Mechanisms Governing Phosphorus Retention in Streams

by

Donna Jean D'Angelo

Dissertation submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy
in
Biology

APPROVED:

Jackson R. Webster, Chairman

Ernest F. Benfield

Robert E. Benoit

Theo A. Dillaha

George M. Simmons

April, 1990

Blacksburg, Virginia

Acknowledgements

I would like to extend sincere appreciation to my major professor, Dr. J.R. Webster, for always taking the time to assist me with any difficulties that arose during the course of this project, and for thoroughly reviewing proposals, manuscripts and miscellaneous documents. I also thank my committee (Drs. E.F. Benfield, R.E. Benoit, T.A. Dillaha, and G.M. Simmons) for their assistance with this project through helpful suggestions, constructive critisism, and thorough examination of material submitted to them. A special thank you goes to Dr. E.F. Benfield for his support and candid advice during the difficult portions of this degree program. I also appreciate the support and generous help of my personal friends, as well as graduate students in biology and other fields. Thanks also goes to Sheri Gernhofer, Steve Gollady, and Ben Stout for their help building the artificial stream system. John Hutchens provided valuable sample collection assistance, and John, Nick Zemo, and Chris Marshall helped with sample processing. A am also indebted to all those at the Coweeta Hydrologic Laboratory who provided assistance. Jim Deal and Kitty Reynolds were especially helpful. The mathematical model chapter of this dissertation would not have been possible without the generous help of Dr. Dan Gallagher and John Musson.

Finally, I would like to thank my parents for their constant support, and my Mother for always telling me to do whatever would make me happy--and meaning it.

This work was supported by an NSF doctoral disseration improvement grant (#), with additional funding from the VPI&SU graduate student development project and Sigma Xi.

Table of Contents

List of Illustrations

List of Tables

1.0 General Introduction

A nutrient is defined as a chemical element necessary for life. In streams, phosphorus is typically one of the most important nutrients and often limits microbial (algae, bacteria, and fungi) growth. As a result, retention of phosphorus within streams largely determines productivity. Factors that influence retention include temperature (Elwood et al. 1981b), velocity (Bencala 1983), and organic matter (Mullholland et al. 1984).

Watershed input-output budgets have been commonly used to evaluate nutrient retention characteristics (Borman et al. 1974). These studies provide information about nutrient flux through ecosystems but offer little information about mechanisms governing nutrient dynamics. In contrast, nutrient spiralling, as described by Webster and Patten (1979), provides a method to evaluate retention and the mechanisms governing it. A nutrient spiral is defined as the distance traveled by a nutrient ion as it completes one cycle from dissolved form to particulate form and back to dissolved form. The distance a nutrient ion travels in dissolved form is called the uptake length and typically accounts for > 90% of spiralling length (Newbold et al. 1983). Uptake length is commonly used instead of spiralling length, because unlike spiralling length, uptake length can be measured without the use of radiotracers.

Nutrient spiralling, developed in the late 70's and early 80's, is a relatively new concept. Work on spiralling length (or uptake length) has just begun to allude to possible mechanisms of solute retention and the relative importance of these mechanisms (see Solute Working Group 1990 for a review of concepts and methodology). Recent

nutrient retention studies have shown phosphorus retention to be affected by both physical (e.g. temperature, velocity) and biological (e.g. microbial activity, organic matter biomass) factors. However, these studies have yielded conflicting information as to the relative importance of these factors. For example, Gregory (1978) and Elwood et al. (1981) demonstrated that uptake was mostly biotic, while Meyer (1979) found that uptake was determined by physical factors in the streams she studied. This contradiction suggests that streams may range from those driven primarily by biological mechanisms to streams driven almost entirely by physical factors with most streams falling somewhere between these extremes. The relative importance of physical and biological factors may vary spatially and temporally within a stream.

This study was designed to systematically identify and examine factors that influence nutrient retention. More specifically, the objectives of this study were:

1) Examine microbial colonization and breakdown characteristics of leaves with different amounts of structural rigidity, under different constrainment techniques, to gain insight into how these characteristics may affect nutrient retention.

2) Use artificial streams to separate and identify factors governing nutrient retention by controlling flow and using different amounts and types of leaf material.

3) Evaluate how land-use practices may alter phosphorus retention mechanisms by comparing results of nutrient releases in natural streams draining undisturbed mixed-hardwood watersheds with releases in streams draining disturbed watersheds (i.e. watersheds that had been logged and planted in white pine).

2.0 Literature Review

2.1 Phosphorus sources

Phosphorus is commonly a limiting nutrient in streams (Hynes 1970). Most phosphorus is bound organically in cellular constituents. The only significant form of inorganic phosphorus is orthophosphate (PO_4) (Wetzel 1983). Phosphorus inputs are primarily dissolved or course particulate (Meyer et al. 1981). Major outputs are dissolved forms and fine particulate material transported as bedload and suspended load.

Phosphorus enters streams from precipitation either directly as channel interception or indirectly as thru-fall and runoff. Thru-fall precipitation may leach significant quantities of phosphorus from vegetation. Leaves and other riparian material also contribute nutrients when they enter the stream as litterfall or blowin (Fisher and Likens 1973).

In forested headwater streams, leaf inputs are the major source of organic carbon (e.g. Minshall 1967; Fisher and Likens 1973) and also contribute substantial amounts of nutrients. For example, in Hubbard Brook, Fisher and Likens (1973) found that leaching from leaves accounts for 28% of the total annual phosphorus input. After a leaf falls into the stream and is wetted, leaching occurs rapidly within the first 24 hours and then gradually diminishes (Nykvist 1963). Following initial leaching, fungi colonize the leaves and breakdown cellulose, pectin, and some lignin (Suberkropp and Klug 1980; Chamier and Dixon 1982). Fungi breech the epidermis producing points of entry for

bacteria (Kaushik and Hynes 1968; Barlocher and Kendrick 1974). Fungi and bacteria increase the protein content of the leaves so that it is more palatable for macroinvertebrates, and soften leaf material making it more prone to physical breakdown.

During the course of leaching and breakdown, leaves undergo changes in chemical composition. Initial leaching results in a decline in phosphorus. Meyer (1980) reported that during the first week, leaf phosphorus declined from 0.035% to 0.030%. Following leaching, colonizing microbes immobilize nitrogen and phosphorus causing and increase in nitrogen and phosphorus as percent dry weight (Kaushik and Hynes 1968; Howarth and Fisher 1976; Suberkropp and Klug 1976a; Meyer 1980; Barlocher 1985; Paul et al. 1983). Nitrogen and phosphorus eventually begin to decline along with structural constituents such as hemicelluloses and celluloses (Godshalk and Wetzel 1978), while lignin increases as percentage ash free dry weight (%AFDW)(Suberkropp and Klug 1976b; Paul et al. 1983).

Breakdown rates of leaves appear to be correlated with lignin (Sedell et al. 1975; Suberkropp and Klug 1976b; Triska and Sedell 1976; Paul et al. 1983) and nitrogen concentrations in the leaves (Kaushik and Hynes 1971; Sedell et al. 1975; Godshalk and Wetzel 1978). External supplies of dissolved inorganic nitrogen (DIN) also influence breakdown with systems rich in nitrogen typically having faster breakdown rates than nitrogen poor systems (e.g. Rosset et al. 1982; Meyer and Johnson 1983). Nutrient addition studies have verified this characteristic and shown that nitrogen accelerates breakdown (Hynes and Kaushik 1969; Howarth and Fisher 1976; Fairchild et al. 1984). while additions of phosphorus usually have little effect (Fairchild et al. 1984; Brock et al. 1985). However, there are exceptions to the above studies. Data collected by Triska and Sedell (1976) did not show an acceleration of breakdown with the addition of ni-

trogen and work done by Elwood et al 1981 showed that phosphorus additions do accelerate breakdown.

Leaf breakdown is also faster in the the presence of invertebrate shredders (Cummins et al. 1973; Wallace et al. 1982; Kirby et al. 1983; Rounick and Winterbourn 1983; Cuffney et al. 1984; Mutch and Davies 1984; Benfield and Webster 1985; Smith 1986). Shredders accelerate leaf breakdown via cominution of leaf material and stimulation of microbial metabolism (Mulholland et al. 1984), hastening the release of leaf nutrients into the stream.

2.2 Phosphorus uptake and transformations

Phosphorus is taken up by algae and fungi as dissolved inorganic phosphorus (DIP) and by bacteria as either DIP or dissolved organic phosphorus. Microbes incorporate dissolved phosphorus into cellular constituents and thereby serve as an important particulate organic phosphorus retention mechanism. Phosphorus is then released through secretions of dissolved organic colloids or particulate sloughing (Wetzel 1983).

Other factors that influence nutrient transformation are invertebrate comminution of coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM), and abiotic processes. Leaf shredding invertebrates tear leaf material, releasing nutrients and accelerating breakdown of CPOM to FPOM. Abiotic processes include adsorption of dissolved phosphorus onto particulates, leaching from organic matter, formation of particulates by coagulation of dissolved material, and deposition and entrainment of particulate nutrients.

2.3 Factors affecting phosphorus uptake

Phosphorus entering streams is taken-up according to first order kinetics (Simmons and Cheng 1985). Uptake is influenced by both biotic (microbes, macroinvertebrates, and detritus) and abiotic (water velocity and sorption onto particles) factors. Biotic factors appear to be more important than abiotic factors in regulating uptake in most streams (Ball and Hooper 1961; Gregory 1978; Vincent and Downs 1980; Elwood et al. 1981b; Mulholland et al. 1985). However, Meyer (1979) found that in the streams she worked in, abiotic factors were more important. Bond (1979) suggested that under limiting conditions, nutrient concentrations are controlled by the biota. For example, microbial uptake has been shown to account for about 80-91% of uptake, with physical sorption being responsible for only 9-20% (Gregory 1978; Elwood et al. 1981).

Biotic uptake is a two step process involving both adsorption of nutrients onto the cell wall or membrane and then transport into the organism (Chen 1974; Elwood et al. 1981). The rate of uptake is dependent on various factors including nutrient concentration and temperature (Chen 1974; Elwood et al. 1981).

In streams, CPOM from allochthonous leaf inputs provides an important site of attachment and food source for microbes. As a result, nutrient uptake onto CPOM is an important nutrient retention mechanism. Newbold et al. (1983) found that CPOM and associated microbes took up 60% of available phosphorus, and Mulholland et al. (1985) showed a seasonal correlation between nutrient retention and the biomass of CPOM in Walker Branch. Mulholland et al. (1984,1985) also found that uptake corresponded with microbial colonization. Therefore, leaves with different colonization patterns and breakdown rates would be expected to produce different seasonal phosphorus uptake patterns.

Leaves with a high nitrogen to lignin ratio breakdown quickly (Melillo et al. 1982) and support higher levels of microbial activity than leaves with lower nitrogen to lignin ratios. (Kaushik and Hynes 1968; Triska 1970; Suberkropp and Klug 1976). Leaves that breakdown quickly include herbaceous plants (Peterson and Cummins 1974) and leaves from early successional tree species such as dogwood (Benfield and Webster 1985), black locust (Meyer and Johnson 1983), and yellow-poplar (Thomas 1970). Leaves that colonize quickly and sustain high levels of microbes would be expected to retain nutrients effectively at first but would not be expected to be retentive over an annual cycle because the leaves breakdown rapidly and do not remain in the stream.

Leaves from intermediate and late successional tree species such as maple and oak (Peterson and Cummins 1974) generally have slower breakdown rates. As a result, these tree species would be expected to be less retentive initially, but because they disappear from the stream more slowly than faster decomposing species, should be more retentive on an annual cycle.

Physical sorption of nutrients onto particles is primarily determined by the magnitude and rate of suspension and settling (Newbold et al. 1983). Direct exchange, in the absence of water or particle movement, is negligible (Newbold et al. 1983). As a result, storms and other factors that increase particle suspension will have a large impact on uptake. Storms and changes in water velocity in general also affect uptake length less directly. Uptake length (U) is a function of both nutrient flux (F), the total amount of a nutrient that passes through a cross section of the stream, and the rate of uptake (R) (i.e. $U = F/R$) (Newbold et al. 1983). As water velocity increases, nutrient flux increases. Therefore, uptake length would also be expected to increase. However, as water velocity and flux increase, R may also increase because the fresh supply of water moving past microoranisms continually restores the concentration gradient necessary for effective uptake of nutrients (Whitford and Schumacher 1964; Lock and John 1979; Mulholland

et al. 1985). Therefore, increases in uptake length may not be proportional to increases in water velocity (Newbold et al. 1983).

2.4 Spiralling

Because spiralling length provides an important index of stream nutrient retention, it also has implications concerning production and efficiency. Newbold et al. (1982b) suggested that production, the capacity of a body of water to support growth in biomass, is expected to be a function of retention and recycling. Therefore, factors such as microbial uptake and adsorption that shorten uptake length should increase productivity. Factors that increase uptake length such as increases in water velocity (Newbold et al. 1983) and loss of CPOM (Mulholland et al. 1985b) should decrease productivity.

Elwood et al. (1983) proposed that spiralling length is also an index of stream efficiency and compared it to Fisher and Likens' (1973) ecosystem efficiency, which is a measure of carbon respired per carbon supply. The two indices are similar but not identical because ecosystem efficiency is dependent on stream length (Fisher 1977), whereas spiralling length is independent of length (Newbold 1982a). Therefore, spiralling length can be used to compare streams or stream reaches of different lengths (Newbold et al. 1982a). Elwood et al. (1983) and (Newbold et al. 1982a) suggested that for two identical streams with equal supplies of a limiting nutrient, the stream with the shorter nutrient spiral is most efficient and most productive.

Spiralling length is the best indicator of stream nutrient retention efficiency, but, because uptake length has been shown to account for almost 90% of the total spiralling length (Newbold et al. 1983) and to eliminate the necessity of using radiotracers, this

study will focus on nutrient uptake length as an indicator of stream nutrient retention efficiency.

3.0 Effects of constrainment techniques on leaf breakdown

3.1 Abstract

Breakdown rates and microbial colonization patterns of dogwood and oak leaves were measured between November and June of 1987-88 and 1988-89. Leaves were placed in artficial streams in bags, packs, and unconstrained. Discharge was maintainted at approximately 0.25 L/s, and no shredders were present in the streams. Microbial biomass as ATP increased from near 0 mg/g AFDW in November to over 8 mg/g AFDW in June. Microbial respiration increased from about 0.01 ug glucose respired/hr-g AFDW in November to about 0.03 ug/hr-g AFDW in June. Microbial biomass and activity were significantly greater on dogwood leaves than on oak leaves. Dogwood and oak leaf breakdown rates were fastest when unconstrained, -0.0034 and -0.0027 degree-day^{-1}, respectively. Breakdown rates of dogwood leaves were faster in bags (-0.0025 degree-day^{-1}) than in packs (-0.0015 degree-day^{-1}), while rates of oak leaves were not significantly different between bags and packs (-0.0014 and -0.0018 degree-day^{-1}, respectively). Breakdown rates of dogwood and oak leaves obtained in this study were much slower than those obtained by other investigators either in the presence or absence of shredders. A comparison of results from this study with results from other

studies revealed that dogwood leaves may be affected more by turbulence, while oak leaves may be influenced more by shredder activity.

3.2 Introduction

In forested headwater streams, leaf inputs are the major source of organic carbon (e.g. Minshall 1967; Fisher and Likens 1973). Timing of leaf inputs, conditioning rates, and time of disappearance from the stream are important factors governing macroinvertebrate populations as well as secondarily influencing higher trophic levels (Cummins 1989). After leaves enter the stream, they are broken down by physcial processes such as leaching and abrasion and biological processes such as microbial degredation and invertebrate feeding (e.g. Kaushik and Hynes 1968; Kaushik and Hynes 1971; Cummins 1974; Petersen and Cummins 1974). A wide range of leaf breakdown rates have been observed. Previous studies have shown that leaves from herbaceous plants (Petersen and Cummins 1974) and labile leaves such as dogwood (Benfield and Webster 1985), black locust (Meyer and Johnson 1983), and tulip-poplar (Thomas 1970) breakdown rapidly. More refractory leaf species such as oak (e.g. Petersen and Cummins 1974) generally have slower breakdown rates.

Species-specific breakdown rates have been shown to be influenced by both internal and external factors. Internal factors include leachability of dissolved organic components (e.g. Suberkropp et al. 1976), nitrogen content (e.g. Kaushik and Hynes 1971), and amount of structural polymers such as lignin and cellulose (e.g. Cromack and Monk 1975; Godshalk and Wetzel 1978). External factors include nutrient concentration of the water (e.g. Rosset et al. 1982), current velocity (e.g. Chergui and Pattee 1988), temper-

ature (e.g. Hauer et al. 1986), and invertebrate shredders (Cummins et al. 1973; Wallace et al. 1982; Kirby et al. 1983; Rounick and Winterbourn 1983; Cuffney et al. 1984; Mutch and Davies 1984; Benfield and Webster 1985; Smith 1986).

Most information on breakdown has been obtained by placing leaves in mesh bags or by stacking the leaves on top of one another and loosely sewing them together into packs (e.g. Peterson and Cummins 1974; Benfield et al. 1979; Brock et al. 1982; Iverson et al. 1982). Two exceptions are studies done by Cummins et al. (1980) and Wallace et al. (1982). Cummins et al. (1980) introduced unconstrained basswood leaves, and basswood leaves in bags (1 mm mesh) and packs into a region of a first-order stream that did not have basswood trees nearby and determined decomposition rates. Decomposition rates of loose leaves were calculated with the use of a length-weight regression developed using the dry basswood leaves before they were placed in the stream. They determined that packs provided a good representation of decomposition rates of loose leaves but that small mesh bags did not. Wallace et al. (1982) examined leaf decomposition rates in an undisturbed first-order stream and a first-order stream that had been treated with methoxyclor to kill the macroinvertebrates. They found that removal of shredders substantially decreased export of CPOM and FPOM from the stream. They proposed that the decrease in export was due to a decrease in leaf shredding by macroinvertebrates. Despite these studies, differences in breakdown between unconstrained and constrained leaves have not been clearly demonstrated. Some studies indicated that breakdown rates obtained from leaves in bags and packs were not different (Webster and Waide 1982; Mutch et al. 1983), while others found that leaves in packs broke down faster than leaves in bags (Cummins et al. 1980). Bags have been shown to reduce gas exchange and render leaves less vulnerable to leaching and physical abrasion (Peterson and Cummins 1974). Packs may also limit gas exchange but should not interfere with leaching or protect the leaves from abrasion.

