

## Effects of upland disturbance and instream restoration on hydrodynamics and ammonium uptake in headwater streams

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**Abstract.** Delivery of water, sediments, nutrients, and organic matter to stream ecosystems is strongly influenced by the catchment of the stream and can be altered greatly by upland soil and vegetation disturbance. At the Fort Benning Military Installation (near Columbus, Georgia), spatial variability in intensity of military training results in a wide range of intensities of upland disturbance in stream catchments. A set of 8 streams in catchments spanning this upland disturbance gradient was selected for investigation of the impact of disturbance intensity on hydrodynamics and nutrient uptake. The size of transient storage zones and rates of  $\text{NH}_4^+$  uptake in all study streams were among the lowest reported in the literature. Upland disturbance did not appear to influence stream hydrodynamics strongly, but it caused significant decreases in instream nutrient uptake. In October 2003, coarse woody debris (CWD) was added to ½ of the study streams (spanning the disturbance gradient) in an attempt to increase hydrodynamic and structural complexity, with the goals of enhancing biotic habitat and increasing nutrient uptake rates. CWD additions had positive short-term (within 1 mo) effects on hydrodynamic complexity (water velocity decreased and transient storage zone cross-sectional area, relative size of the transient storage zone, fraction of the median travel time attributable to transient storage over a standardized length of 200 m, and the hydraulic retention factor increased) and nutrient uptake ( $\text{NH}_4^+$  uptake rates increased). Our results suggest that water quality in streams with intense upland disturbances can be improved by enhancing instream biotic nutrient uptake capacity through measures such as restoring stream CWD.

**Key words:** catchment disturbance, stream restoration, hydrodynamics, transient storage, nutrient uptake, ammonium, coarse woody debris, military reservation.

Stream ecosystems are strongly influenced by inputs of water, sediment, nutrients, and organic material from their surrounding catchments (Hynes 1975). Headwater streams are important sites of nutrient and organic matter processing and retention and can alter the delivery of these constituents to downstream ecosystems (Alexander et al. 2000, Peterson et al. 2001). Stream nutrient uptake is influenced by hydrological, geomorphological, and biological factors, including ambient nutrient concentrations (Dodds et al. 2002, Webster et al. 2003), water residence times (Valett et al. 1996), water temperature (Butturini and Sabater 1998), stream size (Wollheim et al. 2001), benthic leaf litter (Mulholland et al. 1985), periphyton biomass (Martí et

al. 1997), and ecosystem metabolism rates (Hall and Tank 2003).

Stream hydrodynamic properties, in particular transient storage, are potential regulators of nutrient uptake (Grimm and Fisher 1984, Jones and Holmes 1996, Valett et al. 1996, Mulholland et al. 1997, Hall et al. 2002, Ensign and Doyle 2005). Transient storage is the temporary hydrologic retention of stream water that moves downstream more slowly than water in the main channel (Bencala and Walters 1983). Transient storage zones can occur in surface (e.g., backwaters and eddies) or subsurface (hyporheic) areas (Harvey et al. 1996). Modeling studies suggest that increasing transient storage may increase nutrient uptake (Mulholland and DeAngelis 2000). However, results from empirical studies have been equivocal. Nutrient uptake increased with transient storage in several studies (Valett et al. 1996, Mulholland et al. 1997, Gücker and Boëchat 2004, Ensign and Doyle 2005), but Hall et al. (2002) found that  $\text{NH}_4^+$  uptake was only weakly related to transient storage and that no

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relationship existed between transient storage and P uptake. Other studies have found no relationship between transient storage and nutrient uptake (Martí et al. 1997, Butturini and Sabater 1999, Webster et al. 2003, Niyogi et al. 2004), and Valett et al. (2002) found that P uptake velocity declined as transient storage increased.

Stream ecosystems are influenced in many ways by the natural input of coarse woody debris (CWD) from the surrounding catchment (Harmon et al. 1986). Debris dams can shape stream channel morphology by altering water velocity, streambed erosion patterns, and dissipating energy (Bilby and Likens 1980, Bilby 1981). CWD often increases hydrological heterogeneity by creating backwaters and eddies (Trotter 1990). CWD dams facilitate the deposition and retention of dissolved, fine particulate, and coarse particulate organic matter (DOM, FPOM, and CPOM, respectively) in streams (Naiman and Sedell 1979, Bilby and Likens 1980, Bilby 1981, Molles 1982, Smock et al. 1989, Trotter 1990, Ehrman and Lamberti 1992, Bilby and Bison 1998). Retention of CPOM by debris dams and the subsequent colonization by heterotrophic organisms may lead to increased nutrient uptake (e.g., P uptake rates increased in response to increases in benthic leaf litter in a woodland stream; Mulholland et al. 1985). N uptake rates associated with debris dams were faster than rates associated with other stream habitats (Munn and Meyer 1990), and N uptake lengths decreased (indicating an enhancement of N retention) in response to the experimental addition of logs to streams (Wallace et al. 1995).  $\text{NH}_4^+$  and  $\text{PO}_4^{3-}$  uptake velocities decreased after removal of CWD from a blackwater stream (Ensign and Doyle 2005).

Catchment land use affects instream habitats (e.g., abundance of CWD dams) as well as the rate at which water, nutrients, and organic materials are delivered to streams (Richards et al. 1996). Deforestation strongly affects the amount and timing of the delivery of water (e.g., Webster et al. 1990), sediment inputs (e.g., Gurtz et al. 1980), and nutrient export (e.g., Likens et al. 1970) to streams.  $\text{NH}_4^+$  uptake rates in forested stream reaches greatly exceeded rates in deforested stream reaches (Sweeney et al. 2004). Forest disturbance (previously logged catchments) increased organic matter export from streams (especially during storm events), and this increase was related primarily to a decrease in woody debris dams in disturbed streams (Webster et al. 1990). The presence of an intact riparian zone mitigates some landuse impacts (e.g., Lowrance et al. 1984, Gregory et al. 1991, Richards et al. 1996). However, less is known about how intense, localized upland disturbances impact streams with intact riparian zones.

Stream restoration projects have the potential to ameliorate some of the impacts of catchment-scale disturbances on hydrodynamics and nutrient cycling in streams, and restoration efforts have increased significantly in recent years (Bernhardt et al. 2005b). A wide variety of goals are stated for restoration projects (Bernhardt et al. 2005b) but, to be ecologically successful, these efforts must attempt to restore function as well as structure to streams (Palmer et al. 2005). Billions of dollars are spent restoring streams and rivers, but few studies have examined the effect of these restoration efforts on important stream functions such as hydrodynamics and nutrient cycling.

Our study addressed 2 questions concerning controls on stream hydrodynamics and nutrient uptake: 1) How does upland disturbance influence stream hydrodynamics and nutrient uptake in streams with intact riparian zones? 2) How effective are instream restorations (CWD additions) at mitigating these disturbances?

Fort Benning Military Installation (FBMI) provides a unique opportunity to examine the effects of upland disturbance on streams because of the broad range of disturbance intensities found within a small, relatively homogenous region (i.e., numerous stream reaches of comparable morphology, shading, and discharge can be found). Moreover, FBMI offers an excellent opportunity to evaluate the effects of instream restoration on stream ecosystem characteristics impacted by upland disturbance. Upland disturbance has led to decreased abundance of CWD in FBMI streams (Maloney et al. 2005), and low vegetative cover in highly disturbed catchments has increased stream flashiness and sediment load and decreased streambank stability, leading to increased burial of CWD (Maloney et al. 2005). CWD export may be greater in flashier, more disturbed streams because the lengths of pieces of CWD are smaller than widths of FBMI streams (Maloney et al. 2005). The combined effects of increased burial and export of CWD are that the relative abundance of CWD ( $\text{m}^2$  CWD/ $\text{m}^2$  streambed) decreases with increased disturbance intensity (Maloney et al. 2005). Our paper presents results from an instream restoration project involving CWD additions to several streams along the upland disturbance gradient in an attempt to restore hydrodynamic and structural complexity to enhance biotic habitat and nutrient cycling.

