J. N. Am. Benthol. Soc., 1991, 10(3):225-237

Mechanisms of stream phosphorus retention: an experimental study

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Abstract. Using the spiralling concept, this study assessed the relative importance of temperature, current velocity, leaf biomass, fine particulate organic matter, and leaf type in determining phosphorus retention in woodland streams. To accomplish this objective, streamside artificial streams and two contrasting leaf types were used. A labile leaf type (dogwood), typical of successional forest vegetation, and a more refractory leaf type (oak) characteristic of mature forest species were chosen. Leaves were picked just before abscission and air dried. Dogwood leaves were added to three streams and oak leaves to three other streams. Phosphorus uptake experiments were conducted in the streams during November 1987–June 1988 and November 1988–June 1989. All streams were least retentive of phosphorus in December, the coldest month of the year, and more retentive in the warmer spring and summer months. Phosphorus uptake was not correlated with microbial biomass or activity on leaves or with leaf biomass. However, streams with oak leaves were more retentive than streams with dogwood leaves. Measurements of penetrance (i.e., weight required to push a metal rod through the leaf) revealed that dogwood leaves were softer than oak leaves. The soft dogwood leaves were less effective at retarding water flow and therefore velocity was typically faster in dogwood streams ($p < 0.05$; Pearson's correlation). This higher velocity apparently contributed to lower retention. These results suggest that phosphorus retention under conditions of this experiment was governed primarily by temperature and water velocity. Coarse and fine particulate organic matter biomass and composition did influence retention, but their impact was secondary to the effects of temperature and velocity.

Key words: stream, nutrients, phosphorus, temperature, velocity, CPOM, FPOM, logging.

Productivity in many streams is limited by availability of phosphorus (Elwood et al. 1981), which in turn is determined both by supply from the drainage basin and by processes within the stream (Webster and Swank 1985). Land-use practices such as logging can severely alter phosphorus supply and instream processes by changing physical and biological characteristics of streams. For example, canopy removal by logging increases stream temperatures (Brown and Krygier 1971, Swift and Messer 1971, Swift 1982) and reduces allochthonous inputs to streams (Webster and Waide 1982), thereby shifting the stream energy base to autochthonous production (Hains 1981). Lack of rainfall interception by the canopy and decreased evapotranspiration result in elevated stream flow (Swank et al. 1988). Higher stream flows increase nutrient export (Swank 1988) and sediment loads (Lieberman and Hoover 1948, Bormann et al. 1974). Benthic organic matter storage also decreases (Golladay et al. 1989).

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Watershed nutrient budgets have been used as an ecosystem-level approach to assess overall ecosystem function or response to disturbances such as logging (Bormann et al. 1974). Although budgets can provide information on changes in nutrient flux through ecosystems, they provide little information on internal processes or mechanisms governing nutrient dynamics. Furthermore, most watershed studies have relied on terrestrial processes to explain differences in nutrient budgets and paid little attention to in-stream processes (Webster and Swank 1985). To fully understand the impact of watershed disturbance, in-stream material and nutrient processes must also be understood. Previously, stream studies that attempted to evaluate stream nutrient dynamics applied a budget approach to stream segments similar to the approach used for watersheds (Meyer and Likens 1979, Fisher and Likens 1973, Triska et al. 1982). Consequently, unless in-stream processes were measured separately (e.g., Naiman and Mellilo 1984), stream budgets provided little information about mechanisms and processes.

Spiralling, as defined by Webster and Patten (1979), provides a method to both evaluate eco-

system function and investigate internal processes. Spiralling couples the processes of nutrient uptake, transformation, and release with downstream transport (Webster and Patten 1979). A nutrient spiral is defined as the distance required for a nutrient ion to complete one cycle from dissolved form to particulate form and back to dissolved form (Newbold et al. 1981). The distance a nutrient ion travels in dissolved form, before being removed from solution, is defined as uptake length. The distance a nutrient ion travels in particulate form before being released back into the water in dissolved form is the turnover length. Summation of uptake length and turnover length yields spiralling length (Elwood et al. 1981). Streams with short spiralling lengths are more efficient at retaining nutrients than streams with longer spiralling lengths (Elwood et al. 1983). The nutrient uptake rate (1/s) can also be calculated by multiplying the inverse of the uptake length (1/m) by stream velocity (m/s).

Using the spiralling concept, we assessed the relative importance of temperature, current velocity, fine benthic organic matter, leaf biomass, and leaf type in determining phosphorus retention. Because phosphorus dynamics are governed by a complex interaction of these factors, an artificial stream system was used to maintain control and more effectively identify important mechanisms governing phosphorus retention. Uptake length is the best indicator of stream nutrient retention efficiency because it has been shown to account for almost 90% of the total spiralling length (Newbold et al. 1983). Also, rather than using radiotracers as in previous studies of phosphorus spiralling (Mulholland et al. 1985), we used small additions of stable phosphorus to measure phosphorus uptake length and uptake rate as indicators of stream retention. A short uptake length and/or fast uptake rate identifies a retentive system, while a longer uptake length and/or slower uptake rate is indicative of a less retentive system.