Because one of the primary impacts of constrainment technique is to decrease exposure to physical and microbial processing, it is suggested that the extent to which constrainment method influences breakdown may vary from species to species depending upon leaf physical rigidity. Therefore, a constrainment technique that is acceptable for one species may be unacceptable for another. This study was designed to determine if leaves such as dogwood and oak, which differ in structural rigidity, are affected differently by constrainment technique. I hypothesize that leaves with more structural rigidity should be affected less by constrainment technique than more fragile leaves.

3.3 Methods

Dogwood and oak leaves were collected just prior to abscission in the fall of 1987 and 1988. Leaves were air dried for several weeks. Leaf bags of each species were made by placing 10 g of dry leaf material into plastic pecan bags (5 mm mesh openings). Leaf packs of each species were made by weighing 10 g of dry leaf material, soaking the leaves in water until softened, and loosley sewing the leaves together with fishing line (12 lb test).

The study streams consisted of lengths of plastic drain pipe 15 m long, 20 cm wide, with a 2 % slope. Each stream was partially filled with 5 - 10 cm of gravel. Water was piped from a natural stream through a headbox with a series of faucets (1987-88) or v-notches (1988-89) so that the streams had a discharge of approximately 0.25 L/s. During certain times of the year, debris partially blocked the water intake pipe resultig in fluctuating discharges throughout the study. Macroinvertebrates did not colonize the streams through the intake pipe, and throughout the study no macroinvertebrates were

found in the stream. In November 1987 (year 1) and November 1988 (year 2) leaf bags (year 1), or leaf packs and unconstrained leaves (year 2), were placed in the streams. Periodically, between November and June of both years, three bags or packs of each leaf type were removed from the streams to determine leaf breakdown rates, total kjeldhal nitrogen (TKN), total phosphorus (TP), and percent ash. Leaf disks (1.5 cm diameter) were cut from randomly selected leaves in each pack to determine microbial biomass and microbial activity. Area to dry weight conversions of leaf disks were calculated so that microbial biomass and activity could be determined on a per gram and per area basis. Analyses on each pack were done in triplicate. Between November 1988 and June 1989, this procedure was repeated with leaf packs and loose leaves. At the end of the 1989 sampling period, all loose leaves were removed from the streams, dryed, and ashed to determine the breakdown rate of loose leaves.

Leaf packs or bags (with disks removed) were dried (60°C) and weighed. Leaf material was ground in a Whiley mill (1 mm mesh) and then three 0.25 g sub-samples from each bag or pack were ashed at 550 °C for 30 min. to determine ash free dry weight (AFDW). Post leaching AFDW of leaf material remaining and days or degree days were log transformed and regressed to determine breakdown rates. To determine TKN, ground leaf material was digested with H_2SO_4, and ammonium was measured using a cyanurate-salicylate reaction (Reynolds and Deal 1986). To determine TP, ground leaf material was digested with perchloric acid, and TP was measured as soluable reactive phosphorus (SRP)(Reynolds and Deal 1986). Chemical analyses of digested material were done on a Technicon autoanalyzer II.

Microbial biomass was estimated as ATP content according to (Suberkropp et al. 1983). ATP was extracted from each disk by placing it in 5 mL of cold 1.2N H_2SO_4 plus 5 mL of tris buffer. The ATP was then brought to a pH of 7.5 with NaOH and frozen at -4 °C. At a later date, three subsamples of each extract were analyzed photometrically

with a Lab-Line photometer (model 9140). Luciferin luciferase (0.4 mL) was added to a 0.1 mL aliquot of each sample and ATP was determined as a function of the amount of florescence produced.

Microbial activity nf leaf material was estimated by measuring ^{14}C glucose respiration (Williams and Askew 1968; Peters et al. 1989). Individual leaf disks (1 cm diam.) were placed in 25 mL incubation flasks containing 5 mL of sterile water. Labeled ^{14}C (specific activity 304.7 mCi/mole) was added to the water to obtain a concentration of 0.5ug-glucose/L and flasks were sealed with rubber septa. Filter paper treated with phenethylamine was suspended in the flasks to capture ^{14}C respired (Hobbie and Crawford 1969). In preliminary experiments, flasks were incubated from 1 to 4 hours to determine the incubation time that minimized isotopic dilution (i.e. recycling of $^{14}CO_2$, King and Berman 1984). An incubation time of 3 hours was determined to be sufficient. Therefore, flasks were incubated at ambient streams temperatures for 3 hours. At the end of the incubation period, respiration was stopped by adding 2N H_2SO_4 and the filter paper was removed from the flask and placed in a scintillation cocktail for later analysis on a Beckman Model LS-3105T Scintillation Counter.

During the second year of the study, penetrance (i.e. pressure that must be applied to push a metal rod through the leaf) was used as a measure of leaf conditioning (Feeny 1970; Suberkropp and Klug 1981). Three leaves were selected from each pack. Each leaf was held firmly between two plexiglass plates and the mean weight (3 replicates per leaf) required to push a metal rod (5 mm diam) through the leaf was determined. Care was taken to avoid major veins.

3.4 Results

Water temperature in the artificial streams ranged from a low of 1 °C in December to a high of 14 °C in June (Fig. 1). Velocity increased from approximately 0.06 m/s at the onset of the experiment to about 0.12 m/s in June as leaf material in the streams brokedown.

Results revealed significant differences between long term microbial colonization patterns and breakdown characteristics of dogwood and oak leaves. For both species, microbial biomass (Fig. 2) and microbial activity (Fig. 3) increased from November, when the leaves were placed in the streams, to June, when the study was terminated. During year 2, when the leaves were in packs, activity on the dogwood leaves was less than in the previous year when the leaves were in bags. Activity on oak leaves was not different between the two years. Microbial activity and biomass were significantly correlated with temperature ($p < 0.05$).

Microbial activity and biomass were greater on dogwood leaves than on oak leaves during most months. Over all months, microbial activity was significantly higher on dogwood leaves (ANOVA, $p < 0.05$). However, microbial activity was variable so that significant differences on a monthly basis were spotty. Microbial biomass was significantly greater on dogwood leaves than oak leaves (ANOVA, $p < 0.05$) during all months tested except June. During year 2, penetrance data showed that oak was typically tougher than dogwood and significantly tougher on an overall basis (ANOVA, $p < 0.01$)(Fig 4.) illustrating that oak leaves have more structural rigidity than dogwood leaves and that dogwood leaves were conditioned more effectively than oak leaves (sensu Suberkropp and Klug 1981).

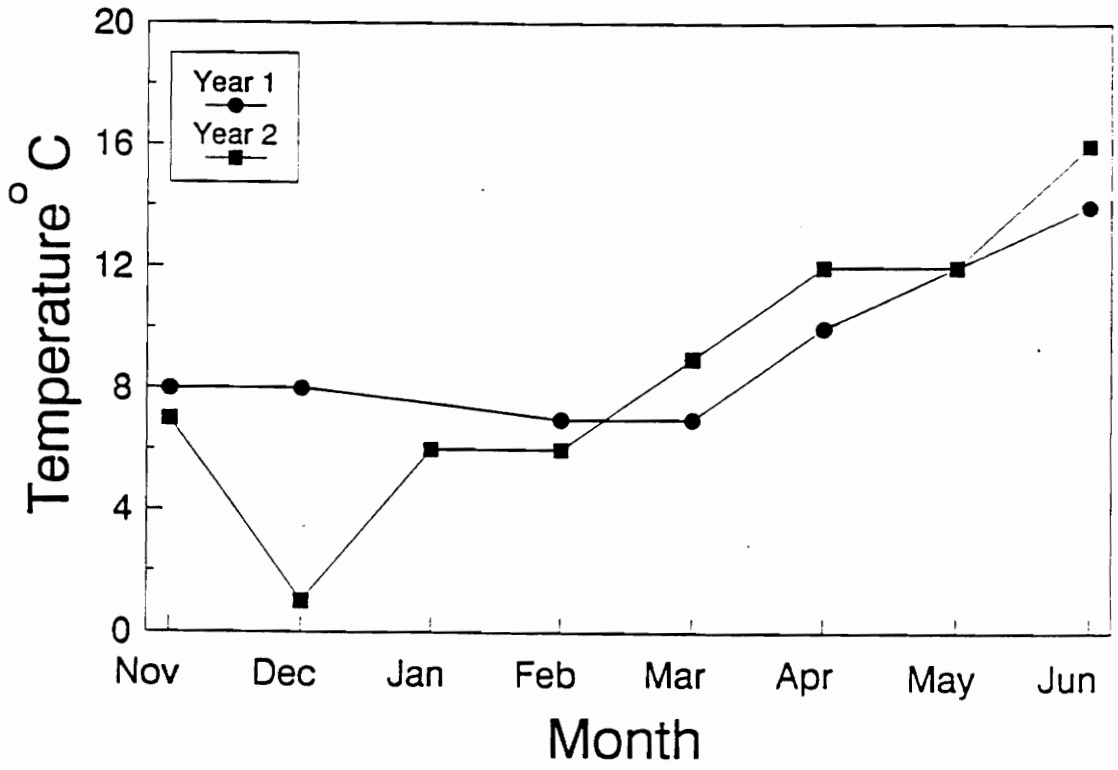

Figure 1. Water temperature (°C) in the artificial streams at the time of the nutrient release

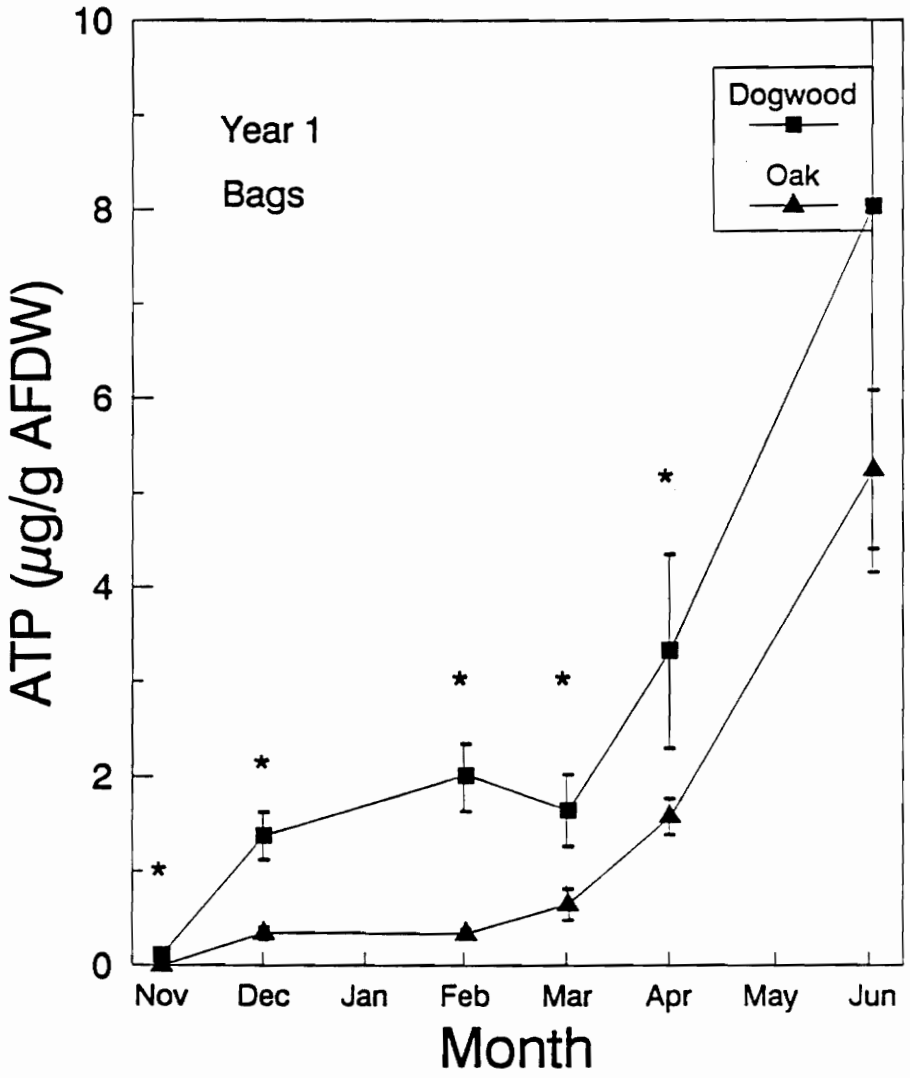

Figure 2. **Microbial biomass of leaves as ATP (ug/g AFDW):** Asterisks denote significance at $p < 0.05$; ANOVA.

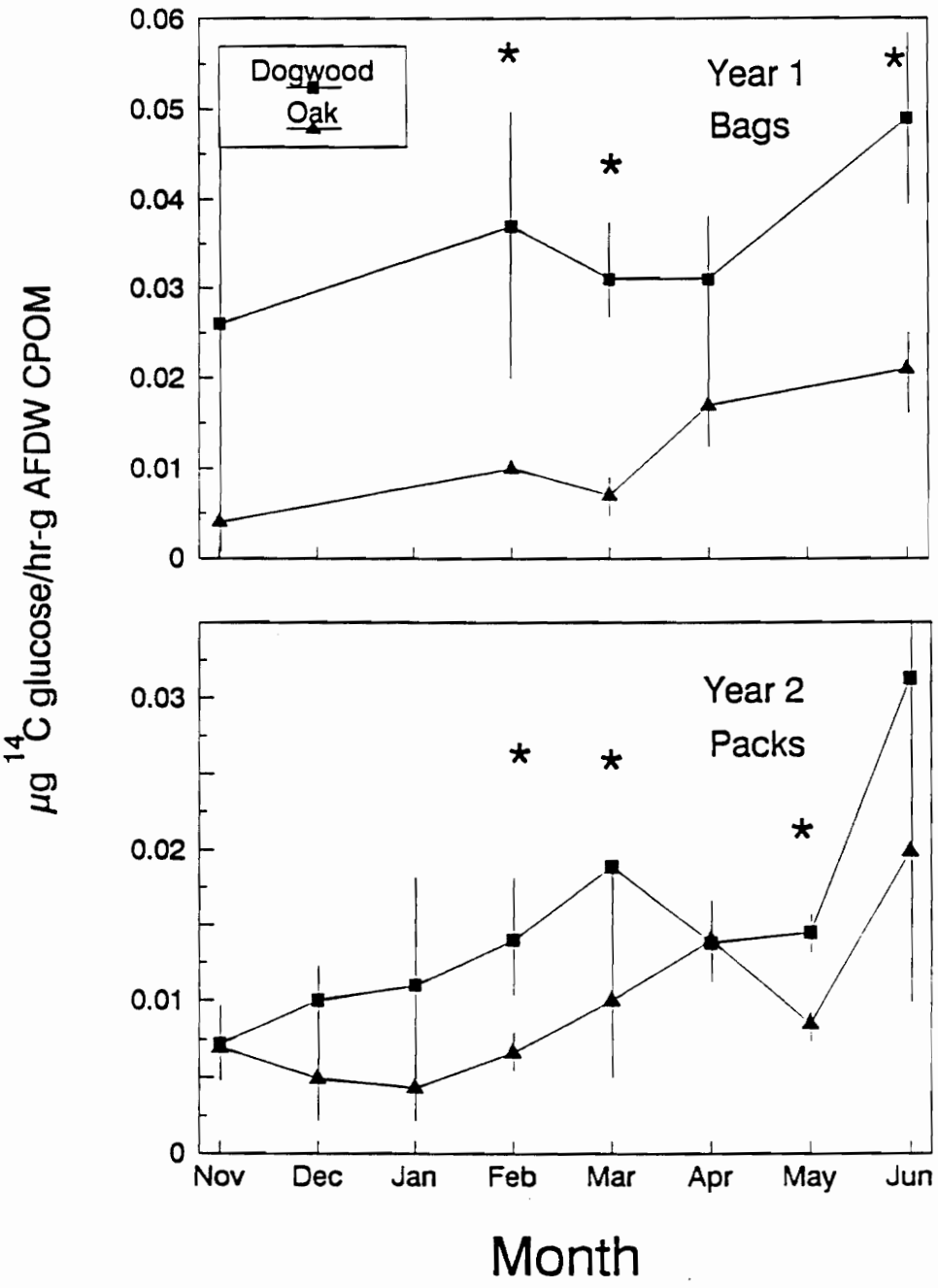

Figure 3. Microbial respiration of leaves (ug glucose respired/g AFDW): Asterisks denote significance at $p < 0.05$; ANOVA.

