Ecology, 71(6), 1990, pp. 2069–2082

2560

HABITAT-SPECIFIC SOLUTE RETENTION IN TWO SMALL STREAMS: AN INTERSITE COMPARISON[1]

NANCY L. MUNN AND JUDY L. MEYER
Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA

Abstract. We measured uptake rates of phosphorus, nitrate, calcium, and dissolved organic carbon within two headwater streams, one in the Appalachian mountains of North Carolina and the other in the Cascade range of Oregon. The major physical differences between these two streams are parent geology and local geomorphic structure. Uptake rates were measured following low-level nutrient releases during summer 1987 in 20-m reaches with different geomorphology. The relative importance of biotic vs. abiotic sorption of nitrogen and phosphorus by sediments from the two streams was assessed by laboratory experiments.

Nitrate-N uptake rates were high for the western stream (11.9 $\mu g \cdot m^{-2} \cdot min^{-1}$) and low for the eastern stream (3.9 $\mu g \cdot m^{-2} \cdot min^{-1}$) during the summer. The debris dam reaches in Oregon were the most retentive of N (shortest uptake length of 17 m). Conversely, soluble reactive phosphorus (SRP) uptake rates were higher for the eastern stream (18.6 $\mu g \cdot m^{-2} \cdot min^{-1}$), primarily through biotic processes. SRP uptake lengths were short for the cobble (32 m), debris dam (35 m), and rock outcrop (40 m) reaches in the eastern stream. Uptake of SRP in either stream was not related to sediment size fraction but rather to a combination of sediment infiltration rates and quality of organic material. Calcium (Ca) uptake lengths were long in the Oregon stream (1278 m) but short in the Appalachian stream (106 m). Surprisingly, the eastern stream was more retentive of Ca than nitrate (shorter uptake lengths for Ca) during this time period. Debris dams greatly enhanced retention of dissolved organic carbon in both streams (60% of all uptake in the eastern stream and 81% in the western stream), although retention was greater in the eastern stream.

The lower uptake rate of phosphorus and higher uptake rate of nitrate in the Oregon stream were expected based on geographic location and parent geology; streams in this area drain catchments of volcanic origin and tend to have low N:P (atomic; 1.8 for the western stream) ratios, indicating potential N limitation. Streams flowing over granitic bedrock, such as the eastern stream, tend to have lower P availability (N:P = 15.5). The combined results of laboratory and field measurements indicate that in the eastern stream, strong biotic control of P uptake coupled with high P demand result in relatively short P uptake lengths and a strong impact of P spiraling on ecosystem dynamics. In the western stream, strong biotic control of N uptake combined with strong N demand result in short N uptake lengths. This is especially true at sites of downed timber that retain both FPOM and CPOM, creating a high N demand (shortening N spirals).

Key words: calcium; dissolved organic carbon; geology; geomorphology; nitrate; phosphorus; retention; spiraling; uptake lengths; uptake rates.

INTRODUCTION

Processes occurring within a stream have a strong impact on the export of nutrients and organic matter from catchments (Meyer and Likens 1979, Swank and Caskey 1982). The net effect of these processes is influenced by the irregular mosaic of different patches typical of small streams (Pringle et al. 1988). Patches composed of debris dams, bedrock outcrops, gravel beds, or cobble–riffles are characterized by differences in biotic properties (Mulholland et al. 1984), fine organic matter accumulations, and the nature and number of retention devices in the stream channel (Speaker et al. 1984). Stream bed patch-type can influence current velocity and particle transport (Young et al. 1978, Brussock et al. 1986, Ward and Aumen 1986) as well as the biomass, trophic structure, and productivity of the animal community (Bowlby and Roff 1986, Huryn and Wallace 1987). In this paper, these patches and the biotic and physical properties associated with each patch type will be referred to as habitats, and a section of stream bed of a particular habitat will be referred to as a reach.

Habitat type may regulate nutrient cycling as well. Coarse particulate organic matter (CPOM; Mulholland et al. 1985) and attached algae (Sebetich et al. 1984) are responsible for most phosphorus uptake in some streams; reaches within a stream with large organic matter accumulations and luxuriant algal growths should have higher nutrient uptake rates than other reaches. The size fraction of sediment particles determines the surface area available for uptake (Meyer 1979)

[1] Manuscript received 10 April 1989; revised and accepted 20 February 1990.

and the permeability of the stream bed (Munn and Meyer 1988). Since mesoscale geomorphological differences in habitat type influence stream bed characteristics, it is not surprising that we find different nutrient uptake rates in stream reaches with different habitat types (Munn 1989). However, the net impact of the different physical, chemical, and biotic attributes of habitat on solute retention is unknown.

On a larger scale, we anticipate differences in solute retention by streams in different geographic regions with different geology, hydrology, and geomorphic structure. Parent geology influences water chemistry and channel geomorphic structure, which in turn affect biotic characteristics of the system. Streams flowing through forested igneous catchments of volcanic origin tend to be relatively rich in phosphorus (P) compared with those of plutonic origin (e.g., Hubbard Brook, New Hampshire), or catchments on sedimentary rock (Dillon and Kirchner 1975). Stream primary production and decomposition in many parts of North America are generally considered potentially P limited (e.g., Elwood et al. 1981, Peterson et al. 1985). However, streams of Southwestern deserts, northern California and the Pacific Northwest are considered nitrogen (N) limited because of low N:P (atomic) ratios (Gregory 1980, Grimm et al. 1981), low nitrate and ammonium concentrations (Fredriksen 1972, Gregory 1980), and active conservation of N by undisturbed catchments (Fredriksen 1972, Scrivener 1975; see Triska et al. 1983). Thut and Haydu (1971) found that over half the surface waters in Washington state have N:P ratios <10, indicating potential N limitation (Redfield 1958). The presence of N-fixing bacteria associated with woody debris and their role in the decomposition of wood in northwest streams (Buckley and Triska 1978) is further evidence of potential N limitation. Geology also affects geomorphic structure through subtle controls of drainage and topography (Hatcher 1988); this includes control over stream sediment and woody debris movement. Thus, differences between streams in potential nutrient limitation and geomorphic structure should result in differences in nutrient retention.

The objectives of this study are: (1) to compare phosphorus, nitrogen, carbon, and calcium uptake rates and uptake lengths at a mesoscale level within two headwater streams that are characterized by different geology and local geomorphic structure; and (2) to identify what physical and biotic factors are important determinants of solute retention at a mesoscale level. Uptake length is a measure of how rapidly an element is removed from the stream water and appears to be a major component in the spiraling length of an element (Mulholland et al. 1985); short uptake lengths imply rapid removal of an element from the water column. The major differences between the two streams in this study are parent geology and the size of the retention structures (snags or debris dams). These data are compared to data from streams in The Hubbard Brook Experimental Forest, New Hampshire, Konza Prairie, Kansas, and Oak Ridge, Tennessee.

Study Sites

This study was conducted on two headwater streams, Hugh White Creek at the Coweeta Hydrologic Laboratory in North Carolina and the stream draining Watershed 2 at the H. J. Andrews Experimental Forest in Oregon; both sites are part of the long-term ecological research (LTER) program. Both streams are relatively high-gradient second-order mountain streams with low dissolved nutrient concentrations (Table 1). Primary production in both streams is limited primarily by light and secondarily by nutrients (Gregory 1980, Lowe et al. 1986). When this study was conducted there was a drought in Oregon (summer 1987) and in North Carolina (spring 1986 through summer 1988).

Hugh White Creek (HWC) drains Watershed 14 in the southern Appalachian mountains (Macon County). HWC is shaded year-round by a dense understory of rhododendron (*Rhododendron maximum*) and drains a mixed mature hardwood forest that has been undisturbed since 1927, except for the demise of American chestnut (*Castanea dentata*). The soils are highly permeable and overlie deeply weathered granitic bedrock (Douglass and Swank 1975, Swank 1986). Stream sediments (overlying the bedrock) range in depth from 0 to 10 cm. Stream substrata vary from steep sections of moss-covered bedrock to infrequent, small pools filled with sediments associated with relatively small debris accumulations. The predominant substrata in HWC are gravel and cobble reaches. Stream discharge is greatest during winter and early spring storms. Air temperature during the solute additions averaged 23°C, and water temperature averaged 18°.

Watershed 2 (WS2) drains an old-growth Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) forest in the western slopes of the Cascade range in Oregon (Franklin et al. 1981). The channel is bedrock constrained, with narrow channel width and steep side slopes. Channel morphology consists of stairsteps of pools and tree-fall zones with some pool and cobble areas (Buckley and Triska 1978, Triska et al. 1982). Although stream substrata are predominantly exposed bedrock of volcanic origin, the channel is dominated by large and relatively stable debris accumulations that shade stream substrata (Froehlich 1973). Stream discharge is greatest in late spring as snow melts. Air temperature during the solute additions averaged 25° and water temperature averaged 17°.