## Methods

### *Study site*

Eight 1<sup>st</sup>- to 2<sup>nd</sup>-order streams on the FBMI were selected for study (Fig. 1). The study streams are

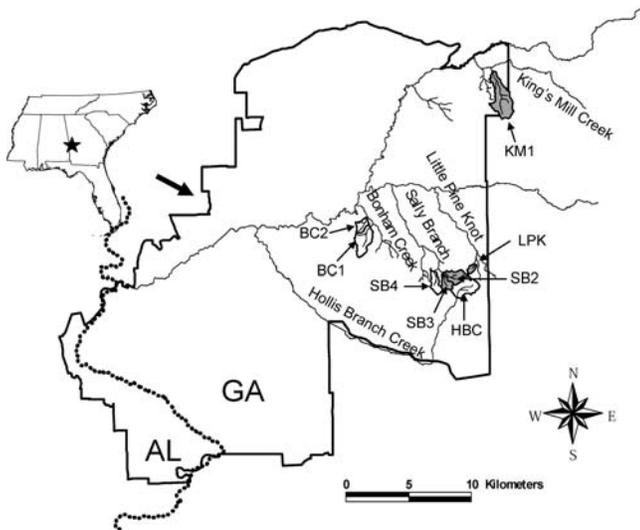


FIG. 1. Study catchments on the Fort Benning Military Installation near Columbus, Georgia. Study catchments include 2 tributaries of Bonham Creek (BC1 and BC2), 3 tributaries of Sally Branch Creek (SB2, SB3, and SB4), 1 tributary of Little Pine Knot Creek (LPK), 1 tributary of King's Mill Creek (KM1), and Hollis Branch Creek (HBC). GA = Georgia, AL = Alabama.

typical low-gradient (range = 0.8–5.1%, mean = 2.1%; Maloney et al. 2005), sandy Southeastern Hills and Plains streams (Felley 1992) with generally intact deciduous riparian canopies (mean summer canopy cover = 94%; Maloney et al. 2005) dominated by blackgum (*Nyssa sylvatica*) and other mesic species. The streams drain catchments ranging in area from 33 to 369 ha within the Southeastern Hills and Plains geophysical province of west-central Georgia (Fig. 1, Table 1; Houser et al. 2005).

The geology and landuse history of the study catchments are detailed in Maloney et al. (2005). The dominant land use in the area was row-crop agriculture and pasture before the land was purchased by the US military in 1918 and 1941/1942 (Kane and Keeton 1998). Forest has been allowed to regrow in many areas of FBMI, and land cover in these areas now consists primarily of oak–pine and southern mixed forest. The underlying soils are sand or sandy clay loam (Omernik 1987). Some areas of the FBMI are used for military training involving infantry and heavy-equipment vehicles. These activities have resulted in some catchments having localized areas with high levels of vegetation and soil disturbance leading to high erosion rates and streams with unstable, organic-poor sediments (Maloney et al. 2005). Other catchments have remained essentially undisturbed since their purchase by the military.

### Disturbance intensity

Disturbance intensity for each stream catchment was quantified by Maloney et al. (2005). They determined land use in each catchment from geographic information system (GIS) data sets (streams: 1:24,000, 1993; soils: 1:20,000, 1998; roads: 10 m, 1995), available digital orthophotography (1:5000, July 1999), digital elevation models (1:24,000, grid size = 10 m, 1993), and Landsat imagery (28.5-m resolution, July and December 1999) provided by Fort Benning personnel and available on the US Department of Defense Strategic Environmental Research and Development Program Environmental Management Program data repository (<https://sempdata.erdc.usace.army.mil>). Disturbance intensity for each catchment was defined as the % of catchment area covered by unpaved roads or bare ground on slopes >5%. At FBMI, unpaved roads mostly are roads and trails used by tracked military vehicles, and much of the bare ground was created by military training using these tracked vehicles. The areas of soil and vegetation disturbance are located mostly in upland areas away from the perennial streams. These upland areas become hydrologically connected to perennial streams via ephemeral drainages that discharge to the perennial stream during storms. The disturbance intensity of the 249 2<sup>nd</sup>-order catchments on the FBMI ranged from 0 to 17% (excluding the 4 most disturbed catchments). Our 8 study streams were in catchments that spanned most of this available range (~3.2–13.7%; Table 1). The relative abundance of submerged CWD decreased significantly (linear regression:  $r^2 = 0.91$ ,  $p < 0.0001$ , excluding BC1 [see below]) with increased disturbance in our study streams, and % areal coverage of CWD ranged from ~3.1 to ~8.9% (except in BC1 where % areal coverage ≈12.6%; Table 1) before CWD additions (see below).

### CWD and stream restorations

CWD was added to streams in 4 of the 8 study catchments (KM1, SB2, SB3, and LPK) that spanned a range of disturbance intensities (~4.6–11.3%; Table 1). Riparian trees used for CWD additions (*N. sylvatica* in KM1, SB2, and SB3, and *Quercus alba* in LPK) were felled and sectioned during August 2003 and allowed to dry for 2 to 3 mo before deployment. Ten CWD additions (~10 m apart) were made over a 100-m reach in each of the 4 streams. Individual CWD additions consisted of 3 logs (~10–20 cm in diameter, 1–2 m long) anchored in the streambed with rebar stakes. CWD additions were not intended to create pool environments, so logs did not span the entire width of the stream and were positioned in a zigzag

TABLE 1. Disturbance intensity, area of study catchments at Fort Benning Military Installation, and % areal coverage of submerged coarse woody debris (CWD) in study streams in October 2003 (before CWD addition) and November 2003 (after CWD addition). See Fig. 1 for stream abbreviations.

Stream	Disturbance intensity (% catchment)	Catchment area (ha)	CWD (% areal coverage)	
			Before	After
Control streams				
BC2	3.15	75	8.92	8.92
HBC	6.62	215	6.34	6.34
BC1	10.46	210	12.62	12.62
SB4	13.65	100	3.11	3.11
Manipulated streams				
KM1	4.63	369	8.60	12.09
SB2	8.12	123	7.30	11.62
SB3	10.49	72	3.70	8.89
LPK	11.26	33	3.79	6.90

arrangement. CWD additions increased the % areal coverage of CWD by ~3.1% (LPK) to ~5.2% (SB3) and resulted in coverage of 6.9% (LPK) to ~12.1% (KM1) of the streambed surface area in the restored streams (Table 1).

#### Field and laboratory methods

Conservative tracer (NaCl) and nutrient ( $\text{NH}_4\text{Cl}$ ) injections were done to determine hydrodynamic properties and nutrient uptake before and ~1 mo after CWD additions were completed (Table 2). Conservative tracer injections were designed to increase specific conductance ~15 to ~45  $\mu\text{S}/\text{cm}$  above background (Table 2), while nutrient injections increased  $[\text{NH}_4^+]$  between ~30 and ~77  $\mu\text{g N}/\text{L}$  (Table 3). Injectate solutions were introduced to surface water at a point of natural constriction as a steady addition of  $\text{Cl}^-$  (as NaCl) or  $\text{NH}_4^+$  (as  $\text{NH}_4\text{Cl}$ ) by a battery-powered fluid metering pump (Fluid Metering, Syosset, New York) over a 1.5- to 2-h period. Specific conductance was monitored with a YSI Model 55 Conductivity Meter (YSI, Yellow Springs, Ohio) at 60-s intervals at 2 stations downstream from the injection site. The upstream sampling site was located  $\geq 10$  m below the injection site (after complete mixing had occurred) and the downstream site was located between 45 and 115 m (Table 2) downstream of the upstream sampling location. The injection was continued until specific conductance had clearly reached a plateau (specific conductance did not increase  $>0.1$   $\mu\text{S}/\text{cm}$  over 5 min).

Triplicate water samples were collected for back-

ground  $[\text{NH}_4^+]$  analysis at the upstream and downstream sampling sites before the  $\text{NH}_4\text{Cl}$  tracer injections. Stream water was collected with a 30-mL plastic syringe and passed through Whatman GF/F glass fiber (0.7- $\mu\text{m}$  nominal cut-off) filters into acid-washed, stream-rinsed 30-mL Nalgene sample bottles. After specific conductance clearly had reached a plateau during the injection, 5 replicate filtered water samples were collected for  $[\text{NH}_4^+]$  analyses at the upstream and downstream sampling sites following the same procedure as above. Filtered samples were stored frozen prior to analysis at Oak Ridge National Laboratory.  $[\text{NH}_4^+]$  was determined by phenate colorimetry (APHA 1992) using an autoanalyzer (Bran Lubbe Model AA3).