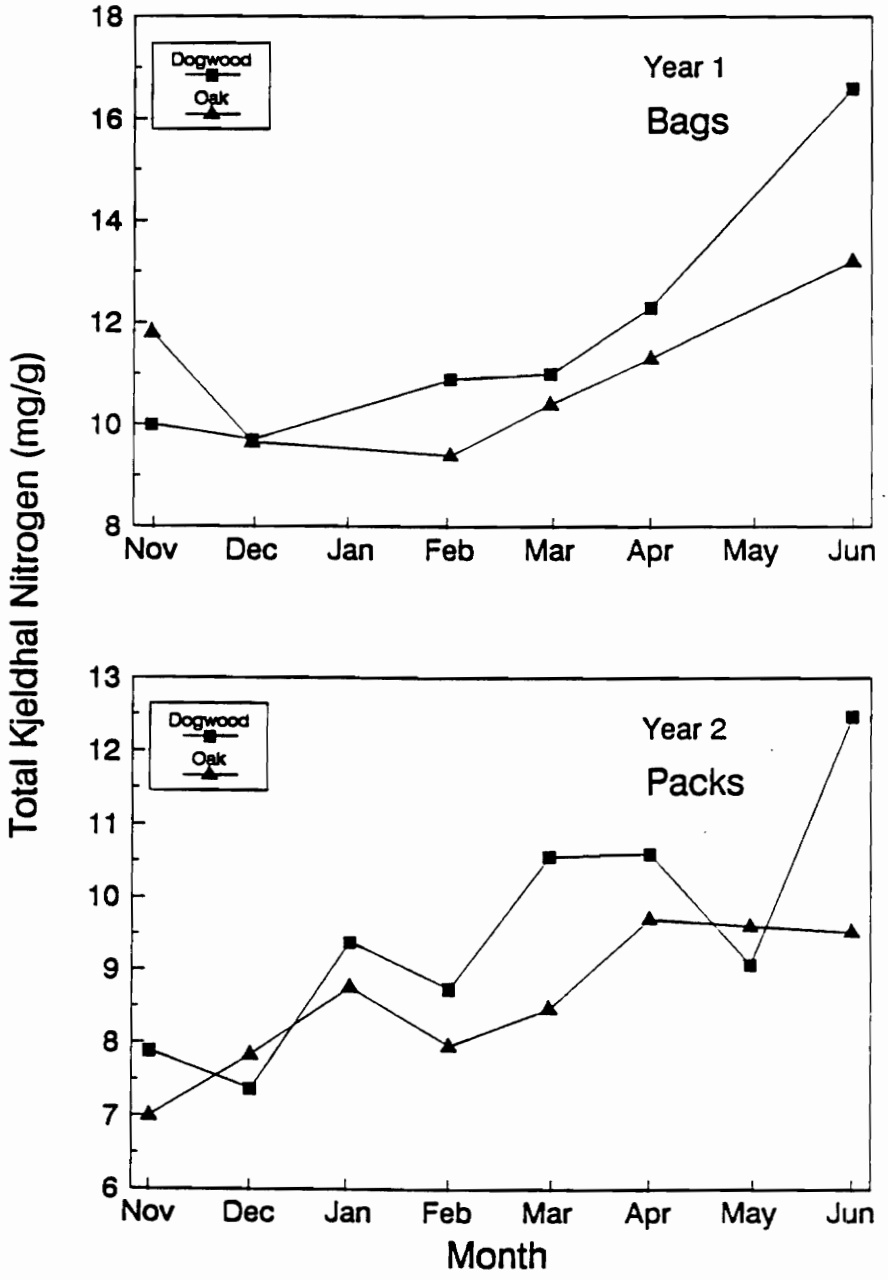

Figure 4. **Total Kjeldhal nitrogen (mg/g) content of dogwood and oak leaves:** during 1987-88 (bags) and 1988-89 (packs)

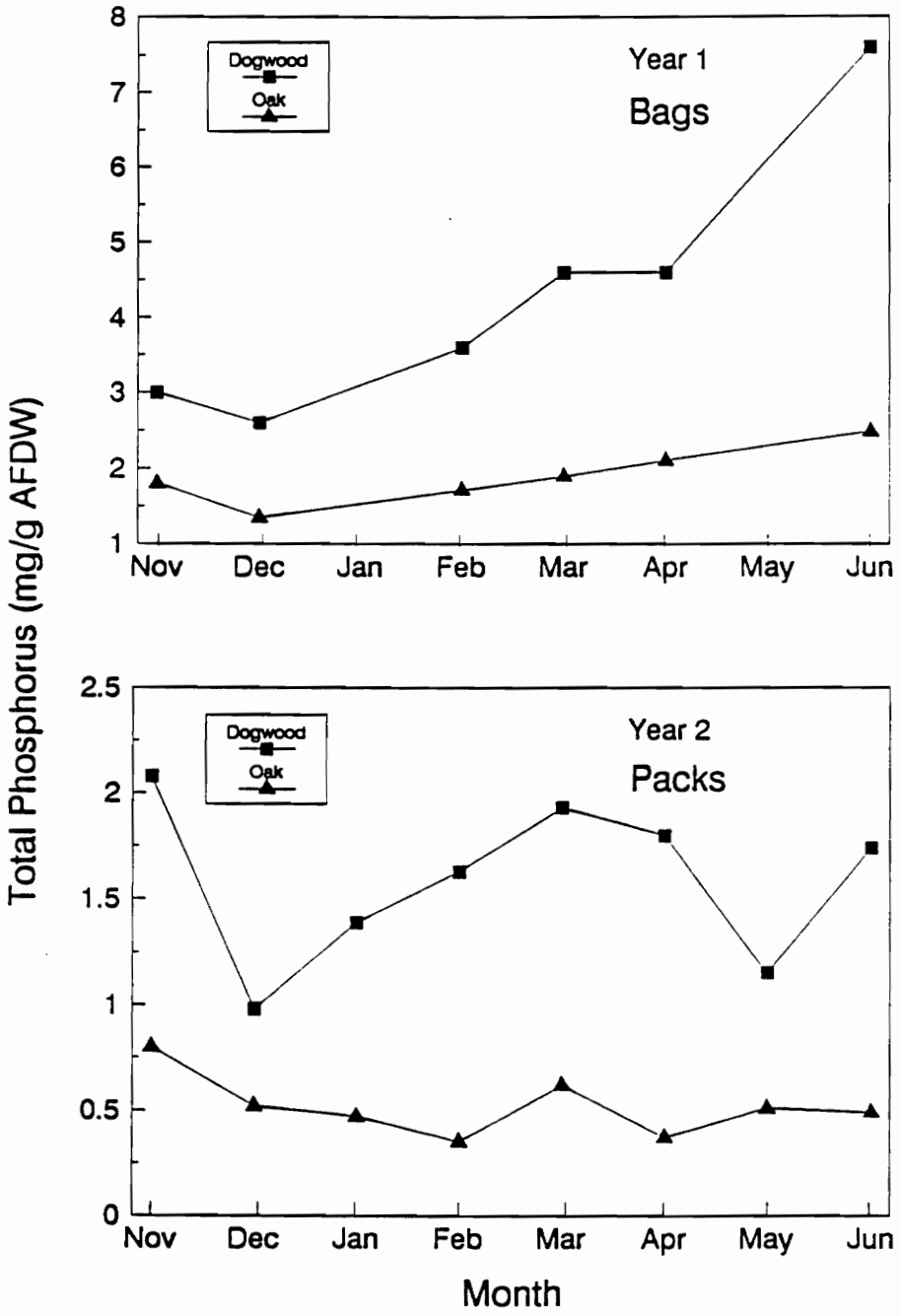

Figure 5. **Total phosphorus (mg/g) content of dogwood and oak leaves:** during 1987-88 (bags) and 1988-89 (packs)

Dogwood leaves contained more TP than oak (ANOVA, $p < 0.0001$) during both years of the experiment (Fig. 5). Dogwood leaves also typically had a higher TKN content than oak leaves although this difference was significant only during the second year of the study (ANOVA, $p < 0.001$)(Fig 5). Furthermore, dogwood leaves only contain about half the lignin of oak leaves (Webster and Benfield 1986). Thus, dogwood leaves have a much lower lignin to nitrogen ratio than oak leaves. Melillo et al. (1982) showed that leaves with lower lignin to nitrogen ratios breakdown more quickly than leaves with higher ratios.

When leaves were placed in the streams, in either bags or packs, dogwood leaves lost more weight due to leaching of soluble components during the first 3 days in the stream than oak leaves. Dogwood leaves had a 30% weight loss while oak leaves lost only about 20% of their weight. In addition to leaching more soluble material than oak leaves, dogwood leaves contain less fiber (Benfield unpublished data).

When leaves were placed in bags, dogwood leaves broke down significantly faster than oak leaves (ANOVA, $p < 0.05$) based on days (dogwood = -0.019/day; oak = -0.011/day) and per degree-day (dogwood = -0.0025/degree-day; oak = -0.0015/degree-day). When the leaves were in packs there was no difference between dogwood and oak breakdown rates (Fig. 6)(dogwood = -0.012/day and 0.0015/degree-day; oak -0.014/day and 0.0018/degree-day). Bags and packs were placed in the stream during different years, however, calculation of breakdown rates based on degree days allowed for direct comparison. There was no difference between the breakdown rates of oak leaves in bags and packs (-0.0014/degree-day and -0.0018/degree-day respectively). In contrast, dogwood leaves decomposed faster in bags (-0.0025/degree-day) than in packs (-0.0015/degree-day)(ANOVA; $p < 0.05$)(Fig 7). For both species, loose leaves decomposed much more quickly

(dogwood = -0.0034/degree-day; oak = -0.0027/degree-day) than leaves in bags or packs (Table 1)(ANOVA).

3.5 Discussion

Results from this study, and comparisons with other studies, revealed that water velocity, feeding by invertebrates, and constrainment method, affected dogwood and oak leaves to different extents. The more fragile dogwood leaves were affected more by physical factors such as velocity and constrainment, while the more fibrous oak leaves were impacted more by invertebrate feeding.

Natural streams at Coweeta Hydrologic Laboratory, North Carolina, have higher discharges than the artificial streams I used. Discharge and velocity are typically correlated, and it is expected that breakdown rates obtained from these studies may be due to differences in velocity. Breakdown rates obtained in this study were much slower than rates obtained in natural streams in the absence of shredders (Wallace et al. 1982)(Table 1). Comparing rates obtained in this study with those of Wallace et al. (1982) revealed that dogwood leaves broke down 4.2 times faster in the natural streams than in the artificial streams while oak leaves only broke down 2.8 times faster. This suggests that the higher velocity in the natural streams affected dogwood leaves to a greater extent than oak leaves.

Comparing rates obtained by Wallace et al. (1982) in 1st order streams and rates obtained by Webster and Waide (1982) in a 2nd order stream with higher discharge also suggest that dogwood leaves may be affected more by phycical factors than oak leaves (Table 1). Shredding of leaves by invertebrates also appeared to affect dogwood and oak

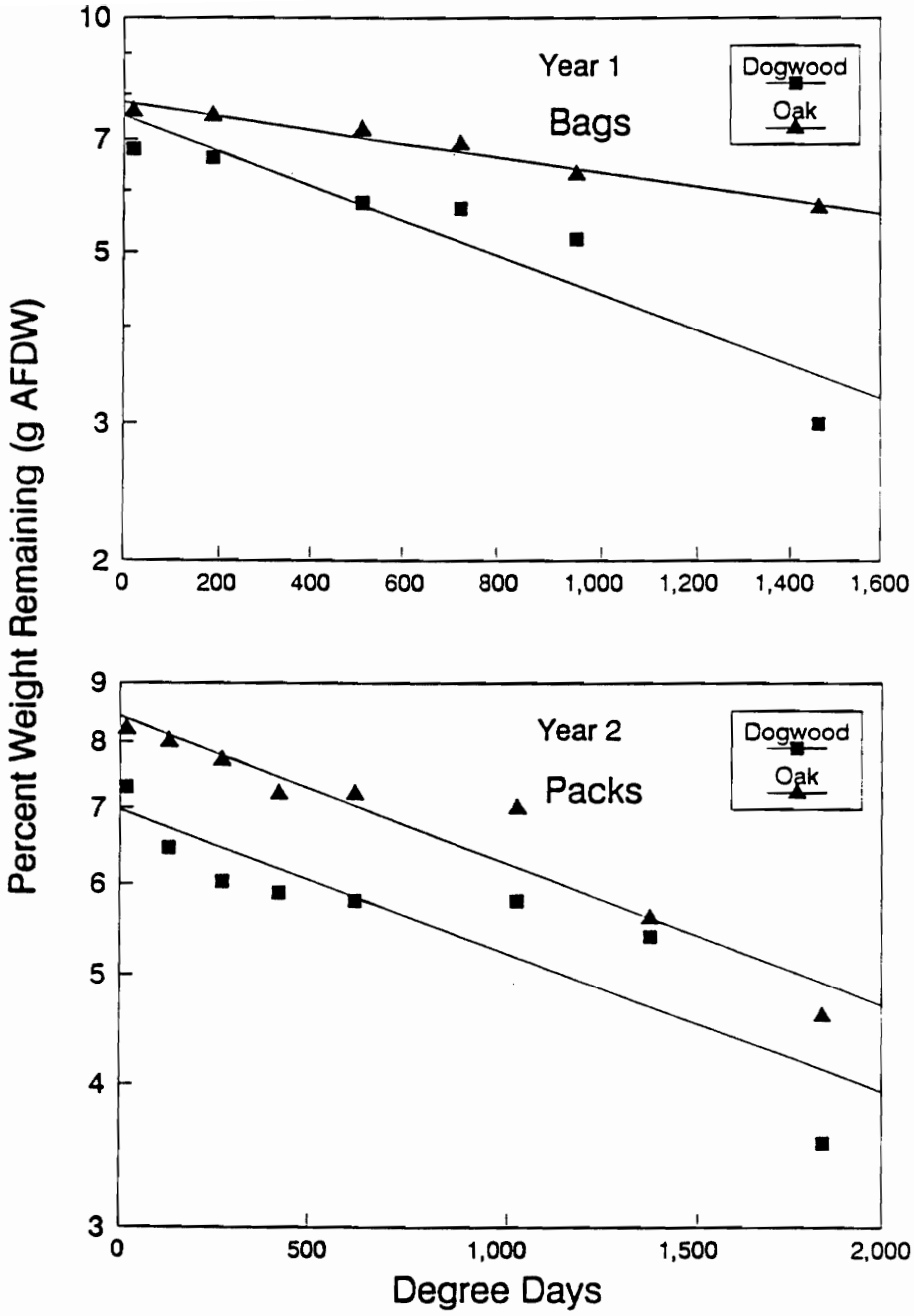

Figure 6. **Dogwood and oak leaf biomass remaining in bags or packs:** as a function of degree-days. Initial biomass = 10.0 g

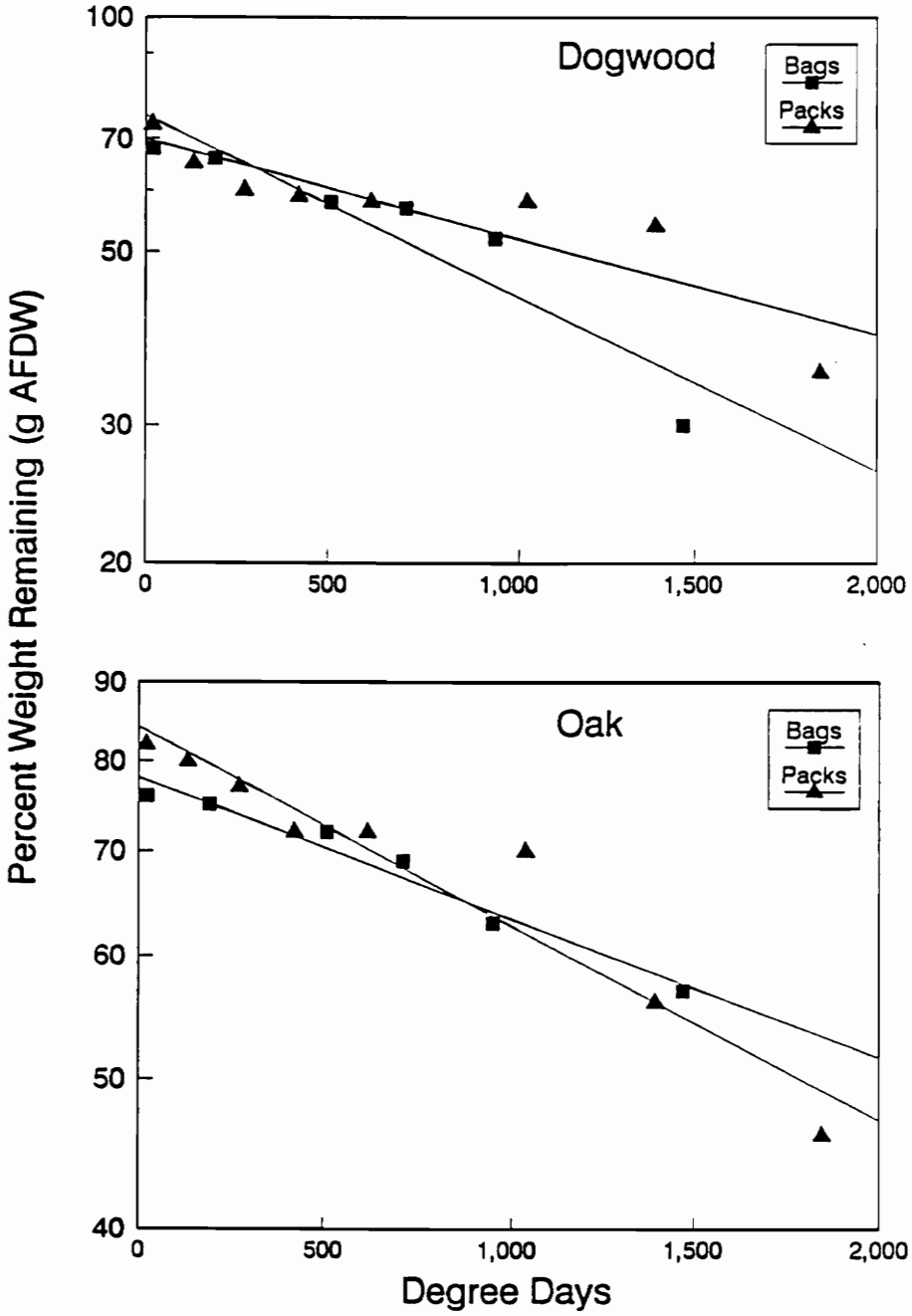

Figure 7. **Comparison of dogwood biomass remaining:** in bags and packs and oak biomass in bags and packs as a function of degree-days. Initial biomass = 10.0 g

Table 1. Leaf breakdown rates

Treatment	Leaf Breakdown per degree-day Dogwood	Oak	Discharge (L/s)	Source
Artificial Streams-No Shredders				
Bags	-0.0025 Aa	-0.0014 Ba	0.25	This study
Packs	-0.0015 Ab	-0.0018 Ba	0.25	
Loose	-0.0034 Ac	-0.0027 Bb	0.25	
1st Order Streams-No Shredders				
Bags	-0.0106 A	-0.0040 B	1.0-2.0	Wallace et al. 1982
Moderate Velocity-Shredders				
Bags	-0.0169 A	-0.0108 B	1.0-2.0	
2nd Order Streams-Shredders				
Bags	-0.023 A	-0.008 B	17.7	Webster and Waide 1982
Packs	-0.012 A	-0.008 B	17.7	

[1]Upper case letters indicate a significant difference between leaf type at $p < 0.05$ with ANOVA. Lower case letters indicate a significant difference between treatment at $p < 0.05$ with ANOVA.

leaves to different extents. Comparing Wallace et al. (1982) data from a 1st order streams with and without shredders revealed that in the prescence of shredders, dogwood leaves decomposed 1.6 times faster than without shredders while rates for oak leaves were 2.7 times faster with shredders than without. This comparison suggests that discharge may be a more important determinant of breakdown rates for dogwood leaves, while shredders may be more important to the structurally tough oak leaves.