Methods

Short-term solute releases were conducted during summer 1987 in HWC and WS2 to compare solute uptake rates in HWC and WS2. The releases were repeated in reaches characterized by different habitat type to examine the influence of habitat on uptake rates. Sediment cores were removed from each reach and subsampled for identification of physical and biotic factors important in solute retention. Laboratory sorption experiments were conducted to address the importance of biotic, physical, and chemical mechanisms of uptake.

Field methods.—Twenty-metre reaches of stream bed characterized as predominantly cobble, gravel, debris dam, or rock outcrop were identified within each of the two streams. Rock outcrop reaches are characterized by relatively high entrainment of materials (Gurtz and Wallace 1984) and are covered with moss that acts as a filtering mechanism for particles in suspension (Smith-Cuffney and Wallace 1987). Cobble-riffle reaches had the largest size fraction of sediment (80% by mass >2 mm), and pools associated with debris accumulations are depositional areas for fine materials during low flow. Debris dams in HWC were underlain primarily by gravel whereas in WS2, debris accumulations were almost exclusively over exposed bedrock. Two 20-m reaches of each of the four habitats were selected for study in each stream, except that there were no 20-m reaches of gravel in WS2. The surface area and slope of each reach were measured, as was the surface area of wetted wood in debris dam reaches (de Vries 1974, Wallace and Benke 1984).

To quantify element uptake by different habitats, phosphorus, nitrate, calcium, and dissolved organic carbon were added to WS2 in July 1987 and to HWC in August 1987. Initially, rhodamine dye and chloride were dripped into each 20-m reach to observe mixing and to quantify time of travel through the reach (Munn and Meyer 1988). This was done to estimate how much time was required for thorough mixing of the injectate and stream water throughout each reach; that is, for the concentration of the conservative tracer, chloride, to achieve a plateau. The injectate was dripped into the reach ≈1 m upstream from the head of each reach; the stream was confined at this point to ensure thorough mixing before entering the stream. Solutes were dripped into each reach for 90 min at a constant rate of 100 mL/min. For the first 40 min, concentrations in the reach were allowed to stabilize and reach a plateau, and no samples were taken. For the next 50 min, samples were collected in the middle of the stream at 5-m intervals every 10 min in 250-mL acid-washed polyethylene bottles and filtered immediately (GF/C filters). To reduce the number of additions, phosphorus (as NaH_2PO_4) and nitrate (as $NaNO_3$) were added together and calcium (as $CaCl_2$) and dissolved organic carbon (DOC as sucrose) were added together. For HWC, stream water concentrations during the releases were 6 μg/L SRP, 20 μg/L NO_3-N, and 4 mg/L Ca and DOC; the atomic N:P declined from 15.5 to 11.5. For WS2, the Ca and DOC concentrations were the same as HWC but SRP was increased to 15 μg/L and NO_3-N was increased to 10 μg/L; N:P remained at 1.8. Chloride (as NaCl) was included with all additions as a conservative tracer to calculate downstream losses due to dilution (from riparian inputs) and dispersion (Bencala et al. 1987). Chloride concentrations increased from ambient levels of 1–2 mg/L to ≈6 mg/L. Chloride dilution (from injectate to when mixed with stream water) was also used to estimate discharge (Q) within each reach (Stream Solute Workshop, *in press*). Solute releases were repeated at eight reaches in HWC and six reaches in WS2. A release could not be replicated at a reach since previous releases would influence subsequent releases when repeated closely in time (D. D'Angelo, Virginia Polytechnic Institute and State University, *personal communication*).

TABLE 1. Physical and chemical characteristics of Hugh White Creek (Coweeta Hydrologic Laboratory, North Carolina) and WS2 (H. J. Andrews Experimental Forest, Oregon). Element concentrations are ambient concentrations immediately prior to solute additions.

	Hugh White Creek	Watershed 2
Watershed area (ha)	61	60
Maximum elevation (m)	996	1060
Minimum elevation (m)	708	525
Channel length (m)	1077	1100
Average annual precipitation (cm)	200	225
Chemistry*		
NO_3-N (μg/L)	6.0	2.0
SRP (μg/L)	1.0	5.0
DOC (mg/L)	1.0	2.0
Ca (mg/L)	0.6	4.0
Cl^- (mg/L)	0.5	2.0
pH	6.6	6.5
N:P	15.5	1.8

* SRP = soluble reactive phosphorus; DOC = dissolved organic carbon; N:P = atomic ratios of (ammonium + nitrate)-N:SRP during summer 1987 (baseline).

Five sediment cores (2 cm diameter, 0–5 cm depth) were removed from the sediments of cobble, gravel, and debris dam reaches and subsampled for organic matter content (percent OM), density of bacteria (which were preserved in buffered formalin), and chlorophyll (chl a) analyses. While the 2-cm core does not adequately sample sediments with larger particle size (e.g., cobble reaches), this core size was chosen as a compromise between adequate sampling and stream bed destruction. Since it was not possible to take cores from rock outcrop reaches, samples for these reaches were obtained from ceramic tiles that had been in the stream for 3 mo prior to removal (for HWC) or by scraping the rock surface (for WS2). Woody material within debris dams may be a major substrate for biota, but was not sampled in this study.

To quantify the percent stream bed bottom covered by each habitat within each stream, the habitat type was visually determined at 5-m intervals along the 'tire length of each stream ($n > 190$ for each stream). The percent surface area of each habitat was used to estimate the percent contribution by each habitat to element uptake and to calculate an average uptake rate weighted for percent habitat type in each stream.

Element uptake is expressed as both an uptake rate and uptake length. Uptake rates were calculated from the decrease in element concentration (over background concentration corrected for dilution) multiplied by discharge Q for the 20-m reach divided by the surface area of the reach (Δconcentration $\times$ Q/surface area). Uptake length is the average distance travelled downstream by an element before it is taken up. To calculate uptake length, the concentration of the element (ln observed concentration/ln predicted concentration) is plotted vs. distance downstream. The slope of this line is the distance rate constant (per metre), and the inverse of the slope is the uptake length (metres). Both methods of expressing uptake are used in the literature (e.g., Grimm et al. 1981, Newbold et al. 1981), and thus are useful to calculate here for comparative purposes. Both expressions are an index of how rapidly an element is removed from the stream water. A comparison of the two models will be illustrated for one set of data within the *Results: Uptake rate and length models*. The conditions necessary for these two models to apply are: (1) channel and flow characteristics are reasonably uniform, (2) uptake of nutrient by stream bed is directly proportional to concentration, and (3) release of nutrient from the bottom does not significantly affect nutrient concentration during the measurement period (Stream Solute Workshop, *in press*). Since both the added solutes and conservative tracer yielded plateau concentrations within similar time periods, the conditions of the model were satisfied for the releases reported here.

Laboratory experiments.—The P and N (as NH_4-N) sorption capacity of sediments from both streams was examined in laboratory sorption experiments, since uptake rates of some elements are greatly influenced by the extent of sorption by sediments (Newbold et al. 1981). Laboratory experiments were used to examine mechanisms of sorption that would be difficult to address under field conditions. Sediment subsamples were exposed to solutions of different P or N concentrations, and a plot made of the amount of P or N sorbed by each sample against the concentration in solution at the end of the incubation period. This technique was used to answer four questions: (1) the relative importance of biotic vs. abiotic mechanisms of N and P uptake, (2) the effect of sediment size fraction on sediment P sorption characteristics, (3) the sorption capacities of P for sediment from different habitats (HWC only), and (4) the influence of temperature on P uptake (HWC only). Ammonium sorption was measured instead of nitrate sorption since later field work revealed that ammonium uptake rates were greater than nitrate uptake rates in HWC (Munn 1989). While the ammonium data are not directly comparable to the field data for nitrate reported here, they do provide valuable information about mechanisms of N uptake in the two streams.

Sediment sorption capacities were determined from incubations of sediments in P- or NH_4-N-enriched stream water using Taylor and Kunishi's (1971) procedure with modifications by Meyer (1979) and Klotz (1985). Incubations were initiated by adding washed sediment (6 mL) to filtered stream water (50 mL) with P or N concentrations ranging from 1 μg/L to 2 mg/L. Flasks were incubated at 11°C unless noted otherwise, and flasks were shaken vigorously for 5 s every 10 min. Incubations were stopped after 1 h (for P incubations) or 5 h (for N incubations) by filtration, and the filtrate was analyzed for soluble reactive phosphorus (SRP) or NH_4-N. The difference between concentration in the water before and after the incubation was used to calculate the amount of P (or N) sorbed or desorbed by the sediments.

The influence of biotic vs. abiotic mechanisms of sorption was investigated through incubations of living (unsieved) and sterile sediments from each stream. Sediments were sterilized by exposure to 2×10^4 Gy from a ^{60}Co source. If biotic uptake is the primary mechanism of nutrient removal from stream water, then lower filtrate concentrations would be expected in incubations with living sediments; however, if abiotic mechanisms predominate, then no difference in filtrate concentrations between the two treatments would be expected.