#### Characterization of physical variables and basic hydrodynamics

Basic physical measurements made at each site included water temperature (at upstream and downstream sampling locations), reach length (distance between upstream and downstream sampling locations), and stream wetted width (5-m intervals along the study reach). Reach travel time was calculated as the difference between the times at which the upstream and downstream station specific conductance breakthrough curves reached the point of maximum rate of increase per unit time. Average stream surface-water velocity ( $u$ ) was determined by dividing reach length by reach travel time. Stream discharge at each station ( $Q_i$ ) was determined from the increase in streamwater specific conductance during the injection using the equation

$$Q_i = \frac{Q_{\text{pump}} \times \text{Cond}_{\text{inj}}}{(\text{Cond}_i - \text{Cond}_b)}, \quad [1]$$

where  $Q_{\text{pump}}$  is the injection rate of the NaCl solution,  $\text{Cond}_{\text{inj}}$ ,  $\text{Cond}_i$ , and  $\text{Cond}_b$  represent the specific conductance of the injection solution, the specific conductance at station  $i$  during the injection, and the background specific conductance at station  $i$  before the injection, respectively. Mean depth ( $d$ ) was calculated using the equation

$$d = \frac{Q}{uw}, \quad [2]$$

where  $Q$  is the stream discharge and  $w$  is the mean wetted width.

#### Hydrodynamic characterization

Specific conductance values at each station were corrected for background concentrations by subtracting pre-injection values from all measurements. Solute

TABLE 2. Physicochemical data for all conservative tracer and nutrient injections done before and after addition of coarse woody debris (CWD) to manipulated streams. NaCl and NH<sub>4</sub>Cl injections were conducted separately before CWD addition. Therefore, the data for each are reported in separate rows. *w* = mean wetted width, *d* = mean depth, *Q* = discharge, *u* = mean surface-water velocity, Cond = specific conductance,  $\Delta C_{\text{cond}} = \text{Cond}_{\text{plateau}} - \text{Cond}_{\text{initial}}$ . See Fig. 1 for stream abbreviations.

Stream	Before/after	Injection date	Reach length (m)	<i>w</i> (m)	<i>d</i> (m)	<i>Q</i> (L/s)	<i>u</i> (m/s)	Water temperature (°C)	Cond (µS/cm)	$\Delta C_{\text{cond}}$ (µS/cm)
Control										
BC2	Before (NaCl)	15 October	45	0.83	0.11	2.7	0.03	17.9	18.9	46.8
	Before (NH <sub>4</sub> <sup>+</sup> )	29 October								
HBC	After	19 November	110	0.90	0.15	7.3	0.05	17.4	24.5	28.9
	Before (NaCl)	15 October								
	Before (NH <sub>4</sub> <sup>+</sup> )	28 October								
BC1	After	18 November	60	1.93	0.13	15.2	0.06	18.8	14.0	21.0
	Before (NaCl)	16 October								
	Before (NH <sub>4</sub> <sup>+</sup> )	29 October								
SB4	After	19 November	80	1.28	0.18	11.5	0.04	17.3	26.4	27.8
	Before (NaCl)	15 October								
	Before (NH <sub>4</sub> <sup>+</sup> )	29 October								
	After	20 November		1.55	0.06	9.0	0.09	15.6	20.2	31.1
Manipulated										
KM1	Before (NaCl)	13 October	105	2.03	0.14	31.2	0.11	18.8	14.4	15.6
	Before (NH <sub>4</sub> <sup>+</sup> )	27 October								
	After	17 November								
SB2	After	17 November	115	2.21	0.15	23.0	0.07	16.6	11.7	21.2
	Before (NaCl)	14 October								
	Before (NH <sub>4</sub> <sup>+</sup> )	28 October								
SB3	After	18 November	100	1.82	0.10	13.7	0.08	18.2	19.0	18.8
	Before (NaCl)	14 October								
	Before (NH <sub>4</sub> <sup>+</sup> )	28 October								
LPK	After	18 November	65	1.34	0.07	5.3	0.06	16.9	23.1	34.8
	Before (NaCl)	14 October								
	Before (NH <sub>4</sub> <sup>+</sup> )	28 October								
	After	19 November		1.07	0.05	4.8	0.09	17.5	16.0	32.3

TABLE 3. Summary data for nutrient (NH<sub>4</sub><sup>+</sup>) injection experiments done before and after addition of coarse woody debris to manipulated streams.  $\Delta C_{\text{NH}_4} = [\text{NH}_4^+]_{\text{plateau}} - [\text{NH}_4^+]_{\text{initial}}$ , *k* = fractional NH<sub>4</sub><sup>+</sup> uptake rate from water per unit distance, *V<sub>f</sub>* = NH<sub>4</sub><sup>+</sup> uptake velocity, *U* = mass removal rate of NH<sub>4</sub><sup>+</sup> from water per unit area. See Fig. 1 for stream abbreviations.

Stream	Before/after	Upstream [NH <sub>4</sub> <sup>+</sup> ] (µg N/L)	$\Delta C_{\text{NH}_4}$ (µg/L)	<i>k</i> (/m)	<i>V<sub>f</sub></i> (mm/s)	<i>U</i> (µg NH <sub>4</sub> <sup>+</sup> -N m <sup>-2</sup> s <sup>-1</sup> )
Control						
BC2	Before	6.6	59.3	0.0075	0.030	1.71
	After	4.1	73.3	0.0037	0.031	2.22
HBC	Before	3.1	42.4	0.0024	0.014	0.60
	After	9.4	44.2	0.0026	0.017	0.71
BC1	Before	1.8	39.8	0.0047	0.026	1.03
	After	5.3	47.4	0.0028	0.026	1.18
SB4	Before	19.2	29.6	0.0000	0.000	0.00
	After	17.9	51.8	0.0000	0.000	0.00
Manipulated						
KM1	Before	3.7	38.6	0.0016	0.023	0.83
	After	4.7	46.6	0.0029	0.030	1.35
SB2	Before	6.1	49.6	0.0006	0.006	0.28
	After	9.0	41.9	0.0018	0.014	0.56
SB3	Before	6.4	47.9	0.0027	0.013	0.58
	After	3.4	43.2	0.0039	0.016	0.68
LPK	Before	4.1	55.2	0.0014	0.005	0.27
	After	5.2	77.4	0.0021	0.013	0.92

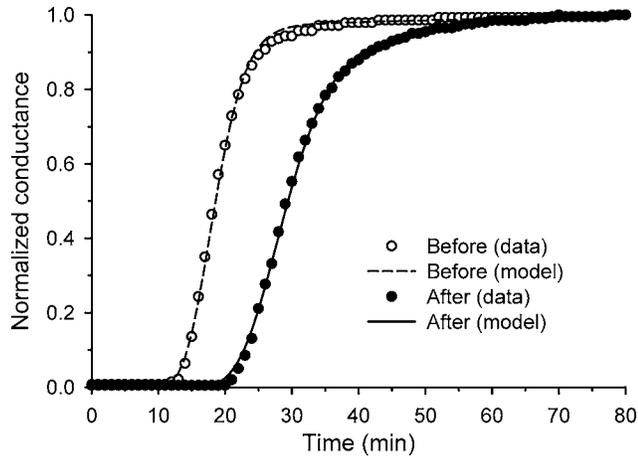


FIG. 2. Observed and modeled normalized conductance at the downstream sampling station of Kings Mill Creek during conservative tracer injections before (13 October 2003) and after (17 November 2003) addition of coarse woody debris to the stream.

transport was modeled by the stochastic version (Hart 1995) of the transient storage model, which is essentially equivalent to the partial differential equation formulation (Bencala and Walters 1983). In this version, parameter estimation relies on an automated minimum sum of squares method (Hart et al. 1999) and on visual inspection (Thomas et al. 2003). The 1<sup>st</sup>-order decay coefficients ( $\lambda_c$  and  $\lambda_s$ ) were set to 0 when calculating transient storage zone characteristics because  $\text{Cl}^-$  and, therefore, specific conductance were assumed to behave conservatively.

The stochastic version of the transient storage model (Hart 1995) provided a good fit to the conservative tracer data for each stream before and after addition of CWD. For example, Fig. 2 shows the normalized conductance (equal to specific conductance at time  $t$  divided by steady-state specific conductance) tracer curve and the model fit for NaCl injections conducted in KM1 before (13 October 2003) and after (17 November 2003) addition of CWD.

Several metrics useful in assessing general hydrodynamic and transient storage zone characteristics were calculated. These metrics included main channel cross-sectional area ( $A$ ;  $\text{m}^2$ ), transient storage zone cross-sectional area ( $A_s$ ;  $\text{m}^2$ ), relative size of the transient storage zone ( $A_s/A$ ), mean surface-water velocity ( $u = Q/A$ ;  $\text{m/s}$ ), and the hydraulic retention factor ( $R_t = A_s/Q$ ;  $\text{s/m}$ ), which represents the time water spends in the transient storage zone for each meter advected downstream (Morrice et al. 1997). The fraction of the median travel time attributable to transient storage was calculated over a standardized length of 200 m ( $F_{\text{med}}^{200}$ ; Runkel 2002).