Methods

Artificial streams

Six artificial streams, 20 m long and 20 cm wide, were constructed of plastic drain pipe on a platform over a weir pond at Coweeta Hydrologic Laboratory, North Carolina. The bottom of each artificial stream was layered with gravel to a depth of 5–10 cm. Water was piped from the natural stream into a headbox, which fed the artificial streams. Inflow was regulated by either faucets feeding each stream or v-notches in the headbox. Because the canopy over the weir pond was open relative to other portions of the natural stream, the aritifical streams were covered with shade cloth (80%) to more closely approximate natural solar input and algal growth (Fig. 1).

Leaf breakdown

Dogwood and white oak leaves were picked in autumn 1987 and 1988, just before abscission, and air dried. During the first year of the experiment (November 1987–June 1988), 10 g of dry leaves of each species were placed in plastic mesh bags (mesh size = 5 mm). During year 2 (November 1988–June 1989), most of the leaves of each species were placed in the streams unconstrained, instead of in leaf bags, to allow leaf fragments to more readily leave the streams. However, to facilitate calculation of breakdown rates and determination of microbial biomass and activity on the leaves, some leaves were fastened into leaf packs. Leaf packs were made by weighing 10 g of dry leaf material, soaking the leaves in water until softened, and loosely sewing the leaves together with fishing line (12 lb test). Dogwood leaves were placed in three streams and oak leaves in the other three study streams. During the first year, 85 g/m^2 of dry leaves were placed in each stream (in bags) to approximate mean annual leaf biomass in Coweeta streams. In the second year, 300 g/m^2 of dry leaves were placed in each stream (200 g loose and 100 g in packs) to approximate autumn in-stream leaf biomass.

One leaf bag was removed from each of the six streams (i.e., three dogwood and three oak leaf bags) at 2–6-wk intervals (concurrent with phosphorus uptake experiments) to determine leaf breakdown rates. Three leaf discs (1.5-cm diameter) were cut from randomly selected leaves in each bag or pack to determine microbial biomass and activity. Leaf bags or packs removed from each artificial stream were replaced by leaf packs conditioned for the same length of time in extra artificial streams so that

the amount of coarse particulate organic matter (CPOM) in the streams was not reduced by pack removal.

Retrieved leaves were dried (60°C for >24 h) to a constant weight. Dried leaf material was ground in a Wiley mill (1-mm mesh), and 0.25-g subsamples were ashed at 550°C for 30 min. Leaf breakdown rates were calculated on ash free dry mass (AFDM) using a negative exponential model.

During year 1, microbial biomass on leaves was estimated as ATP (Suberkropp et al. 1983). ATP was extracted for 10 min from 1.5-cm leaf discs (three replicates per bag or pack) placed in 5 mL of cold 1.2 N H_2SO_4 plus 5 mL of tris buffer. The ATP extract was then brought to a pH of 7.5 with NaOH and frozen at −4°C for not more than one month. Later, ATP extracts were thawed and 0.1-mL aliquots were added to 0.4 mL luciferin-luciferase. ATP content was measured on a Lab-line Model 9140 ATP photometer. Enzyme solutions and ATP standards were made with tris buffer. Standards were run in triplicate to generate a standard curve. Tris buffer without ATP was used as a blank.

During year 2, penetrance was used as a measure of leaf conditioning or change in the toughness of the leaf matrix (Feeny 1970, Suberkropp and Klug 1981). Three leaves were selected from each bag or pack. Single leaves were held firmly between two plexiglass plates with a hole through the middle and the mean weight (three replicates per leaf) required to push a metal rod (5-mm diameter) through an intervein area of the leaf was determined.

During both years, microbial activity was estimated as ^{14}C-glucose respiration (Williams and Askew 1968, Peters et al. 1989). Three leaf discs (1.5-cm diameter) were taken from each bag or pack. Each disc was placed in an incubation flask with 5 mL of autoclaved stream water. ^{14}C-glucose (specific activity 304.7 mCi/mmole) was added to the water to obtain a concentration of 0.5 μg-glucose/L and the flasks were sealed with rubber septa. Flasks with sterile water were used as blanks. Based on preliminary experiments to determine the incubation time that allowed maximum time for uptake of $^{14}CO_2$ while minimizing isotopic dilution (i.e., recycling of $^{14}CO_2$, King and Berman 1984), flasks were incubated at ambient tempratures for 3 h. At the end of incubation, respiration was stopped with 0.2 mL of 6 N H_2SO_4. Strips of phenethlamine-saturated filter paper suspended from the rubber septum absorbed $^{14}CO_2$ that evolved during the experiment (Hobbie and Crawford 1969). The filter paper was removed and placed in a scintillation cocktail for counting on a Beckman Model LS-3105T Liquid Scintillation Counter.

FIG. 1. Artificial stream system (June 1988) located at Coweeta Hydrologic Laboratory, Macon County, North Carolina. Three streams contained dogwood leaves and three streams contained oak leaves in mesh bags. Extra streams were used to hold replacement leaf bags or packs.

Fine benthic organic matter

Fine benthic organic matter (FBOM) was sampled at the end of year 1 and concurrently with phosphorus uptake experiments during year 2. An FBOM sample was collected from each stream by isolating a randomly selected 5.5-cm length of stream and suctioning all sediments from this area into a 1-L nalgene bottle. The volume of the sediment-water slurry was recorded, and a

20-mL sub-sample was filtered through a preashed 0.45-μm, type A/E Gelman filter, dried, and ashed, to determine FBOM per mL of slurry. The FBOM per mL, multiplied by the total volume of the slurry, was then divided by the area sampled to obtain FBOM/m².