Nutrient content of the leaf material may have also influenced microbial biomass and thereby breakdown rates. Dogwood leaves contained more TKN and TP than oak leaves. Both dogwood and oak leaves supported levels of microbial activity and biomass that continued to increase for 9 months at these slow rates of decomposition, but activity and biomass were generally higher on dogwood than oak leaves. It has been suggested that leaves with a higher TKN content support higher levels of microbial activity and breakdown more quickly than leaves with less abundant microbial communities (Triska et al. 1982).

Differences in microbial activity appeared to govern breakdown. Dogwood leaves supported significantly more microbial activity and broke down significantly faster than oak leaves. Furthermore, dogwood leaves in bags supported significantly higher microbial activity and broke down more quickly than dogwood leaves in packs. Microbial activity and breakdown rates of oak leaves in bags and packs were similar.

In addition to supporting higher levels of microbial activity, dogwood leaves were softer than oak leaves (i.e. less force is required to penetrate the leaf matrix). Perhaps as a result of this softness, dogwood leaves may be affected more by constrainment than tougher leaf species such as oak. Dogwood leaves in packs, even when loosely tied, stacked closely on one another. Consequently, microbial activity of dogwood leaves in packs was less than activity on dogwood leaves in bags. Visual observation of dogwood leaf packs revealed that inner leaves were less damaged than outer leaves. In bags, the

leaves were more spread out and were less likely to have other leaves on both sides. Microbial activity of oak leaves was not related to constrainment method.

A wide variety of studies have been done on leaf breakdown. This study supports previous conclusions that chemical composition of leaves, velocity, and shredders influence leaf breakdown. But perhaps a more important conclusion to be drawn from this study is that species with different amounts of structural components are differentially affected by constrainment techniques and that velocity and/or shredders may be more important to some leaf species than others.

4.0 Mechanisms of phosphorus retention in artificial streams

4.1 Abstract

This study was designed to investigate mechanisms of phosphorus retention in streams and to determine how changes in these mechanisms that result from logging may affect phosphorus retention. To accomplish this objective, 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. Dogwood leaves were added to three streams and oak leaves to the three other streams. Nutrient releases were conducted in the streams between November 1987 - June 1988 and November 1988 - June 1989. A biotic-uptake experiment revealed that greater than 60% of uptake was biotic. Consequently, phosphorus retention was strongly correlated with temperature. 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 revealed that dogwood leaves were softer than oak leaves. The soft dogwood leaves were less effective at retarding the flow of water ($p < 0.05$; Pearsons) and therefore velocity was typcially

faster in dogwood streams. This increase in velocity apparently contributed to a decrease in retention. These results suggest that phosphorus retention is governed primarily by temperature and velocity. The coarse and fine particulate organic matter biomass and composition did influence retention but their impact was secondary to the effects of temperature and velocity.

Keywords: stream, nutrients, phosphorus, temperature, velocity, CPOM, FPOM, logging.

4.2 Introduction

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 processsing within the stream (Webster and Swank 1985). Land-use practices such as logging can severely alter phosphorus supply and processing by changing physical and biological characteristics of the stream. For example, removal of the canopy 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).

Watershed nutrient budgets have been used as an ecosystem level approach to assess overall ecosystem function or response to disturbances such as logging (e.g. Borman et al. 1974). Although budgets can provide information on changes in nutrient flux through the ecosystem, 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 processing (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 looked at stream segments and applied a budget approach similar to the approach used for watersheds. (Meyer and Likens 1979; Fisher and Likens 1973;Triska et al. 1982). Consequently, unless instream processes were measured separately (e.g. Naiman and Mellilo 1984), stream budgets also provided little information about mechanisms and processes.

Spiralling as defined by Webster and Patten (1979) provides a method to both evaluate ecosystem 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 referred to 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 the uptake length and the turnover length yields the spiralling length (Elwood et al. 1981). Streams that have short

spiralling lengths are more efficient at retaining nutrients than streams that have longer spiralling lengths (Elwood et al. 1983). The phosphorus uptake rate (sec^{-1}) can also be calculated by multiplying the inverse of the uptake length (m^{-1}) by the stream velocity (m/s).

Using the spiralling concept, this study assessed the relative importance of temperature, current velocity, sediment biomass, 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. A numerical model was also developed to help separate and identify phosphorus retention mechanisms. Because it integrates both uptake length and turnover length, spiralling length is the best indicator of stream nutrient retention efficiency. However, because uptake length has been shown to account for almost 90% of the total spiralling length (Newbold et al. 1983) and to eliminate the necessity of using radiotracers, we used nutrient uptake length and uptake rate as indicators of stream nutrient retention. A short uptake length and/or fast uptake rate signifies a retentive system, while a longer uptake length and/or slower uptake rate is indicative of a less retentive system.

4.3 Methods

Artificial Streams

Six artificial streams, approximately 20 m long and 20 cm wide, were constructed of plastic drain pipe and placed on a platform over an unused weir pond at Coweeta Hydrologic Laboratory, North Carolina. The bottom of each 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 either by faucets feeding each stream or v-notches in the headbox. The streams were covered with shade cloth (80%) to limit solar input and prevent them from becoming autotrophic (Fig. 8).

Leaf Breakdown

Dogwood and white oak leaves were picked just prior to abcission and air dried. During the first year of the experiment (year 1), ten g of dry leaves of each species were placed in pecan bags (mesh size = 5mm). During year 2, most of the leaves were placed in the streams unconstrained, instead of in leaf bags, to allow leaf fragments to more readily leave the streams. However to faciliate 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). Bags (year 1) or loose leaves and packs (year 2) of dogwood leaves were placed

Figure 8. **Artificial stream located at the Coweeta Hydrologic Laboratory:** Macon County, North Carolina. Three streams contained dogwood leaves and three streams contained oak leaves. Extra streams were used to hold replacement leaf bags or packs.

in three streams and bags or loose leaves and packs of oak leaves were placed in the other three study streams. During the first year of the study, 85 g/m^2 of leaves were placed in each stream and during the second year 300 g/m^2 of leaves were placed in each stream. Leaf bags or packs were also placed in extra artificial streams and used to replace bags or packs removed from the study streams.

One leaf bag or pack was removed from each stream at two to six week intervals (concurrent with nutrient releases) 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 that were removed from each artificial stream were replaced with leaf packs from the extra artificial streams so that the amount of CPOM in the artificial streams was not reduced due to pack removal.

Retrieved leaves were dried (60°C for > 24 hr) and weighed. Leaf material was then ground in a Wiley mill (1 mm mesh) prior to percent ash. Percent ash was determined by ashing 0.25 g of dry leaf material at 550°C for 30 minutes. Leaf breakdown rates were calculated on ash free dry weight using a negative exponential model.

During year 1, microbial biomass on leaves was estimated as ATP (Suberkropp et al. 1983). ATP was extracted from 1 cm leaf discs placed in 5 mL of cold 1.2N H_2SO_4 plus 5 mL of TRIS buffer. 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 defrosted and 0.1-mL aliquots were added to 0.4 mL luciferin-luciferase. ATP content was 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.

During the 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. Each leaf was held firmly between two

plexiglass plates with a hole through the middle and the mean weight (3 reps per leaf) required to push a metal rod (5 mm diam.) through the hole and leaf was determined. Care was taken to avoid major veins.

During both years, microbial activity was estimated as ^{14}C glucose respiration (Williams and Askew 1968; Peters et al. 1989). Leaf disks (approx. 1 cm diameter) were placed in incubation flasks with 5 mL of sterile stream water. ^{14}C labeled glucose (specific activity 304.7 mCi/mmole) was added to the water to obtain a concentration of 0.5 ug-glucose/L and the flask was sealed with a rubber septa. Based on preliminary experiments in which flasks were incubated for periods ranging from 1 to 4 hr to determine the incubation time required to minimize isotopic dilution (i.e. recycling of $^{14}CO_2$ King and Berman 1984), flasks were subsequently incubated at ambient stream temperatures for 3 hr. At the end of the incubation period, respiration was stopped with 0.2 mL of 6N H_2SO_4. Strips of phenethlamine saturated filter paper suspended from the rubber septa were used to capture $^{14}CO_2$ that evolved during the experiment (Hobbie and Crawford 1969). The filter paper was removed from the flasks and placed in a scintillation cocktail for counting on a Beckman Model LS-3105T Liquid Scintillation Counter.

Fine Benthic Organic Matter

Fine benthic organic matter (FBOM) was sampled at the termination of the first sampling season and concurrent with nutrient releases during the second sampling season. A FBOM sample was collected from each stream by isolating a 5.5 cm length of stream and suctioning all sediments from this area into a 1-L nalgene bottle. The vol-

ume of the sediment-water slurry was recorded and a 120-mL aliqout removed. A 20-mL sub-sample of the aliquot was then filtered through a pre-ashed 0.45 um Gelman filter, dried, and ashed, to determine FBOM biomass per mL of slurry. The FBOM biomass per mL, multiplied by the total volume of the slurry, was then divided by the area sampled to obtain the FBOM biomass per m^2.

Nutrient Uptake Length

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

At the downstream end of the reach, water samples were taken at 5 to 10 minute intervals to measure the rise in nutrient concentrations. When the nutrient concentration reached a plateau, water samples were immediately taken at 5 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 minute intervals for an additional 30 minutes to measure decline in nutrient concentrations. Samples were filtered as they were collected (0.45 μGelman A/E glass fiber filters) and then taken to the laboratory and refrigerated (4 °C). Samples were frozen or analyzed within 24 hr for SRP and chloride.

Nutrient releases were conducted in the streams between November 1987-June 1988 and November 1988-June 1989 at 2-6 week intervals. Each year, prior to adding leaves to the streams, nutrient releases were conducted to determine the variability inherenet in the streams and their sediments.

Biotic-Abiotic Uptake

To determine the ratio of biological uptake of phosphorus to abiotic uptake of phosphorus, streams were chlorinated after the last nutrient release of each sampling season. Chlorination was achieved by minimizing flow of water into the streams and pouring a chlorine solution into the streams. At the end of the first sampling season, an 8-L hypochlorite chlorine 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 below), the following year 8 L of a 4 g/L solution was used resulting in a 0.5 g/L concentration. Two hours after chlorination, stream flow was resumed and nutrient releases were conducted as described previously. Because chlorine interferes with the labeled glucose assay described above, chlorination effectiveness was determined as a decrease in live microbial biomass (i.e. ATP) or as a decrease in colony forming units (CFU's) on standard 1.5% agar plates with 1% yeast extract. Three grams of dry leaf material (about 2.7 g dry) were blended in a Waring blender with 20 ml sterile water. Dilutions (10^{-2} to 10^{-6}) of the leaf-water slurry were were plated in triplicate for each stream to estimate CFU's.

Laboratory Analyses

All chemical analysis were performed at Coweeta Hydrologic Laboratory. The protocol for water chemistry analysis used at Coweeta was described in detail by Reynolds and Deal (1986). Phosphorus and chloride were analyzed using a 3-channel Technicon Autoanalyzer-II system. Soluable reactive phosphorus concentrations were measured using the ammonium-molybdate reaction. Chloride was determined using the ferricyanide method (Reynolds and Deal 1986).

Data Analyses

Figure 9 is an example of a chloride curve produced from water samples collected at the downstream site from the nutrient release. 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 station. The difference between the time at which half of the solution was released and the time for half of the chloride to pass the station is the nominal transport time (Triska et al. 1989). Velocity was calculated as distance divided by nominal transport time. For nutrient releases that we did not have a chloride curve, velocity was determined by releasing rhodomine dye into the stream and measuring the travel time. Because velocity determined from the rhodomine dye is the maximum velocity, a regression equation was calculated for velocity obtained from chloride data versus velocity from rhodomine dye releases. This equation was used to convert the maximum velocity obtained from the rhodomine dye to an average velocity comparable to velocity obtained from chloride data.

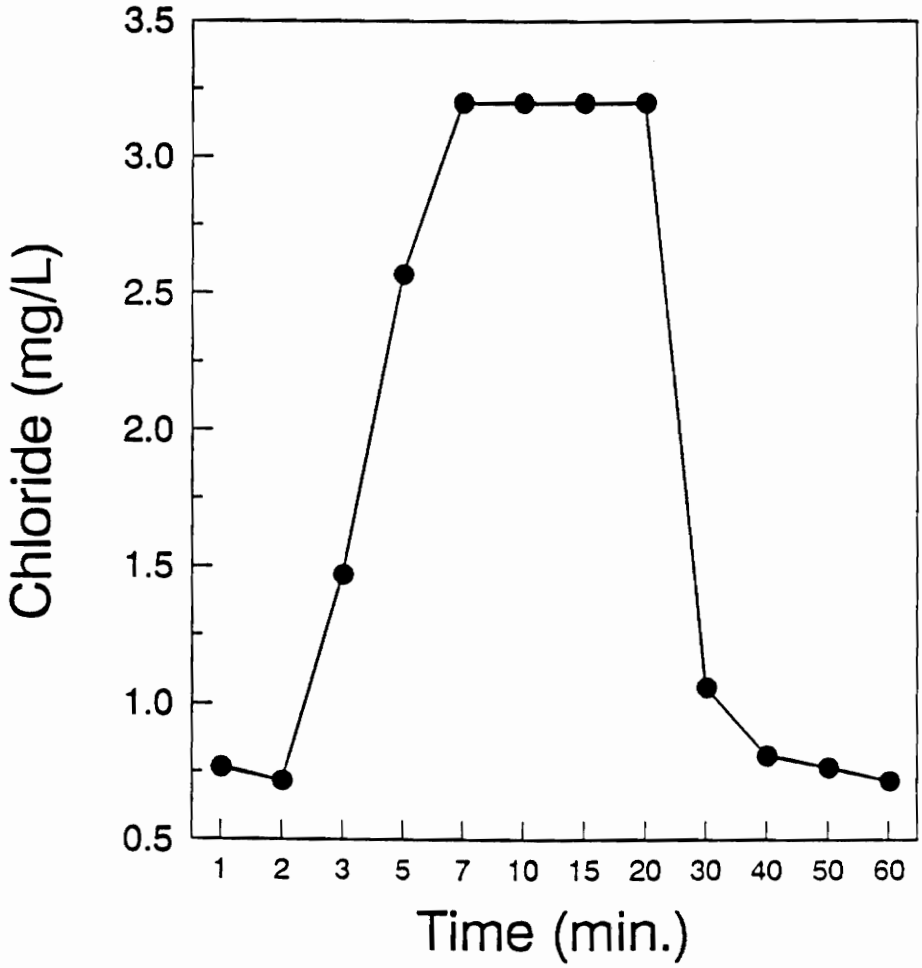

Figure 9. Example chloride curve produced from samples collected at the downstream site

Figure 10 shows the downstream decline in chloride and phosphorus concentrations. The decline in phosphorus concentration is a result of dilution, dispersion, and uptake. Chloride, however, is conservative in these streams, and therefore the decline in chloride concentration is a result only of dilution and dispersion. Therefore, the chloride data was used to adjust the phosphorus data to eliminate losses due to dilution and dispersion. Corrected phosphorus data was then expressed as a percent of upstream concentration. For this example, about 70% of the phosphorus released into the stream was removed from solution, either biotically or abiotically, in the first 10-15m. After correction, uptake of phosphorus (m^{-1}) was calculated (Fig. 10). The inverse of the rate of decline of phosphorus concentration per unit length yields uptake length, i.e., the average distance that a nutrient travels before being sorbed onto particulates or taken up by the biota (Elwood et al. 1981). Uptake rate (s^{-1}) can then be obtained by multiplying the decline in nutrient concentration (i.e. the rate at which a nutrient atom is removed from the water column) (m^{-1}) by velocity (m/s).

4.4 Results

Physical parameters

Water temperatures in the artificial streams ranged from 1°C to 14°C during both years. Minimum temperatures occurred in December and maximum temperatures in June. (Fig. 11).