The influence of sediment size fraction on P uptake was investigated since P sorption increases as particle size decreases in some streams (Meyer 1979). Sorption capacities were quantified for sediments sieved into four size fractions (0.1–0.4, 0.4–1.0, 1–2, and >2 mm). Iron and aluminum concentrations and organic content of sieved sediments from both streams were measured to examine the influence of the chemical nature of the sediments on P sorption.

Incubations were conducted to determine the P sorption capacities of sediment collected from cobble, gravel, and debris dam reaches. Finally, the influence of temperature on P uptake was examined by incubating flasks at 4°, 11°, and 18°; sediments used were collected from HWC during autumn 1987.

Phosphorus uptake from sorption experiments is frequently expressed by two indices, the equilibrium P concentration (EPC) and the sorption index (see Meyer 1979, Klotz 1985). EPC is the SRP concentration at which there is neither adsorption nor desorption of P by the sediments, and is interpolated from regressions of final SRP concentrations in the incubation flasks and the amount of P adsorbed or desorbed from the sediments. The capacity of the sediments to maintain low P concentrations in the stream water at or near the

EPC is crucial to the concept of a river as a self-purifying system; a low EPC indicates a large capacity of the sediments to adsorb P. The sorption index is calculated as the amount of P absorbed (micrograms per gram sediment) from an initial P concentration of 2 mg/L divided by the SRP concentration in the solution after the 1-h incubation. The sorption index is a useful indicator of the P buffering capacity of sediments; a high index value indicates that a large amount of P can be sorbed by the sediment without increasing the concentration in the water at equilibrium (Meyer 1979). Of the two indices, EPC is the best indicator of the sorption capacity of sediments in HWC and WS2 since the EPC represents sorption at normal stream water concentrations, whereas the sorption index is calculated from incubations conducted at concentrations far greater than normal concentrations for the two streams.

Laboratory analyses.—Soluble reactive phosphorus (SRP) was determined on the P samples using the ammonium-molybdate reaction (Murphy and Riley 1962). Nitrate was determined using a hydrazine reduction method with a Technicon Autoanalyzer II system (Downes 1978). Calcium concentrations were quantified using a Perkin-Elmer 5000 Atomic Absorption spectrophotometer. Dissolved organic carbon was analyzed on a Model 700 TOC Analyzer (Oceanography International Corporation). Chloride concentrations were determined with an automated ferricyanide technique (APHA 1985). For all analytical methods, standard error was <5% of the mean value.

Organic matter content of sediments was estimated from mass loss at combustion (450°). Bacterial density was estimated with acridine orange direct counts (Hobbie et al. 1977), and chl *a* concentrations of sediment subsamples with a Turner fluorometer after acetone extraction (Strickland and Parsons 1972). Acid-extractable iron and aluminum concentrations were determined by atomic absorption spectrophotometry after HCl digestion of the sediments (Meyer 1979).

Results

Uptake rate and length models.—To demonstrate how models of uptake rate and length are fitted to raw data, examples of data from SRP releases at cobble reaches within HWC and WS2 are illustrated in Fig. 1. SRP concentrations measured (observed; $n = 50$) during the releases along each 20-m reach were plotted along with the predicted SRP concentration based on measured dilution of the conservative tracer (chloride) (Fig. 1A). The differences between predicted and observed concentrations (in the example, ≈3.1 and 0.8 μg/L for HWC and WS2, respectively) were multiplied by discharge for the reaches (4.0 and 1.4 L/s) and then divided by the surface area of the reaches (34 and 22 m^2) yielding uptake rates of 22 and 3 $\mu g \cdot m^{-2} \cdot min^{-1}$ for HWC and WS2, respectively. Uptake lengths were calculated with further manipulation of the data in Fig.

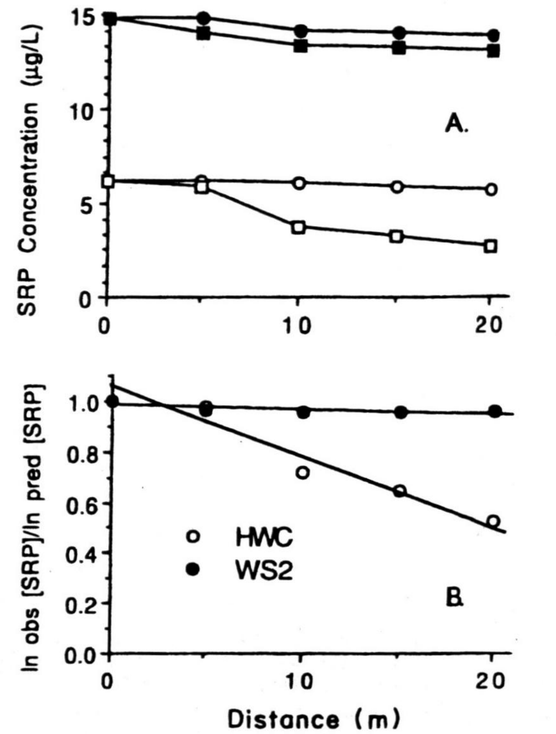

FIG. 1. (A) Predicted (circles; based on chloride dilution) and observed (squares) soluble reactive phosphorus (SRP) concentrations in cobble reaches in HWC (solid symbols) and WS2 (open symbols). All standard deviations were smaller than the size of the symbols. Uptake rates were calculated from the decrease in SRP concentration (difference between circle and square symbols) multiplied by discharge for the 20-m reaches divided by reach surface area. (B) Uptake lengths for cobble reaches in HWC and WS2 were calculated from plots of (ln observed [SRP]/ln predicted [SRP]) vs. distance downstream. The slope of a line fitted through the points is the distance rate constant and the inverse of the slope is the uptake length (m).

1, wherein (ln observed [SRP]/ln predicted [SRP]) were plotted vs. distance downstream (Fig. 1B). Straight lines were fitted through the points, and uptake lengths were calculated as the inverse of the slopes. The slope of the lines in Fig. 1B are 0.03 and 0.0015 m^{-1} for HWC and WS2, respectively, yielding uptake lengths of 32 and 666 m.

Solute releases.—Uptake rates of SRP were greater in all reaches in HWC than in any reach in WS2 (ANOVA, $P = .004$; Table 2). Uptake rates were lowest in debris dam reaches in WS2. In HWC, SRP uptake lengths were longest for gravel reaches, although there were no consistent differences in uptake between other habitat types in HWC.

Rates of nitrate uptake were similar for the two streams (ANOVA, $P = .054$; Table 2); however, when rock outcrop reaches were excluded from the analysis, WS2 had greater nitrate uptake than HWC ($P = .014$). The highest uptake rate was for debris dam reaches in WS2 and the lowest for cobble reaches in HWC. Nitrate

TABLE 2. Uptake rates and uptake lengths of four elements in reaches of different habitat types in Hugh White Creek (HWC), North Carolina, and the stream draining Watershed 2 (WS2), Oregon. There were no gravel reaches in the Oregon stream. Values are means for two replicate reaches since paired t tests indicated no significant difference ($P > .06$) in uptake rates between replicate sites.

		Cobble	Gravel	Debris dam	Rock outcrop
Uptake rates					
Phosphorus	HWC	21.90	14.49	20.19	18.69
(SRP, $\mu g \cdot m^{-2} \cdot min^{-1}$)	WS2	2.97†	...	0.15†	3.42†
Nitrate-N	HWC	0.39	5.13	4.59	7.77
($\mu g \cdot m^{-2} \cdot min^{-1}$)	WS2	9.18†	...	16.20†	5.37
Calcium	HWC	2.73	3.03	5.25	5.64
($mg \cdot m^{-2} \cdot min^{-1}$)	WS2	0.39†	...	0.33†	0.63†
DOC	HWC	8.97	0.90	19.59	5.37
($mg \cdot m^{-2} \cdot min^{-1}$)	WS2	0.14†	...	0.91†	0.31†
Uptake lengths (m)					
Phosphorus	HWC	32	188	35	40
	WS2	666	...	1000*	188
Nitrate	HWC	500*	600	1278	136
	WS2	119	...	17	56
Calcium	HWC	72	163	82	86
	WS2	6500	...	666	375
DOC	HWC	47	167*	39	69
	WS2	2300*	...	113	83*

* Indicates only one replicate used for uptake length since uptake length of the other replicate was longer than could be estimated; when the uptake rate is zero the uptake length is infinite.

† Indicates significant difference between the HWC and WS2 uptake rate for that habitat. The statistical difference between reaches could not be tested for uptake length since some values were infinite.

uptake lengths were longest for HWC reaches. Debris dam reaches in Oregon were the most retentive of nitrate (shortest uptake length) of all reaches for either stream.