Phosphorus uptake length

To determine phosphorus uptake lengths, a solution containing soluble reactive phosphorus (SRP, as Na_2HPO_4) and chloride (NaCl) was released at a constant rate into each stream for a period (10–20 min) determined by preliminary experiments to be sufficient to allow the downstream concentration to reach a plateau. SRP and Cl^- concentrations added were sufficient to raise stream concentrations to 5–10 × ambient levels (about 30 μg/L SRP and 3 mg/L Cl^- for all experiments) and were high enough to allow uptake length to be measured. Chloride is conservative in most streams and was used to account for dilution and dispersion (Bencala et al. 1987).

At the downstream end of the reach, water samples were taken at 1–3-min intervals to measure the rise in concentration. After the concentration reached a plateau (based on preliminary experiments), water samples were taken at five stations (4 m apart) along the stream. Solution input was then stopped, and sampling continued at the downstream end of the reach at 5–10-min intervals for an additional 30 min to measure the decline in concentration. Samples were filtered as they were collected (0.45-μm Gelman A/E glass fiber filters) and then frozen or analyzed within 24 h for SRP and Cl^-.

Biotic-abiotic uptake

To determine the ratio of biotic to abiotic uptake of phosphorus, streams were chlorinated after the last uptake experiment of each year. Chlorination was achieved by minimizing water flow into the streams and pouring a chlorine solution into the streams. In year 1, an 8-L hypochlorite solution (0.5 g/L) was added to the streams resulting in a stream chlorine concentration of about 62.5 mg/L. Because only about 50% of the microbes were killed at this concentration (see Results), 8 L of a 4-g/L solution was used in year 2 resulting in a 0.5-g/L concentration. Two hours after chlorination, stream flow was resumed and phosphorus uptake was measured as described previously. Because chlorine interfered with the labeled glucose assay described above (apparently by accelerating respiration of stressed microbes or abiotically oxidizing the glucose to CO_2), chlorination effectiveness was determined as a decrease in live microbial biomass (i.e., ATP) or as a decrease in bacterial colonies on standard 1.5% agar plates with 1% yeast extract. Three grams of wet leaf material (about 2.7 g dry) were blended in a Waring blender with 20 mL of sterile water. Dilutions (10^{-2} to 10^{-6}) of the leaf-water slurry were plated in triplicate for each stream to estimate number of colonies.

Laboratory analyses

All chemical analyses were performed at Coweeta Hydrologic Laboratory. Phosphorus and chloride were analyzed using a 3-channel Technicon Autoanalyzer-II system. Soluble reactive phosphorus concentrations were measured using the ammonium-molybdate reaction. Chloride was determined using the ferricyanide method.

Data analyses

Figure 2 is an example of chloride concentrations measured at the downstream end of the artificial streams during one phosphorus uptake experiment. These data were used to calculate stream velocity by integrating the area under the curve and determining the time for half of the chloride to pass the downstream end. The difference between the time at which half of the solution was released and the time for half of the chloride to pass the downstream station is the nominal transport time (Triska et al. 1989). Velocity was calculated as distance divided by nominal transport time. For phosphorus uptake experiments where we did not generate a chloride curve, velocity was determined by releasing rhodomine dye into the stream and measuring travel time. Because velocity determined by rhodomine dye is the maximum velocity, a regression equation was calculated for velocity obtained from chloride data versus velocity from rhodomine dye releases from experiments when both chloride and rhodomine dye were released. This equation was used to convert maximum velocity to average velocity.

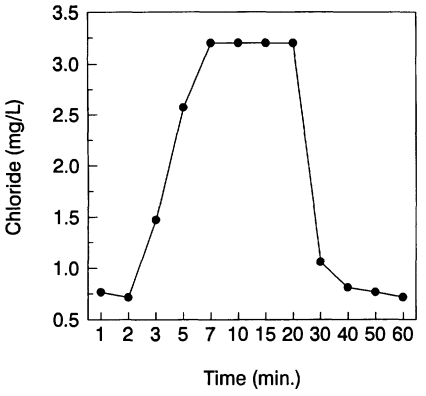

FIG. 2. Example of chloride concentrations measured at the downstream site during one uptake experiment. Mean stream velocity was calculated by determining the area under the curve and the travel time for half of the chloride relative to the time when half of the chloride had been released.

Figure 3 shows the downstream decline in average chloride and phosphorus concentrations during the plateau portion of the release pulse. The decline in phosphorus concentration was a result of dilution, dispersion, and uptake. Chloride, however, is conservative in these streams, and therefore the decline in chloride concentration was a result only of dilution and dispersion. Chloride data were used to correct the phosphorus data to account for losses due to dilution and disperion.

$$[SRP]_{corr} = ([Cl_o]/[Cl_i])[SRP_i]$$

where: o = upstream-most station
i = downstream station

Corrected phosphorus concentrations were then expressed as a percent of upstream concentration. For this example, about 70% of the phosphorus released into the stream was removed from solution, by either biotic or abiotic processes, in the first 15 m. Uptake of phosphorus per unit stream length was calculated as the slope of the regression line relating the natural logarithm of the corrected phosphorus concentration to distance. The inverse of the uptake rate of phosphorus per unit length is phosphorus uptake length (m), i.e., the average distance a phosphorus atom travels before being sorbed onto particulates or taken up by the biota (Elwood et al. 1981). Uptake rate per unit time (1/s) was then obtained by multiplying the uptake rate per unit distance (1/m) by water velocity (m/s).