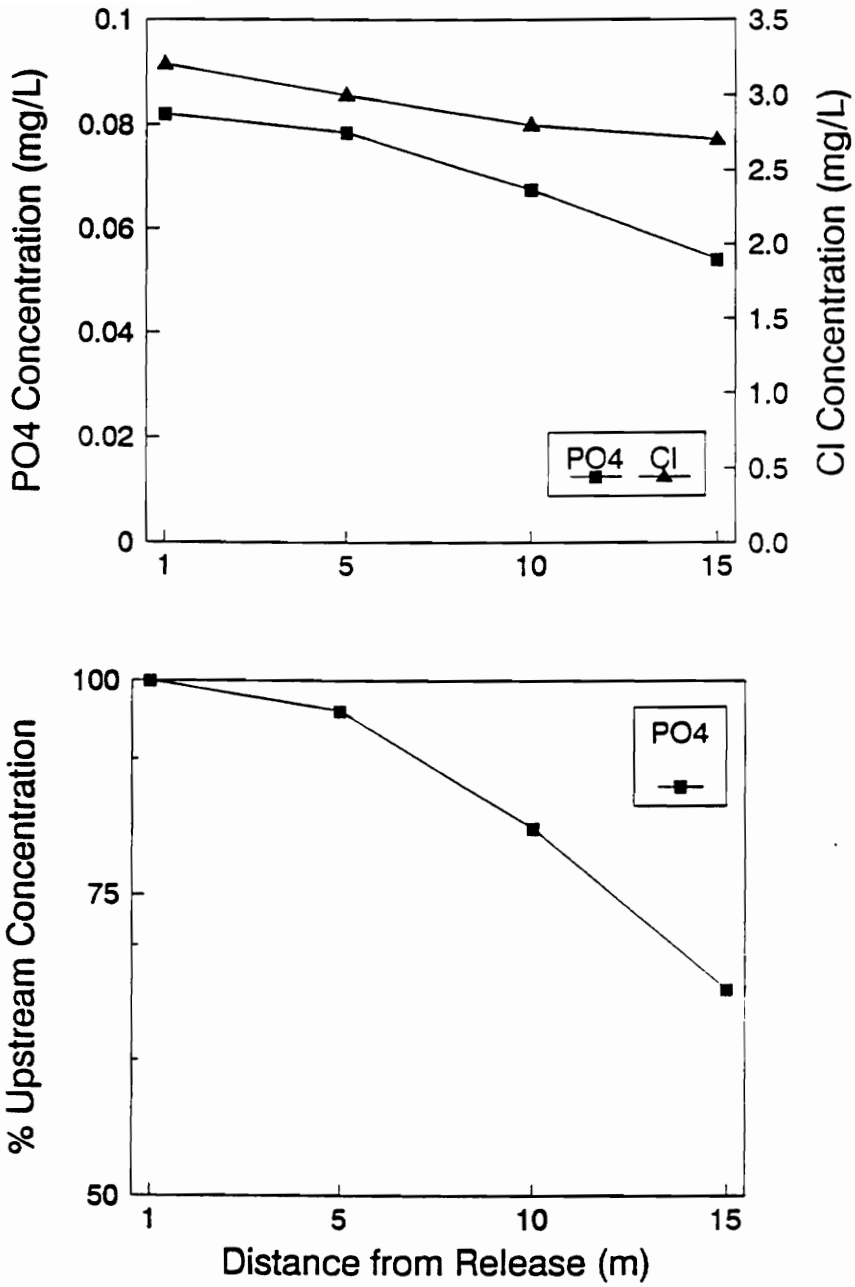

Figure 10. **Example chloride curve and phosphorus curves produced from samples collected along the length of the stream:** The upper panel shows the decline in phosphorus and chloride concentration from the upstream to downstream site. The lower panel shows the phosphorus data corrected for losses due to dilution and dispersion and expressed as a percent of the upstream concentration.

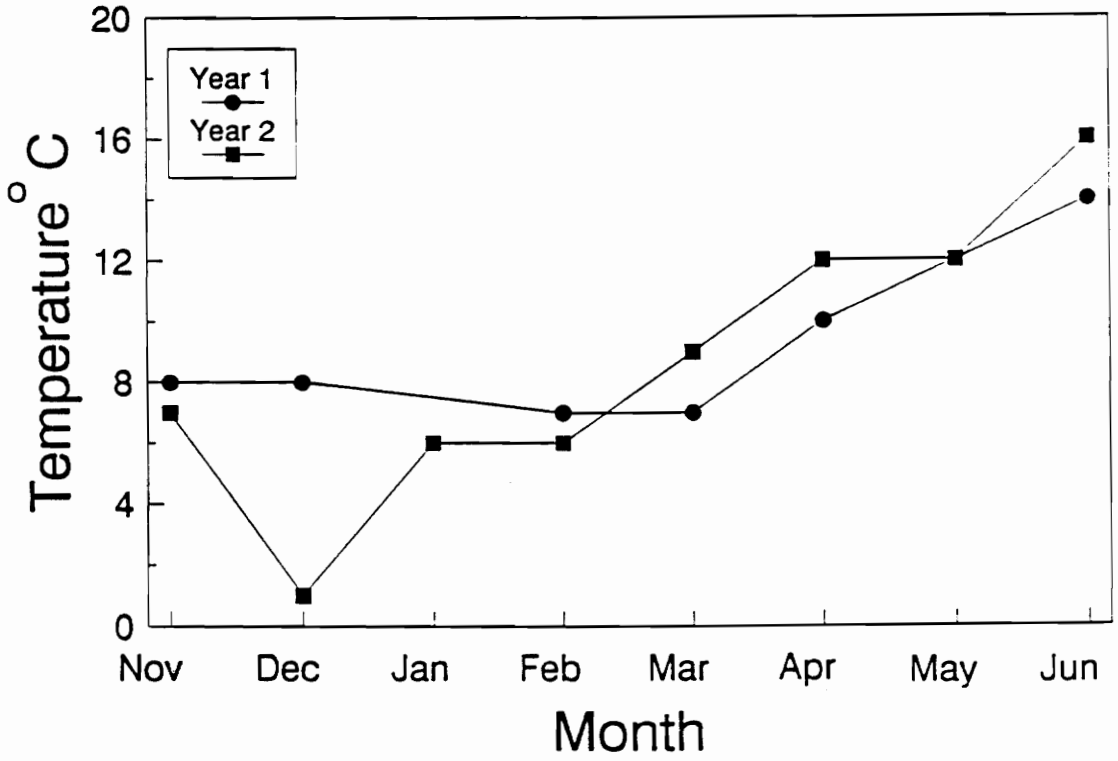

Figure 11. Mean monthly water temperature (°C) in the artificial streams: at the time of the nutrient releases.

Discharge in the artificial streams was initially set at 0.5 L/s, however, at this discharge there was very little uptake. Therefore, in January the discharge was reduced to 0.25 L/s. Discharge was maintained at 0.25 L/s throughout the rest of the study. During year 1, when the leaves were in bags, there was no difference between velocity in the dogwood and oak streams and velocity remained at about 0.12 m/s between January and June (Fig. 12). During year 2, when the majority of the leaves were unconstrained, dogwood leaves, which were less rigid, were less effective at retarding waterflow in the streams. Consequently, velocity in the dogwood streams increased more than in the oak streams and was significantly greater ($p < 0.01$) than in the oak streams during the latter months of the experiment (Fig. 12). Mean velocity of dogwood streams doubled from 0.07 m/s to 0.14 m/s, while mean velocity of oak streams only increased from 0.06 m/s to 0.09 m/s.

Biological Parameters

During year 1 of the experiment, dogwood leaves decomposed significantly faster than oak leaves (ANOVA, $p < 0.0001$) (Fig. 13) 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 biomass due to leaching and therefore maintained a higher biomass throughout the year. Microbial biomass (Fig. 14) and activity (Fig. 15) were greater on dogwood leaves than on oak leaves for all sample dates, and overall mean microbial biomass and activity on dogwood (0.025 ug glucose/hr/g AFDW; 2.45 ug ATP/g AFDW) were significantly greater (ANOVA, $p < 0.05$) than on oak (0.01 ug glucose/hr/g AFDW; 1.79 ug ATP/g AFDW). This concurs with the findings of Mulholland et al. (1984) and Elwood et al.

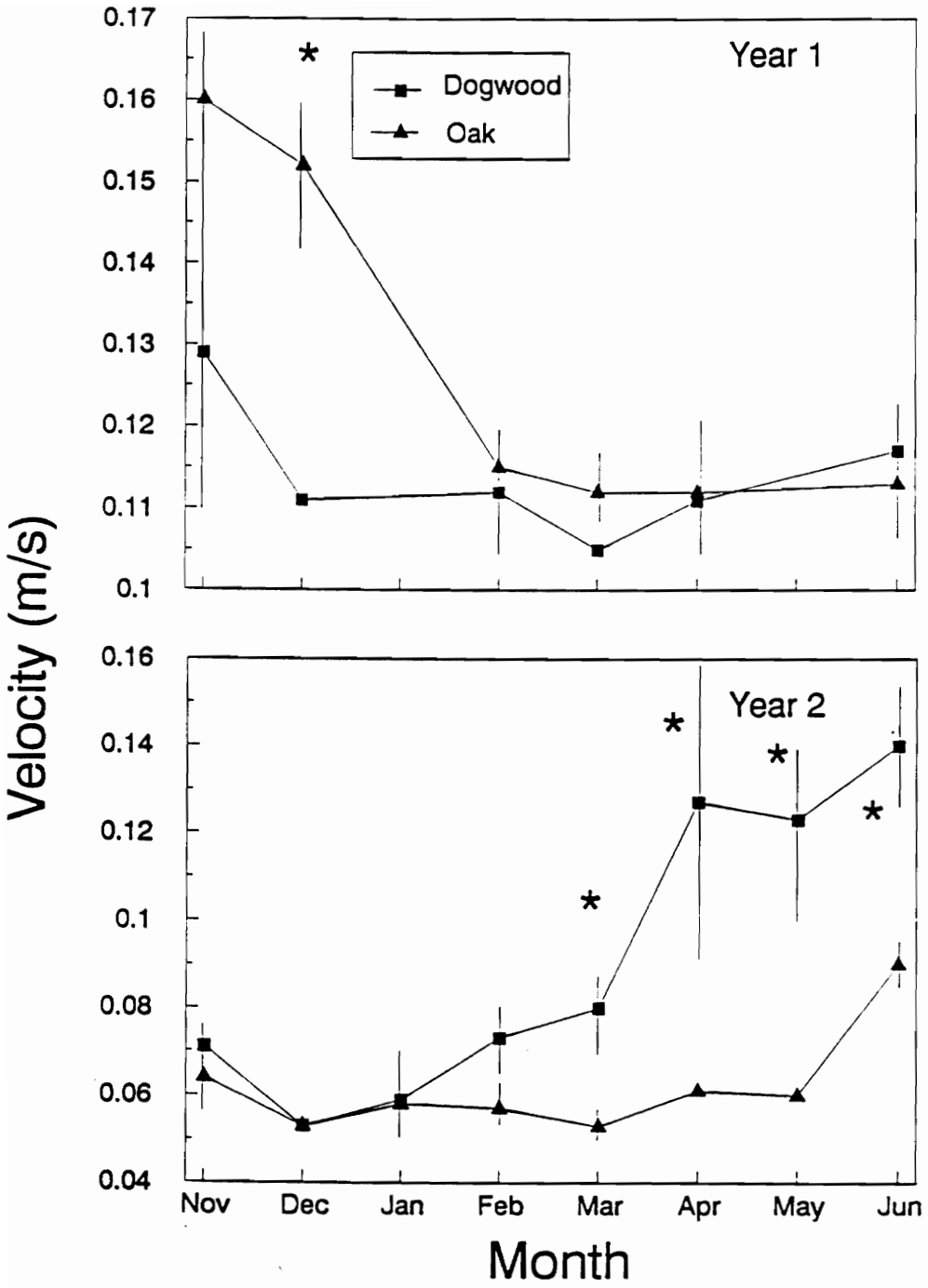

Figure 12. Mean velocity (m/s) in the streams with dogwood and oak leaves (n = 3): Discharge was reduced from 0.5 L/s to 0.25 L/s between December 1987 and February 1988 and maintained there for the remainder of the study. Asterisks denote significance at $p < 0.05$(ANOVA)

(1988) who also found that decaying dogwood leaves had higher microbial biomass and activity than oak leaves.

Penetrance data revealed that dogwood leaves were typically softer than oak leaves (Fig. 16). Weakness was positively correlated with microbial respiration ($p < 0.001$) and stream velocity ($p < 0.05$) (i.e. as the leaves softened, velocity increased). This relationship suggests that velocity in the dogwood streams may have been greater than in the oak streams because dogwood leaves had less structural rigidity and were therefore less of an impediment to the flow of water. Leaves were enclosed in mesh bags during year 1 of the experiment and there was no effect of physical differences in leaf types on velocity.

FBOM biomass was measured at the termination of the first sampling period, and after each nutrient release of the second sampling period. FBOM biomass ranged from 3.1 to 150 g AFDW/m^2. FBOM biomass was lowest in stream 1 and greatest in stream 6 (Fig. 17). Average FBOM biomass ranged from about 10.7 g AFDW/m^2 in December (FBOM biomass was not measured in November) to 27.7 g AFDW/m^2 by June. Ratios of leaf to FBOM biomass at the start of the 1988-89 sampling period were approximately 22:1 and decreased to about 4:1 by the end of the sampling period.

Biotic-Abiotic Uptake

Based on a comparison of uptake length in chlorinated and non-chlorinated streams, at least 60% of uptake can be attributed to biotic factors (Table 2). For both biotic-abiotic uptake comparisons, uptake length in the chlorinated streams was about 2.5 times longer in the non-chlorinated streams than in the chlorinated streams. For the first run, microbial biomass (ATP) was reduced 46%. For run 2, when a higher chlorine

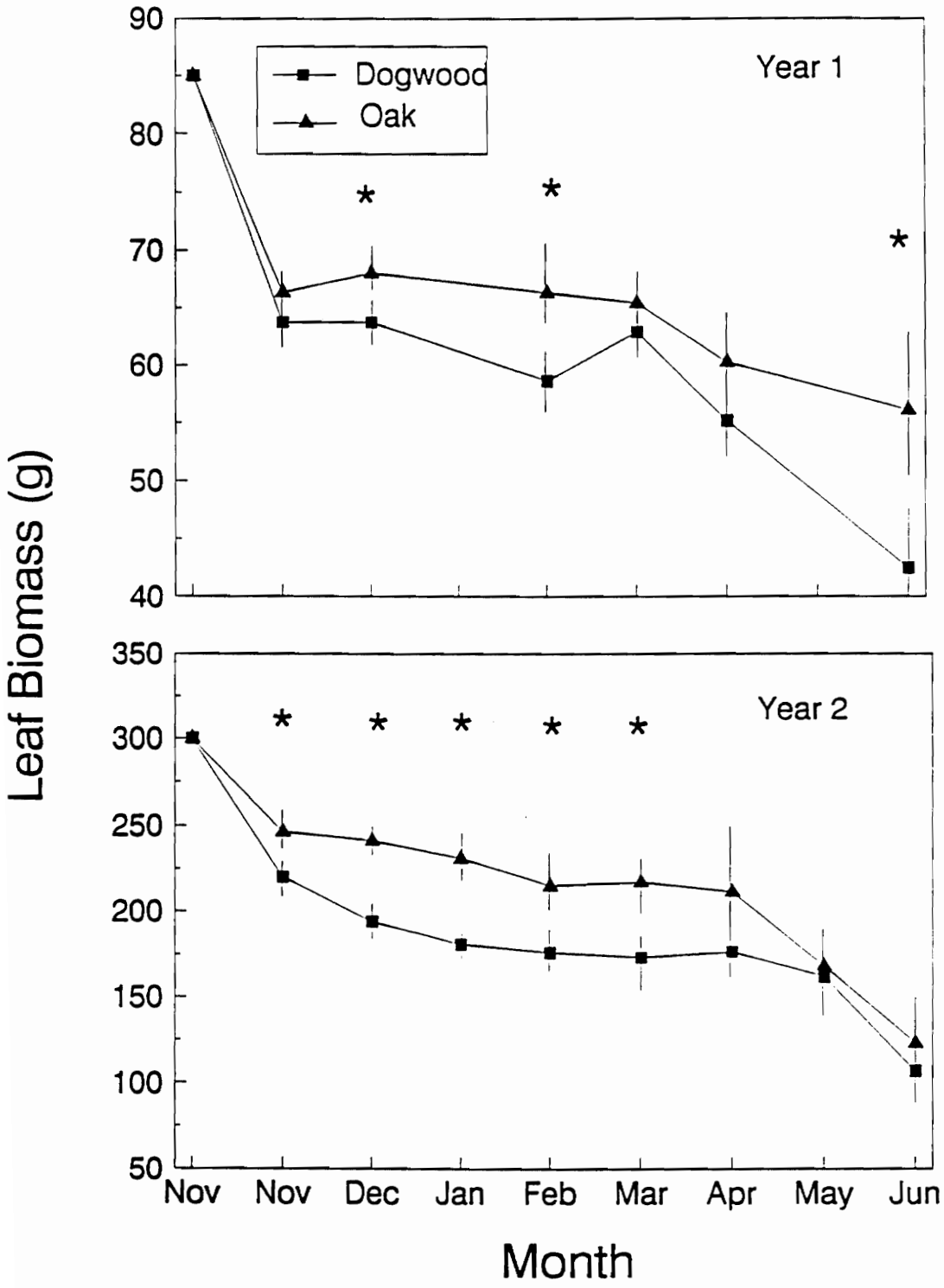

Figure 13. Mean leaf biomass (g/m^2) of dogwood and oak leaves ($n = 3$) during year 1 and 2: Asterisks denote significance at $p < 0.05$ (ANOVA).

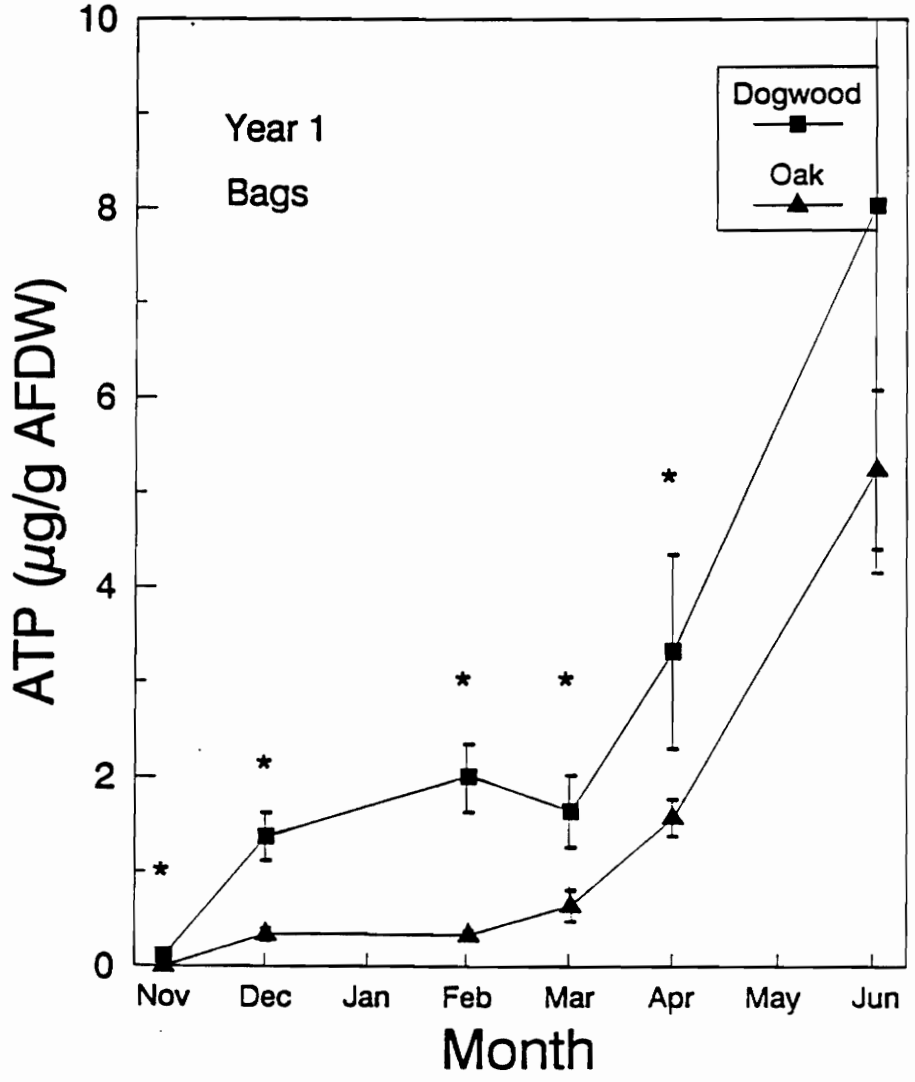

Figure 14. **Microbial biomass (ATP ug/g AFDW) of dogwood and oak leaves:** Asterisks denote significance at $p < 0.05$ (ANOVA).