#### Calculation of $\text{NH}_4^+$ uptake parameters

$[\text{NH}_4^+]$  was corrected for dilution using the conservative tracer additions and background  $[\text{NH}_4^+]$  from pre-injection data (as in Webster and Ehrman 1996). Total  $\text{NH}_4^+$  uptake rate, expressed as a fractional uptake rate from water per unit distance ( $k$ ,  $/\text{m}$ ), was calculated using the equation

$$k = \frac{(\ln([\text{NH}_4^+]_{\text{UP}}) - \ln([\text{NH}_4^+]_{\text{DN}}))}{l}, \quad [3]$$

where  $l$  is the reach length and  $[\text{NH}_4^+]_{\text{UP}}$  and  $[\text{NH}_4^+]_{\text{DN}}$  are the background-corrected  $[\text{NH}_4^+]$  of the upstream and downstream stations (Newbold et al. 1981, 1983, Stream Solute Workshop 1990). The inverse of  $k$  is the uptake length ( $S_w$ ;  $\text{m}$ ) of  $\text{NH}_4^+$  (or the average distance an  $\text{NH}_4^+$  ion travels in the water column before it is removed or transformed by physical or biological processes; Newbold et al. 1981).

$S_w$  and  $k$  are often functions of  $Q$  and are difficult to use when comparing nutrient uptake from streams of different sizes. Uptake velocity (or mass-transfer coefficient;  $V_f$  [ $\text{m/s}$ ]) corrects for the effects of depth and water velocity on nutrient uptake (Davis and Minshall 1999) and represents the benthic demand for a nutrient relative to its concentration in the water column (Hall et al. 2002).  $V_f$  was calculated from  $k$  using the equation

$$V_f = kud, \quad [4]$$

where  $u$  is the mean surface-water velocity and  $d$  is the mean water depth (Stream Solute Workshop 1990).

Total  $\text{NH}_4^+$  uptake also was calculated as a mass removal rate from water per unit area ( $U$ ;  $\mu\text{g NH}_4^+\text{-N m}^{-2} \text{s}^{-1}$ ) using the equation

$$U = \frac{Fk}{w}, \quad [5]$$

where  $F$  is the mean flux of  $\text{NH}_4^+\text{-N}$  in stream water in the experimental reach (equal to the product of mean  $[\text{NH}_4^+]$  and mean  $Q$ ) and  $w$  is the mean wetted width of the stream reach (Newbold et al. 1981, 1983).

Nutrient addition experiments do not permit measurement of ambient uptake rates because nutrient enrichments generally lead to underestimates of  $k$  and overestimates of  $U$  occurring at ambient conditions (Mulholland et al. 1990, 2000a, 2002, Dodds et al. 2002, Payn et al. 2005). We attempted to limit this problem by using low levels of enrichment that were similar between time periods (before and after CWD addition) within a given stream and among streams (Table 3). Enrichment concentrations also were within the observed range of ambient and storm concentrations observed in the study streams (Houser et al. 2006).

These precautions were used to permit a useful comparison of  $\text{NH}_4^+$  uptake among our study streams.

### Statistical analysis

The effects of disturbance intensity (% catchment disturbed) on stream hydrodynamic characteristics ( $A_s$ ,  $A_s/A$ ,  $F_{\text{med}}^{200}$ ,  $u$ , and  $R_h$ ) and  $\text{NH}_4^+$  uptake metrics ( $k$ ,  $V_f$ , and  $U$ ) were tested by regression analysis. The effect of  $u$  on  $k$  and the effect of % cover of CWD and  $A_s/A$  on  $\text{NH}_4^+ V_f$  also were examined using regression analysis.

A modified before–after control–intervention (BACI; Green 1979) approach (in which both control and intervention [CWD addition] locations were replicated; Underwood 1994) was used to examine the effects of CWD additions on stream hydrodynamic and nutrient uptake characteristics. After:before [A:B] ratios were calculated for each hydrodynamic and  $\text{NH}_4^+$  uptake metric in each stream. All ratios were  $\sqrt{x}$  transformed. The effects of CWD addition on each variable were evaluated by comparing the transformed A:B ratios of the 4 control streams to the transformed A:B ratios of the 4 intervention (= manipulation [CWD addition]) streams using the Satterthwaite approximation of the  $t$ -test. All statistical analyses were conducted using SAS (version 8.0; SAS Institute, Cary, North Carolina).

## Results

Most physical and chemical variables were similar before and after CWD addition within each stream. The range of wetted widths (0.83–2.21 m) and mean depths (0.04–0.18 m) was relatively narrow (Table 2).  $Q$  ranged from 2.7 L/s (BC2) to 31.2 L/s (KM1) (Table 2).  $Q$  increased in some streams and decreased in others after CWD addition. The ranges of background specific conductance and water temperatures were similar during injections made before (13.1–23.3  $\mu\text{S}/\text{cm}$  and 14.0–20.3°C, respectively) and after (11.7–26.4  $\mu\text{S}/\text{cm}$  and 15.6–18.8°C, respectively) CWD addition (Table 2).

### Relationships with disturbance intensity gradient

**Hydrodynamic variables.**—As was the case in previous studies (Houser et al. 2005, Maloney et al. 2005), one stream (BC1) was omitted from all regression analyses. This catchment had a notably broader, flatter forested floodplain that appeared to protect the stream from effects of disturbance and had received some restoration of upland areas before our study (Houser et al. 2005, Maloney et al. 2005).

No strong relationships were observed between

stream hydrodynamics and disturbance intensity before CWD additions (Table 4).  $A_s$  ranged from 0.006 to 0.024  $\text{m}^2$ .  $A_s$  appeared to decrease with disturbance intensity (Fig. 3A), but the relationship was not statistically significant ( $p = 0.13$ ).  $A_s/A$  ranged from 0.080 to 0.333 (Table 4, Fig. 3B), and  $F_{\text{med}}^{200}$  ranged from 0.072 to 0.250 (Table 4, Fig. 3C). Mean  $u$  ranged from 0.3 m/s to 1.5 m/s (Table 4, Fig. 3D), and  $R_h$  ranged from 0.75 s/m to 7.44 s/m (Table 4, Fig. 3E).

**$\text{NH}_4^+$  uptake characteristics.**—Before CWD additions,  $[\text{NH}_4^+]$  ranged from 1.8 to 19.2  $\mu\text{g N}/\text{L}$  (Table 3) and was not related to disturbance intensity. However,  $\text{NH}_4^+$  uptake decreased with disturbance intensity.  $k$  ranged between 0 (values below detection were assumed to be 0) and 0.0075/m,  $V_f$  ranged from 0 to 0.030 mm/s, and  $U$  ranged from 0 to 1.71  $\mu\text{g NH}_4^+-\text{N m}^{-2} \text{ s}^{-1}$  (Table 3). All 3 metrics decreased as disturbance intensity increased ( $k = -0.0005[\text{disturbance intensity}] + 0.0061$ ,  $r^2 = 0.47$ ,  $p = 0.09$ ;  $V_f = -0.0028[\text{disturbance intensity}] + 0.0348$ ,  $r^2 = 0.88$ ,  $p = 0.002$ ;  $U = -0.13[\text{disturbance intensity}] + 1.66$ ,  $r^2 = 0.73$ ,  $p = 0.01$ ; Fig. 4A–C). All 3 uptake metrics suggest that the ability of FBMI streams to remove  $\text{NH}_4^+$  from the water column decreases as disturbance increases.

$k$  was not related  $Q$ , but it decreased strongly as  $u$  increased ( $r^2 = 0.87$ ,  $p = 0.002$ ). Because most of the variation in  $k$  was a function of  $u$  and  $V_f$  corrects for differences in  $u$  and mean depth,  $V_f$  appeared to be a more appropriate comparative metric of  $\text{NH}_4^+$  uptake than  $k$  in these streams. Both Davis and Minshall (1999) and Hall et al. (2002) came to similar conclusions. However, in our study, variation in  $k$  was the result of  $u$  alone and not  $Q$  or specific discharge ( $Q/w$ ) as seen previously.  $V_f$  was positively related to the relative abundance of submerged CWD ( $V_f = 0.0031[\text{CWD}] - 0.0082$ ,  $r^2 = 0.76$ ,  $p = 0.005$ ; Fig. 5A) but not to  $A_s/A$  ( $p > 0.20$ ; Fig. 5B).