Calcium uptake rates were near zero in WS2, and Ca uptake lengths were long, especially for cobble reaches (Table 2). There was greater Ca uptake in HWC than WS2 for all habitat types ($P = .021$). Gravel reaches in HWC had longer uptake lengths than any other habitat type in this stream. Surprisingly, HWC was more conservative of Ca than nitrate (shorter uptake lengths for Ca). Conversely, of the four elements examined, WS2 was least conservative of Ca and most conservative of nitrate.

Uptake rates of DOC were greater for all reaches in HWC than WS2, with the exception of gravel reaches in HWC (ANOVA, $P = .065$ for all data; $P = .025$ when gravel reaches from HWC were excluded from the analysis). Within each stream, DOC retention was greatest within debris dam reaches.

Intersite comparison of physical and biotic parameters.—The 20-m reaches of the two streams had similar stream bed surface areas (t test, $P = .07$) and slopes ($P = .72$; Table 3); however, discharge during the nutrient releases was greater in the eastern stream ($P < .01$). The surface area of wood in debris dam reaches was 0.67 m^2 of wood per linear metre of stream in HWC compared with 1.45 m^2/m of stream in debris dam

TABLE 3. Physical and biotic parameters for 20-m reaches of different habitat types within Hugh White Creek, North Carolina, and the stream draining Watershed 2, Oregon. The value for each habitat type is the mean of two replicate reaches since there were no significant differences between the replicate reaches. Bacterial densities per unit area of sediment include both rods and cocci. $n = 10$. ND indicates no data.

	Stream area (%)	Surface area (m^2)	Slope (%)	Q (L/s)	Organic content (%) $\bar{X}$	Organic content (%) SD	Chl a ($\mu g/cm^2$) $\bar{X}$	Chl a ($\mu g/cm^2$) SD	Bacterial density (10^8 cells/cm^2) $\bar{X}$	Bacterial density SE
Hugh White Creek										
Cobble	29.0	34.2	10.5	4.0	1.4	0.1	0.32	.18	36.1	4.4
Gravel	33.0	27.2	9.0	5.0	1.6	0.1	0.96	.29	19.0	1.7
Debris dam	27.0	32.3	12.5	4.2	2.0	0.3	0.34	.36	24.8	2.2
Rock outcrop	11.0	32.2	19.0	3.1	23.3	2.4	0.12	.03	ND	
Watershed 2										
Cobble	11.6	22.2	6.0	1.4	6.6	1.4	1.2	1.0	29.7	5.0
Debris dam	55.8	26.0	14.5	0.9	26.2	11.3	1.4	0.62	39.2	2.2
Rock outcrop	32.6	25.8	14.0	0.7	51.1	9.1	ND		ND	

reaches in WS2. These values are within ranges presented previously; low-order streams with old-growth catchments in Oregon tend to retain more coarse particulate matter than low-order hardwood catchments in North Carolina (Wallace and Benke 1984, Harmon et al. 1986), likely a response to the constrained channels and larger debris size in the Cascade stream.

There was no difference in sediment percent OM or chl a concentrations between replicate habitat types (e.g., no difference in percent OM between Cobble I and Cobble II) in either HWC or WS2 (paired t tests, $P > .05$). Thus, data for replicate reaches were combined for further analyses.

Sediment percent OM was greater in WS2 than HWC for cobble ($t = 4.971$, $P < .0005$), debris dam ($t = 2.741$, $P = .014$), and rock outcrop ($t = 2.953$, $P = .014$) reaches. Sediment chl a concentrations were also greater in WS2 than HWC for cobble ($t = 2.594$, $P = .03$) and debris dam ($t = 4.470$, $P = .001$) reaches. Bacterial density was greater in WS2 than in HWC in all reaches measured ($P = .0008$). In summary, the western stream had lower discharge and larger debris accumulations with greater sediment OM content, chl a concentration, and bacterial density (Table 3).

Habitat comparison of physical and biotic parameters.—There was no significant difference in sediment percent OM between habitats in WS2 (ANOVA, $F = 2.645$, $P = .08$), likely due to large variability in the data within each habitat type (Table 3). There was no difference in chl a concentrations between cobble and debris dam reaches in WS2. Rock outcrop reaches in HWC had greater sediment percent OM ($F = 182.1$, $P < .0005$) and sediment chl a concentrations ($F = 5.268$, $P = .008$) than other HWC reaches, although there were no differences between cobble, debris dam, and gravel reaches. There was no difference in bacterial density between habitat types in either HWC or WS2 ($P > .05$).

Correlation analyses.—The relationship between discharge, biotic parameters, and element uptake was examined through correlation analysis to determine relatedness of these parameters (significant at $P < .05$). Nitrate retention was greatest in reaches with greater chl a concentration ($r = 0.90$) and decreased with discharge ($r = -0.75$). Conversely, SRP retention was highest in reaches with high discharge ($r = 0.88$), low chl a concentrations ($r = -0.97$), and low bacterial density ($r = -0.93$); however, when correlations were performed separately for each stream, there was no significant relationship between biotic factors, discharge, and SRP uptake. SRP retention was greatest in reaches with low nitrate retention ($r = -0.83$). The most important determinant of SRP and nitrate retention was stream location, that is, either HWC or WS2. There was no relationship between Ca or DOC uptake and any biotic parameter; however, Ca uptake was greatest in reaches with high SRP uptake rates ($r = 0.87$). DOC uptake and Ca uptake were also positively correlated ($r = 1.00$).

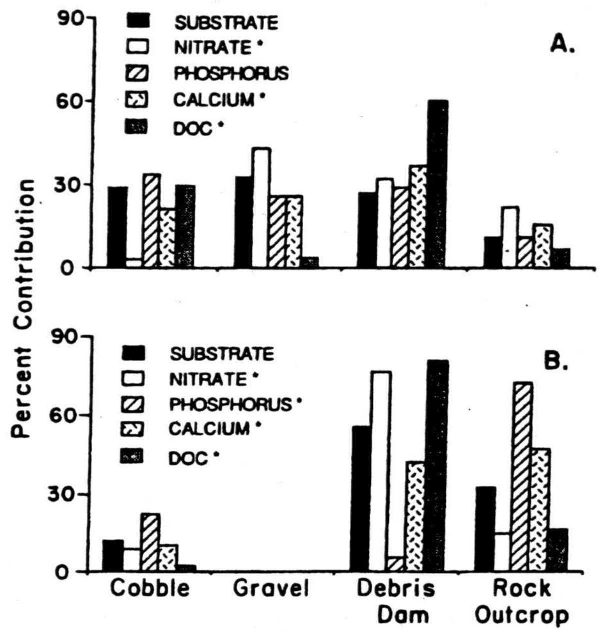

FIG. 2. Percent contribution of uptake weighted by the relative abundance of different habitats to total uptake of the element in Hugh White Creek (A) and the stream draining Watershed 2 (B) during summer 1987. * indicates distributions of element uptake that depart significantly (χ^2 goodness of fit) from the distribution of stream area among habitats.

Effect of local geomorphology.—When uptake was weighted by the relative abundance of different habitats within each stream, gravel reaches were the most retentive of nitrate in HWC (Fig. 2A), whereas debris dam accumulations retained the most nitrate in WS2 (Fig. 2B). Rock outcrop reaches retained the most Ca and SRP in WS2. Calcium retention in HWC was mediated primarily by debris dam reaches (37%), although there was significant retention by all habitat types. In HWC, uptake of SRP was proportional to the relative amounts of different habitats (chi-square goodness of fit, $P = .43$); that is, habitat did not affect SRP retention in this stream. DOC uptake occurred primarily at debris dam reaches in both HWC (60%) and WS2 (81%). The difference observed in distribution between element uptake vs. stream bed area among habitats for most elements reflects the dependence of uptake on specific physical or biotic attributes of the local geomorphology. The average uptake rates and lengths of SRP, NO_3-N, Ca, and DOC (weighted for habitat type) were strikingly different between the two streams (Table 4), although no between-stream statistical significance can be inferred due to the lack of replicate streams.

Laboratory experiments.—EPCs were lower for untreated sediments than for sterilized sediments in both streams (Table 5; $P < .05$), and lower for HWC (1.0 μg/L) than WS2 (5.4 μg/L; $P < .05$). However, there

TABLE 4. Average uptake rates and uptake lengths of four elements in Hugh White Creek, North Carolina, and the stream draining Watershed 2, Oregon, weighted for the relative abundance of each habitat type.