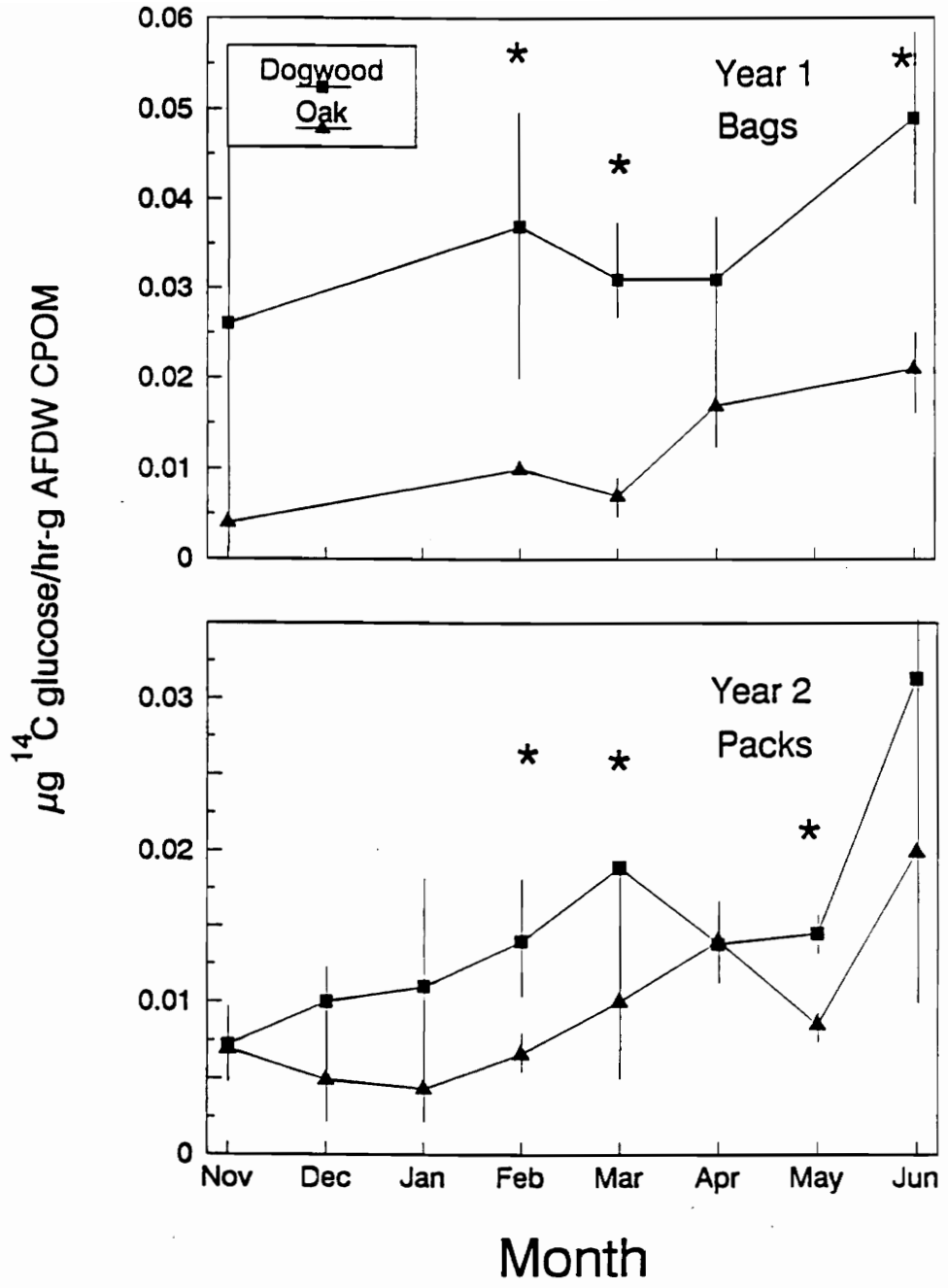

Figure 15. Microbial respiration (ug glucose/g AFDW) of dogwood and oak leaves during year 1 (1987-88) and year 2 (1988-89).: Asterisks denote significance at $p < 0.05$ (ANOVA).

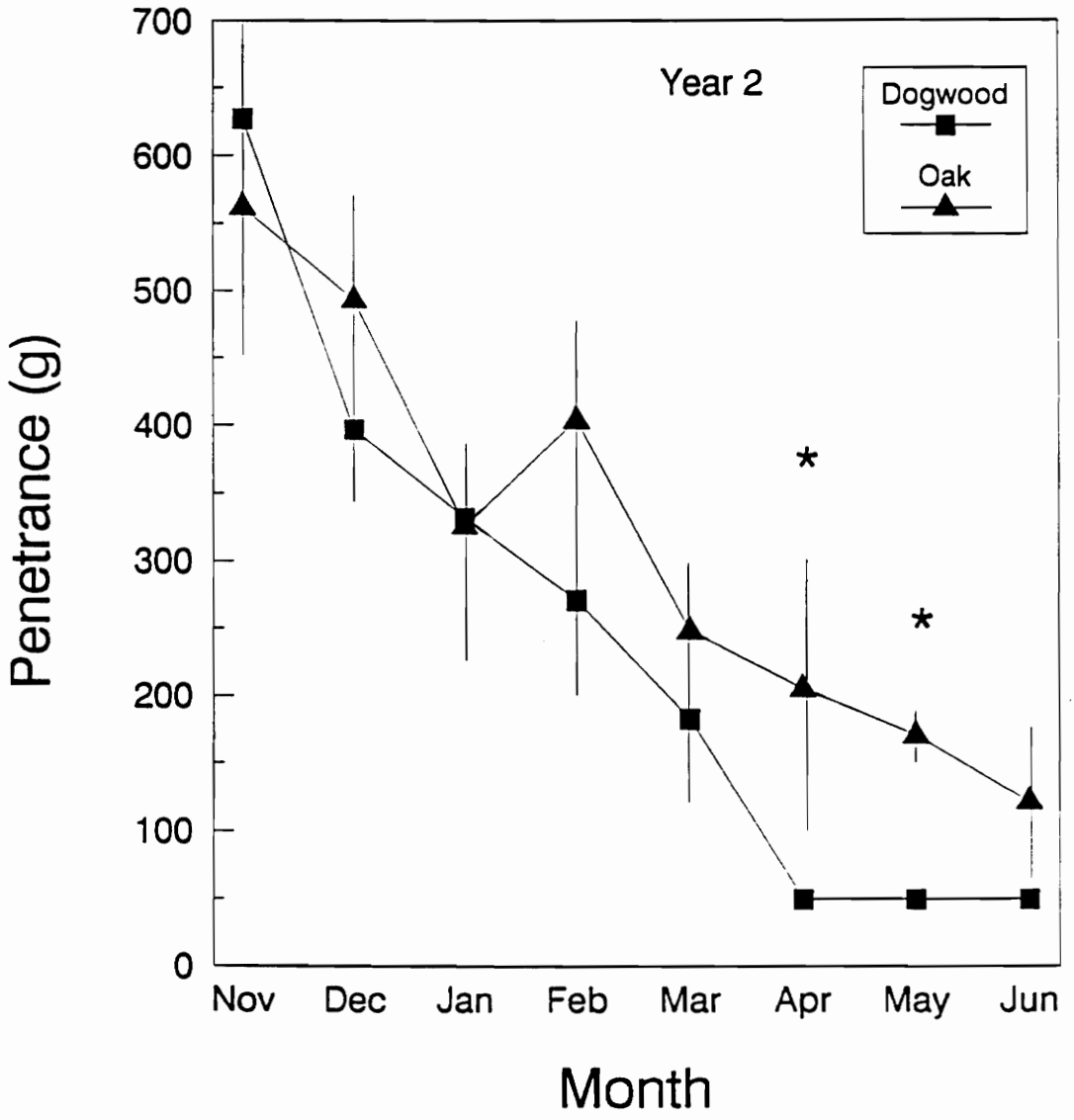

Figure 16. Mean penetrance of leaf material as mg pressure (n = 3.): Asterisks denote significance at $p < 0.05$ (ANOVA).

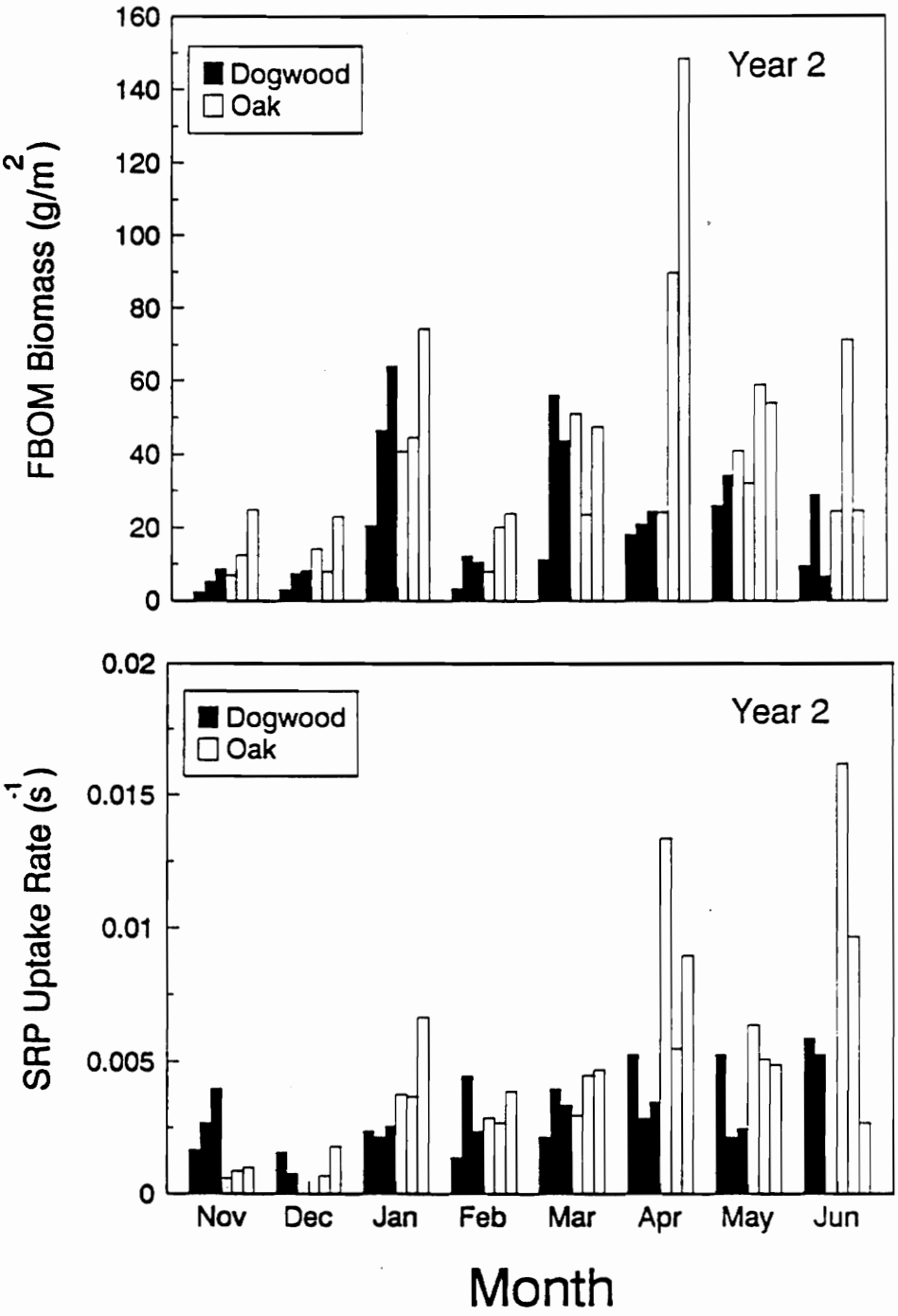

Figure 17. FBOM (g AFDW/m^2) and phophorus uptake rate (sec^{-1}): Individual bars indicate individual streams from left to right 1,3,5,2,4,6, where 1, 3, and 5 contained dogwood leaves and 2, 4, and 6 contained oak leaves

concentration was used, colony reductions indicate that 85% of the microbes were killed or inactivated. Therefore the 40% reduction in uptake that resulted 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 (Fig. 18) or uptake rate (Fig. 19), 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, uptake decreased in the dogwood streams and remained about the same in the oak streams.

In November 1988, just after leaves were placed in the streams, dogwood leaves retained significantly more phosphorus than oak leaves (ANOVA, $p < 0.05$). By December, there was no difference in phosphorus retention between dogwood and oak leaves. Post December, oak leaves retained significantly more phosphorus than dogwood during all months except February and June when retention by oak was not significantly greater (ANOVA, $p = 0.27$ for February; $p = 0.64$ for June). Nutrient releases from year 1 followed this same pattern, but not as clearly. Based on mean nutrient uptake data for November-June 1987-88 and 1988-89, oak leaves retained significantly more phosphorus than dogwood leaves (ANOVA, $p < 0.0007$)(Table 3).

Table 2. Uptake lengths (m) in chlorinated and non-chlorinated streams for June 1987 and June 1988

Year	1987/88		1988/89	
Treatment	No-chlorine	Chlorine	No-chlorine	Chlorine
UPTAKE LENGTH(M)	34.1	89.4	36.5	83.0
ATP (ug/g AFDW)	6.5	3.5	-	-
Colony Forming Units	-	-	51.0	7.6

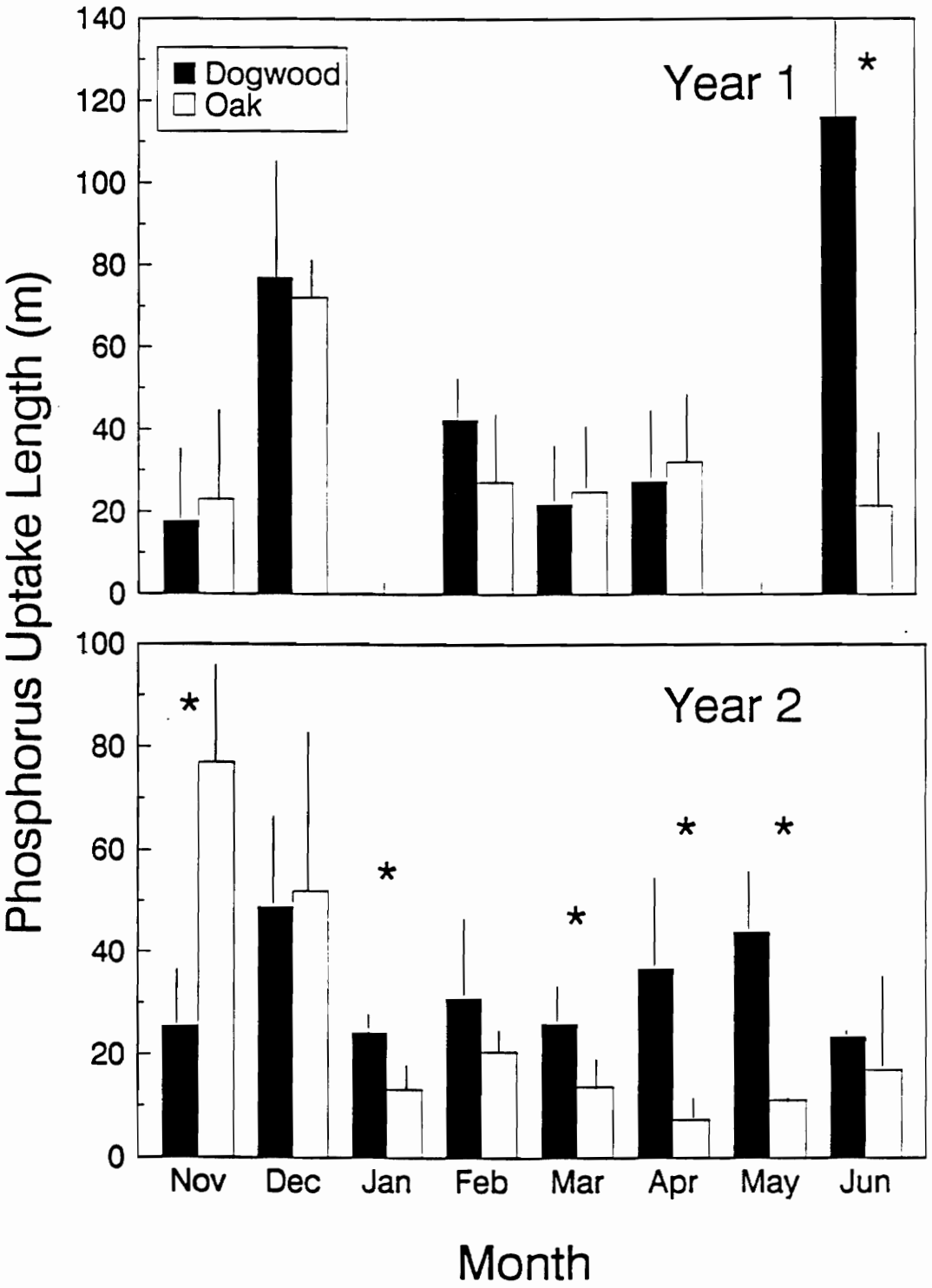

Figure 18. **Mean phosphorus uptake length (m) in streams with dogwood and oak leaves:** Asterisks denote significance at $p < 0.05$ (ANOVA).