Statistical analyses

Statistical analyses were conducted using mainframe SAS software procedures for analysis of variance (ANOVA) and Pearson's correlations. Two sets of ANOVAs and correlations were run. One set of ANOVAs was run for each variable grouped by leaf type with all dates combined. A second set was run with leaf types grouped and each sample date evaluated separately. Significance values noted in the text are for analyses conducted with all dates combined. Significant differences noted on the figures are for each sample date examined separately. Correlations were based on individual streams and dates (n = approx. 72) or were grouped by sample date (n = approx. 12).

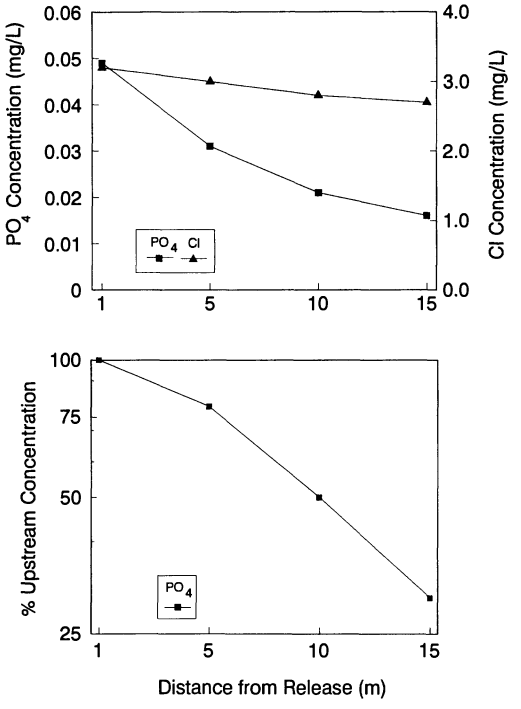

FIG. 3. Example of mean chloride and phosphorus concentrations during the plateau at sites along the length of the stream. The upper panel shows the downstream decline in chloride and phosphorus concentration. The lower panel shows the downstream decline in phosphorus concentration after correction for losses due to dilution and dispersion and expressed as a percentage of upstream concentration.

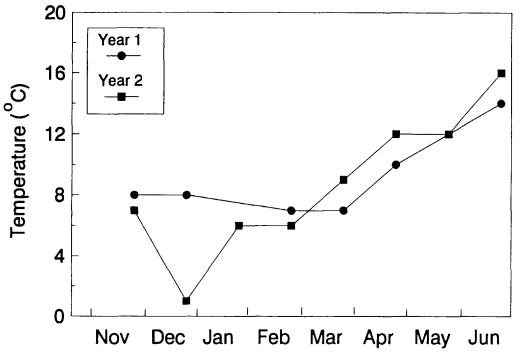

FIG. 4. Mean monthly water temperature (°C) in the artificial streams at the time of the phosphorus uptake experiments during year 1 (1987–1988) and year 2 (1988–1989).

Results

Physical variables

Water temperature in the artificial streams ranged from 1°C to 16°C during the study. Minimum temperatures occurred in December and maximum temperatures in June (Fig. 4). Discharge was initially set at 0.5 L/s; however, phosphorus uptake was negligible at this discharge. Therefore, in January 1988, discharge was reduced to 0.25 L/s and maintained at that level for the remainder of the study. When discharge was at 0.5 L/s, velocity was higher in the oak streams. After the discharge was lowered to 0.25 L/s in January of year 1 (when leaves were in bags), velocity did not differ between dogwood and oak streams and remained at about 0.12 m/s between January and June (Fig. 5). During year 2, when the majority of the leaves were unconstrained, the less rigid dogwood leaves were less effective at retarding waterflow in the streams. Velocity in the dogwood streams increased more than in the oak streams during the study and was significantly greater ($p < 0.01$) than in the oak streams during the later months of the experiment (Fig. 5). Mean velocity of dogwood streams doubled from 0.07 to 0.14 m/s, while mean velocity of oak streams increased only from 0.06 to 0.09 m/s.

Biological variables

During year 1, dogwood leaves decomposed significantly faster than oak leaves (ANOVA, $p < 0.0001$) (Fig. 6) with decomposition rates of 0.0025 and 0.0015 per degree-day, respectively. During year 2, there was no difference in decomposition rates (0.0015 and 0.0018 per degree-day). However, oak leaves lost less weight through leaching and therefore maintained a higher biomass throughout the year. Oak leaf biomass with significantly greater (ANOVA, $p < 0.05$, $n = 3$) than dogwood leaf biomass on most sample dates. Microbial biomass (Fig. 7) and respiration (Fig. 8) were greater on dogwood leaves than on oak leaves on all sample dates, and overall mean microbial biomass and glucose respiration on dogwood (2.45 μg ATP/g AFDM; 0.025 μg glucose/h/g AFDM) were significantly greater (ANOVA, $p < 0.05$) than on oak (1.79 μg ATP/g AFDM; 0.01 μg glucose/h/g AFDW).