	Hugh White Creek	Watershed 2
Uptake rate		
Phosphorus (SRP, $\mu g \cdot m^{-2} \cdot min^{-1}$)	18.64	1.54
Nitrate-N ($\mu g \cdot m^{-2} \cdot min^{-1}$)	3.90	11.86
Calcium ($mg \cdot m^{-2} \cdot min^{-1}$)	3.83	0.43
DOC ($mg \cdot m^{-2} \cdot min^{-1}$)	8.78	0.63
Uptake length (m)		
Phosphorus	85	697
Nitrate	689	42
Calcium	106	1278
DOC	87	357

was no difference in SRP sorption indices between untreated vs. sterilized sediments for both HWC ($t = 1.85$, $P = .14$) and WS2 ($t = 1.83$, $P = .14$). Since the untreated vs. sterilized treatment lines on the sorption plot converged at higher ambient SRP concentrations for sediments from both streams, SRP sorption indices (initial concentration 2 mg/L) reflected physico-chemical sorptive capacity of the sediments (no difference between biotic and abiotic uptake at this concentration), whereas EPC (always <11 μg/L) was more responsive to biotic activity.

Uptake of NH_4-N by untreated sediments was greater than uptake by sterilized sediments ($P < .01$ for both streams), suggesting that biotic processes maintain the low ambient NH_4-N concentrations in both streams. Sorption of ammonium was greater for WS2 sediments than HWC ($P < .01$).

There was strong SRP sorption by HWC and WS2 sediments, with the smaller size fractions sorbing more P (Table 6). The sorption index decreased with an increase in sediment particle size for both HWC (ANOVA, $F = 272.5$, $P < .0005$) and WS2 (ANOVA, $F = 89.34$, $P < .0005$), but there was no observable relationship between EPC and particle size with sediments from either stream. There was no consistent pattern between sediment size fraction and Al or Fe concentrations in either stream. However, concentrations of both cations in HWC were highest for sediments >2 mm. Sediments from HWC and WS2 did not differ in either Al ($P = .53$) or Fe ($P = .55$) concentrations. There was no relationship between sediment chemical parameters (Fe, Al, and percent OM) and SRP sorption index (based on correlation analyses). These data suggest that chemical interactions are not as important as biotic interactions in maintaining the low stream water SRP concentrations.

The P sorption index was highest for sediment from debris dam reaches and lowest for sediment from cobble reaches in HWC (Table 6; ANOVA, $P < .005$, $n = 3$). The EPC was lowest for sediment from debris dam reaches with the largest surface area : volume ratio, and highest for the cobble reaches.

Finally, EPC was lowest for sediment incubated at 4°C (2.9 μg/L SRP) and 11° (3.1 μg/L) and highest for sediment incubated at 18° (13.0 μg/L). Stream water temperature when the sediments were collected for this experiment was 9°.

DISCUSSION

Biotic uptake of P and N.—Microbial processes appear to be maintaining low SRP and NH_4-N concentrations in both HWC and WS2. Biotic sorption of P by sediments is more important than abiotic sorption in both streams as indicated by the low EPC values for untreated sediments when compared with EPC values for sterilized sediments (Table 5; EPC is a better indicator of P sorption capacity than sorption index at the low stream water concentrations measured at the two sites). Gregory (1978) also demonstrated the importance of biotic uptake of P by stream sediments in a nearby Oregon mountain stream. While the EPC is higher in WS2 than HWC, the values are similar to baseline SRP concentrations in each stream (Table 1). Since EPC for sterilized sediments in HWC is approximately equal to the stream water concentration at 0 m during the solute additions, essentially all SRP uptake measured during the additions in HWC was due to biotic processes. In WS2, the EPC for sterilized sediments is less than the augmented stream water concentration during the additions, and therefore a greater portion of uptake is probably due to abiotic processes than in HWC.

The inconsistent pattern in EPC for sediments of different size fractions (Table 6) indicates that differences in uptake rate observed between sites is not simply a surface area phenomenon. SRP retention was very low in debris dam reaches (long uptake lengths) in WS2, and retention in debris dam reaches was no different from rock outcrop or cobble reaches in HWC (Table 2). High retention was expected in debris dam

TABLE 5. The sorption index ($\bar{X} \pm 1$ SD, $n = 6$) and equilibrium phosphorus concentration (EPC) of soluble reactive phosphorus (SRP) in untreated and radiation-sterilized sediment from Hugh White Creek (HWC), North Carolina, and the stream draining Watershed 2 (WS2), Oregon.

		SRP sorption index (X/ln C)*	EPC (μg/L)
HWC	Untreated	16.0 ± 1.2	1.0
	Sterilized	18.4 ± 2.0	10.7
WS2	Untreated	16.9 ± 2.3	5.4
	Sterilized	14.3 ± 1.1	8.6

* X = μg/g sediment, adsorbed from an initial SRP percentage of 2 mg/L; C = final SRP concentration after 1-h incubation.

TABLE 6. The sorption index ($\bar{X} \pm 1$ SD; see Table 5 footnote for explanation), equilibrium phosphorus concentration (EPC), aluminum (Al), and iron (Fe) concentrations of sediment from Hugh White Creek (HWC) and the stream draining Watershed 2 (WS2).

	Sediment size (mm)	SRP sorption index	EPC (μg/L)	OM (%)	[Al] (mg/g)	[Fe] (mg/g)
HWC	>2	13.5 ± 0.6	5.9	1.59	60.48	29.73
	1–2	17.9 ± 0.5	4.4	1.61	28.14	13.85
	0.4–1	23.6 ± 1.0	2.3	1.13	24.78	12.29
	0.1–0.4	34.7 ± 0.8	4.5	2.09	37.80	18.46
WS2	>2	11.7 ± 1.8	4.2	7.53	39.27	19.25
	1–2	18.7 ± 1.5	3.7	8.22	51.66	25.22
	0.4–1	24.0 ± 2.7	4.2	5.75	55.02	27.32
	0.1–0.4	36.2 ± 1.1	3.7	6.43	38.22	18.22
SRP sorption capacities of sediments from three habitat types in HWC						
Cobble		1.5 ± 0.7	13.5			
Gravel		3.3 ± 0.3	11.8			
Debris dam		13.9 ± 0.8	8.0			

reaches because they have a greater percentage of fine-grained sediment and thus the greatest surface area available for uptake. This hypothesis is supported by laboratory experiments in which unsieved sediments from debris dam reaches in HWC had lower EPC than other habitat types (Table 6). These results contradict the results from sieved sediments, suggesting that the low EPC associated with debris dam sediments has to do with something that is removed in the sieving process. However, low uptake rates in debris dam reaches may be mitigated by low sediment infiltration rates in the fine sediment associated with debris dams (Munn and Meyer 1988), resulting in less surface area in contact with the nutrient supply. The effect of low infiltration rates would not be encountered in the laboratory experiments because of greater contact between the sediments and nutrients in the flask. The lack of relationship between sediment chemical (Al and Fe concentrations and OM content) and physical factors to P sorption, and the stronger relationship with biotic factors, indicates strong biotic control of SRP uptake by stream sediments; hence, P dynamics appear to be important to stream metabolic processes, especially in HWC.

Although the EPC is very similar in Bear Brook (Hubbard Brook, New Hampshire; ≈ 2 μg/L P; Meyer 1979) to HWC and WS2, mechanisms for maintaining low P concentrations are different. While P concentrations are primarily under biotic control in HWC and WS2, abiotic sorption maintains the low concentrations in Bear Brook (Meyer 1979). P sorption in Bear Brook increases as particle size decreases, and is highly correlated with OM content and acid-extractable Al content (Meyer 1979). This is not the case in HWC or WS2.

The N sediment sorption experiments suggest that NH_4-N uptake by stream sediments is primarily a biotic process, especially at low stream water concentrations. Biotic uptake by WS2 sediments are able to maintain lower NH_4-N concentrations than uptake by HWC sediments. While these data are not directly comparable with field data for NO_3-N, they do demonstrate the importance of N sorption. As part of another study at Coweeta, uptake lengths for NH_4-N were much shorter than for NO_3-N (Munn 1989), indicating that N removal by sediments is an important process and that the mechanisms involved warrant further investigation.

Influence of geomorphology.—Despite evidence that benthic organic matter is a source of interstitial DOC (Crocker and Meyer 1987), there was a net removal of DOC in debris dam reaches. Debris dams greatly enhance retention of CPOM (Speaker et al. 1984), which promotes increased channel roughness and accumulation of FPOM (secondary trapping). Although there were no significant differences in sediment OM content between habitats (due to large variability within habitat types), debris dam reaches tended to have greater benthic organic matter accumulations, especially in the western stream with greater accumulations of large woody debris. In both streams, debris dams were the major sites of DOC uptake (Fig. 2; 60% of all uptake in HWC and 81% in WS2). Physical adsorption of DOC to stream sediments occurs most rapidly (Dahm 1981), but most DOC uptake in undisturbed streams is mediated by the benthic microbial community (Kuserk et al. 1984). Bacterial density was not much greater in reaches with greater OM, suggesting that differences in uptake rates were not due to difference in microbial metabolism; however, reaches with greater OM should be able to support greater bacterial production (which may not be reflected in density measurements) and have greater surface area for fungal communities that were not measured. Also, the woody debris may be a substrate for biota important in DOC retention, but biotic communities on wood substrates were not sampled.