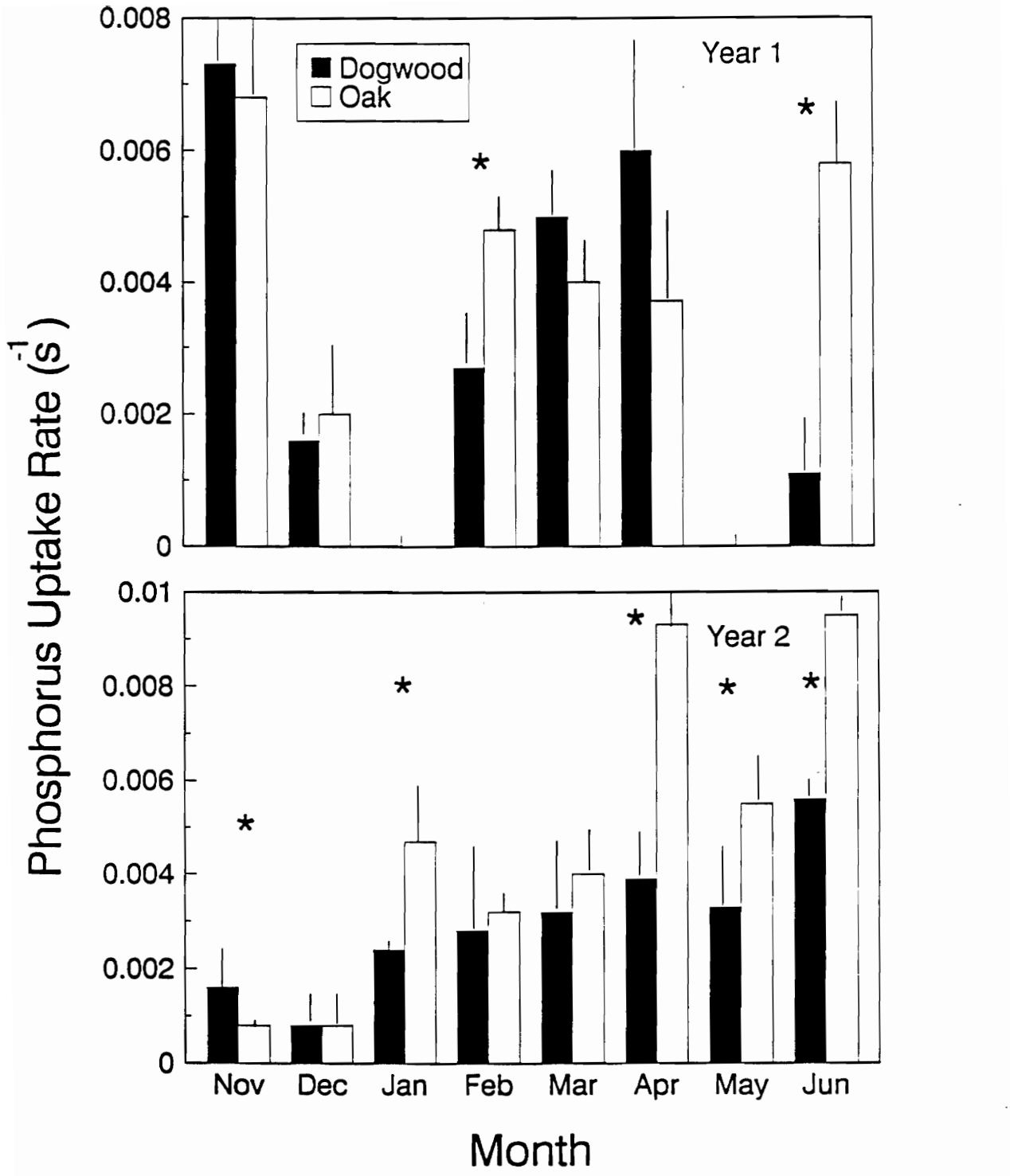

Figure 19. Mean phosphorus uptake rate (sec^{-1}) in streams with dogwood and oak leaves: Asterisks denote significance at $p < 0.05$ (ANOVA).

Table 3. Mean uptake lengths (m) in streams with dogwood leaves and streams with oak leaves.

	UPTAKE LENGTH (m)		
YEAR	DOGWOOD	OAK	p value
1987-88	57.9	38.8	0.01
1988-89	32.2	22.8	0.001

4.5 Discussion

Among the complex factors governing phosphorus retention (e.g. temperature, velocity, and organic matter biomass, composition, and associated characteristics), temperature appears to be one of the most important. Chen (1974) demonstrated that the rate of microbial uptake of phosphorus was temperature dependent. Slowest uptake rates occurred at 4°C and increased until a threshold 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 my study and others (McColl 1974; Corning et al. 1989) support the conclusion that temperature may be a primary determinant of phosphorus retention. Uptake was strongly correlated with temperature ($p < 0.0001$) with lowest rates of uptake in December, the coldest month, and the highest rates in the warm spring and summer months. Temperature control of phosphorus retention likely occurred because microbes account for 60-80% of uptake in these streams. This contrasts with the findings of Meyer (1979) for a New Hampshire stream but is in line with conclusions of Gregory (1978) and Elwood et al. (1981) who found that microbes were responsible for the majority of uptake ($> 80\%$).

Discharge and velocity may also be an important determinants of phosphorus retention. Early in this study, when discharge was set at 0.50 L/s, no measurable retention of phosphorus was observed. Therefore, discharge was lowered to 0.25 L/s and kept there fore the remainder of the study. At a discharge of 0.25 L/s measurable retention occurred. Although discharge was kept constant, changes in velocity occurred during the study as a result of changes in leaf structural rigidity did affect uptake (see below).

In addition to physical factors such as temperature, discharge, and velocity; organic matter biomass and composition also affected retention. Biomass in the streams was in

the form of dogwood and oak leaves (i.e. CPOM), and FBOM that accumulated in stream sediments. CPOM biomass was not correlated with phosphorus uptake (Pearson correlation, $p > 0.05$); however, streams with oak leaves were more retentive than streams with dogwood leaves. Greater relative retention in streams with oak leaves became more pronounced as the year progressed and occurred despite higher microbial biomass and activity on dogwood leaves. Gregory (1978), comparing conifer needles and maple leaves, found that organic matter quality and ability to support microbial growth greatly affected retention. According to Gregory's (1978) results, it was expected that higher microbial biomass and activity on the dogwood leaves would result in a greater retentive ability. Elwood et al. (1981) also found a correlation between microbial respiration and uptake onto oak leaves but no correlation for dogwood or maple leaves. This information indicates that a difference in retention capability is reflected only if there is a large disparity in the ability of organic matter to support microbial growth or in organic matter structure.

Species-specific differences in leaf structure were correlated with retention. As both leaf types became more penetrable, velocity in the streams increased; however, velocity increased more in dogwood than in oak streams. This velocity increase resulted in a a loss of retentive ability (as uptake length or uptake rate) for dogwood streams relative to oak streams. Although the rate of algal uptake of nutrients increased with increasing flow (Whitford and Schumacher 1964; McIntire 1966), removal efficiency decreased (Meyer 1979) because at higher discharges, there was less contact between water and sediments. As a result, even though the rate of uptake may be greater, the proportion of material removed from a volume of water is less. At slow flows, there is more contact between the water and sediment and consequently more uptake (Bencala 1983). Therefore, although the type of CPOM may not directly affect phosphorus retention, phosphorus retention may be indirectly affected via changes in stream velocity.

In contrast to the lack of corrleation between CPOM biomass and retention, FBOM biomass, which was about 1/4 of CPOM biomass, was significantly correlated with retention ($p < 0.001$). A spot check of microbial activity done on FBOM in November 1988 showed that microbial activity on the FBOM was approximately equal to activity 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 et al. (1990) also found that FBOM was more retentive than CPOM, whereas Newbold et al. (1983) and Mulholland et al. (1984) found that CPOM was more retentive of phosphorus. The apparent disparty between these studies may be due to differences in FBOM quality. FBOM in this study and that of Munn et al.'s (1990) Coweeta stream study may have been better quality (i.e. able to support more microbial activity) than that of Mulholland et al. (1984).

The ratio of leaf biomass to FBOM biomass also appeared to be important. During year 1, when leaf biomass in the streams was only 85 g/m^2, differences in nutrient retention by dogwood and oak leaves were 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, species-specific effects on uptake were masked by FBOM variability. During year 2, when leaf biomass was higher (300 g/m^2) and FBOM biomass was monitored, effects of leaves on phosphorus uptake were more visable. Furthermore, early in the study (November-January) FBOM effects appeared to be operating within leaf effects. However, by Febuary, FBOM biomass had increased and leaf biomass decreased to the point that FBOM control was evident and species-specific differences became less apparent (Fig. 17).

These results demonstrate that no single factor is responsible for phosphorus retention in my experiment, but rather that it was governed by a dynamic interaction of factors. Temperature appeared to be the primary factor that determined phosphorus

retention. Within the constraints of temperature, velocity differences, which occurred due to changes in leaf structural rigidity, resulted in species specific differences in uptake. FBOM became more important as its biomass increased and leaf biomass decreased. Although the artificial streams provided a template with which to investigate these factors in a somewhat controlled system (Solute Workshop Group 1990), it is important to recognize that in natural streams, discharge is not constant and therefore seasonal patterns may be different 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, increases throughout winter and spring, then declines again through summer. Therefore, it is expected that streams would be most retentive 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 stream in eastern Tennessee. Their data illustrated this expected trend except that they found uptake to be lowest in August because discharge was higher than normal. Munn and Meyer (1990) obtained similar results from a stream at Coweeta. They 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 they observed between the two years of their study. It is likely that they found CPOM biomass to be most important, while in this study temperature was most important, because in the artificial streams discharge was kept relatively constant. In the natural streams, the effects of warm temperatures and high microbial respiration are likely offset by higher discharges that increase the downstream flux of nutrients and decrease uptake (Whitford and Schumacher 1964; Lock and John 1979; Mulholland et al. 1985).

Although these results suggest that temperature is a prime determinant of retention, results from natural streams (see chapter 5.0) indicate that discharge may be more 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 increases 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 retention. However, the lack 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 allothonous leaf material (Webster and Waide 1982) and decrease in benthic organic matter storage should (Golladay et al. 1989) also accentuate this decrease in retentive ability. Input-output studies of logged watersheds support this conclusion (Borman et al. 1974). Therefore, by understanding mechanisms governing phosphorus retention and their relative importance over a range of conditions, we can begin to evalute the consequences of land-use practices prior to their implimentation.

5.0 Phosphorus retention in streams draining pine and hardwood watersheds

5.1 Abstract

This study was designed to determine how watershed-use affects stream nutrient retention efficiency. Nutrient retention was compared in streams draining 3 even-aged white pine watersheds and 3 mixed hardwood watersheds. Watersheds of similar area and stream discharge were chosen. Nutrient uptake was measured monthly in each watershed along with temperature, discharge, velocity, coarse particulate organic matter (CPOM) biomass, fine particulate organic matter (FBOM) biomass, and microbial respiration associated with FBOM. Average nutrient retention was not different between streams draining pine and hardwood watersheds and there were no significant differences between physical (temperature, velocity, and discharge) or biological (CPOM, FBOM, and respiration) parameters based on watershed type. However, discharge was more variable in the pine streams and phosphorus uptake was negatively correlated with discharge, therefore, nutrient retention was also more variable. Because storms affected discharge and nutrient retention more in pine streams than in mixed hardwood forest streams and because discharge returned to baseline more quickly in pine streams, it can be suggested that discharge regimes and nutrient dynamics of streams draining pine

watersheds are less resistant to change but return more quickly to baseline (i.e. are more resiliant) than streams draining mixed hardwood forests.

5.2 Introduction

Small watersheds provide a convenient means of examining whole ecosystem phenomena (Monk et al. 1977). At Coweeta and other sites, watershed nutrient studies have been used to assess consequences of land-use practices (Odum 1969; Likens and Borman 1974; Monk et al. 1977). Nutrient studies have been used because they provide an integrative measure of ecosystem responses to disturbances (e.g. changes in stability; Monk et al. 1977). It has been suggested that disturbed ecosystems are less efficient and retentive than mature ecosystems (Fisher and Likens 1973; but see Vitousek and Reiner 1975; Van Voris et al. 1980). Because land disturbances ultimately affect stream ecosystems, stream nutrient studies are an important part of land-use assessment. In streams, spiralling length, which incorporates nutrient cycling and downstream transport, can be used as a measure of retention efficiency (Newbold et al. 1982a). In this study, a component of nutrient spiralling length, uptake length, is used as a means of measuring differences in the phosphorus retention capabilities of streams draining hardwood and white pine watersheds.

Much of the forested land in the Southeast is dominated by pine trees. In addition, many mixed forests and other land types are being logged and turned into pine plantations. Because pine trees intercept (Helvey 1967) and transpire more water than hardwoods (Swank and Douglass 1974), conversion of lands from mixed hardwood forests to pine forests results in decreased water yields (Swank and Miner 1968). Decreased

water yield is expressed in terms of lower stream discharge and water velocity. Furthermore, annual litterfall is lower in pine watersheds than in hardwood watersheds (Cromack and Monk 1975) and is comprised predominantly of wood and pine needles, which breakdown slowly in streams and do not support high levels of microbial biomass or respiration (Triska et al. 1982).

Previous work on phosphorus retention in streams has revealed that retention is strongly infuenced by physical and biological factors such as stream velocity and CPOM and FBOM biomass and quality. Various researchers have shown that phosphorus uptake decreases with increasing stream velocity (Meyer 1979; Newbold et al. 1983; Mulholland et al. 1985).

Uptake and sorption of phosphorus onto CPOM and FBOM are primarily due to biotic mechanisms such as incorporation by microbes. In most studies of phosphorus retention, biotic uptake accounted for greater than 60% of retention (see Chapter 4; Gregory 1978; Elwood et al. 1981. However, Meyer (1979) found that in her streams uptake was mostly abiotic. Although little work has been done on FBOM quality, a study done in artificial streams showed that CPOM quality influences phosphorus uptake (see Chapter 4). Higher quality leaf material is quickly colonized and conditioned by microbes. As a result, high quality leaf material looses rigidity and biomass more quickly and therefore is less effective at retarding waterflow. Consequently, stream velocity increases and nutrient retention decreases.

This study was designed to examine physical and biological characteristics (e.g. discharge, velocity, organic matter biomass and composition) of streams draining white-pine and mixed-hardwood watersheds in conjunction with phosphorus retention characteristics to determine if the two watershed types have different phosphorus retention capabilities and what factors are important in regulating retention.

5.3 Methods

Description of watersheds

Watersheds used in this study are located at the Coweeta Hydrologic Laboratory, a 2270-ha experimental forest in the Nahantahala Mountains of western North Carolina. Temperature in this region is moderate with an annual mean of 13°C and average annual rainfall of about 2 m (Swift et al. 1988). Watersheds at Coweeta are designated as either experimental or reference. Reference watersheds have not been disturbed since 1900-1924 when the entire area was selectively logged. For this study, three reference watersheds (#2,14,18) were chosen along with three experimental watersheds (#1,3,17) that had been cut and planted in white pine. Watershed 1 was cut in 1956-57 and planted in white-pine in 1957. Watershed 3 was used for agriculture between 1940 and 1952 and then planted in white pine with some yellow poplar in the upper reaches. Watershed 17 was cut in 1942, regrowth was recut annually between 1942 and 1955, and the watershed was planted in white pine in 1956 (Swank and Douglass 1977). Basin sides and stream banks are unstable in the pine watersheds, perhaps as a result of loss of surface soil following cutting or lack of understory vegetation. Consequently, streams draining the pine watersheds are down-cut further and have more FBOM deposits than the hardwood watershed streams. Pine and hardwood watersheds have approximately the same area, slope, and stream discharge. Watersheds were chosen from the northeast and southwest sides of the basin to get watersheds of similar elevation. Watershed physical characteristics are summarized in Table 4.

Table 4. Physical characteristics of pine and hardwood watersheds used in this study[1].

Vegetation Type	Pine			Hardwood		
Watershed	1	3	17	2	14[2]	18
Aspect	SE	SE	NW	SE	NW	NW
Area (ha)	16	9	13	12	14[3]	13
Watershed Elevation (m)						
Maximum	988	931	1021	1004	992	993
Minimum	755	739	760	709	707	726
Stream slope in study area(cm/m)	16	14	20	18	13	23
Mean Ann. Dischg. (L/s) 88-89	1.91	1.30[4]	2.38	2.65	2.80[4]	2.35
Maximum	4.27	-	5.84	5.22	-	4.41
Minimum	0.52	-	0.29	0.44	-	0.43
mean SRP (ug/L)	< 2.0	< 2.0	< 2.0	< 2.0	< 2.0	< 2.0

[1]Data from this study and Swank and Crossley (1988)
[2]Tributary used
[3]Estimated from topographic map
[4]Estimated from ratio of area to discharge of similar watershed type

Nutrient Uptake

Nutrient releases were conducted in the streams at monthly intervals between October 1988 and September 1989 to determine nutrient retention. A 20-30 m reach of stream was chosen at the downstream-most section of each watershed, just above the weir. One exception was that one of the hardwood streams drains a sub-watershed of a larger watershed (14), and this reach was at the downstream-most end of the non-gauged sub-watershed. A nutrient solution containing phosphate (as Na_2HPO_4), and chloride (as NaCl) was released into each stream for a time period sufficient to allow the nutrient concentration to plateau (20-40 min). Nutrient concentrations added were sufficient to raise stream nutrient concentrations to 5-10x ambient levels (about 30 ug/L soluable reactive phosphate-- SRP--and 3 mg/L Cl), which were sufficient to measure nutrient uptake. Chloride (as NaCl) is conservative in most streams and was used to account for nutrient dilution and dispersal (Bencala et al. 1987).

