

STREAM NUTRIENT UPTAKE, FOREST SUCCESSION, AND BIOGEOCHEMICAL THEORY

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Abstract. Theories of forest succession predict a close relationship between net biomass increment and catchment nutrient retention. Retention, therefore, is expected to be greatest during aggrading phases of forest succession. In general, studies of this type have compared watershed retention efficiency by monitoring stream nutrient export at the base of the catchment. As such, streams are viewed only as transport systems. Contrary to this view, the nutrient spiraling concept emphasizes transformation and retention of nutrients within stream ecosystems. In this paper, we address how biogeochemical theory developed for forests may apply to lotic ecosystems in the context of catchment-level succession. Using measures of nutrient spiraling to document uptake, we focus on later seral stages by comparing streams draining second-growth (i.e., 75–100-yr stands) and old-growth (i.e., >400 yr) forests of the southern Appalachian Mountains, USA. Standing stocks of large woody debris (LWD) in old-growth streams were orders of magnitude greater than in second-growth streams where logging practices removed LWD from stream channels. Debris dams were also more frequent in old-growth streams. Solute injections were used to quantify retention of dissolved inorganic phosphate (PO₄-P), the limiting nutrient in Appalachian streams. Uptake velocities in old-growth streams were significantly greater than in second-growth streams and were closely related to debris dam frequency, LWD volume, and the proportion of fine-grained (<2 mm) sediments present in the stream bed. These data suggest that streams of old-growth forests have greater demand for PO₄-P compared to streams draining aggrading second-growth catchments. Finally, we present a schematic model of forest succession, aquatic–terrestrial interaction, and biogeochemical functioning in stream ecosystems emphasizing that the successional time course of retention in lotic ecosystems may be very different than that predicted for forests.

Key words: *Appalachian Mountains, USA; aquatic–terrestrial interaction; forest succession; large woody debris; nutrient retention; nutrient uptake; old-growth and second-growth forest; streams, uptake lengths.*

INTRODUCTION

A great deal of research has addressed how ecosystem metabolism, accumulation of biomass, and nutrient retention change with time after disturbance. Much of this work has addressed the functioning of forest ecosystems following timber harvest (Vitousek and Reiners 1975, Likens et al. 1978, Gorham et al. 1979). Bormann and Likens (1979) emphasized that succession in northern hardwood forests should include phases differing in ecosystem biomass. Their Biomass Accumulation Model predicted that following a relatively short phase of “reorganization,” forest organic matter (OM) would increase rapidly reflecting high net biomass increments during an “aggrading” phase. Their model further predicted that senescence of older trees would eventually generate gaps that reduce forest biomass during the “transition phase.” In late stages of succession (i.e., hundreds of years post disturbance), the forest becomes a stable mosaic of gaps and inter-

ceding stands that functions at steady state. More than 20 yr after its publication, this model of forest growth remains a central tenet of successional theory for forest ecosystems.

Characteristics of elemental cycling are also expected to vary with successional state. Odum (1969) hypothesized that, compared to rates of transport across ecosystem boundaries, internal cycling of nutrients dominates biogeochemical fluxes during later stages of succession. Vitousek and Reiners (1975) challenged this hypothesis by emphasizing a close relationship between net biomass increment and retention of nutrients by hardwood forests. Their model predicts that retention is greatest during the aggrading phases of forest succession and that later stages show little retention, reflecting the relatively invariant OM storage characteristic of steady state conditions in old-growth forests.

In studies addressing succession at the watershed scale, retention has been monitored at the base of the catchment as export in stream water. This approach attributes processes occurring within streams to terrestrial ecosystems (*sensu* Burns 1998) and assumes streams act solely as transport systems. In fact, streams are active ecosystems that process and transform nu-

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trients and OM. At the same time, most streams are strongly influenced by their surrounding catchments (Hynes 1975) and respond to physical and ecological processes occurring over the terrestrial landscape. In this paper, we investigate long-term dynamics of stream succession by addressing how fundamental theories of forest biogeochemical functioning apply to lotic ecosystems of forested catchments.

Nutrient retention in streams

The nutrient spiraling concept (Webster 1975, Newbold et al. 1983) emphasizes the use, transformation, and retention of nutrients within stream ecosystems. In lotic ecosystems, the downstream flow of water displaces materials and elongates nutrient cycles, effectively forming nutrient spirals (Webster 1975). A nutrient completes a spiral when having been released to the water in mineral form it becomes incorporated into organic form, and is again released to solution following mineralization (Newbold et al. 1983). Thus the spiraling length is the amount of downstream displacement that occurs during a complete spiral. The spiraling length is the sum of the turnover length and the uptake length (Newbold et al. 1983). The uptake length is the mean distance traveled by a nutrient as an inorganic solute before it is removed from solution. The turnover length is the distance it is transported in organic form (Newbold et al. 1983). Because nutrients contained in benthic OM are relatively immobile compared to dissolved materials, uptake lengths typically represent the majority of the spiraling distance in forested headwater streams (Newbold et al. 1983, Mulholland et al. 1985). While uptake lengths do not directly quantify mineralization rates, they are sensitive to recycling of nutrients (Mulholland et al. 1995, Martí et al. 1997) and have frequently been used to represent nutrient retention in stream ecosystems.

Uptake lengths for elements like phosphorus (P) and nitrogen (N) vary among streams reflecting differences in physical, chemical, and biological conditions. Research has shown that uptake lengths are influenced by water residence times (Valett et al. 1996, 1997), stream size (Wollheim et al. 2001), water temperature (Butturini and Sabater 1998), standing stocks of benthic leaf litter (Mulholland et al. 1985) and periphyton standing crop (Martí et al. 1997). Recent research has emphasized the influence of interstitial (i.e., hyporheic) processes on nutrient dynamics (Valett et al. 1996, Mulholland et al. 1997). In these and related studies, surface–subsurface interaction has been represented by numerical models that characterize such exchange as transient or dead zone storage (Bencala and Walters 1983, D'Angelo et al. 1993).

Succession in lotic ecosystems

Temporal succession is common in many streams at both community and ecosystem levels (Fisher et al. 1982, Peckarsky 1986). Generally, studies of stream

succession have focused on recovery from endogenous events such as floods (Fisher et al. 1982, Scrimgeour and Winterbourn 1989, Valett et al. 1994) where disturbance is restricted to aquatic components of the landscape and does not occur at the scale of the entire catchment. Fisher (1990) suggested that because of the endogenous nature of these disturbances, stream ecosystem recovery may be best addressed by stability theory (i.e., with measures of resistance and resilience) as compared to theories of ecological succession.

For streams in forested landscapes, wildfires (Minshall et al. 1989) and clear-cut timber harvesting (Hamon et al. 1986) are exogenous disturbances that occur at scales large enough to impact entire catchments. A number of studies have addressed succession in streams following clear-cutting (Meyer and Tate 1982, Webster et al. 1983, Golladay and Webster 1988, Stone and Wallace 1998). For the most part these studies have focused on immediate (i.e., decadal) impacts including altered OM standing stocks (reflecting pulsed inputs or removal of allochthonous material; Hedin et al. 1988, Bilby and Ward 1991), increased autochthonous production (Webster et al. 1983, Sabater et al. 2000), enhanced sediment inputs (Waters 1995), alterations in water quality and nutrient export (Bormann et al. 1974, Sollins et al. 1980), or changes to macroinvertebrate (Stone and Wallace 1998) and fish (Dolloff 1993, Hartman et al. 1996) assemblages.

In this paper, we address how retention theory (sensu Vitousek and Reiners 1975, Hedin et al. 1995) may apply to lotic ecosystems over the more extended time course of catchment-level succession. To supplement existing studies of stream succession, we focus on later seral stages by comparing nutrient uptake in streams draining second-growth (i.e., 75–100-yr stands) and old-growth (i.e., >400 yr) forests. First, we compared structural components of old-growth and second-growth streams that have been shown to be key regulators of nutrient dynamics in forested streams. Then, using solute injection experiments, we quantified nutrient spiraling indices to characterize nutrient retention. While we recognize that uptake rates alone do not directly quantify retention, we focus on discrete measures of whole-system demand and relate them to differences in nutrient retention. Our comparison of ecosystem structure and functioning in replicate stream systems suggests that, contrary to their terrestrial counterparts, streams of old-growth forests remain more retentive of dissolved nutrients compared to streams of aggrading second-growth catchments. We propose that this is an inherent aspect of allochthonous-based lotic ecosystems that results from critical aquatic–terrestrial interactions characteristic of the late stages of terrestrial succession. These interactions drive nutrient demand within streams and are lacking in those draining younger aggrading forests. Thus, the successional time course of biogeochemical functioning for forested streams, and potentially for other allochthonous-based