Debris accumulations also increased nitrate retention, primarily at the western site (Fig. 2). High nitrate uptake rates for debris dam reaches in WS2 would have a strong influence on the export of N from the catchment since debris dams are so abundant in WS2. In HWC, nitrate retention in gravel reaches was greater than expected; infiltration into the sediments was most rapid in cobble habitats resulting in more contact between the nutrient and sediment (Munn and Meyer 1988), and more surface area was available for uptake with the fine-grained sediments associated with debris dams. High retention in gravel reaches may be a compromise between these two processes.

Despite low channel roughness and consequently relatively small available surface area, rock outcrops exhibited high Ca retention in both streams and high nitrate retention in the eastern stream. Moss communities covering the rock surfaces are a physically stable substrate, which enhances biological stability (Gurtz and Wallace 1984) and leads to relatively high respiration rates (Naiman and Sedell 1980, Naiman 1983). Perhaps these factors resulted in an increased demand for Ca and nitrate.

Although habitat type did not influence P retention in HWC, P retention occurred primarily in rock outcrop reaches in WS2. Rock outcrop reaches in the western stream had high organic content, although neither chl *a* nor bacteria were sampled for this substrate. However, the forest canopies over these reaches tended to be more open than for other reaches, and chl *a* concentrations were high in a nearby stream (Gregory 1980). Periphyton associated with rock outcrops may be an important sink of P from stream water in WS2.

Cobble and gravel reaches tended to have low retention of nutrients and DOC (with the exception of reasonably high uptake of P in cobble reaches in HWC), despite relatively high rates of infiltration into the sediments (Munn and Meyer 1988). While this is of minor significance in WS2 where cobble–riffle reaches comprise only 12% of the total stream bed area, it is of greater importance in HWC where cobble and gravel habitats together account for 62% of the stream bed area. Higher flushing rates through the sediments of these habitats may result in a less stable and less productive epibenthic community, resulting in a lower nutrient demand.

In summary, local geomorphology influenced the retention of solutes in two headwater streams. The physical differences between different habitats and the response of the biotic community to these differences altered the demand for nutrients. For example, gravel beds were not important in the retention of nutrients and DOC, despite the relatively large reactive surface area available. In the western stream dominated by large debris dams, cobble–riffle reaches tended to have low retention of the added solutes. Low retention by a habitat does not exert a large influence on overall stream retention when the habitat is not prevalent in the stream (e.g., nitrate retention in cobble reaches for WS2, Tables 2 and 4) but has a greater impact when the habitat is well represented (e.g., P retention in gravel reaches for HWC, Tables 2 and 4); thus, each habitat within a stream has specific properties that differ in retention capacities. In further studies of solute retention, it is important to stratify sampling by habitat type to fully understand retention of solutes by the mosaic of habitats characterizing the stream as a whole.

Intersite comparison.—The lower uptake rates of P in WS2 compared with HWC (Table 4) were expected based on the geographic location of each stream. In their survey of the relationship between geology and P export, Dillon and Kirchner (1975) found that P export was greater on forested igneous catchments of volcanic origin (such as WS2) than those of plutonic origin or catchments of sedimentary rock. While Dillon and Kirchner (1975) could not explain the cause for this difference, parent geology could influence water chemistry and the chemistry of stream bed sediments as well as channel structure; therefore, while geology influences the sources of the nutrients, it may also affect nutrient utilization by soils and sediment resulting in different ratios of elements once they reach the stream water. This may account for the different N:P ratios in HWC vs. WS2. N:P was higher for HWC than for WS2, suggesting a greater potential for P limitation in HWC (Redfield 1958). This was substantiated by the greater retention of P in HWC. Although P uptake was biotic in both streams, the strongest predictor of P retention was parent geology and not biotic parameters, since the western stream had greater densities of bacteria and chl a (Table 3), but much less P retention (Table 4). Sediment organic content, chl *a* concentrations, and bacterial density are better predictors of where within a stream P retention is greatest (Mulholland et al. 1983, Triska et al. 1983).

In contrast to P, nitrate uptake rates were much greater for the Oregon stream than the North Carolina stream (Table 4), with the highest uptake rates for the WS2 debris dam reaches (Table 2). The uptake rates appear to be related to chl a concentrations; however, N:P appears to be the strongest predictor of nitrate retention between streams. Nitrate retention was greatest in WS2 where stream water N:P was lowest, suggesting a potential for N limitation (Redfield 1958). However, N:P for HWC was between 10 and 20, which is in the range considered to be indicative of either N or P limitation (Redfield 1958). While P retention was much greater than nitrate retention in this stream, later experiments in artificial channels constructed over a nearby stream indicated that ammonium retention was high, similar to SRP, and that both ammonium and SRP retention were much greater than nitrate retention (Munn 1989). Unfortunately, ammonium retention was not measured in WS2, but we predict that ammonium retention would be greater than nitrate retention since ammonium is easier than nitrate to assimilate biotically and since most ammonium uptake is through biotic mechanisms (based on laboratory experiments).

The uptake rate of P in a first-order Tennessee stream was at a seasonal low in the summer at a rate of 1.3 $\mu g \cdot m^{-2} \cdot min^{-1}$ (uptake length of 97 m; Mulholland et al. 1985), based on radiotracer releases. While the uptake rate of P is greater in HWC, the uptake length is similar. Also, the uptake rate of P in WS2 is similar to the Tennessee stream, but the uptake length is much longer in WS2. The differences in uptake lengths vs. rates are probably a result of different methodologies in conducting the releases and calculating the uptake rates. The Tennessee study used a radiotracer release as opposed to a nonradioactive solute in this study; however, the major difference is in the method of calculating uptake rate. In the Tennessee stream, the uptake rate (micrograms per square metre per minute) was calculated by multiplying the time-specific P uptake rate (per minute) by the concentration of SRP and the average water depth (see Mulholland et al. 1985: Table 2). In contrast, the uptake rate in this study has the same units, but is calculated by multiplying the change in SRP by the discharge divided by the surface area of the reach. Because of these differences in calculating uptake rates, it is more useful to focus on the differences in uptake length between the streams, therefore, we conclude that P retention is similar in HWC and the Tennessee stream, but much less in WS2. During the summer in the Tennessee stream, CPOM is at a minimum, P demand is low, and hence uptake lengths are long relative to other seasons (Mulholland et al. 1985). Our study suggests that summertime P demand in WS2 is lower than HWC or the Tennessee stream, based on the long uptake lengths. Thus, even in the summer when CPOM quality and quantity are at a seasonal low in the eastern streams, P demand is relatively high and P is rapidly sorbed by biotic components of the stream.

By reworking P uptake data from Meyer (1978), we were able to calculate rough estimates of uptake length at two sites characterized by different geomorphic structure in a small stream, Bear Brook, at the Hubbard Brook Experimental Forest, New Hampshire. During summer releases (July and August 1976), uptake lengths ranged from 5 to 21 m for a rock outcrop site with abundant moss and from 10 to 67 m for a cobble–riffle site with small debris dams and tree roots. Meyer (1979) found the bryophyte community to be efficient in P retention but concluded that this substrate was not important as a P sink in Bear Brook since it covered only 2% of the stream area. Nevertheless, both sites in Bear Brook exhibited strong P retention, and were more retentive than WS2 and slightly more retentive than HWC (based on Mann-Whitney *U* tests) during this season. The mechanism of P uptake in Bear Brook is also different; uptake is primarily abiotic and strongly controlled by sediment particle size and Al content (Meyer 1979). This abiotically sorbed P may be available for use by the biota over a long time period.

Although no nitrate uptake was detected when nitrate or nitrate + DOC was added to Bear Brook, New Hampshire, there was significant retention of ammonium when the ammonium concentration was increased two orders of magnitude over background concentrations (Richey et al. 1985). By examining Fig. 1 of Richey et al. (1985), we estimated the uptake length of ammonium in Bear Brook to be 200 m, although a considerable portion of this was subsequently nitrified and lost as nitrate. In field flume experiments at Coweeta, retention of ammonium was greater than nitrate (e.g., uptake length of 32 m for ammonium and 320 m for nitrate, Munn 1989); this is not surprising since ammonium is a less costly form of N to assimilate biotically. Thus, we conclude that Bear Brook is not highly retentive of nitrate when compared to WS2; nitrate retention in Bear Brook is more similar to HWC.