### Effects of CWD addition

**Hydrodynamic variables.**—Hydrodynamic variables did not change appreciably between before and after sampling periods in control streams (all A:B ratios  $\approx 1$ ; Fig. 6, open bars). In contrast, all hydrodynamic variables changed after CWD additions in the manipulated streams (Table 4).  $A_s$ ,  $A_s/A$ ,  $F_{\text{med}}^{200}$ , and  $R_h$  increased strongly (A:B ratios  $> 1$ ), and  $u$  decreased (A:B ratio  $< 1$ ) in manipulated streams (Table 4, Fig. 6). The differences in A:B ratios between control and manipulated streams were significant ( $p < 0.05$ ) or marginally significant ( $0.05 < p < 0.10$ ) for all hydrodynamic variables (see Fig. 6 for individual  $p$ -values). These results suggest that CWD addition decreased the rate at which water moved through

TABLE 4. Hydrodynamic properties obtained from conservative tracer (NaCl) injections done before and after addition of coarse woody debris to manipulated streams.  $Q$  = discharge,  $u$  = mean surface-water velocity,  $A$  = stream channel cross-sectional area,  $A_s$  = transient storage zone cross-sectional area,  $A_s/A$  = relative size of transient storage zone,  $F_{\text{med}}^{200}$  = fraction of median travel time from transient storage over a standardized length of 200 m,  $R_h$  = hydraulic retention factor. See Fig. 1 for stream abbreviations.

Stream	Before/after	$Q$ (L/s)	$u$ (m/s)	$A$ (m <sup>2</sup> )	$A_s$ (m <sup>2</sup> )	$A_s/A$	$F_{\text{med}}^{200}$	$R_h$ (s/m)
Control								
BC2	Before	2.7	0.03	0.089	0.020	0.226	0.184	7.44
	After	7.3	0.05	0.137	0.026	0.194	0.162	3.63
HBC	Before	15.8	0.07	0.215	0.021	0.100	0.091	1.36
	After	15.2	0.06	0.244	0.028	0.114	0.103	1.83
BC1	Before	6.9	0.04	0.176	0.021	0.117	0.105	2.98
	After	11.5	0.04	0.236	0.033	0.141	0.123	2.88
SB4	Before	7.1	0.14	0.051	0.017	0.333	0.250	2.39
	After	9.0	0.09	0.097	0.026	0.267	0.211	2.88
Manipulated								
KM1	Before	31.2	0.11	0.294	0.024	0.080	0.072	0.75
	After	23.0	0.07	0.339	0.085	0.250	0.200	3.69
SB2	Before	14.6	0.15	0.099	0.018	0.180	0.153	1.22
	After	13.7	0.08	0.176	0.039	0.220	0.180	2.82
SB3	Before	5.6	0.10	0.059	0.010	0.177	0.150	1.86
	After	5.3	0.06	0.093	0.026	0.281	0.219	4.91
LPK	Before	3.0	0.11	0.028	0.006	0.225	0.184	2.06
	After	4.8	0.09	0.054	0.035	0.640	0.390	7.26

streams by decreasing  $u$  and increasing transient storage.

*NH<sub>4</sub><sup>+</sup> uptake metrics.*— $\text{NH}_4^+$  uptake metrics did not change in any consistent manner between before and after sampling periods in control streams, but all 3  $\text{NH}_4^+$  uptake metrics increased after CWD addition in manipulated streams (Table 3).  $k$  decreased strongly in 2 control streams (51% and 41% in BC2 and BC1, respectively), whereas  $k$  increased in all 4 manipulated streams (45–196%) after CWD addition (Table 3). Eighty percent of the after-manipulation variance in  $k$  was explained by a strong negative relationship with  $u$  ( $p = 0.007$ ), further indicating that  $V_f$  is a more robust comparative metric of  $\text{NH}_4^+$  uptake than  $k$  in FBMI streams.  $V_f$  increased 23 to 154% in manipulated streams after CWD addition, and the increases were greater in manipulated streams than in any control stream (Table 3).  $U$  increased 61 to 235% in manipulated streams after CWD addition, and the increases were greater in all manipulated streams (except SB3) than in any control stream (Table 3).

Mean A:B ratios for all 3 nutrient uptake metrics were  $\sim 1$  in control streams (Fig. 7), whereas mean A:B ratios for all 3 nutrient uptake metrics were  $\sim 2$  in manipulated streams (Fig. 7). The A:B ratio for  $k$  was significantly greater in manipulated than in control streams ( $t$ -test,  $p = 0.01$ ). Differences in A:B ratios of  $V_f$  and  $U$  for manipulated and controls streams were only marginally significant ( $t$ -test,  $0.05 < p < 0.1$ ) because  $V_f$  and  $U$  in one of the manipulated streams (SB3)

changed very little after CWD addition and our sample size was small (4 streams per treatment). All 3 metrics suggest that CWD additions resulted in an increase in  $\text{NH}_4^+$  uptake in these streams.

## Discussion

### *Relationships with disturbance intensity gradient*

Transient storage zones were small in FBMI streams.  $A_s$  and  $A_s/A$  values for FBMI streams were comparable to values reported for Walker Branch, Tennessee (Mulholland et al. 1997, Hart et al. 1999), and Aspen Creek and Rio Calaveras, New Mexico (Morrice et al. 1997), but they were lower than values reported for other headwater streams (Table 5). A strong relationship between  $A_s/A$  and discharge (either  $Q$  or  $Q/w$ ) has been observed in several studies (Valett et al. 1996, Butturini and Sabater 1999, Hall et al. 2002). However, as in several New Zealand tussock streams (Niyogi et al. 2004),  $A_s/A$  was not significantly related to  $Q$ ,  $Q/w$ , or  $u$  ( $p > 0.1$  in all cases) in FBMI streams.

No other published studies have directly examined the effect of upland disturbance on transient storage, but several studies have investigated general hydrodynamic responses to the abundance of CWD. These studies have shown that as CWD abundance decreases (as was seen along our upland disturbance gradient), hydrologic retention decreases because  $u$  increases and hydrodynamic heterogeneity decreases (e.g., backwaters and eddies became less common; Trotter 1990,