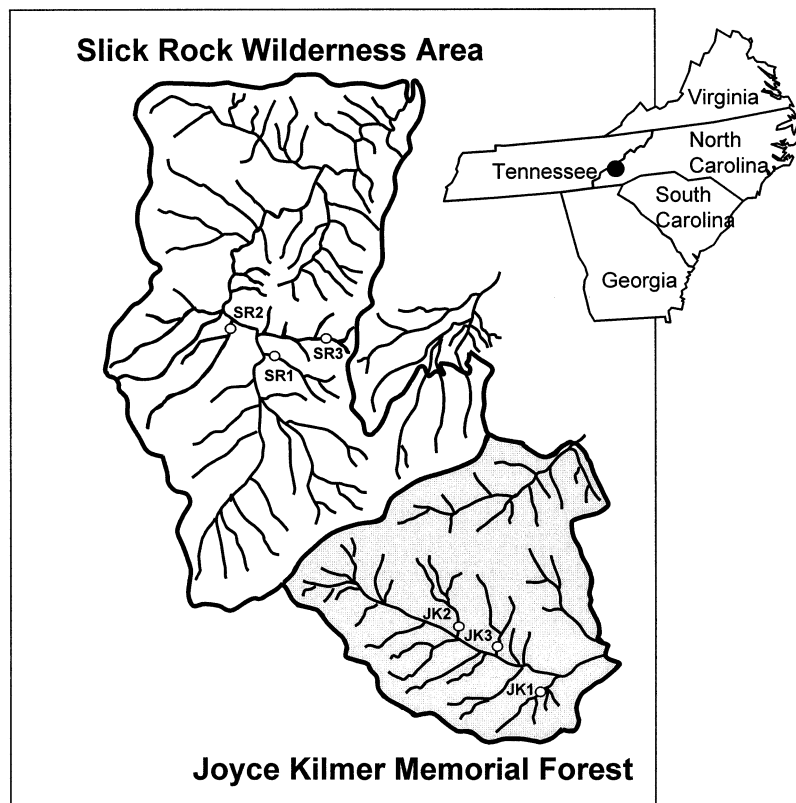


FIG. 1. Map of the southeastern United States showing the location of the Joyce Kilmer–Slick Rock Wilderness Area. The detailed map shows study sections of streams draining old-growth (JK1–JK3) and second-growth (SR1–SR3) catchments. The dark lines indicate watershed and wilderness boundaries.

ecosystems, may be very different than that predicted for forests. Finally, we present a conceptual model that provides a series of predictions relating the stages of forest succession, aquatic–terrestrial interaction, and biogeochemical functioning in stream ecosystems.

STUDY SITE

The research was conducted in streams of the Joyce Kilmer–Slick Rock (JKSR) Wilderness Area in the Nantahala National Forest, Graham County, North Carolina, USA, during July and August of 1998 (Fig. 1). The JKSR Wilderness Area includes the Joyce Kilmer Memorial Forest (JK), a 1540 ha forest preserve ranging in elevation from 670 m to 1600 m. The JK forest was never logged due to the construction of a nearby dam that flooded the only railroad access to the forest. The forest is composed of mixed hardwood stands, many of which are >400 yr old. Catchments in the adjacent Slick Rock (SR) Wilderness Area cover 4550 ha ranging from 330 m to 1600 m elevation and are characterized by similar mixed hardwood and evergreen stands. The SR forests were logged from 1917 until the construction of the Calderwood Lake Dam in 1922 (Cheoa Ranger District Office, USDA Forest Service, *personal communication*).

Three streams (first or second order) within the JK

and SR forests were selected as study sites (Fig. 1, Table 1). Streams in the JKSR Wilderness Area are characterized by soft waters of low ionic strength. While high elevation streams of the nearby Smoky Mountains periodically receive atmospheric N inputs that result in elevated nitrate-nitrogen ($\text{NO}_3\text{-N}$) concentrations (Flum and Nodvin 1995), our sites were of relatively low elevation (658–820 m, Table 1) and no significant relationship between elevation and N concentration was observed across the study streams.

METHODS

In July 1998, stream ecosystem structure and biogeochemical functioning were characterized by mapping the stream channel, quantifying standing stocks of benthic materials, and by executing solute injections to assess differences in stream hydrology and nutrient uptake.

Stream reach structure: channel geomorphology, light, and organic matter standing stocks

Following the definitions of Gregory et al. (1991), we measured widths of the wetted channel (WC) and active channel (AC) along with valley floor widths (VFW) on 7–13 transects established along each study reach. Light was quantified as photon flux density

($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) with a LI-1000 Photometer (Li-Cor, Lincoln, Nebraska, USA) set to integrate one-minute intervals during midday at each of the transects.

Stream bed sediment composition was assessed with granulometry techniques (Bevenger and King 1995). A single longitudinal transect was randomly placed in a zigzag pattern and sampled at one meter intervals over the length of each study reach. Proportion of observations belonging to a given size class was calculated based on a minimum of 200 data points for each stream.

Epilithic OM and chlorophyll standing stocks were quantified as the mean of three composite samples taken from random locations along the stream reach. Each composite sample included scrapings from known areas of three cobbles (~ 10 cm diameter) collected randomly within a 10 m radius of the chosen sample site. Rocks were scraped in the field and composite slurries were filtered through pre-ashed and weighed glass fiber filters (Pall Gelman Type AE, Pall Life Sciences, Ann Arbor, Michigan, USA) that were placed on ice for transport back to the laboratory. In the laboratory, filters were bisected and used to quantify epilithic OM as ash-free dry mass (AFDM) following standard methods and chlorophyll *a* using buffered acetone extraction (Wetzel and Likens 1991).

Standing stock of large woody debris (LWD) was measured using the line-transect method (Wallace and Benke 1984). Because of small stream widths, we established a single longitudinal transect that extended the entire length of each study reach and quantified the location and diameter of all wood that intersected the transect. Volume of woody debris per square meter of stream bottom was quantified following Wallace and Benke (1984). Wood mass per unit area ($\text{g AFDM}/\text{m}^2$) was calculated using a specific gravity of $0.356 \text{ g AFDM}/\text{cm}^3$ (Wallace et al. 2000).

We measured debris dam frequency by recording their number and location along the length of the study reach in each stream. Debris dams were defined as accumulations of OM that spanned the width of the stream and included at least one piece of woody debris with a minimum diameter of 5 cm.

Chemical properties of water and sediment

Water samples were filtered within six hours of collection using glass fiber filters (Whatman GFF, $0.70\text{-}\mu\text{m}$ pore size) and frozen until analyzed. During solute injection experiments, temperature, dissolved oxygen (DO), DO saturation (%), and temperature-compensated electrical conductivity were recorded at 15-s intervals using automated sondes (Hydrolab Model 4A, Austin, Texas, USA). Values recorded before the initiation of the injections were used to characterize background stream conditions. Background water samples were analyzed for a variety of dissolved constituents. Laboratory detection limits for each analyte were determined with the Method Detection Limit approach

(American Public Health Association 1998) and are presented preceding the method reference. Concentrations of chloride (Cl), ammonium nitrogen ($\text{NH}_4\text{-N}$) and nitrate nitrogen ($\text{NO}_3\text{-N}$) were determined on an Autoanalyzer II (Technicon, Emeryville, California, USA). Chloride was analyzed with the mercuric thiocyanate–ferric nitrate method (0.39 mg/L , Zall et al. 1956). The phenolphthorite method (0.007 mg/L , Solorzano 1969) and cadmium–copper reduction (0.001 mg/L , Wood et al. 1967) were used to determine $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$, respectively. The molybdate–antimony method (0.001 mg/L , Murphy and Riley 1962) was used to determine ortho-phosphate ($\text{PO}_4\text{-P}$) as soluble reactive phosphorus. Dissolved organic carbon was determined via persulfate digestion (0.7 mg/L , Menzel and Vaccaro 1964) on a Model 700 Total Organic Carbon Analyzer (Oceanographic International, College Station, Texas, USA). Total inorganic nitrogen (TIN) is the sum of $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$, and atomic ratios of N:P were calculated from TIN and $\text{PO}_4\text{-P}$ concentrations.

Solute injections, transport modeling, and nutrient uptake

Co-injections of a conservative tracer (i.e., Cl) and a biologically active solute ($\text{PO}_4\text{-P}$) were executed in each stream during summer baseflow. A concentrated solution of Cl (as NaCl) and $\text{PO}_4\text{-P}$ (as K_2HPO_4) was added at a constant rate to the head of each experimental reach using a fluid metering pump (FMI, Syosset, New York, USA). Tracers were added at a point of natural constriction at the head of each experimental reach and monitored at six to eight equally spaced downstream sampling transects.

Solute injections were carried out from 19 July to 21 July 1998, during daylight hours. Replicate ($n = 3\text{--}5$) background and plateau (i.e., fully mixed tracer content) water samples were collected at each sampling transect and analyzed for solutes.

Solute transport modeling

One-dimensional modeling of transport including inflow and transient storage (Bencala and Walters 1983) was used to characterize hydrologic conditions along each of the study reaches. Conductivity data (converted to Cl concentration using regression curves established in the laboratory) provided by the automated sondes were used to analyze solute transport with the model of Hart (1995). An iterative process of model parameter adjustment was applied to produce predicted values of Cl concentration at the downstream transect and an optimization subroutine used to statistically determine best-fit parameters (Hart 1995, Harvey and Wagner 2000). Reach lengths at each site were established to provide a spatial scale balanced for assessment of nutrient uptake and hydrologic exchange. Damkohler coefficients (Wagner and Harvey 1997) calculated for injection experiments ranged from 0.81 to 4.72 with a

TABLE 1. Physical and chemical properties of the study streams in the Slick Rock Wilderness Area (SR1–SR3) and the Joyce Kilmer Memorial Forest (JK1–JK3).