The uptake rate of nitrate-N for a N + P limited stream in Kansas was 57 $\mu g \cdot m^{-2} \cdot min^{-1}$ (Dr. Cathy Tate, Kansas State University, *personal communication*), three times as high as any of the rates measured in this study. The Kansas data were based on nitrate additions that increased stream water concentrations from near detection limits to ≈ 100 $\mu g/L$, a concentration reached during storm events; however, this is an order of magnitude greater than the augmented concentration in HWC or WS2. Since there is a positive relationship between amount of a nutrient added and uptake rate (Meyer 1979), this difference alone could account for the differences in uptake rate between the streams in this study and the Kansas stream. That is, uptake may be concentration dependent, and the differences in uptake rates could be due to differences in nutrient release technique. There is a second possible explanation for high uptake rates in the Kansas stream. This stream has an open canopy and high standing stocks of chl a. This could result in a greater N demand, and thus greater uptake rates for nitrate (Triska et al. 1983).

Nitrate uptake was measured in a flume experiment in a northern California coastal stream following NO_3-N and PO_4-P amendment (Triska et al. 1983). In treatment channels with light conditions similar to WS2 and HWC, nitrate-N uptake ranged from ≈ 0 to 8 $\mu g \cdot m^{-2} \cdot min^{-1}$ depending on time of day and age of the periphyton community; as the amount of light reaching the channels increased, uptake rates increased, approaching rates to those measured in the Kansas stream. The upper end of this range is within the range measured for WS2 in this study (Table 2). Although the California stream like WS2 is potentially N limited (Triska et al. 1983), adding nitrate had little effect on primary production in the California stream or a stream adjacent to WS2 (Gregory 1980, Triska et al. 1983), even though nitrate levels were near detection limits. The heterotrophic communities were probably energetically based on DOC and dependent on upstream supplies of detritus. These findings support previous conclusions that primary production in small streams with forested catchments is light limited, despite low concentrations of nutrients (Gregory 1980, Triska et al. 1983, Lowe et al. 1986).

Uptake of DOC in HWC and WS2 is near the range published previously (see Kuserk et al. 1984); habitat-weighted uptake (measured as C) in HWC is 527 $mg \cdot m^{-2} \cdot h^{-1}$ and WS2 is 38 (note change of units from Table 4) as compared to a range of 6 to 400 $mg \cdot m^{-2} \cdot h^{-1}$ using a variety of techniques. High DOC uptake rates were also calculated for Bear Brook, New Hampshire (McDowell 1985: Table 2); the rates were more similar to HWC than WS2. Using data presented by McDowell (1985: Fig. 1), we estimated DOC uptake length. The lengths range from 56 m for yellow birch leachate to 83 m for spruce leachate, over the course of a 5-h addition. These lengths are in the range presented here for HWC and generally shorter than those in WS2.

As in an earlier study in HWC and a nearby stream (Meyer et al. 1988), uptake rates of DOC in the eastern stream are at the high end of the reported range. Meyer et al. (1988) attribute the high rates to the use of a labile DOC source (sucrose as opposed to leachate) and a consequence of overestimating uptake in stream beds with high channel roughness. Since WS2 has a greater percentage of rock outcrop (Table 3) and the debris dams are underlain primarily by outcrop as opposed to gravel as in HWC, WS2 has a lower channel roughness than HWC. Thus, differences in stream bed roughness may partly account for the difference in uptake rates between these two streams, although uptake lengths are so strikingly different between the two streams that there are probably other reasons as well. In a chamber experiment using material collected from a western Cascade stream, the rate of microbial uptake (measured as C) of DOC was 14 $mg \cdot m^{-2} \cdot h^{-1}$, an estimated 77% of total DOC leachate removed (Dahm 1981). Thus, the total C uptake was 18 $mg \cdot m^{-2} \cdot h^{-1}$; this is in the range reported for WS2 (38 $mg \cdot m^{-2} \cdot h^{-1}$) even though a more labile source of DOC (sucrose) was used in our field addition. However, when the total uptake rate was calculated over the first 9 h of the 48-h chamber experiment, the C uptake rate was 43 $mg \cdot m^{-2} \cdot h^{-1}$ and for the first 20 min, the rate was 442 $mg \cdot m^{-2} \cdot h^{-1}$ (Dahm 1981). This higher rate over the shorter time period is attributed to rapid abiotic uptake initially followed by saturation of the organic substrate (Dahm 1981). An important factor in the chamber experiment is the greater contact between the DOC source and the substrate. Saturation of the substrate is less likely to occur in field additions, and the rates are not likely to vary so strikingly over a 48-h field addition. Rapid infiltration into the sediments in HWC may result in a high initial uptake rate as measured in this study, but over the course of a few hours, the rate may decrease and be more similar to WS2, where the sediments are more shallow.

Synthesis.—In comparing solute retention between ecosystems, it is important to compare field and analytical methodologies as well as final conclusions, because methods strongly influence the results. In further comparative studies, it will be important to standardize methods and to stratify sampling by habitat to better understand whole stream retention of solutes.

The combined results of laboratory experiments and field retention measurements indicate that in HWC, strong biotic control of P uptake coupled with high P demand, result in relatively short P uptake lengths and therefore a strong impact of ecosystem dynamics (microbial processes, decomposition) on P spiraling compared to WS2. In HWC, short uptake lengths of Ca and DOC (particularly at debris accumulations) suggest the demand for these elements could influence ecosystem dynamics. There is no evidence for significant differences between habitats in P uptake for HWC during the summer although debris dams are responsible for most DOC and Ca retention. In WS2, the western stream, strong biotic control of N retention combined with strong N demand result in relatively short N uptake lengths. The results suggest that in WS2, N spiraling may have a strong influence on ecosystem processes. This is especially true at sites of downed timber that retain both FPOM and CPOM, creating a high N demand. Bear Brook, a small forest stream in New Hampshire, was similar to HWC in retention of P and DOC, although the mechanisms for P uptake are quite different. Retention of nitrate was negligible in Bear Brook, similar to HWC, although ammonium (a less costly form of N to assimilate biotically) was taken up in Bear Brook.

These results emphasize the overriding influence of parent geology on ecosystem processes. Geology may be a major determinant of solute retention through direct and indirect processes affecting water chemistry and ratios of elements present in stream water. Geology also determines geomorphic structure of the stream channel, thereby influencing physical and biotic characteristics of the channel that may in turn influence solute retention.

Acknowledgments

Dr. M. Sumner (Agronomy Department, University of Georgia) permitted the use of his atomic absorption spectrophotometer for calcium analyses. The Center for Applied Isotope Studies at the University of Georgia kindly irradiated the sediment samples. Dan Kearns provided valuable and enthusiastic field assistance in Oregon. Dr. Stan Gregory facilitated the work at the H. J. Andrews Experimental Forest in Oregon. Dr. Wayne Swank and the staff at the Coweeta Hydrologic Laboratory provided data and gave logistical assistance. This paper benefited from the advice of two anonymous reviewers and Dr. Stuart Fisher. Support was provided by National Science Foundation grant BSR 8514328.

Literature Cited

APHA. 1985. Standard methods for the examination of water and wastewater. 16th edition. American Public Health Association, Port City, Maryland, USA.

Bencala, K. E., D. M. McKnight, and G. W. Zellweger. 1987. Evaluation of natural tracers in an acidic and metal-rich stream. Water Resources Research 23:827–836.

Bowlby, J. N., and J. C. Roff. 1986. Trophic structure in southern Ontario streams. Ecology 67:1670–1679.

Brussock, P. P., A. V. Brown, and J. C. Dixon. 1986. Channel form and stream ecosystem models. Water Resources Bulletin 21:859–866.

Buckley, B. M., and F. J. Triska. 1978. Presence and ecological role of nitrogen-fixing bacteria associated with wood decay in streams. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen 20: 1333–1339.

Crocker, M. T., and J. L. Meyer. 1987. Interstitial dissolved organic carbon in sediments of a southern headwater stream. Journal of the North American Benthological Society 6: 159–167.

Dahm, C. N. 1981. Pathways and mechanisms for removal of dissolved organic carbon from leaf leachate in streams. Canadian Journal of Fisheries and Aquatic Science 38:68–76.

de Vries, P. G. 1974. Multi-stage line intersect sampling. Forest Science 20:129–133.

Dillon, P. J., and W. B. Kirchner. 1975. The effects of geology and land use on the export of phosphorus from watersheds. Water Research 9:135–148.

Douglass, J. E., and W. T. Swank. 1975. Effects of management practices on water quality and quantity: Coweeta Hydrologic Laboratory, North Carolina. Northeastern Experiment Station, United States Forest Service General Technical Report NE-13.

Downes, M. T. 1978. An improved hydrazine reduction method for the automated determination of low nitrate levels in freshwater. Water Research 12:673–675.

Elwood, J. W., J. D. Newbold, A. F. Trimble, and R. W. Stark. 1981. The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. Ecology 62:146–158.

Franklin, J. F., K. Cromack, Jr., W. Denison, A. McKee, C. Master, J. Sedell, F. Swanson, and G. Juday. 1981. Ecological characteristics of old-growth Douglas-fir forests. United States Forest Service General Technical Report PNW-118.