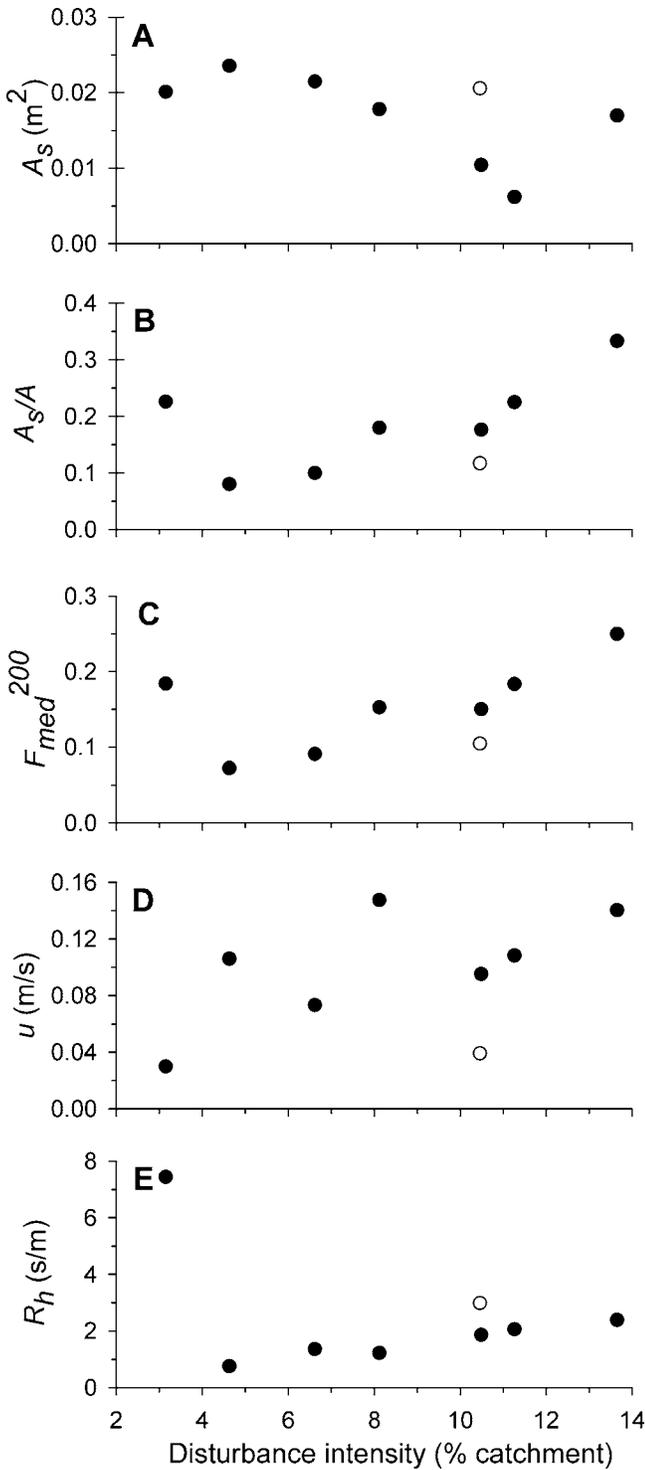


FIG. 3. Relationship between disturbance intensity and absolute size of the transient storage zone ( $A_s$ ; A), relative size of transient storage zone ( $A_s/A$ ; B), the fraction of the median travel time attributable to transient storage over a standardized length of 200 m ( $F_{med}^{200}$ ; C), average surface-water velocity ( $u$ ; D), and hydraulic retention factor ( $R_h$ ; E) before addition of coarse woody debris to streams. The open

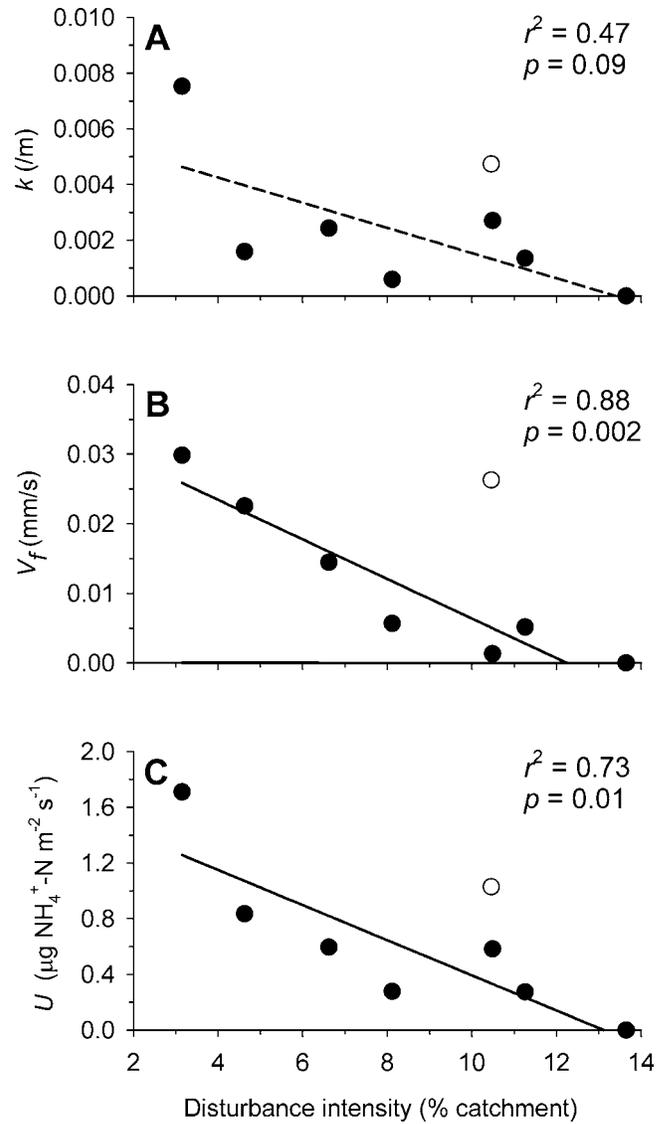


FIG. 4. Relationship between disturbance intensity and the fractional uptake rate of  $NH_4^+$  from water per unit distance ( $k$ ; A),  $NH_4^+$  uptake velocity ( $V_f$ ; B), and the mass removal rate of  $NH_4^+$  from water per unit area ( $U$ ; C). The open circle indicates site BC1 (see Fig. 1 for site name), which was excluded from the statistical analyses (see Results). Solid lines are statistically significant ( $p < 0.05$ ) and dashed lines are marginally significant ( $0.05 < p < 0.10$ ) linear regressions.

Bilby and Bison 1998). Upland disturbance did not cause changes in the hydrodynamics ( $A_s$ ,  $A_s/A$ ,  $F_{med}^{200}$ ,  $R_h$ , or  $u$ ) of FBMI streams. One possible reason for the absence of an observable disturbance effect in

← circle indicates site BC1 (see Fig. 1 for site name), which was excluded from the statistical analyses (see Results).

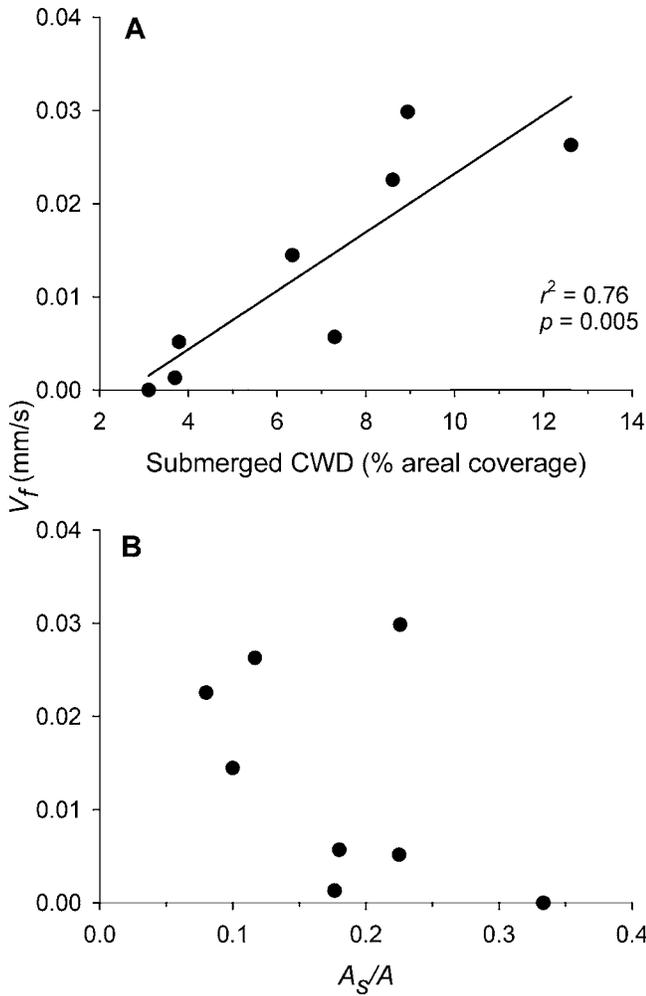


FIG. 5. Relationship between  $\text{NH}_4^+$  uptake velocity ( $V_f$ ) and % areal coverage of submerged coarse woody debris (CWD; A) and relative size of transient storage zone ( $A_s/A$ ; B).

our study is the small size of the transient storage zones in FBMI streams.

FBMI  $V_f$  values were compared only with values from other studies that used the same  $\text{NH}_4^+$  addition method because enrichment methods do not provide true estimates of ambient nutrient  $V_f$ s (Mulholland et al. 1990, 2000a, 2002, Dodds et al. 2002, Payn et al. 2005).  $V_f$  ( $0.015 \pm 0.004$  mm/s [mean  $\pm 1$  SD]) for FBMI streams is lower than any value previously reported from  $\text{NH}_4^+$  addition experiments (Table 6). In fact, only values from the low end of the  $V_f$  ranges reported for Hubbard Brook Experimental Forest streams (Hall et al. 2002), Grand Teton National Park streams (Hall and Tank 2003), and a single date in Riera Major, Spain (Sabater et al. 2000), overlap with any FBMI  $V_f$  values (Table 6).