Site	Name	Elevation (m)	Conductivity ($\mu\text{S}/\text{cm}$)	Temperature ($^{\circ}\text{C}$)	Dissolved oxygen	
					(mg/L)	(% saturation)
SR1	Little Stack Gap	683	10.7–11.1	19.0–19.3	7.0–7.4	75.0–80.3
SR2	Buckeye Branch	667	11.3–11.7	19.1–19.3	7.1–8.1	88.7–92.5
SR3	Big Fat Gap	658	11.5–11.9	19.9–20.1	7.6–8.0	86.5–90.5
JK1	Poplar Cove	744	9.7–10.1	16.3–16.6	8.1–9.0	83.6–91.9
JK2	Adam Camp Branch	820	7.5–7.7	17.6–17.7	7.6–7.9	79.3–82.7
JK3	Indian Springs	753	7.2–7.5	17.1–17.4	7.9–8.4	81.9–87.7

Notes: Data are means \pm 1 SD calculated from 10–14 background samples from each stream. For conductivity, temperature, and dissolved oxygen, values are presented as the limits of \sim 50–100 observations obtained from automated sensors placed in each stream. N:P ratios are calculated from mean TIN and $\text{PO}_4\text{-P}$ concentrations.

mean of 2.51, indicating moderate uncertainty in transient storage modeling (Harvey and Wagner 2000).

Variables obtained from the model characterize features of both the surface channel and storage zone. Surface parameters include water velocity (v , m/s), stream channel cross-sectional area (A , m^2), and dispersion (D , m^2/s). Storage zone parameters are storage zone cross-sectional area (A_s , m^2) and exchange coefficient (α , s^{-1}), a measure of the percent of water entering storage per unit time. The ratio A_s/A was used to represent storage zone size relative to the channel cross-sectional area. Combinations of model parameters were used to calculate the surface water residence time ($T_{\text{Surf}} = 1/\alpha$, min), storage water residence time ($T_{\text{Sto}} = [A_s/(\alpha A)]$, min) and the hydraulic retention factor ($R_H = A_s/Q$, s/m) which represents the amount of time water spends in the storage zone for each meter advected downstream (sensu Morrice et al. 1997).

Analysis of plateau tracer concentrations: dilution and nutrient uptake

Discharge (Q , L/s) at the upstream transect was calculated using dilution gauging methods. Stream depth (z , m) was determined from mean width measures, discharge calculations, and water velocity (provided by model output). Lateral inflow (Q_L , $\text{L}\cdot\text{s}^{-1}\cdot\text{m}^{-1}$) of water without tracer and dilution corrections for plateau $\text{PO}_4\text{-P}$ concentrations were determined following standard techniques (Stream Solute Workshop 1990). Background-corrected and dilution-corrected plateau $\text{PO}_4\text{-P}$ was ln-transformed and regressed against distance downstream. Uptake lengths for $\text{PO}_4\text{-P}$ (S_w , m) were calculated as the negative inverse of the regression coefficient (Stream Solute Workshop 1990). Uptake lengths were normalized to stream depth and water velocity as follows:

$$V_f = \left(\frac{vz}{S_w} \right) 1000 \quad (1)$$

where V_f = uptake velocity (mm/s), z = stream depth (m), v = water velocity (m/s). Uptake rates (U , $\text{mg P}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$) for $\text{PO}_4\text{-P}$ were calculated as the product of the uptake velocity and mean background $\text{PO}_4\text{-P}$ concentration (Stream Solute Workshop 1990):

$$U = V_f [\text{PO}_4\text{-P}] 3.6 \times 10^3 \quad (2)$$

where U = areal $\text{PO}_4\text{-P}$ uptake rate ($\text{mg P}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$), V_f = $\text{PO}_4\text{-P}$ uptake velocity (mm/s), $[\text{PO}_4\text{-P}]$ = mean background $\text{PO}_4\text{-P}$ concentration (mg/L), and 3.6×10^3 = conversion factor to satisfy unit requirements.

Statistical analysis: old-growth vs. second-growth forests

Because of small sample size ($n = 3$ streams/forest type) and associated problems with assumptions of normality and equivalence of variance, we used nonparametric statistical analyses ($\alpha = 0.05$) to compare streams of old-growth and second-growth forests. Wilcoxon signed-ranks test was used to compare physical and chemical measures (e.g., stream geomorphology, solute transport parameters), and variables representing ecosystem structure (e.g., organic matter standing stocks, chlorophyll a) and function (uptake length, velocity, and rate). Spearman rank correlations were calculated for pairs of variables ($n = 6$) to assess relationships among streams or within ($n = 3$) stream groups. All statistical analyses were performed on SAS Version 6 (SAS 1990).

RESULTS

Physical and chemical characteristics of stream water

Electrical conductivity was low in all streams (7.2–11.9 μS , Table 1). While mean values were significantly higher ($P = 0.049$) in old-growth streams, they differed by only 3 μS . Surface water was well oxygenated ($\text{DO} = 7\text{--}9$ mg/L, 75–92% of saturation, Table 1). Percent saturation was 4.3% lower ($P = 0.046$) in old-growth streams. At the same time, mean stream temperature was 2.3 $^{\circ}\text{C}$ higher ($P = 0.046$) in second-growth streams where values ranged from 19.0 $^{\circ}\text{C}$ to 20.1 $^{\circ}\text{C}$ (16.3 $^{\circ}\text{C}$ –17.7 $^{\circ}\text{C}$ for old-growth streams). No significant differences between stream groups existed for any measure of stream chemistry ($P > 0.2$ for all comparisons). Concentrations of $\text{NH}_4\text{-N}$ were all below detection limit (i.e., <0.007 mg/L, Table 1). Mean $\text{PO}_4\text{-P}$ concentrations were similar (~ 0.004 mg/L, Table 1) and ranged only 0.003 mg/L among all streams. In

TABLE 1. Extended.

NH ₄ -N (mg/L)	NO ₃ -N (mg/L)	PO ₄ -P (mg/L)	Atomic N:P	Dissolved organic carbon (mg/L)
<0.007	0.183 ± 0.030	0.005 ± 0.001	57.0	0.4 ± 0.1
<0.007	0.140 ± 0.070	0.005 ± 0.001	25.6	0.4 ± 0.1
<0.007	0.041 ± 0.024	0.003 ± 0.001	17.7	0.6 ± 0.1
<0.007	0.124 ± 0.013	0.005 ± 0.001	83.5	0.5 ± 0.1
<0.007	0.054 ± 0.004	0.004 ± 0.001	63.7	0.7 ± 0.1
<0.007	0.020 ± 0.002	0.006 ± 0.001	16.6	0.5 ± 0.1

contrast, NO₃-N concentrations were higher and spatially more variable. Lowest concentrations were found in the old-growth streams, but values among those streams varied from 0.020 mg/L to 0.124 mg/L. Nitrate-N varied comparably in second-growth streams (Table 1). Mean TIN concentration was never >0.180 mg/L and NO₃-N was the major constituent (83–97%) due to low concentrations of NH₄-N. Atomic N:P ratios reflected variation in NO₃-N concentration and ranged from 16.6 to 83.5 (Table 1). Dissolved organic carbon concentrations were low (~0.5 mg/L) and statistically similar in old-growth and second-growth streams.

Channel and benthic structure

Channel structure did not differ significantly between stream groups (Table 2). Characteristic of headwater streams, VFW was small (~6–8 m, Table 2) and AC widths were only 2–3 m. Consequently, all streams were considered unconstrained (i.e., VFW:AC > 2, Gregory et al. 1991). Photon flux density beneath the canopy was low for all streams (<1% incident light) and did not differ significantly between forest types (Table 2).

Wood storage was greatly reduced in second-growth compared to old-growth streams (Table 2). The number of debris dams in old-growth streams (5.8/100 m) was nearly 20 times that recorded for second-growth streams (Table 2). Total wood volume in old-growth streams was more than two orders of magnitude greater than in second-growth streams (Table 2) representing nearly 170 times the wood biomass found in streams draining the younger forests.

Benthic algal standing crops were low (33 mg/m² chlorophyll *a*), nearly identical, and not significantly different between old-growth and second-growth systems (Table 2). In contrast, mean epilithic OM standing stock in old-growth streams (10.2 g AFDM/m²) was significantly greater ($P = 0.049$) than in second-growth streams (4.1 g AFDM/m², Table 2). Higher epilithic OM in old-growth streams resulted primarily from significantly greater ($P = 0.049$) OM content per unit mass of epilithic material (Table 2).

Relative abundance of sediment size classes (Fig. 2) showed that there were more fine-grained particles in old-growth streams. Old-growth streams were characterized by a bimodal distribution, dominated by the

TABLE 2. Channel geomorphology, light, large woody debris, and epilithic characteristics for old-growth streams of the Joyce Kilmer Memorial Forest and second-growth streams in the Slick Rock Wilderness Area.

