the same processes are responsible for the increases in nitrate demand in CB, we cannot suggest with the same degree of confidence that increasing substrate stability was responsible for the increase in nitrate demand in this site. The substrate size response to wood removal at Crazy Brook was generally consistent with wood removal responses in SRN(w−), however, changes in mean substrate size from 2005 to 2006 were not significant. And, while the number of permanent cross sections

occurring at sites with riffle versus pool habitat changed from five riffles and six pools in 2005 to nine riffles and two pools in 2006 following wood removal, this metric has no replication and therefore cannot be evaluated statistically. Results at CB are broadly consistent with the hypothesized mechanism for increasing nitrate uptake at SRN(w−), however, measurements of overall stream metabolism and gross primary production are needed to test directly whether wood removal enhances N uptake by stimulating periphyton growth in summer.

Seasonality is an important consideration in the interpretation of these results (Tank et al., 2000). The increase in nutrient uptake following wood removal that we observed reflects only the relative demand for nitrate in summer, not annual uptake or retention. Full consideration of the seasonal influences of wood on stream nutrient dynamics is clearly needed before broad conclusions regarding the role of wood in stream nitrogen uptake can be made. The summer uptake velocities measured here also represent potential seasonal nitrogen retention but they do not necessarily represent a true loss of biologically

available nitrogen from the aquatic environment; the dominant mechanism for the actual loss of biologically available nitrogen in streams is denitrification (e.g., Steinhart et al., 2000; Mulholland et al., 2008). The saturated sediments behind large wood and in woody debris dams provide optimal areas for denitrification. Indeed, results from incubations by Steinhart et al. (2000) suggest that denitrification potential is far greater in the sediments associated with debris dams than in other stream sediments within the HBEF. Therefore, although demand for nitrate increased following wood removal, the capacity to remove biologically reactive nitrogen from theses streams may not have changed significantly or maybe even decreased.

Nitrate uptake velocities measured in this study were generally comparable to those from other studies in the northeastern US and in other temperate deciduous forest stream, and although our study reaches were relatively short for the assessment of nitrate uptake in forested streams, in most cases the loss of $^{15}N-NO_3^-$ was clear. Uptake velocities at HBEF and Sleepers River were greater than those reported for the hardwood forest stream in the southern Appalachian Mountains studied by Mulholland et al. (2004), but lower than those reported from streams in the upper peninsula of Michigan (Hoellein et al., 2007). Bernhardt et al. (2002) and Warren et al. (2007) reported a range of uptake from *no detect* to 1.39 mm min^{-1}. Most of our uptake velocity measurements fall within this range, however, peak nitrate uptake velocities reported in the current study (HBEF: 3.45 mm min^{-1}, SR: 2.83 mm min^{-1}) exceed the maximum summer nitrate uptake velocities previously reported from these streams. Greater uptake velocity from a ^{15}N tracer release is consistent with results reported by Mulholland et al. (2004), in which they found that the uptake velocity estimated using a ^{15}N tracer was greater than the uptake velocity estimated from solute additions that increased nitrate concentrations far above background levels. While our findings did not support our initial expectation they are generally consistent with the earlier correlative work at HBEF, which found a positive relationship between phosphate uptake and stream wood volume, but no significant relationship between wood volume and uptake velocities of nitrate or ammonium (Warren et al., 2007).

Our study also supports previous work documenting the influence of wood on the retention of fine inorganic material, solute transport, total stream substrate composition, and the distribution of habitat units in northern forest headwater streams (Bilby & Likens, 1980; Bilby, 1981; Thompson, 1995; Ensign & Doyle, 2005). Overall though, in contrast to our initial expectations, this study did not provide evidence for a positive relationship between wood and nitrate uptake in northern hardwood forest streams during summer. These results suggest that wood accumulation in streams is unlikely to be responsible for trends in declining nitrate export from these systems (e.g., Bernhardt et al., 2005a; Bernal et al., 2012). As wood loading continues to increase in these streams over the next 100 years or more (Warren et al., 2009), the increase in retention of fine materials may ultimately reduce nitrate uptake velocities during spring and summer when periphyton growth on stable substrates would be at its peak. Our results highlight that the structure provided by large wood and debris dams can affect stream N dynamics, and the addition of wood to streams, as a result of either forest successional patterns (e.g., Likens & Bilby, 1982) or management practices, has the potential to alter seasonal and annual stream biogeochemical cycling through a number of pathways.

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