Penetrance data showed that dogwood leaves were typically softer than oak leaves (Fig. 9). Penetrance was negatively correlated with microbial respiration ($p < 0.05$, $r = -0.7422$, $n = 10$) and stream velocity ($p < 0.0001$, $r = -0.7756$, $n = 10$) (i.e., as the leaves softened, microbial respiration and stream velocity increased).

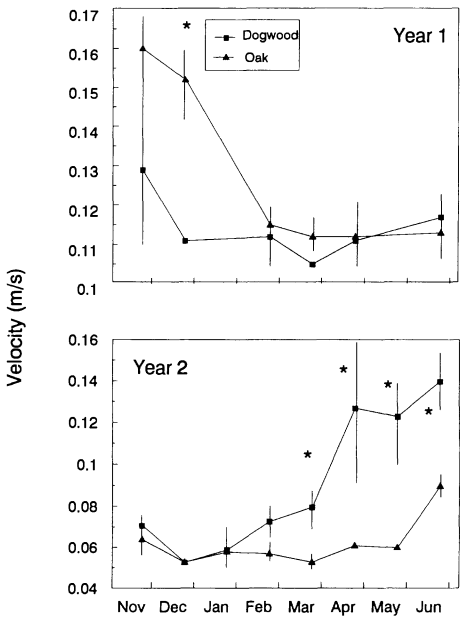

FIG. 5. Mean water velocity (m/s) in the streams with dogwood and oak leaves ($n = 3$) during year 1 (1987–1988) and year 2 (1988–1989). Discharge was reduced from 0.5 to 0.25 L/s between December 1987 and February 1988 of year 1 and maintained there for the remainder of the study. Asterisks denote significance at $p < 0.05$ (ANOVA).

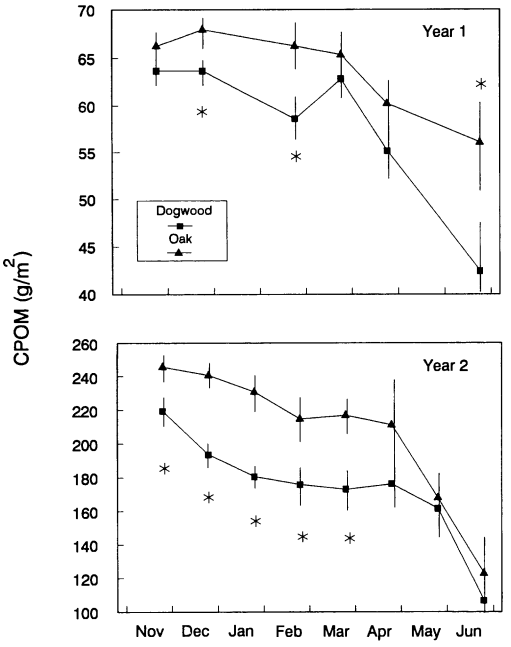

FIG. 6. Mean leaf biomass (g/m²) of dogwood and oak leaves ($n = 3$) during year 1 (1987–1988) and year 2 (1988–1989). Asterisks denote significance at $p < 0.05$ (ANOVA).

FBOM biomass was measured at the termination of year 1 experiments and after each phosphorus uptake experiment in year 2. FBOM biomass ranged from 3.1 to 150 g AFDM/m². FBOM biomass was lowest in stream 1 and greatest in stream 6 (Fig. 10). Average FBOM biomass ranged from about 10.7 g AFDM/m² in December to 27.7 g AFDM/m² by June. Ratios of leaf to FBOM biomass at the start of year 2 were approximately 22:1 and decreased to about 4:1 by the end of the year. A spot check of microbial activity was done in November 1988. Microbial activity on the FBOM was approximately equal to activity on CPOM.

Biotic-abiotic uptake

Based on a comparison of phosphorus uptake lengths in chlorinated and non-chlorinated streams, at least 60% of SRP uptake can be attributed to biotic factors (Table 1). For both biotic-abiotic uptake comparisons (at the end of year 1 and year 2), uptake length was about 2.5 times longer in non-chlorinated streams than in chlorinated streams. For the year 1 study, microbial biomass (ATP) was reduced 46% with chlorination. For the year 2 study, 85% of the microbes were killed or inactivated based on colony reductions. Therefore the 60% reduction in uptake resulting from chlorination is a conservative estimate, and biotic uptake likely accounts for more than 60% of uptake.

Phosphorus retention

In year 2, phosphorus retention, expressed as uptake length or uptake rate (Fig. 11), was generally lowest in December, the coldest month of the year, and then increased throughout winter and spring as temperatures and microbial colonization increased. In year 1, the same pattern was apparent, but by late spring and early summer, retention decreased in the dogwood streams.

In November 1988 (year 2), just after leaves were placed in the streams, streams with dogwood leaves retained significantly more phosphorus than those with oak leaves (ANOVA, $p < 0.05$). By December, there was no difference in phosphorus retention between streams with dogwood and oak leaves. After December, streams with oak leaves retained significantly more phosphorus than those with dogwood during all months except February and June when retention by oak streams was not significantly greater (ANOVA, $p = 0.27$ for February; $p = 0.64$ for June). Phosphorus uptake experiments from year 1 followed this same pattern, but not as clearly. Based on mean uptake data for both years, streams with oak leaves retained

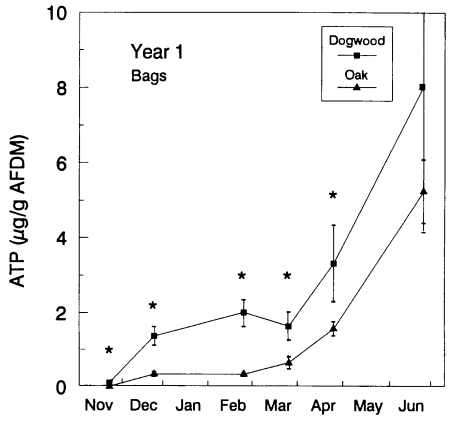

FIG. 7. Microbial biomass (μg ATP/g AFDM) of dogwood and oak leaves during year 1 (1987–1988). Asterisks denote significance at $p < 0.05$ (ANOVA).