Stream reach characteristics	Old-growth streams	Second-growth streams	<i>P</i>
Channel geomorphology			
Valley floor width (VFW, m)	7.93 ± 0.28	6.21 ± 1.34	0.50
Active channel width (AC, m)	2.67 ± 0.70	2.82 ± 0.35	0.51
VFW:AC [†]	3.30 ± 0.97	2.15 ± 0.21	0.27
Light			
PAR photon flux density (μmol·m ⁻² ·s ⁻¹)	14.2 ± 3.4	12.2 ± 1.12	0.51
Large woody debris			
Debris dam frequency (no./100 m)	5.8 ± 2.3	0.30 ± 0.33	0.046
Wood volume (m ³ /m ²)	0.0234 ± 0.0082	0.00014 ± 0.00005	0.049
Wood mass (kg/m ²)	8.335 ± 2.927	0.050 ± 0.032	0.049
Epilithic characteristics			
Chlorophyll <i>a</i> (mg/m ²)	33.1 ± 3.1	33.2 ± 7.4	0.51
AFDM (g/m ²)	10.2 ± 1.2	4.1 ± 0.9	0.049
Organic matter (%)	8.37 ± 0.99	3.57 ± 0.70	0.049

Notes: Data are means ± 1 SE for three streams of each forest type. *P* values derived from Wilcoxon's signed-ranks test are given in the final column.

[†] Mean and SE for VFW:AC were determined from square-root transformed data, and values shown here are back-transformed.

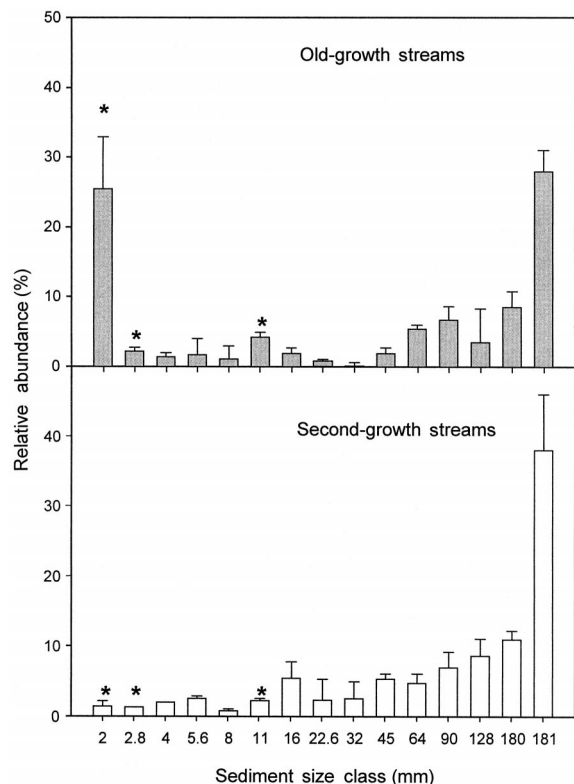


FIG. 2. Relative abundance of sediment size classes in streams of old-growth and second-growth forests. Proportional abundance was determined within each stream, and data were arcsine-square root transformed before calculation of mean and standard error. Bars (mean \pm 1 SE) represent values obtained after back transformation. Significant differences ($P < 0.05$) between old-growth and second-growth streams with regard to the proportion of sediment present in a given size class are identified with an asterisk following nonparametric t tests.

largest and smallest size classes (Fig. 2). In contrast, relative abundance of particles in second-growth streams generally increased with increasing particle size (Fig. 2). In second-growth streams, sediments of the largest size class represented $\sim 38\%$ of all observations, while the smallest size class represented $<2\%$ of sampled particles. Relative abundance differed significantly between stream groups for three size classes, including particles <2 mm, 2–2.8 mm, and 11–16 mm (Fig. 2). While the difference in relative abundance in the <2 mm size class was striking (28.1% vs. 1.6%) relative abundance in the 2.8 mm and 11 mm classes differed by only 0.9% and 2.0% (Fig. 2). Among streams, relative abundance of the smallest size class was positively correlated with wood volume ($r = 0.81$, $P = 0.05$) and debris dam frequency ($r = 0.90$, $P = 0.01$). Despite low statistical power (i.e., $n = 3$), the relationships between abundance of fine sediments and wood volume or debris dam frequency remained significant ($P < 0.0001$) among old-growth streams. In

contrast, these variables were not related significantly ($P > 0.66$) among second-growth streams.

Ecosystem hydrology and transient storage

Stream discharge ranged from 4.2 to 9.9 L/s and mean increase along study reaches was 39% and 25% in old-growth and second-growth streams, respectively. Lateral inflow, wetted stream widths, stream cross-sectional area, water depth, water velocity, and dispersion coefficients did not differ significantly between groups of streams (Table 3).

Streams draining second-growth forests had larger storage zones than streams within the old-growth catchments (Table 3). Absolute size of the transient storage zone (A_S) in second-growth streams was 1.6 times greater ($P = 0.07$, Table 3) than in old-growth streams. Similarly, when normalized to the cross sectional area of the channel water, storage zone area (A_S/A) was 1.5 times higher ($P = 0.05$) in second-growth streams (Table 3). Average storage zone exchange coefficients (α) were nearly identical and did not differ significantly (Table 3).

Average residence times in old-growth and second-growth streams were similar and stream types did not differ significantly in respect to surface water residence time. Mean storage zone residence times (T_{Sto}) were not statistically different between stream groups (Table 3), reflecting low statistical power and variation in storage zone residence times for streams of old-growth forests ($cv = 118\%$). In contrast, the hydraulic retention factor (R_H) did differ significantly between stream types (Table 3) and the mean value for second-growth streams was 2.4 times greater than that for old-growth streams.

Phosphorus uptake and retention

Solute injections increased $PO_4\text{-P}$ by a mean of 0.008 mg/L and 0.011 mg/L in second-growth and old-growth streams, respectively, representing an approximate three-fold increase above background concentrations. Uptake lengths (S_w) were shorter in old-growth streams (Fig. 3A), but S_w did not differ significantly ($P = 0.12$) between forest types. Uptake lengths were correlated only with the number of debris dams ($r = -0.87$, $P = 0.02$), reflecting a decrease in $PO_4\text{-P}$ travel distance with increasing dam abundance.

Uptake velocities (V_i) in old-growth streams averaged 0.18 ± 0.05 mm/s vs. only 0.04 ± 0.02 mm/s in second-growth streams (Fig. 3B), representing significantly greater ($P = 0.046$) ability of old-growth streams to extract $PO_4\text{-P}$ from the water column. Uptake velocities were positively correlated with the volume of woody debris ($r = 0.81$, $P = 0.05$) and even more closely with number of debris dams (Fig. 4A, $r = 0.995$, $P < 0.0001$). Uptake velocities were also positively correlated with the relative abundance of fine sediments (Fig. 4B, $r = 0.90$, $P = 0.01$). At the same time, uptake velocities decreased with increasing transient storage (i.e., A_S/A , Fig. 4C, $r = -0.81$, $P = 0.05$).

TABLE 3. Hydrologic properties of surface and storage zones in study streams of old-growth and second-growth forests.

Measure	Old-growth streams	Second-growth streams	<i>P</i>
Surface flow parameters			
Discharge (<i>Q</i> , L/s)	8.20 ± 0.98	5.50 ± 1.25	0.12
Lateral inflow (\bar{Q}_L , L·s ⁻¹ ·m ⁻¹)	0.126 ± 0.003	0.094 ± 0.017	0.68
Stream width (<i>w</i> , m)	1.58 ± 0.18	2.36 ± 0.59	0.27
Depth (<i>z</i> , m)	0.09 ± 0.03	0.06 ± 0.03	0.26
Stream x.s. area (<i>A</i> , m ²)	0.13 ± 0.02	0.11 ± 0.03	0.48
Velocity (<i>V</i> , m/s)	0.08 ± 0.01	0.06 ± 0.01	0.10
Dispersion (<i>D</i> , m ² /s)	0.07 ± 0.03	0.03 ± 0.01	0.18
Storage zone parameters			
Storage zone x.s. area (<i>A_s</i> , m ²)	0.06 ± 0.003	0.10 ± 0.02	0.07
Normalized storage zone area† (<i>A_s/A</i> , m ² /m ²)	0.50 ± 0.07	0.88 ± 0.05	0.05
Exchange coefficient (<i>α</i> , s ⁻¹)	0.0010 ± 0.0008	0.0013 ± 0.0006	0.65
Residence times			
Surface residence time‡ (<i>T_{surf}</i> , min)	15.8 ± 4.5	13.5 ± 2.6	0.82
Storage residence time‡ (<i>T_{sto}</i> , min)	8.4 ± 2.2	12.1 ± 2.0	0.27
Hydraulic retention factor‡ (<i>R_H</i> , s/m)	0.008 ± 0.001	0.017 ± 0.003	0.05

Notes: Data are means ± 1 SE for three replicate streams from each group. *P* values derived from Wilcoxon's signed-ranks test are given in the final column.