Catchment disturbance intensity significantly affect-

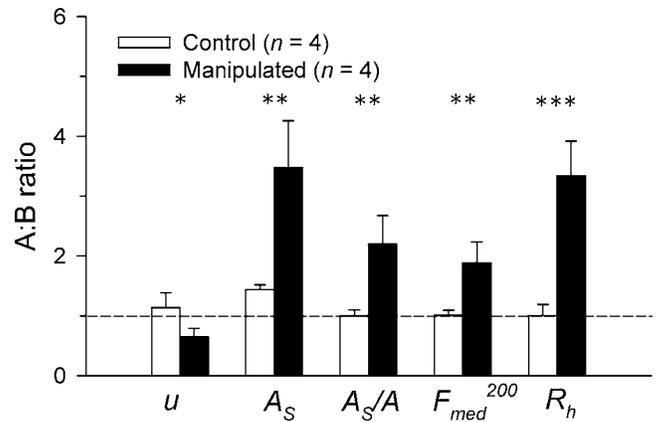


FIG. 6. Mean (+1 SE) after:before (A:B) manipulation ratios of hydrodynamic properties (surface water velocity [ $u$ ], size of transient storage zone [ $A_s$ ], relative size of transient storage zone [ $A_s/A$ ], the fraction of the median travel time attributable to transient storage over a standardized length of 200 m [ $F_{med}^{200}$ ], and the hydraulic retention factor [ $R_h$ ]) in control and manipulated streams. Dashed line indicates an A:B ratio equal to 1, indicating no change between the 2 sampling periods. \*  $p < 0.1$ , \*\*  $p < 0.05$ , \*\*\*  $p < 0.01$ .

ed nutrient-uptake metrics despite the low uptake rates in FBMI streams.  $\text{NH}_4^+$  uptake decreased significantly as disturbance intensity increased across FBMI streams. Deforestation decreased  $\text{NH}_4^+$  uptake rates but had little effect on P uptake rates in eastern North America Piedmont watersheds (Sweeney et al.

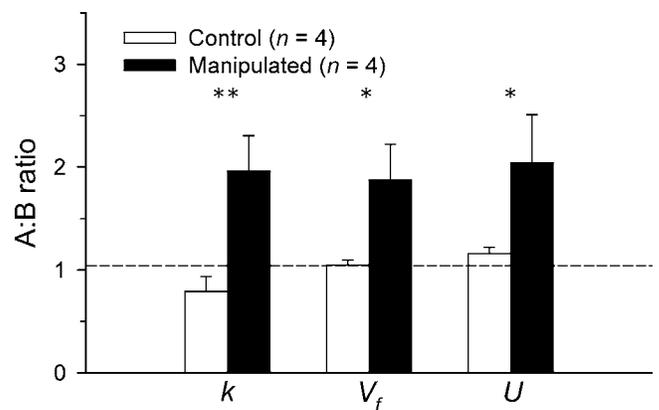


FIG. 7. Mean (+1 SE) after:before (A:B) manipulation ratios of  $\text{NH}_4^+$  uptake characteristics (fractional uptake rate of  $\text{NH}_4^+$  from water per unit distance [ $k$ ], uptake velocity [ $V_f$ ], and the mass removal rate of  $\text{NH}_4^+$  from water per unit area [ $U$ ]) in control and manipulated streams. Dashed line indicates an A:B ratio = 1, indicating no change between the 2 sampling periods. All differences in A:B ratios between control and manipulated streams were significant. \*  $p < 0.1$ , \*\*  $p < 0.05$ , \*\*\*  $p < 0.01$ .

TABLE 5. Transient storage zone characteristics for published conservative tracer injection experiments. FBMI = Fort Benning Military Installation,  $A$  = stream channel cross-sectional area,  $A_s$  = transient storage zone cross-sectional area,  $A_s/A$  = relative size of transient storage zone. Blanks indicate data not available.

Location	$A_s$ (m <sup>2</sup> )		$A_s/A$		Reference
	Mean $\pm$ 1 SD	Range	Mean $\pm$ 1 SD	Range	
FBMI streams	0.017 $\pm$ 0.006	0.006–0.024	0.180 $\pm$ 0.083	0.080–0.333	Our study
Walker Branch, Tennessee	0.008		0.084		Mulholland et al. (1997)
	0.013 $\pm$ 0.005	0.006–0.024	0.109 $\pm$ 0.027	0.075–0.170	Hart et al. (1999)
North Carolina coastal plain streams					
Slocum Creek	0.149 $\pm$ 0.022		0.33		Ensign and Doyle (2005)
Snapping Turtle Creek	0.23 $\pm$ 0.066		0.416		Ensign and Doyle (2005)
Coweeta Hydrologic Lab, North Carolina					
Ball Creek	0.400		3.883		D'Angelo et al. (1993)
Pine catchments ( $n = 3$ )	0.022		1.000		D'Angelo et al. (1993)
Hardwood catchments ( $n = 3$ )	0.030		1.364		D'Angelo et al. (1993)
Snake Den Branch	0.100	0.090–0.110	1.475	1.33–1.62	Thomas et al. (2003)
Hugh White Creek	0.129		1.491		Mulholland et al. (1997)
Joyce Kilmer Memorial Forest, North Carolina (3 old-growth streams)	0.06 $\pm$ 0.005		0.50 $\pm$ 0.12		Valett et al. (2002)
Slick Rock Wilderness Area, North Carolina (3 2 <sup>nd</sup> -growth streams)	0.10 $\pm$ 0.032		0.88 $\pm$ 0.09		Valett et al. (2002)
Hubbard Brook Experimental Forest, New Hampshire	0.058 $\pm$ 0.049	0.015–0.260	0.405 $\pm$ 0.158	0.16–0.71	Hall et al. (2002)
Sycamore Creek, Arizona	0.743 $\pm$ 0.455	0.288–1.258	4.16 $\pm$ 3.094	0.9–7.5	Martí et al. (1997)
New Mexico streams					
Aspen Creek	0.0008		0.08		Morrice et al. (1997)
Rio Calaveras	0.0030		0.10		Morrice et al. (1997)
Gallina Creek	0.230		4.6		Morrice et al. (1997)

2004). Time since clear-cutting (reference stream relative to streams with catchments logged 10 and 30 y previously) had little effect on  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  uptake rates in Coweeta, North Carolina, streams (Webster et al. 1991). However,  $\text{NO}_3^- V_f$  was lower in disturbed (pasture) than in pristine (tussock) streams in New Zealand (Niyogi et al. 2004), and  $\text{NH}_4^+ V_f$  decreased as the % of catchment covered by high-intensity urban development increased in Chattahoochee River tributaries (Meyer et al. 2005).

Our results are consistent with the notion that catchment disturbance leads to decreases in instream nutrient uptake. As forested catchments become increasingly disturbed, the abundance of CWD in streams declines (Harmon et al. 1986, Golladay et al. 1989, Webster et al. 1990, Maloney et al. 2005). CWD dams tend to increase organic matter deposition and retention in streams (Naiman and Sedell 1979, Bilby 1981, Smock et al. 1989), and benthic organic matter (BOM) is highly correlated with CWD abundance in FBMI streams (Maloney et al. 2005). The combination of increased substrata stability and increased organic matter retention associated with woody debris dams

and the subsequent microbial colonization should lead to increased nutrient uptake rates when CWD is added back onto the streambed.

$\text{NH}_4^+ V_f$  was positively correlated with CWD abundance, and rates increased when CWD was added to FBMI streams. These results are consistent with findings from other forested stream studies. N uptake rates associated with debris dams are faster than rates associated with other stream habitats (Munn and Meyer 1990). Experimental log additions led to increased N uptake rates (shorter  $S_w$ ) in Cunningham Creek, North Carolina (Wallace et al. 1995).  $\text{NH}_4^+$  and  $\text{PO}_4^{3-}$  uptake rates decreased relative to rates in a reference stream in response to litter exclusion and wood removal from 2 Coweeta streams (Webster et al. 2000), and  $\text{NH}_4^+$  and  $\text{PO}_4^{3-} V_f$ s decreased after CWD removal from a North Carolina coastal blackwater stream (Ensign and Doyle 2005).  $\text{PO}_4^{3-}$  uptake rates were highly correlated with CWD abundance in mountain streams of North Carolina (Valett et al. 2002). Taken together, these results suggest that woody debris plays an important role in regulating nutrient retention in streams.