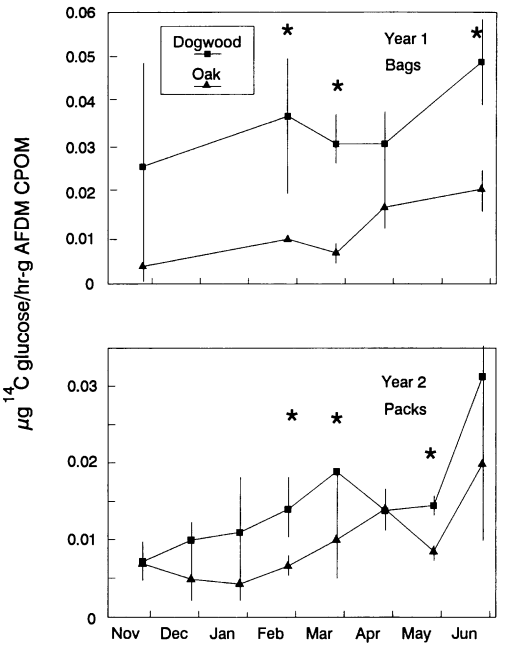

FIG. 8. Microbial respiration (μg glucose respired/g AFDM) of dogwood and oak leaves during year 1 (1987–1988) and year 2 (1988–1989). Asterisks denote significance at $p < 0.05$ (ANOVA).

significantly more phosphorus than those with dogwood leaves (ANOVA, $p < 0.0007$) (Table 2). Species-specific differences in retention were not a result of microbial biomass or activity associated with the different species, as there was no relationship between microbial biomass or activity and retention. In contrast, FBOM was correlated with retention ($p < 0.001$, $r = -0.675$, $n = 70$).

Discussion

Among the complex factors governing phosphorus retention, temperature and velocity appear to be most important. Chen (1974) demonstrated that the rate of microbial uptake of phosphorus was temperature dependent. Uptake rates were slowest at 4°C and increased until a maximum was reached at about 30°C. Elwood et al. (1981), conducting uptake experiments with phosphorus, also found that uptake was slower at colder temperatures. Results from our study and others (McColl 1974, Corning et al. 1989) support the conclusion that temperature may be a primary determinant of phosphorus retention. Temperature control of phosphorus retention likely occurred because chlorination experiments indicated that microbes account for greater than 60% of the uptake in these streams. This contrast with the findings of Meyer (1979) for a New Hampshire stream but agrees with conclusions by Gregory (1978) and Elwood et al. (1981) who found that microbes were responsible for most phosphorus uptake (>80%) in Oregon and Tenessee streams, respectively.

Velocity differences in the streams occurred as a result of differences in breakdown rates and structural characteristics of leaf types, and these differences influenced retention. As both dogwood and oak leaves became softer and more penetrable, stream velocity increased in streams with unconstrained leaves; however, velocity increased more in dogwood than in oak streams. Increased velocity resulted in loss of retentive ability (as measured by phosphorus uptake length or uptake rate) for dogwood streams relative to oak streams, and the difference became more pronounced as the year progressed. Removal efficiency may decrease (Meyer 1979) because at higher velocity there is less contact between water and sediments. At slow velocity, there is more contact between the water and sediment and consequently more nutrient uptake (Bencala 1983).

Although leaf structural characteristics indirectly influenced retention through changes in water velocity, leaf biomass (i.e., CPOM) and

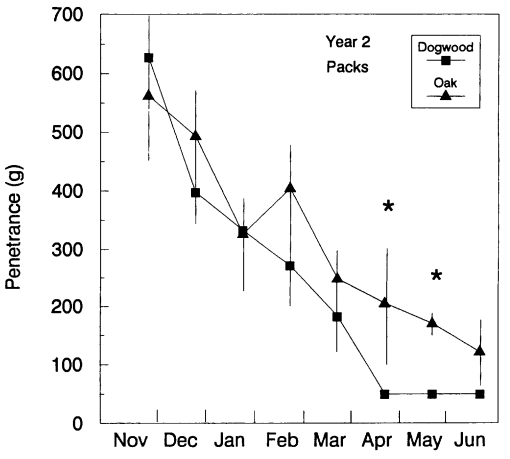

FIG. 9. Mean penetrance of leaf material as mg pressure ($n = 3$) during year 2 (1988–1989). Asterisks denote significance at $p < 0.05$ (ANOVA).