† Means and SE were calculated on square-root transformed data, and tabular values were back-transformed.

‡ Means and SE were calculated on inverse transformed data, and tabular values were back-transformed.

In old-growth streams, PO₄-P uptake per square meter of stream bottom (*U*) averaged 2.65 ± 0.55 mg P·m⁻²·h⁻¹ and was significantly greater (*P* = 0.046) than in second-growth streams (0.73 ± 0.23, Fig. 3C). Due, in part, to low variability in ambient PO₄-P concentrations, correlations between measures of stream structure and *U* were nearly identical to those for *V_f*.

DISCUSSION

Large woody debris

Wood standing stocks and debris dam frequency were greater in old-growth streams than in adjacent logged streams, despite 75 yr of forest regeneration. Our mean value of ~8 kg/m² is comparable to measures from other streams in old-growth deciduous forests of the southeastern United States (7.6–10 kg/m²; Triska and Cromack 1980, calculated from Silsbee and Larson 1983, calculated from Hedman et al. 1996).

Large woody debris standing stocks in second-growth streams of the Slick Rock Wilderness Area were lower than those recorded for other southeastern second-growth forests of comparable age. For example, Silsbee and Larson (1983) reported mean wood volumes in streams of second-growth catchments in the Smoky Mountains that were 60 times greater than our estimates for second-growth catchments. Differences in LWD standing stocks may have resulted from a number of factors, including differential mortality or tree harvest selection. However, it is more likely that differences relate to the logging methods employed in the Slick Rock Wilderness Area.

In the southern Appalachian Mountains, standing stock of LWD in streams draining midsuccessional

(i.e., 40–70 yr post disturbance) forests was found to depend largely on residual wood from previous stand-forming disturbances (Hedman et al. 1996). Dolloff (1993) and Benfield (1995) emphasized the use of railroads constructed along stream beds of the southern Appalachian Mountains as a method for removing timber from low order catchments. In this manner, low order streams were developed as “conduits” for wood transport and LWD was removed for rail construction. Rail remnants were evident in two of our second-growth study catchments. While logging practices may differ in their treatment of instream LWD (Waters 1995), the very low standing stocks of wood and nearly complete absence of debris dams in Slick Rock streams suggest removal of carryover debris.

As suggested by the Biomass Accumulation Model and supported by comparable models of LWD loading following catchment-level disturbance (e.g., Webster et al. 1992, Hedman et al. 1996), aggrading second-growth forests have contributed little lasting wood to streams of the Slick Rock Wilderness Area. Senescence of mature trees provides the necessary elements to build debris dams and initiate long-term retention of wood. Triska et al. (1982) estimated that this would require 150 yr of forest regrowth for streams of the Pacific Northwest, USA. Webster et al. (1992) suggested that as much as 300 yr of hardwood forest regrowth would be needed to reestablish pre-disturbance LWD standing stocks in the southern Appalachian deciduous forest.

Stream bed sediments

Across all study streams, the abundance of fine sediment was closely related to the quantity of wood mea-

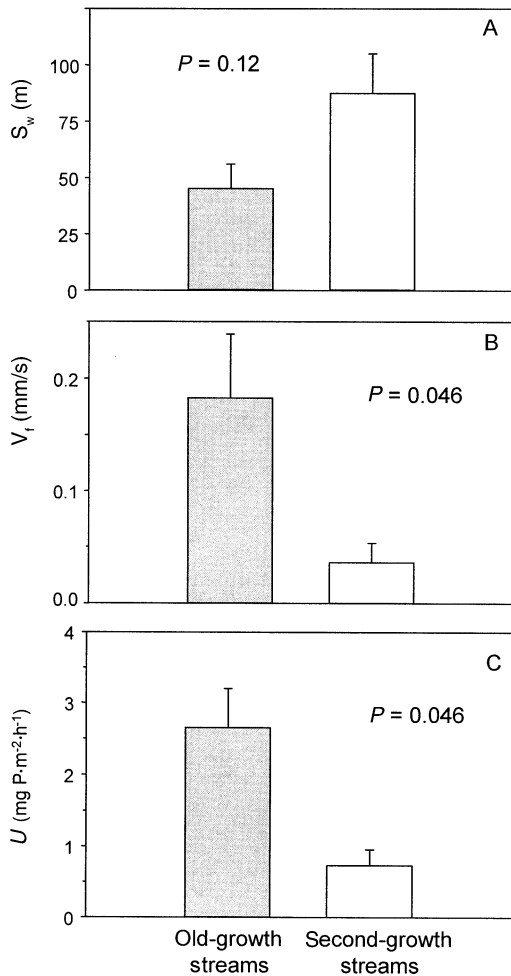


FIG. 3. Nutrient retention measures in old-growth and second-growth streams including (A) uptake length (S_w ; m), (B) uptake velocity (V_i ; mm/s), and (C) uptake rate (U ; $\text{P}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$). Data are means \pm 1 SE, and P values reflect results of nonparametric t tests between groups.

sured both as standing stock and debris dam frequency. This association between fine sediment and wood abundance was evident among streams draining old-growth catchments. On the other hand, wood and fine sediment were uncommon and their abundance unrelated when analysis was restricted to second-growth streams.

During forest harvest and other agricultural practices, large quantities of fine sediments are introduced to streams draining impacted basins (Waters 1995). This may have been the case for streams of the Slick Rock Wilderness Area. However, following re-vegetation, bank stabilization, and decreased erosion, sediment input to the stream is eventually reduced. We contend that the lack of LWD and loss of debris dams has decreased the capacity for Slick Rock streams to retain smaller particles, resulting in a net loss of fine-grained sediments. Monitoring of clear-cut and reference forests (Monk 1975) and experimental removal of LWD (Bilby 1981, Diez et al. 2000) have documented drastic

losses of sand and silt from impacted stream beds. The loss of fine-grained sediment may generate substantially different bed conditions within a reach including altered surface area and bed permeability (Chapman 1989).

Light availability and epilithic characteristics

Well developed forest canopies and understory vegetation reduced light to $<1\%$ of incident levels in all study streams. Typical of headwater streams in the southern Appalachian region, standing stocks of chlorophyll a were low at all sites. Epilithic OM standing stocks, however, were significantly greater in old-growth streams, suggesting more extensive development of heterotrophic components of benthic biofilms. In combination with increased debris dam frequency and greater abundance of fine sediments, greater epilithic OM suggests a more biologically active benthic environment.

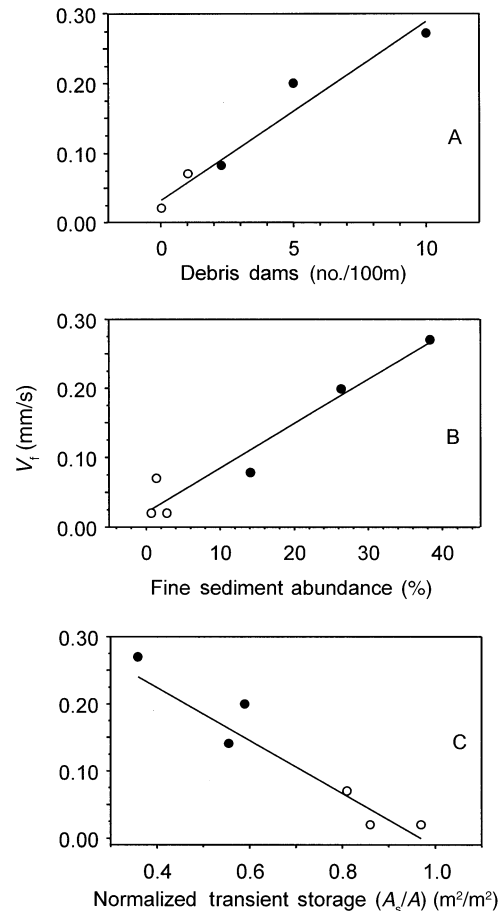


FIG. 4. (A) Relationship between uptake velocity (V_i ; mm/s) and debris dam frequency. Note that a single data point is hidden on this plot. (B) Relationship between uptake velocity and relative abundance (%) of fine (<2 mm) sediments. (C) Relationship between uptake velocity and size of the normalized transient storage zone (A_s/A ; m^2/m^2) in old-growth (solid symbols) and second-growth (open symbols) streams.

Hydrologic characteristics

In-channel hydrologic characteristics were similar among sites and typical of montane streams of the mesic southeastern United States (D'Angelo et al. 1993). Others have indicated that presence of debris dams and LWD reduces channel velocity (Wallace et al. 1995). In our study, however, no significant differences were observed between streams of old-growth and second-growth forests despite large differences in wood content (Tables 2 and 3). Lack of distinction between mean velocities may be due to low statistical power. However, it may also reflect variation in stream gradient and the fact that tracer-derived velocities integrate short (i.e., thalweg) and long (i.e., interstitial) flow paths (Stream Solute Workshop 1990).