$\text{NH}_4^+$  uptake in forested streams is largely a biotic process (Munn and Meyer 1990, Mulholland et al. 2000b).  $\text{NH}_4^+$  taken up by microbes can be used either for assimilation or nitrification. In many streams, a large fraction of  $\text{NH}_4^+$  uptake is used for nitrification (e.g., Richey et al. 1985, Webster et al. 1991, Peterson et al. 2001, Bernhardt et al. 2002). However, in some streams (e.g., streams in Grand Teton National Park [Hall and Tank 2003] and FBMI),  $\text{NH}_4^+$  uptake appears to be used in some other way. If a significant fraction of  $\text{NH}_4^+$  uptake had been used in nitrification, downstream increases in  $[\text{NO}_3^-]$  should have been observed during our  $\text{NH}_4^+$  injections. However, a downstream increase in  $[\text{NO}_3^-]$  was observed in only one stream (BC1), and the increase was minimal ( $0.6 \mu\text{g NO}_3^- \text{-N/L}$  over a 60-m reach).  $[\text{NO}_3^-]$  did not change or decreased in transit in all other streams in our study. This result suggests that the  $\text{NH}_4^+$  uptake rates observed in our study were largely assimilation rates, although we cannot rule out the possibility that nitrification may have contributed to the decline in added  $\text{NH}_4^+$  and increased  $\text{NO}_3^-$  uptake prevented an increase in  $[\text{NO}_3^-]$ .

Both BOM (Maloney et al. 2005) and dissolved organic C concentrations (Houser et al. 2006) decrease with increased catchment disturbance in FBMI streams. Gross primary production (GPP) is minimal ( $\text{GPP} < 0.4 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) in FBMI streams (except during spring months before leaf-out), but ecosystem respiration (ER) rates decrease with disturbance intensity (Houser et al. 2005). The decreases in  $\text{NH}_4^+$   $V_f$  and both BOM and ER (but not GPP) with catchment disturbance suggest that  $\text{NH}_4^+$  uptake in FBMI streams is driven largely by heterotrophic assimilation. Hall and Tank (2003) concluded that

heterotrophic microorganisms were using primarily  $\text{NH}_4^+$  and photoautotrophs were using both  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in Grand Teton streams where GPP was significantly related to both  $\text{NH}_4^+$  and  $\text{NO}_3^-$  uptake, and ER was significantly related only to  $\text{NH}_4^+$  uptake.

The role of transient storage in stream nutrient uptake and retention has received much attention in recent years (Grimm and Fisher 1984, Valett et al. 1996, Mulholland et al. 1997, Hall et al. 2002). Modeling studies (Mulholland and De Angelis 2000) and several empirical studies (Valett et al. 1996, Mulholland et al. 1997, Gücker and Boëchat 2004, Ensign and Doyle 2005) suggest that nutrient uptake should increase as transient storage increases, but other studies indicate either a weak (Hall et al. 2002) or no relationship (Martí et al. 1997, Butturini and Sabater 1999, Webster et al. 2003, Niyogi et al. 2004) between nutrient uptake and transient storage. In our study, a significant relationship between  $V_f$  and  $A_s/A$  was not found. In fact, if anything, our data suggest that  $V_f$  decreased as  $A_s/A$  increased in FBMI streams, a result similar to one found by Valett et al. (2002) for  $\text{PO}_4^{3-}$   $V_f$ . The absence of a relationship between nutrient uptake and transient storage may have been a consequence of the low values and small range of  $A_s/A$  among our study streams. However, our results do not indicate a strong role for transient storage in controlling nutrient uptake among streams when taken together with other studies.

#### Effects of adding CWD

The small size of the transient storage zones and low  $\text{NH}_4^+$  uptake rates found in FBMI streams provided ideal conditions for detecting changes in stream hydrodynamics and nutrient uptake following CWD

TABLE 6.  $\text{NH}_4^+$  mass-transfer coefficient values ( $\text{NH}_4^+ V_f$ ) for published  $\text{NH}_4^+$  enrichment experiments. FBMI = Fort Benning Military Installation. Blanks indicate data not available.

Location	$V_f$		Reference
	Mean ( $\pm 1$ SD) (mm/s)	Range (mm/s)	
FBMI streams	0.015 $\pm$ 0.011	0–0.031	Our study
Hubbard Brook Experimental Forest streams, New Hampshire	0.053 $\pm$ 0.037	0.003–0.180	Hall et al. (2002)
Slocum Creek, North Carolina	0.053	0.053	Ensign and Doyle (2005)
Hugh White Creek, North Carolina	0.059	0.059	Hall et al. (1998)
Walker Branch, Tennessee	0.068	0.068	Mulholland et al. (2000a)
Grand Teton National Park streams, Wyoming	0.073 $\pm$ 0.069	0.018–0.210	Hall and Tank (2003)
La Solana, Spain	0.115 <sup>a</sup>		Martí and Sabater (1996)
Riera Major, Spain	0.217 <sup>a</sup>	0.027–0.127	Martí and Sabater (1996)
Kye Burn, New Zealand			Sabater et al. (2000)
East Tributary		0.083–0.483	Simon et al. (2005)
North Tributary		0.067–1.183	

<sup>a</sup> Mean of bedrock and sand-cobble reaches as calculated in Hall et al. (2002)

additions. The severity of the upland disturbance (essentially complete removal of vegetation from upland areas with easily eroded soils) and the absence of CWD and other retention structures in the FBMI streams in highly disturbed catchments probably partially account for the strength of the hydrodynamic and nutrient uptake responses to CWD additions.

None of the hydrodynamic metrics used in our study were a function of level of catchment disturbance or abundance of CWD. Nevertheless, all metrics showed strong responses to CWD addition. The after-manipulation decreases in  $u$  and increases in hydrodynamic metrics related to transient storage are consistent with the results of other studies showing that CWD strongly affects the structure of stream ecosystems by shaping channel morphology (e.g., increasing streambank and streambed stability), decreasing water velocity, and increasing hydrodynamic heterogeneity (Bilby 1981, Trotter 1990, Bilby and Bison 1998). Our results specifically suggest that CWD increases the size of transient storage zones, which can lead to increases in capacity of a stream to remove or transform nutrients through biological or physical processes (Mulholland and DeAngelis 2000). The strong increases in  $F_{\text{med}}^{200}$  in manipulated streams are consistent with increased spatial variation in water velocity (i.e., greater effect of transient storage zones on water travel time through the reach), which also indicates enhancement of stream habitat heterogeneity. The decreases in mean  $u$  and the increases in  $R_h$  in manipulated streams indicate an increase in the potential contact time of sediment-associated stream biota with dissolved constituents during their transit through the stream. Thus, the hydrodynamic changes observed in our study indicate that increasing the abundance of CWD in streams has the potential to increase uptake and retention of organic matter and nutrients.

CWD additions appear to have several positive effects on stream morphology and structure. FBMI streams with greater abundances of CWD experience less scouring of the streambed and greater streambank and streambed stability than streams with lower abundances of CWD (Maloney et al. 2005). In addition, the CWD added to manipulated streams provided more stable substrata for algal and microbial colonization and growth on otherwise shifting, fine-grained streambed sediments; i.e., the logs served as stable substrata and they helped stabilize fine sediments (BJR, personal observation). The increased substrata stability and availability of BOM associated with increased CWD abundance (Maloney et al. 2005) probably increased biotic N demand (evidenced by increased  $\text{NH}_4^+$  uptake rates). Our results also are consistent with results from an earlier disturbance

gradient study showing higher ER with higher CWD abundance in less disturbed streams (Houser et al. 2005).

#### *Implications for stream hydrodynamics and nutrient cycling*

The coupled results from the disturbance intensity gradient and the CWD addition experiment imply that elevated dissolved inorganic N concentrations associated with upland disturbance (Houser et al. 2006) reflect both increased N inputs and reductions in the rate at which N is removed in streams. Thus, water quality in streams with intense upland disturbances should be enhanced by reducing nutrient inputs and by enhancing instream biotic nutrient-uptake capacity through measures such as restoring stream CWD. CWD addition stabilizes stream banks and stream beds and increases BOM retention, the amount of stable substrata for microbial colonization, and the potential contact time between biota and dissolved constituents. This hypothesis is consistent with the observation that long-term reductions in stream  $\text{NO}_3^-$  concentrations in the Hubbard Brook Experimental Forest may be the consequence of increased instream N uptake (as the density of woody debris dams has increased) and reduced N inputs (Bernhardt et al. 2005a).

One of the most important results of our study is that CWD additions appear to provide a fast-response (within 1 mo) mechanism by which some of the effects of upland disturbance on hydrodynamic and nutrient-cycling properties of Southeastern Hills and Plains streams can be mitigated. Our results are promising, but upland restorations (e.g., revegetation of ephemeral corridors) aimed at reducing the sediment load to the stream also will be needed to prevent burial of added CWD in highly disturbed catchments. Thus, long-term monitoring of the current project and similar restoration efforts are needed to determine the duration over which positive effects may persist.

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