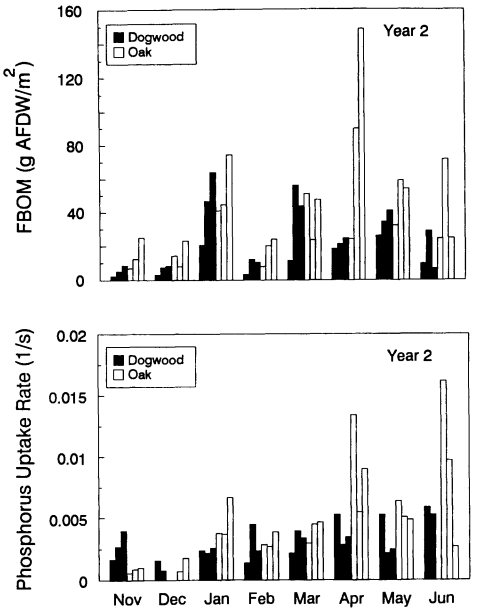

FIG. 10. FBOM (g AFDM/m²) and phosphorus uptake rate (1/s). Individual bars represent individual streams. Streams are ordered from left to right 1, 3, 5, 2, 4, 6 where 1, 3, and 5 contained dogwood leaves and 2, 4, and 6 contained oak leaves. FBOM was inversely correlated with phosphorus uptake rate (ANOVA, $p < 0.001$).

associated microbial biomass and activity, were not correlated with phosphorus retention. In contrast, Gregory (1978), comparing conifer needles and maple leaves, found that the ability of organic matter to support microbial growth greatly affected retention. Elwood et al. (1988) also found a correlation between microbial respiration and uptake by oak leaves but no correlation for dogwood or maple leaves. This information suggests that differences in retention capability are reflected only if there is a large disparity in the ability of organic matter to support microbial growth.

In contrast to the lack of correlation between CPOM biomass and retention, FBOM biomass, which was about ¼ of CPOM biomass, was significantly correlated with phosphorus retention ($p < 0.001$). A spot check of microbial activity done on FBOM in November 1988 showed that microbial activity/g AFDW on the FBOM was approximately equal to activity/g AFDW on CPOM. One possible explanation for the correlation between retention and FBOM is that FBOM has a greater surface area to volume ratio than CPOM. Munn (1990) also found that FBOM was more retentive of phosphorus than CPOM in streams in North Carolina and Oregon, whereas Mulholland et al. (1985) found that CPOM was more retentive of phosphorus in a Tennessee stream. The apparent disparity between these studies may be due to differences in FBOM quality. FBOM in our study and in Munn's (1990) study may have been better quality (i.e., able to support more microbial activity) than that of Mulholland et al. (1985).

The ratio of leaf biomass to FBOM also appears to be related to retention. During year 1, when leaf biomass in the streams was only 85 g dry mass/m², phosphorus uptake by dogwood and oak leaves was not significantly different on a monthly basis, and data collected during the spring showed no clear pattern. Apparently, when leaf biomass was low relative to FBOM biomass, leaf species effects on uptake were masked by FBOM variability. During year 2, when leaf biomass was higher (300 g dry mass/m²) and FBOM biomass was monitored, effects of leaves on phosphorus uptake were more apparent. Early in the study (November-January), FBOM uptake appeared to be less important than whole leaf uptake. However, by February FBOM biomass had increased and leaf biomass had decreased to the point that leaf species differences became less evident (Fig. 10).

Clearly no single factor was responsible for phosphorus retention in our experiment, but rather phosphorus retention was governed by a dynamic interaction of factors among which temperature seemed to be the most important. Within the constraints of temperature, velocity differences (which occurred due to changes in leaf structural rigidity) resulted in species-spe-

TABLE 1. Phosphorus uptake length in sterile and non-sterile streams for June 1988 (Year 1) and June 1989 (Year 2). Microbial biomass (ATP) and number of colonies on agar plates were used as measures of the effectiveness of sterilization.

	1988		1989	
Treatment	Non-chlorine	Chlorine	Non-chlorine	Chlorine
Uptake length (m)	34.1	89.4	36.5	83.0
ATP (μg/g AFDW)	6.5	3.5	—	—
Colony forming units	—	—	51.0	7.6