Historically, the extent of transient storage in streams has been interpreted to represent the degree of ground-water–surface water interaction (Bencala et al. 1984, D'Angelo et al. 1993, Valett et al. 1996, 1997). More recently, others have cautioned that the amount of storage attributed to aboveground areas of slack water (e.g., eddies, backwaters, pools) is unknown (Harvey et al. 1996, Harvey and Wagner 2000). Despite higher LWD standing stocks and increased debris dam frequency, the extent of transient storage was significantly lower in old-growth streams compared to second-growth streams. Both the absolute (A_S) and normalized transient storage size (A_S/A) in second-growth streams were nearly double those in old-growth streams (Table 3). Streams in second-growth catchments lacked significant aboveground storage potential (i.e., few debris dams or large pools). However, bed sediments were dominated by coarse size classes compared to old-growth streams (Fig. 2). Given the close relationship between sediment particle size and hydraulic conductivity (Fetter 1994), we contend that the larger size, lack of fine sediments, and lower OM content of Slick Rock stream beds resulted in greater alluvial hydraulic conductivity. Morrice et al. (1997) documented increased transient storage associated with increasing alluvial hydraulic conductivity in headwater streams of the Rocky Mountains, United States. More extensive surface–subsurface exchange appears to have caused water in second-growth streams to spend significantly more time in storage for each meter of downstream travel (i.e., significantly greater R_H , Table 2).

Nutrient uptake and retention

Streams of the southern Appalachian Mountains are generally P limited (Webster et al. 1995) and PO_4 -P uptake lengths are short compared to those measured for NO_3 -N (Munn and Meyer 1990, Webster et al. 1991). While Meyer and Likens (1979) illustrated that PO_4 -P uptake in a New England stream was primarily abiotic (i.e., due to sorption), Munn and Meyer (1990) showed that PO_4 -P uptake in streams of the Coweeta Hydrologic Laboratory (Otto, North Carolina, USA)

was mainly biotic and this is probably the case for nearby JKSR streams.

Uptake lengths for JKSR streams are relatively short compared to many published values for phosphorus-limited streams from a variety of settings including temperate hardwood forests (Webster et al. 1991, Mulholland et al. 1997), hardwater Mediterranean streams (Martí and Sabater 1996), and Australian highlands (Hart et al. 1992). At the same time, differences in uptake lengths between old-growth and second-growth streams were not significant.

Uptake velocities, V_f , normalize uptake lengths for stream depth and velocity, hence providing a more biological perspective of nutrient transfer from dissolved to particulate components. Thus, Davis and Minshall (1999) argued that V_f may be a better parameter for comparison among streams and for determining the underlying biotic factors that influence nutrient retention. Uptake velocities in Joyce Kilmer streams were much greater than those in the Slick Rock Wilderness Area (Fig. 3B). Relatively few direct measures of uptake velocity are available from the literature, but values can be obtained from other published uptake parameters (Eqs. 1 and 2). In comparison with other studies, PO_4 -P uptake velocities for JKSR old-growth streams are among the highest recorded. Published uptake velocities for phosphorus-limited headwater streams of southeastern deciduous forests range an order of magnitude from 0.007 to 0.07 mm/s (Newbold et al. 1983, Munn and Meyer 1990, Mulholland et al. 1997). Values on the upper end of this range are similar to those we report for streams of second-growth forests in the Slick Rock Wilderness Area while uptake velocities for old-growth streams were greater (0.18 mm/s, Fig. 3B). In addition to greater uptake velocities, old-growth streams displayed significantly higher areal PO_4 -P uptake rates (Fig. 3C) while ambient PO_4 -P concentrations were similar among streams (Table 1). Together these results illustrate significantly greater PO_4 -P uptake in streams draining old-growth streams than in those of second-growth catchments.

Despite earlier studies that showed increased nutrient uptake with greater transient storage (Valett et al. 1996, Mulholland et al. 1997), uptake velocities decreased strongly with increasing storage zone extent (i.e., A_S/A) suggesting that biological retention of P was not dominated by processes occurring within storage zones (i.e., hyporheic processes). Instead, uptake velocities and rates increased with increasing abundance of wood, debris dam frequency, and the proportion of the stream bed composed of fine sediments (Fig. 4). We contend that wood deposited in old-growth streams results in greater nutrient retention (i.e., higher uptake velocities and rates) by (1) retaining fine sediments that promote biological activity due to their high surface area, (2) entraining OM that would otherwise be lost to downstream reaches, and (3) acting as active sites of microbial activity. The retention of particulate organic

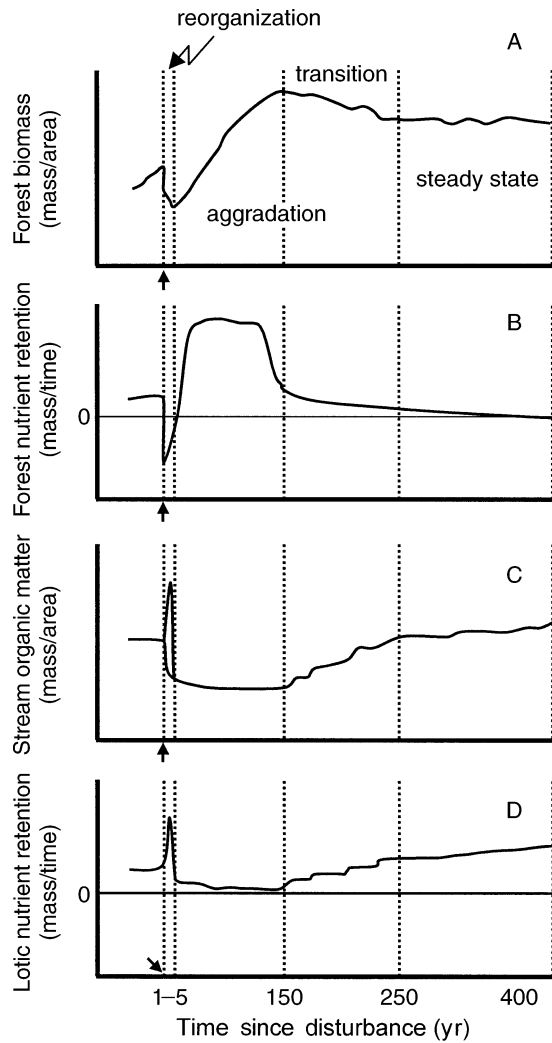


FIG. 5. Proposed successional patterns of organic matter (OM) standing stock and nutrient retention in forests and streams following catchment-level disturbance. (A) Forest biomass as predicted by the Biomass Accumulation Model (Bormann and Likens 1979). (B) Theoretical time course of catchment nutrient retention reflecting net biomass increment associated with forest succession (Vitousek and Reiners 1975). (C) Stream OM standing stock following forest clear-cutting (Harmon et al. 1986, Webster et al. 1995). (D) Proposed successional pattern of nutrient retention within the stream ecosystem. Panels A and B relate OM dynamics and nutrient retention for autochthonous terrestrial ecosystems where metabolic steady state and zero net retention characterize late successional stages. In contrast, stream ecosystems within forested catchments receive substantial allochthonous inputs, and OM dynamics are tied to interaction with the surrounding forest. Immediately following clear-cutting, OM standing stocks may be extremely low or high depending on the removal or addition of wood associated with logging practices (panel C). In either case, retention by the stream is expected to be high (panel D) as a result of temporary increase in autochthonous primary production (following the removal of wood) or increased heterotrophic demand (from pulsed input of logging debris). As succession proceeds, in-stream OM standing stocks decline (panel C) due to biotic processing and the transient nature of input from early successional species. When the surrounding forests enter the transitional phase

material may be of great significance to $\text{PO}_4\text{-P}$ uptake and P standing stock given the propensity for floods to export P from headwater streams (Meyer and Likens 1979). Further, Tank and Webster (1998) showed that wood surfaces can be significant sites of nutrient consumption and that their role as a nutrient sink is enhanced in the absence of more labile OM (i.e., leaves).

Retention and successional theory

Hedin et al. (1995) described the biogeochemical theory of successional response to disturbance as investigated in old-growth forests of Chile. In this, and similar investigations (Vitousek and Reiners 1975, Likens et al. 1978), streams were used to assess biogeochemical status of the watershed, in part because of their propensity to integrate catchment response. The biogeochemical theory of succession emphasizes that the net biomass increment of the vegetation drives nutrient retention in forested catchments. In ecosystems supplied by autochthonous inputs, rates of gross primary production and respiration are expected to be equal, net biomass increments negligible, and net nutrient retention near zero at successional climax. We contend that energy flow and nutrient retention in stream ecosystems should follow a different successional course.

The notion that old-growth streams should be most retentive is common in the literature. Smock et al. (1989) presented a successional interpretation of their experimental manipulations of debris dam frequency by stating that old-growth streams should have considerably greater OM storage and shorter spiraling lengths. While no earlier work is available to compare nutrient spiraling in old-growth and second-growth streams, Triska et al. (1984) provided a detailed N budget for a headwater stream draining a 450-yr-old coniferous forest of the Pacific Northwest, USA. Their seasonal assessment of N transport, storage, and retention showed that on an annual basis the stream was a net sink for N, with retention representing as much as 66% and 48% of input in the summer and fall, respectively. Lower annual retention (34%) was attributed to flooding and export during spring (Triska et al. 1984).