Fredriksen, R. L. 1972. Nutrient budget of a Douglas-fir forest on an experimental watershed in western Oregon. Pages 113–131 *in* J. F. Franklin, L. J. Dempster, and R. H. Waring, editors. Research on Coniferous Forest Ecosystems: a Symposium. United States Forest Service Pacific Northwest Range and Experiment Station, Portland, Oregon, USA.

Froehlich, H. A. 1973. Natural and man-caused slash in streams. Loggers handbook. Volume 33. Pacific Logging Congress, Portland, Oregon, USA.

Gregory, S. V. 1978. Phosphorus dynamics on organic and inorganic substrates in streams. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen 20:1340–1346.

———. 1980. Effects of light, nutrients, and grazing on periphyton communities in streams. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Grimm, N. B., S. G. Fisher, and W. L. Minckley. 1981. Nitrogen and phosphorus dynamics in hot desert streams of southwestern U.S.A. Hydrobiologia 83:303–312.

Gurtz, M. E., and J. B. Wallace. 1984. Substrate-mediated response of stream invertebrates to disturbance. Ecology 65:1556–1569.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133–302.

Hatcher, R. D., Jr. 1988. Bedrock geology and regional geologic setting of Coweeta Hydrologic Laboratory in the eastern Blue Ridge. Pages 81–92 *in* W. T. Swank and D. A. Crossley, Jr., editors. Ecological studies. Volume 66. Forest hydrology and ecology at Coweeta. Springer-Verlag, New York, New York, USA.

Hobbie, J., R. Daley, and S. Jasper. 1977. Use of nucleopore filters for counting bacteria by fluorescent microscopy. Applied Environmental Microbiology 33:1225–1228.

Huryn, A. D., and J. B. Wallace. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. Ecology 68:1932–1942.

Klotz, R. L. 1985. Factors controlling phosphorus limitation in stream sediments. Limnology and Oceanography 30:543–553.

Kuserk, F. T., L. A. Kaplan, and T. L. Bott. 1984. In situ measures of dissolved organic carbon flux in a rural stream. Canadian Journal of Fisheries and Aquatic Science 41:964–973.

Lowe, R. L., S. W. Golladay, and J. R. Webster. 1986. Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. Journal of the North American Benthological Society 5:221–229.

McDowell, W. H. 1985. Kinetics and mechanisms of dissolved organic carbon retention in a headwater stream. Biogeochemistry 1:329–352.

Meyer, J. L. 1978. Transport and transformation of phosphorus in a forest stream ecosystem. Dissertation. Cornell University, Ithaca, New York, USA.

———. 1979. The role of sediments and bryophytes in phosphorus dynamics in a headwater stream ecosystem. Limnology and Oceanography 24:365–375.

Meyer, J. L., and G. E. Likens. 1979. Transport and transformation of phosphorus in a forest stream ecosystem. Ecology 60:1255–1269.

Meyer, J. L., C. M. Tate, R. T. Edwards, and M. T. Crocker. 1988. The trophic significance of dissolved organic carbon in streams. Pages 269–278 *in* W. T. Swank and D. A. Crossley, Jr. Ecological studies. Volume 66. Forest hydrology and ecology at Coweeta. Springer-Verlag, New York, New York, USA.

Mulholland, P. J., J. W. Elwood, J. D. Newbold, J. R. Webster, L. A. Ferren, and R. E. Perkins. 1984. Phosphorus uptake by decomposing leaf detritus: effect of microbial biomass and activity. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen 22:1899–1905.

Mulholland, P. J., J. D. Newbold, J. W. Elwood, L. A. Ferren, and J. R. Webster. 1985. Phosphorus spiralling in woodland streams: seasonal variations. Ecology 66:1012–1023.

Mulholland, P. J., J. D. Newbold, J. W. Elwood, and C. L. Hom. 1983. The effect of grazing intensity of phosphorus spiralling in autotrophic streams. Oecologia (Berlin) 58: 358–366.

Munn, N. L. 1989. The role of stream substrate and local geomorphology in the retention of nutrients in headwater streams. Dissertation. University of Georgia, Athens, Georgia, USA.

Munn, N. L., and J. L. Meyer. 1988. Rapid flow through the sediments of a headwater stream in the southern Appalachians. Freshwater Biology 20:235–240.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27:31–36.

Naiman, R. J. 1983. The annual pattern and spatial distribution of aquatic oxygen metabolism in boreal forest watersheds. Ecological Monographs 53:73–94.

Naiman, R. J., and J. R. Sedell. 1980. Relationships between metabolic parameters and stream order. Canadian Journal of Fisheries and Aquatic Science 37:834–847.

Newbold, J. D., J. W. Elwood, R. V. O'Neill, and W. Van Winkle. 1981. Measuring nutrient spiralling in streams. Canadian Journal of Fisheries and Aquatic Sciences 38: 860–863.

Peterson, B. J., J. E. Hobbie, A. E. Hershey, M. A. Lock, T. E. Ford, J. R. Vestal, V. L. McKinley, M. A. J. Hullar, M. C. Miller, R. M. Ventullo, and G. S. Volk. 1985. Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorus. Science 229:1383–1386.

Pringle, C. M., R. J. Naiman, G. Bretschko, J. R. Karr, M. W. Oswood, J. R. Webster, R. L. Welcomme, and M. J. Winterbourn. 1988. Patch dynamics in lotic systems: the stream as a mosaic. Journal of the North American Benthological Society 7:503–524.

Redfield, A. C. 1958. The biological control of chemical factors in the environment. American Scientist 46:205–221.

Richey, J. S., W. H. McDowell, and G. E. Likens. 1985. Nitrogen transformations in a small mountain stream. Hydrobiologia 124:129–139.

Scrivener, J. C. 1975. Water, water chemistry, and hydrochemical balance of dissolved ions in Carnation Creek Watershed, Vancouver Island, July 1971–May 1974. Fisheries and Marine Technical Report Number 564, Department of the Environment, Ottawa, Ontario, Canada.

Sebetich, M. J., V. C. Kennedy, S. M. Zand, R. J. Avanzino, and G. W. Zellweger. 1984. Dynamics of added nitrate and phosphate compared in a northern California woodland stream. Water Resources Bulletin 20:93–101.

Smith-Cuffney, F. L., and J. B. Wallace. 1987. The influence of microhabitat on availability of drifting invertebrate prey to a net-spinning caddisfly. Freshwater Biology 17:91–98.

Speaker, R., K. Moore, and S. Gregory. 1984. Analysis of the process of retention of organic matter in stream ecosystems. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen 22:1835–1841.

Stream Solute Workshop. *In press.* Concepts and methods for assessing solute dynamics in stream ecosystems. Journal of the North American Benthological Society.

Strickland, J. D. H., and T. R. Parsons. 1977. A practical handbook of seawater analysis. Second edition. Fisheries Research Board of Canada, Ottawa, Ontario, Canada.

Swank, W. T. 1986. Biological control of solute losses from forest ecosystems. Pages 85–139 *in* S. T. Trudgill, editor. Solute processes. John Wiley & Sons, New York, New York, USA.

Swank, W. T., and W. H. Caskey. 1982. Nitrate depletion in a second-order mountain stream. Journal of Environmental Quality 11:581–584.

Taylor, A. W., and H. M. Kunishi. 1971. Phosphate equilibria on stream sediment and soil in a watershed draining an agricultural region. Journal of Agricultural and Food Chemistry 19:827–831.

Thut, R. N., and E. P. Haydu. 1971. Effects of forest chemicals on aquatic life. *In* J. T. Krygier and J. D. Hall, editors. A Symposium on Forest Land Uses and Stream Environment. Continuing Education Publications, Oregon State University, Corvallis, Oregon, USA.

Triska, F. J., V. C. Kennedy, R. J. Avanzino, and B. N. Reilly. 1983. Effects of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. Pages 129–159 *in* F. D. Fontaine III and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science, Michigan, USA.

Triska, F. J., J. R. Sedell, and S. V. Gregory. 1982. Coniferous forest streams. Pages 292–332 *in* R. L. Edmonds, editor. Analysis of coniferous forest ecosystems in the western United States. International Biological Program Synthesis Volume 14. Hutchinson Ross, Stroudsburg, Pennsylvania, USA.

Wallace, J. B., and A. C. Benke. 1984. Quantification of wood habitat in subtropical Coastal Plain streams. Canadian Journal of Fisheries and Aquatic Sciences 41:1643–1652.

Ward, G. M., and N. G. Aumen. 1986. Woody debris as a source of fine particulate organic matter in coniferous forest stream ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 43:1635–1642.

Young, S. A., W. P. Kovalak, and K. A. Del Signore. 1978. Distances travelled by autumn-shed leaves introduced into a woodland stream. American Midland Naturalist 100:217–222.