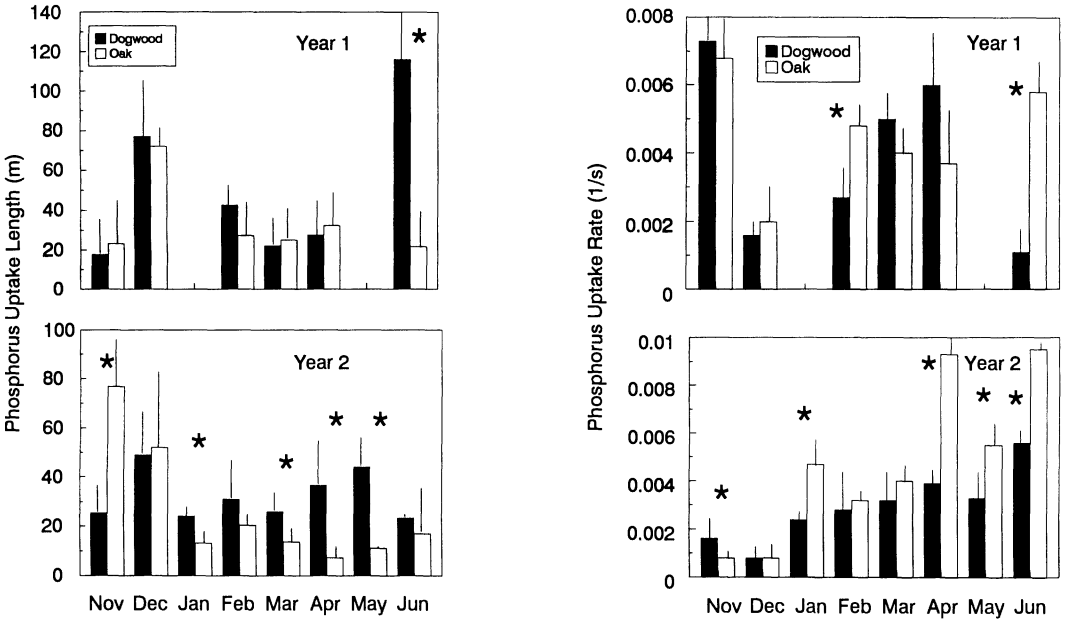

FIG. 11. Mean phosphorus uptake length (m) (left panels) and mean phosphorus uptake rate (1/s) (right panels) during year 1 (1987–1988) and year 2 (1988–1989) in streams with dogwood and oak leaves ($n = 3$). Asterisks denote significant difference between streams at $p < 0.05$ (ANOVA).

cific differences in uptake. FBOM appeared to became more important as FBOM biomass increased and leaf biomass decreased.

Although the artificial streams provided a template with which to investigate these factors in a somewhat controlled system (Stream Solute Workshop 1990), it is important to recognize that in natural streams, discharge is not constant and therefore seasonal patterns may differ and the relative importance of different components may also vary. In natural streams in the southern Appalachain Mountains, discharge is typically lowest in the fall, higher throughout winter and spring, then declines again through summer. Therefore, streams are expected to be most retentive of phosphorus in fall when CPOM biomass is high and discharge is low and in summer when temperatures are high and discharge is low.

Mulholland et al. (1985) lumped data from several years to obtain seasonal uptake characteristics of a stream in eastern Tennessee. Their data illustrated a trend of highest retention in late autumn and lowest retention in summer. Munn (1989), working in a Coweeta stream, attributed changes in uptake primarily to CPOM and microbial activity but noted that discharge was also an important factor and probably accounted for differences in uptake that were observed between the two years of her study. In contrast to the findings of Mullholland et al. (1985) and Munn (1989), we found temperature to be the more important regulator of phosphorus retention. Temperature was probably most important because it regulated microbial activity, which was significantly correlated with retention ($p < 0.05$, $r = 0.572$). This conclusion may have been reached because we kept discharge constant. In natural streams, effects of warm temperatures and high microbial respiration are likely offset by higher discharges that increase the downstream flux of nutrients and

TABLE 2. Mean phosphorus uptake length (m) in streams with dogwood leaves and streams with oak leaves averaged over the months of November to June. p values indicate significant difference between uptake in dogwood and oak streams (ANOVA).

	Uptake length (m)		
Year	Dogwood	Oak	p value
1987–1988	57.9	38.8	0.01
1988–1989	32.2	22.8	0.001

decrease uptake (Whitford and Schumacher 1964, Lock and John 1979, Mulholland et al. 1985).

Mulholland et al. (1990) demonstrated that stable isotope releases involving substantial increases in nutrient concentrations overestimate uptake length compared with radiotracer methods. In their study of Walker Branch, Tennessee, they estimated that biological uptake of SRP was saturated at less than 10 $\mu g/L$. Though we kept our release concentrations as low as possible, the results from Walker Branch suggest that our limited ability to find significant differences related to biomass or microbial activity may have been because biological uptake was saturated. Thus our results show the differences in water velocity among streams caused by structurally different leaf types.

Results from our artificial stream studies suggest that temperature and velocity are the prime determinants of phosphorus retention. Results from natural streams (D'Angelo 1990) show that discharge may be most important. Identification of important phosphorus retention mechanisms allows us to predict effects of certain land-management practices. For example, logging and the resultant loss of canopy cover increase the amount of light that reaches a stream and thereby increases stream temperature (Brown and Krygier 1971) and algal growth (Hains 1981). Given a constant discharge, increased temperatures and algal uptake should increase phosphorus retention. However, the loss of vegetative cover also results in less evapotranspiration and an increase in stream flow (Swank et al. 1988), which should cause a net decrease in retention. The decrease of an autumn input of allochthonous leaf material (Webster et al. 1990) and decrease in benthic organic matter storage (Golladay et al. 1989) should also accentuate this decrease in retentive ability. Input-output studies of logged watersheds support this conclusion (Bormann et al. 1974). Therefore, by understanding mechanisms governing phosphorus retention and their relative importance over a range of conditions, we can begin to evaluate the consequences of land-use practices before their implementation.

Acknowledgements

We thank B. M. Stout and S. W. Golladay for their help in building the artificial stream system. We also express our appreciation to all those at the Coweeta Hydrologic Laboratory who provided assistance, with a special thanks to Jim Deal for his instruction and assistance on the Technicon Autoanalyzer II and Kitty Reynolds for general laboratory help. This work was supported by a doctoral dissertation improvement grant (#BSR8719571) from the National Science Foundation (NSF) with partial support from a grant (#BSR8514328) from NSF for Coweeta Hydrologic Laboratory as a site in the Long Term Ecological Research Program.

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Received: 3 December 1990
Accepted: 30 May 1991