In general, streams are allochthonous-based systems where OM dynamics are dictated by import from the surrounding catchment (Fisher and Likens 1973). In undisturbed streams that drain old-growth forests, rates of primary production are light limited (Gregory 1979), ecosystem metabolism is dominated by heterotrophic respiration, and P/R ratios are low (Bott et al. 1978, Minshall et al. 1983). As streams and their surrounding

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(panel A), streams accumulate OM (panel C) and are characterized by high levels of nutrient retention during late successional stages (panel D).

catchments recover from disturbance they are linked to each other by flows of matter and energy. Forest succession models predict senescence of older trees during later stages of succession. These allochthonous inputs provide continuous loading of OM into streams that drain old-growth forests. Accumulation of carbon-rich woody debris and other forms of OM ensures a continuous demand for nutrients (Fig. 5), reflecting the environmental stoichiometry (sensu Elser and Urabe 1999) of the detrital pool.

This perspective differs from that provided by Grimm (1987) who tested the Vitousek and Reiners (1975) retention model following flooding in Sycamore Creek, a Sonoran Desert stream. Her study generally supported the proposal that diminished net biomass increment and reduced retention capacity are characteristic of late stages of stream succession. To some degree, OM dynamics and N retention in Sycamore Creek are expected to be analogous to forests because of the strong influence of autochthonous autotrophic processes (Busch and Fisher 1981, Fisher et al. 1982) and reduced interactions between the ecosystem and its surroundings (i.e., low rates of allochthonous OM loading, Schade and Fisher 1997).

In many ways, forested streams are more analogous to soils (sensu Wagener et al. 1998) in that they are allochthonous systems that remain retentive in late stages of forest succession. Sollins et al. (1980) emphasized that soils of an old-growth coniferous forest remained retentive of many elements, especially N and P. They noted that deep soil solutions collected beneath horizons that support most biotic activity were enriched in dissolved solutes compared to stream water concentrations measured at the weir. Together, these observations suggest retention along the stream-riparian corridor. Further, Sollins et al. (1980) stated that the biogeochemical theory of Vitousek and Reiners (1975) seemed applicable to soils in that systems gaining OM continue to be retentive of inorganic nutrients. We argue that this perspective applies to both soils and streams as subsystems of old-growth catchments with accumulating OM pools.

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LITERATURE CITED

American Public Health Association, American Water Works Association, Water Environment Federation. 1998. Method detection limit. Pages 1-17-1-18 in *Standard methods for examination of water and wastewater*. 20th edition.

- American Public Health Association, Washington, D.C., USA.
- Bencala, K. E., V. C. Kennedy, G. E. Zellweger, A. P. Jackman, and R. J. Avanzino. 1984. Interactions of solutes and streambed sediment. I. An experimental analysis of cation and anion transport in a mountain stream. *Water Resources Research* **20**:1797-1803.
- Bencala, K. E., and R. A. Walters. 1983. Simulation of solute transport in a mountain pool-and-riffle stream: a transient storage model. *Water Resources Research* **19**:718-724.
- Benfield, E. F. 1995. Historical land-use and streams. *Bulletin of the North American Benthological Society* **12**:241-248.
- Bevenger, G., and R. King. 1995. A pebble count procedure for assessing watershed cumulative effects. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station Research Paper RM-RP-319.
- Bilby, R. E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. *Ecology* **62**:1234-1243.
- Bilby, R. E., and J. W. Ward. 1991. Characteristic and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in Southwestern Washington. *Canadian Journal of Fisheries and Aquatic Sciences* **48**:2499-2508.
- Bormann, F. H., and G. E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. *American Scientist* **67**:660-669.
- Bormann, F. H., G. E. Likens, T. G. Siccama, R. S. Pierce, and J. S. Eaton. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. *Ecological Monographs* **44**:255-277.
- Bott, T. L., J. T. Brock, C. E. Cushing, S. V. Gregory, D. King, and R. C. Petersen. 1978. A comparison of methods for measuring primary productivity and community respiration in streams. *Hydrobiologia* **60**:3-12.
- Burns, D. A. 1998. Retention of NO₃-N in an upland stream environment: a mass balance approach. *Biogeochemistry* **40**:73-96.
- Busch, D. E., and S. G. Fisher. 1981. Metabolism of a desert stream. *Freshwater Biology* **11**:301-308.
- Butturini, A., and F. Sabater. 1998. Ammonium and phosphate retention in a Mediterranean stream: hydrological versus temperature control. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:1938-1945.
- Chapman, D. W. 1989. Critical review of variables used to define effects of fines in redds of large salmonoids. *Transactions of the American Fisheries Society* **117**:1-21.
- D'Angelo, D. J., J. R. Webster, S. V. Gregory, and J. L. Meyer. 1993. Transient storage in Appalachian and Cascade mountain streams as related to hydraulic characteristics. *Journal of the North American Benthological Society* **12**:223-235.
- Davis, J. C., and G. W. Minshall. 1999. Nitrogen and phosphorus uptake in two Idaho (USA) headwater wilderness streams. *Oecologia* **119**:247-255.
- Díez, J. R., S. Larrañaga, A. Elosegui, and J. Pozo. 2000. Effect of removal of wood on streambed stability and retention of OM. *Journal of the North American Benthological Society* **19**:621-632.
- Dolloff, C. A. 1993. Large woody debris, fish habitat, and historical land use. Biodiversity and coarse woody debris in Southeastern forests. USDA Forest Service General Technical Report SE-94:130-138.
- Elser, J. J., and J. Urabe. 1999. The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. *Ecology* **80**:735-751.
- Fetter, C. W. 1994. *Applied hydrogeology*. Third edition. Macmillan, New York, New York, USA.
- Fisher, S. G. 1990. Recovery processes in lotic ecosystems: limits of successional theory. *Environmental Management* **14**:725-736.

- Fisher, S. G., J. F. Lawrence, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* **52**:93–110.
- Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* **43**:421–439.
- Flum, T., and S. C. Nodvin. 1995. Factors affecting stream-water chemistry in the Great Smoky Mountains, USA. *Water, Air and Soil Pollution* **85**:1707–1712.
- Golladay, S. W., and J. R. Webster. 1988. Effects of clearcut logging on wood breakdown in Appalachian mountain streams. *American Midland Naturalist* **119**:143–155.
- Gorham, E., P. M. Vitousek, and W. A. Reiners. 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annual Review of Ecology and Systematics* **10**:53–84.
- Gregory, S. V. 1979. Primary production in Pacific Northwest streams. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *Bioscience* **41**:540–541.
- Grimm, N. B. 1987. Nitrogen dynamics during succession in a desert stream. *Ecology* **68**:1157–1170.
- 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.
- Hart, B. T., P. Freeman, and I. D. McKelvie. 1992. Whole-stream phosphorus release studies: variation in uptake length with initial phosphorus concentration. *Hydrobiologia* **235/236**:573–584.
- Hart, D. R. 1995. Parameter estimation and stochastic interpretation of the transient storage model for solute transport in streams. *Water Resources Research* **29**:89–98.
- Hartman, G. F., J. C. Scrivener, and M. J. Miles. 1996. Impacts of logging in Carnation Creek, a high-energy coastal stream in British Columbia, and their implication for restoring fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences* **53**:237–251.
- Harvey, J. W., and B. J. Wagner. 2000. Quantifying hydrologic interactions between streams and their subsurface hyporheic zones. Pages 3–44 in J. A. Jones and P. J. Mulholland, editors. *Streams and ground waters*. Academic Press, San Diego, California, USA.
- Harvey, J. W., B. J. Wagner, and K. E. Bencala. 1996. Evaluating the reliability of the stream tracer approach to characterize stream–subsurface water exchange. *Water Resources Research* **32**:2441–2451.
- Hedin, L. O., J. J. Armesto, and A. H. Johnson. 1995. Patterns of nutrient loss from unpolluted old-growth temperate forests. *Ecology* **76**:493–509.
- Hedin, L. O., M. S. Mayer, and G. E. Likens. 1988. The effect of deforestation on organic debris dams. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* **23**:1135–1141.
- Hedman, C. W., D. H. Van Lear, and W. T. Swank. 1996. In-stream large woody debris loading and riparian forest seral stage associations in the southern Appalachian Mountains. *Canadian Journal of Forest Research* **26**:1218–1227.
- Hynes, H. B. N. 1975. The stream and its valley. *Verhandlungen der Internationalen Vereinigung für Limnologie* **19**:92–99.
- Likens, G. E., F. H. Bormann, R. S. Pierce, and W. A. Reiners. 1978. Recovery of a deforested ecosystem: replacing biomass and nutrients lost in harvesting northern hardwoods may take 60 to 80 years. *Science* **199**:492–496.
- Martí, E., N. B. Grimm, and S. G. Fisher. 1997. Pre- and post-flood retention efficiency of nitrogen in a Sonoran Desert stream. *Journal of the North American Benthological Society* **16**:805–819.
- Martí, E., and F. Sabater. 1996. High variability in temporal and spatial nutrient retention in Mediterranean streams. *Ecology* **77**:854–869.
- Menzel, D. W., and R. F. Vaccaro. 1964. The measurement of dissolved organic and particulate carbon in seawater. *Limnology and Oceanography* **9**:138–142.
- 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., and C. M. Tate. 1982. The effects of watershed disturbance on organic carbon dynamics of a stream. *Ecology* **64**:33–44.
- Minshall, G. W., J. T. Brock, and J. D. Varley. 1989. Wildfires and Yellowstone stream ecosystems. *Bioscience* **39**:707–715.
- Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, and R. L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs* **53**:1–25.
- Monk, C. D. 1975. Nutrient losses in particulate form as weir pond sediments from four unit watersheds in the southern Appalachians. Pages 862–867 in F. G. Howell, J. D. Gentry, and M. H. Smith, editors. *Mineral cycling in southeastern ecosystems*. ERDA Symposium Series (CONF-740513), Springfield, Virginia, USA.
- Morrice, J. A., H. M. Valett, C. N. Dahm, and M. E. Campana. 1997. Alluvial characteristics, groundwater–surface water exchange and hydrologic retention in headwater streams. *Hydrological Processes* **11**:253–267.
- Mulholland, P. J., E. R. Marzolf, S. P. Hendricks, R. V. Wilkerson, and A. N. Baybayan. 1995. Longitudinal patterns of nutrient cycling and periphyton characteristics in streams—a test of upstream–downstream linkage. *Journal of the North American Benthological Society* **14**:357–370.
- Mulholland, P. J., E. R. Marzolf, J. R. Webster, D. R. Hart, and S. P. Hendricks. 1997. Evidence that hyporheic zones increase heterotrophic metabolism and phosphorus uptake in forest streams. *Limnology and Oceanography* **42**:443–451.
- Mulholland, P. M., J. D. Newbold, J. W. Elwood, L. A. Ferren, and J. R. Webster. 1985. Phosphorus spiraling in a woodland stream: seasonal variations. *Ecology* **66**:1012–1023.
- Munn, N. L., and J. L. Meyer. 1990. Habitat-specific solute retention in two small streams: an intersite comparison. *Ecology* **71**:2069–2082.
- Murphy, J., and J. P. Riley. 1962. Determination of phosphate in natural waters. *Analytica Chimica Acta* **27**:31–36.
- Newbold, J. D., J. W. Elwood, R. V. O'Neill, and A. L. Sheldon. 1983. Phosphorus dynamics in a woodland stream ecosystem: a study of nutrient spiraling. *Ecology* **64**:1249–1265.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* **164**:262–270.
- Peckarsky, B. L. 1986. Colonization of natural substrates by stream benthos. *Canadian Journal of Fisheries and Aquatic Sciences* **43**:700–709.
- Sabater, F., A. Butturini, E. Martí, I. Muñoz, A. Romaní, J. Wray, and S. Sabater. 2000. Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *Journal of the North American Benthological Society* **19**:609–620.
- SAS. 1990. SAS statistical software. Version 6.0. SAS Institute, Cary, North Carolina, USA.
- Schade, J. D., and S. G. Fisher. 1997. Leaf litter in Sonoran

- Desert stream ecosystem. *Journal of the North American Benthological Society* **16**:612–626.
- Scrimgeour, G. J., and M. J. Winterbourn. 1989. Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia* **171**:33–44.
- Silsbee, D. G., and G. L. Larson. 1983. A comparison of streams in logged and unlogged areas of Great Smoky Mountains National Park. *Hydrobiologia* **102**:99–111.
- Smock, L. A., G. M. Metzler, and J. E. Gladden. 1989. The role of organic debris dams in the structuring and functioning of low-gradient headwater streams. *Ecology* **70**:764–775.
- Sollins, P., C. C. Grier, R. Fogel, F. M. McCorison, and K. Cromack, Jr. 1980. The internal elemental cycles of an old-growth Douglas-fir ecosystem in western Oregon. *Ecological Monographs* **50**:261–285.
- Solorzano, L. 1969. Determination of ammonia in natural waters by the phenylhypochlorite method. *Limnology and Oceanography* **14**:799–801.
- Stone, M. K., and J. B. Wallace. 1998. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. *Freshwater Biology* **39**:151–169.
- Stream Solute Workshop. 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. *Journal of the North American Benthological Society* **9**:95–119.
- Tank, J. T., and J. R. Webster. 1998. Interaction of substrate and nutrient availability on wood biofilm processes in streams. *Ecology* **79**:2168–2179.
- Triska, F. J., and K. Cromack, Jr. 1980. The role of wood debris in forests and streams. Pages 171–190 in R. H. Waring, editor. *Forests: fresh perspectives from ecosystem analysis*. Oregon State University Press, Corvallis, Oregon, USA.
- Triska, F. J., J. R. Sedell, K. Cromack, Jr., S. V. Gregory, and F. M. McCorison. 1984. Nitrogen budget for a small coniferous forest stream. *Ecological Monographs* **54**:119–140.
- 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*. Hutchinson Ross, Stroudsburg, Pennsylvania, USA.
- Valet, H. M., C. N. Dahm, M. E. Campana, J. A. Morrice, M. A. Baker, and C. S. Fellows. 1997. Hydrologic influences on groundwater–surface water ecotones: heterogeneity in nutrient composition and retention. *Journal of the North American Benthological Society* **16**:239–247.
- Valet, H. M., S. G. Fisher, N. B. Grimm, and P. Camill. 1994. Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. *Ecology* **75**:548–560.
- Valet, H. M., J. A. Morrice, C. N. Dahm, and M. E. Campana. 1996. Parent lithology, groundwater–surface water exchange and nitrate retention in headwater streams. *Limnology and Oceanography* **41**:333–345.
- Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. *Bioscience* **25**:376–381.
- Wagener, S. M., M. W. Oswood, and J. P. Schimel. 1998. Rivers and soils: parallels in carbon and nutrient processing. *Bioscience* **48**:104–108.
- Wagner, B. J., and J. W. Harvey. 1997. Experimental design for estimating parameters of rate-limited mass transfer: analysis of stream tracer studies. *Water Resources Research* **33**:1731–1741.
- 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.
- Wallace, J. B., J. R. Webster, S. E. Eggert, and J. L. Meyer. 2000. Small wood dynamics in a headwater stream. *Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen* **27**:1361–1365.
- Wallace, J. B., J. R. Webster, and J. L. Meyer. 1995. Influence of log additions on physical and biotic characteristics of a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences* **52**:2120–2137.
- Waters, T. F. 1995. Sediments in streams: sources, biological effects, and control. *American Fisheries Society Monograph* **7**. American Fisheries Society, Bethesda, Maryland, USA.
- Webster, J. R. 1975. Analysis of potassium and calcium dynamics in stream ecosystem on three southern Appalachian watersheds of contrasting vegetation. Dissertation. University of Georgia, Athens, Georgia, USA.
- Webster, J. R., D. J. D'Angelo, and G. T. Peters. 1991. Nitrate and phosphate uptake in streams at Coweeta Hydrologic Laboratory. *Verhandlungen der Internationalen Vereinigung für Limnologie* **24**:1681–1686.
- Webster, J. R., S. W. Golladay, E. F. Benfield, J. L. Meyer, W. T. Swank, and J. B. Wallace. 1992. Catchment disturbance and stream response: an overview of stream research at Coweeta Hydrologic Laboratory. Pages 232–252 in P. J. Boon, P. Calow, and G. E. Petts, editors. *River conservation and management*. John Wiley & Sons, New York, New York, USA.
- Webster, J. R., M. E. Gurtz, J. J. Hains, J. L. Meyer, W. T. Swank, J. B. Waide, and J. B. Wallace. 1983. Stability of stream ecosystems. Pages 355–395 in J. R. Barnes and G. W. Minshall, editors. *Stream ecology: application and testing of general ecological theory*. Plenum Press, New York, New York, USA.
- Webster, J. R., J. B. Wallace, and E. F. Benfield. 1995. Organic processes in streams of the eastern United States. Pages 117–188 in C. E. Cushing, K. W. Cummins, and G. W. Minshall, editors. *Ecosystems of the world 22: river and stream ecosystems*. Elsevier, New York, New York, USA.
- Wetzel, R. G., and G. E. Likens. 1991. *Limnological analyses*. Springer-Verlag, New York, New York, USA.
- Wollheim, W. M., B. J. Peterson, L. A. Deegan, J. E. Hobbie, B. Hooker, W. B. Bowden, K. E. Edwardson, D. B. Arscott, A. E. Hershey, and J. Finlay. 2001. Influence of stream size on ammonium and suspended particulate nitrogen processing. *Limnology and Oceanography* **46**:1–13.
- Wood, E. D., F. A. J. Armstrong, and F. A. Richards. 1967. Determination of nitrate in seawater by cadmium–copper reduction to nitrite. *Journal of the Marine Biological Association of the United Kingdom* **47**:23–31.
- Zall, D. M., D. Fisher, and M. D. Garner. 1956. Photometric determination of chlorides in water. *Analytical Chemistry* **28**:1665.