At the downstream end of the reach, water samples were taken every 5-10 min. from the onset of the nutrient release to when the nutrient concentration had plateaued. Previous released demonstrated that a nutrient release of about 30-50 minutes was sufficient to allow the stream to plateau, or about 10 times the travel time for rhodomine dye to pass the downstream sample site. When the nutrient concentration reached a plateau, water samples were taken at 5 stations (5 m apart) along the stream. Solution input was then stopped and sample collection continued at the downstream end of the reach at 5-10 minute intervals for an additional 30 minutes. Samples were filtered as they were collected (0.45 μGelman A/E glass fiber filters). Water samples were taken to the laboratory and refrigerated (4 °C). Samples were frozen for not more than 3 months or analyzed within 24 hrs for SRP and chloride (Cl).

All chemical analyses of water samples were performed at Coweeta Hydrologic Laboratory. The protocol for water chemistry analysis used at Coweeta was described in detail by Reynolds and Deal (1986). Phosphorus and chloride were analyzed using a 3-channel Technicon Autoanalyzer-II system. SRP concentrations were measured using the ammonium-molybdate reaction. Chloride was determined using the ferricyanide method.

Figure 20 is an example of the chloride curve produced from water samples collected at the downstream site from the nutrient release. 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 station. The difference between the time at which half of the solution was released and the time for half of the chloride to pass the station is the nominal transport time (Triska et al. 1989). Velocity equals distance divided by nominal transport time. For nutrient releases without a chloride curve, velocity was determined by releasing rhodomine dye into the stream and measuring travel time. Because velocity determined from the rhodomine dye is maximum velocity, a regression equation relating nominal transport time and maximum velocity was used to convert maximum velocities obtained from rhodomine dye releases to an average velocity comparable to the nominal transport time obtained from chloride data.

Figure 21 shows the downstream decline in phosphorus and chloride concentrations. The decline in phosphorus concentration is a result of dilution, dispersion, and uptake. Chloride is concervative in these streams and therefore the decline in chloride concentration is due solely to dilution and dispersion. Therefore, the downstream decline in chloride concentration was used to correct phosphorus data for losses due to dilution and dispersion. After correction, phosphorus data was expressed as a percent of the upstream concentration and uptake (m^{-1}) was calculated as the slope of the line relating ln C to x. (Fig. 21). The inverse of the uptake rate yields uptake length, in other

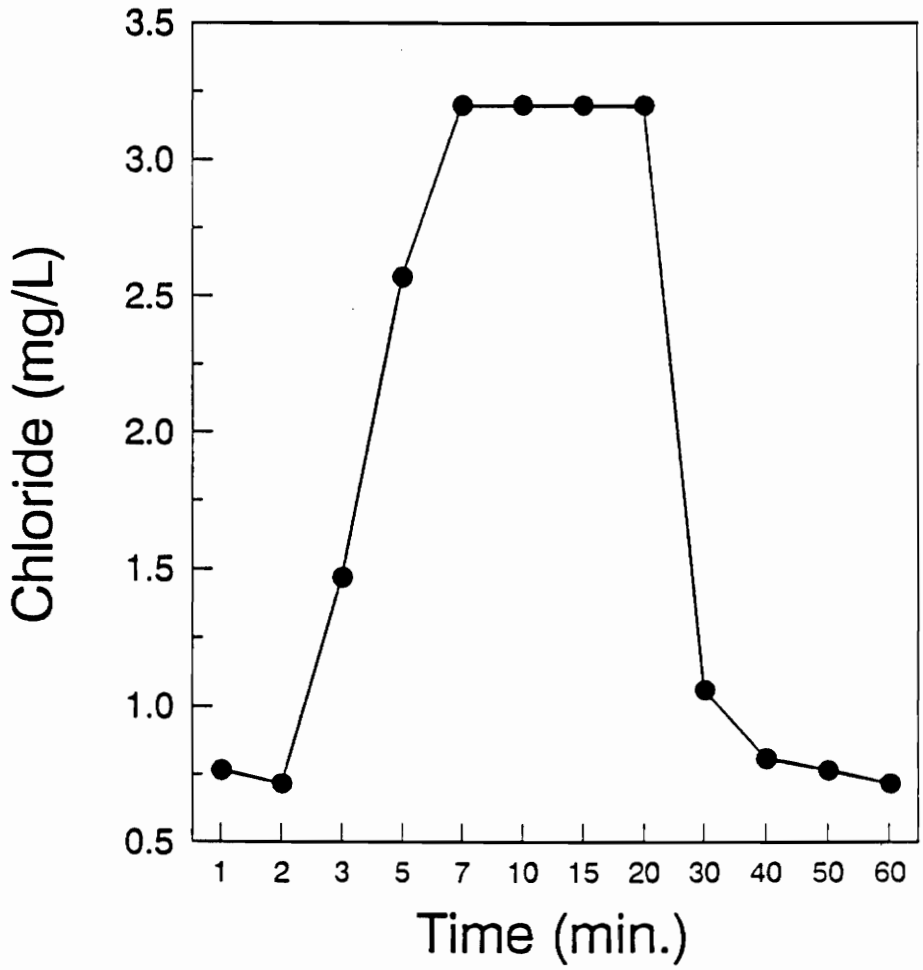

Figure 20. Example chloride curve produced from samples collected at a downstream site

words, the average distance that a nutrient atom travels before being sorbed onto particulates or taken up by the biota (Newbold et al. 1981). The uptake rate (s^{-1}) was calculated by multiplying uptake per unit length (m) by the velocity (m/s).

Benthic samples

In addition to the nutrient releases, CPOM and FBOM samples were taken at three randomly chosen sites in each stream. Samples were taken with a metal core (0.071 m^2) that was pushed into the sediment. CPOM was removed from the core, placed in a ziploc bag, and later dried and sorted to determine dry weight of leaves and sticks. Sediments in the core were repeatedly stirred to a depth of 10cm and sucked with a suction pump through a 250-um mesh net into a bucket. The volume of the bucket was recorded and a 125-mL aliquot of the FBOM/water slurry was removed from the bucket for filtration. Filtered material was then dryed, weighed, and ashed, to determine total FBOM AFDW/m^2

Microbial activity was determined by measuring ^{14}C glucose respiration. Five-mL aliquots of an FBOM slurry were pipetted into incubation flasks. Labeled ^{14}C glucose (specific activity 304.7 mCi/mmole) was added to the slurry to obtain a concentration of 0.5 ug-glucose/L and the flask was sealed with a rubber septa. Filter paper suspended in the flasked was soaked with phenethylamine to capture the ^{14}C respired (Mulholland et al. 1985b). The slurry was inclubated for 3 hr based on a preliminary study in which an incubation curve was run to determine the incubation time that minimized isotopic dilution (King and Berman 1984). At the end of the incubation period, respiration was stopped by adding 0.2 mL of 6 N H_2SO_4 and the filter paper was removed from the flask and placed in scintillation cocktail for counting on a Beckman scintillation counter.

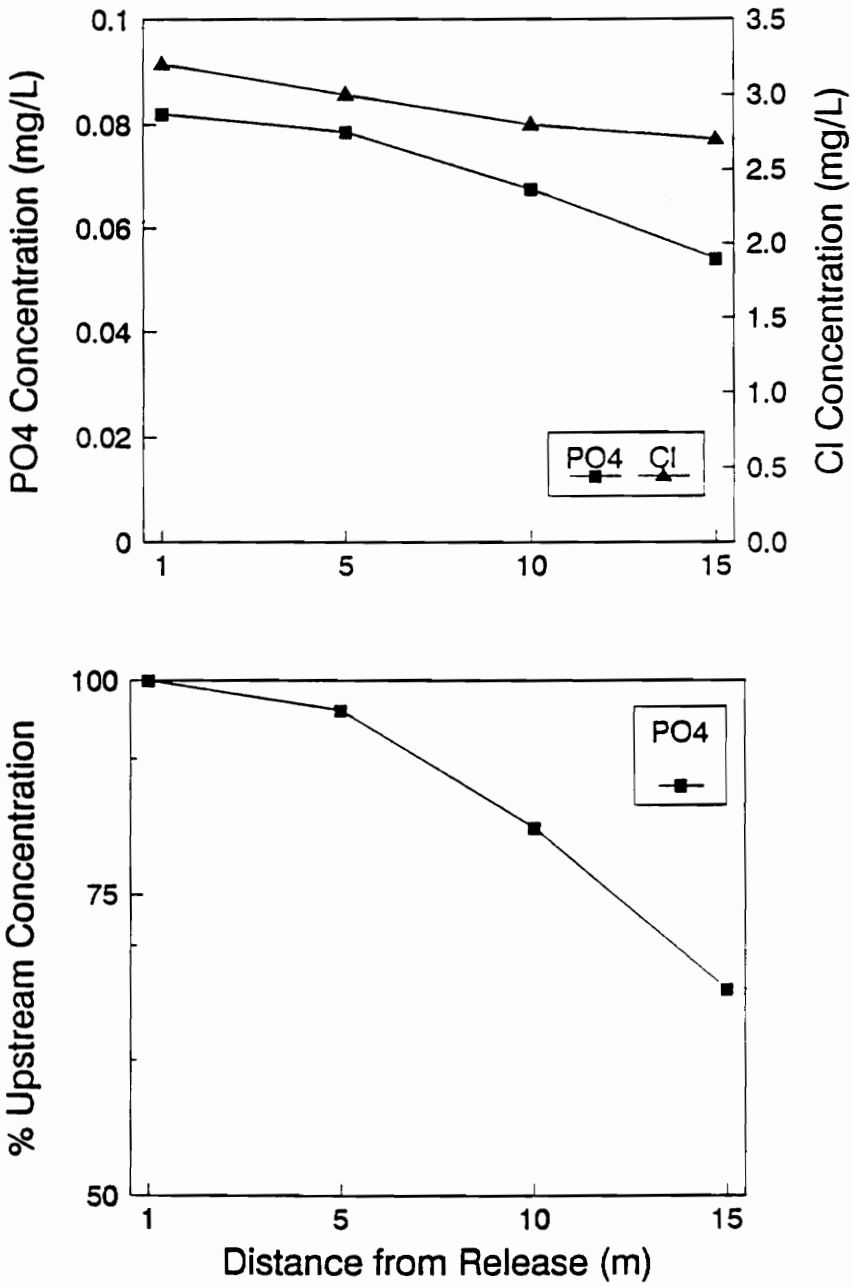

Figure 21. **Example chloride and phosphorus curve produced from samples collected at sites along the length of the stream:** The upper panel shows the downstream decline in phosphorus and chloride concentrations. The lower panel shows the phosphorus data corrected for losses due to dilution and dispersion and expressed as a percentage of the upstream concentration.

Another 5-mL aliquot of the original slurry was collected on a pre-ashed 0.45-um Gelman filter, dried, weighed, and ashed to determine AFDW.

5.4 Results

Physical parameters

There were no significant differences in stream temperature between hardwood and pine streams. Mean water temperature in October was 10 °C, dropped to a low of 6 °C in January, and rose to a maximum temperature of 16 °C in July (Fig 22).

Discharge for two of the pine watersheds and two of the hardwood watersheds was obtained from the weirs. Discharge was significantly lower in the pine watersheds ($p < 0.05$) and more variable (mean = 2.38 L/s, standard deviation (s) = 1.91) than in the hardwood watersheds (mean = 2.35 L/s, s = 1.32) on a yearly basis (Fig. 23). Discharge in the pine streams increased to a greater extent in response to storms than in the hardwood streams and dropped to lower levels during the dryer periods (e.g. January thru May). For both canopy types, lowest discharges occurred in autumn (0.5 L/s), increased in February to about 3.7 L/s, declined to about half of February levels in the spring, and reached yearly highs of over 4.0 L/s in June and July. In late summer and early fall, discharge again dropped to about 2.0 L/s (Fig 23). Velocity exhibited a pattern similar to discharge and was significantly correlated with discharge ($r = .806$; $p < 0.0001$) (Fig. 24). There was no significant difference between velocity of the two watershed types (ANOVA, $p > 0.05$).

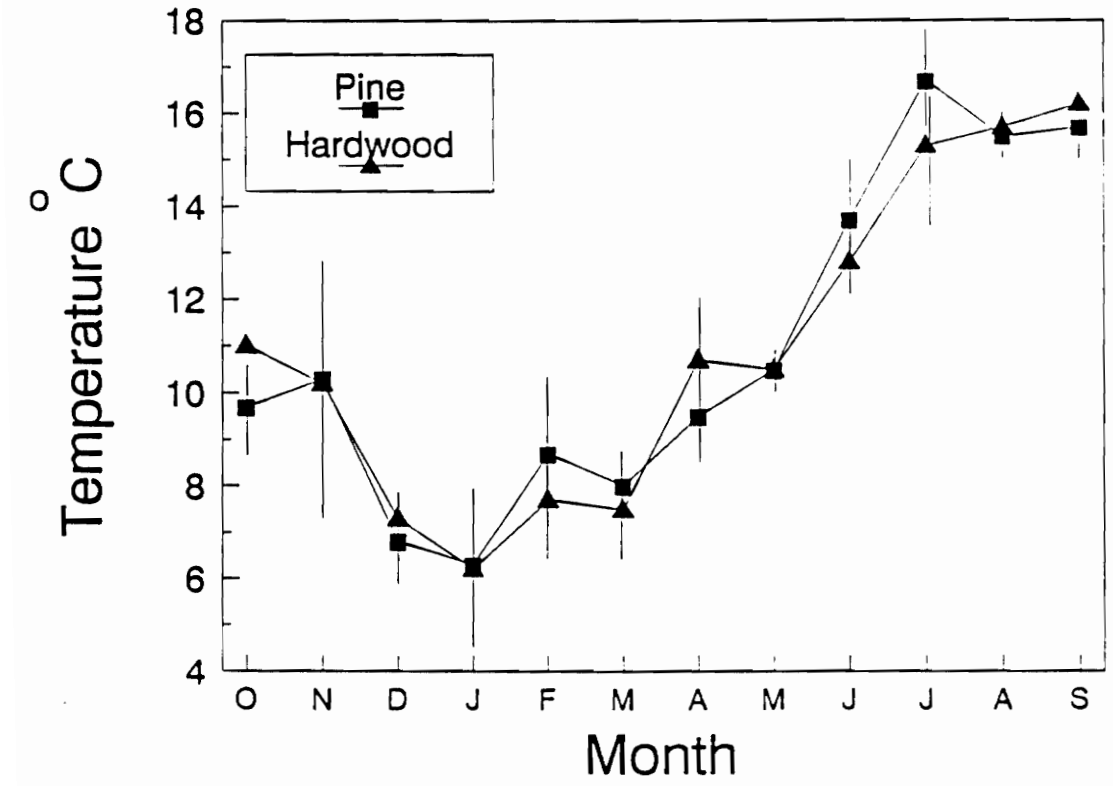

Figure 22. Mean monthly water temperature (°C) in the pine and hardwood watershed streams: at the time of the nutrient releases.

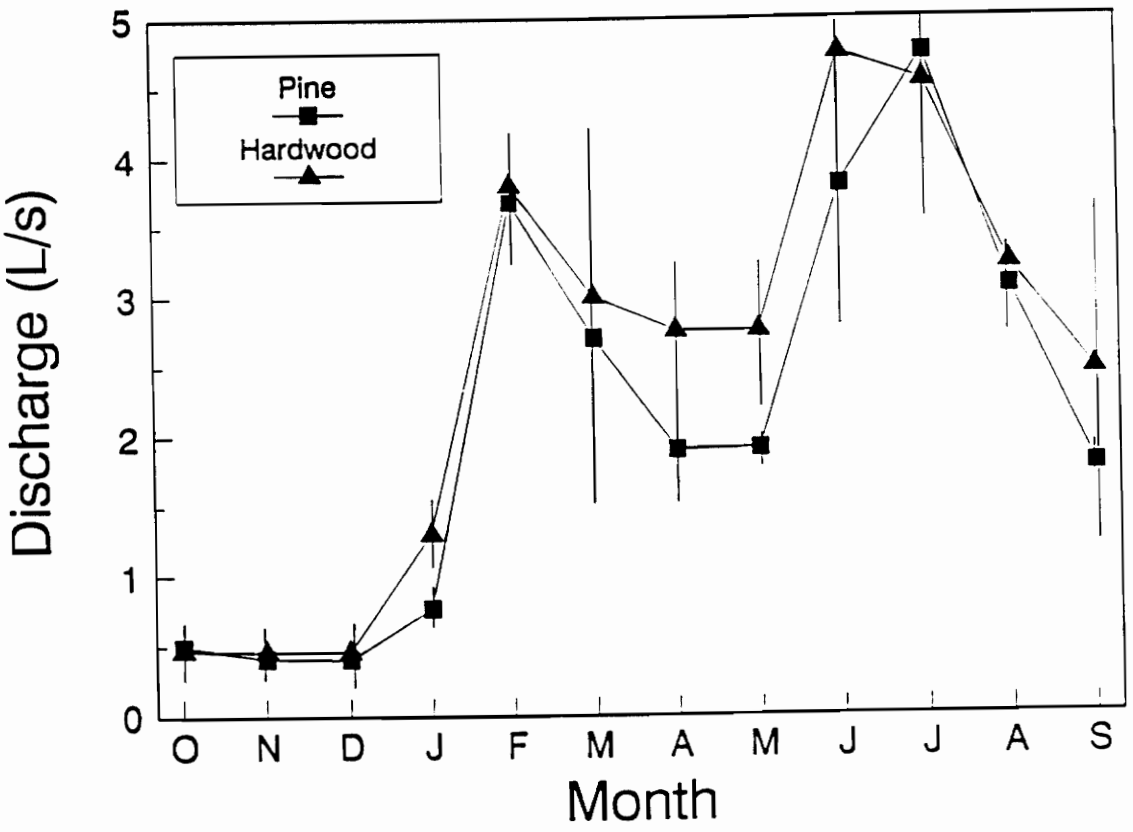

Figure 23. **Mean monthly discharge (L/s) for two of the pine watersheds (1,17) and two of the hardwood watersheds (2,18):** Discharge was not available for the other watersheds. Discharge was determined from weirs located at the base of each watershed.

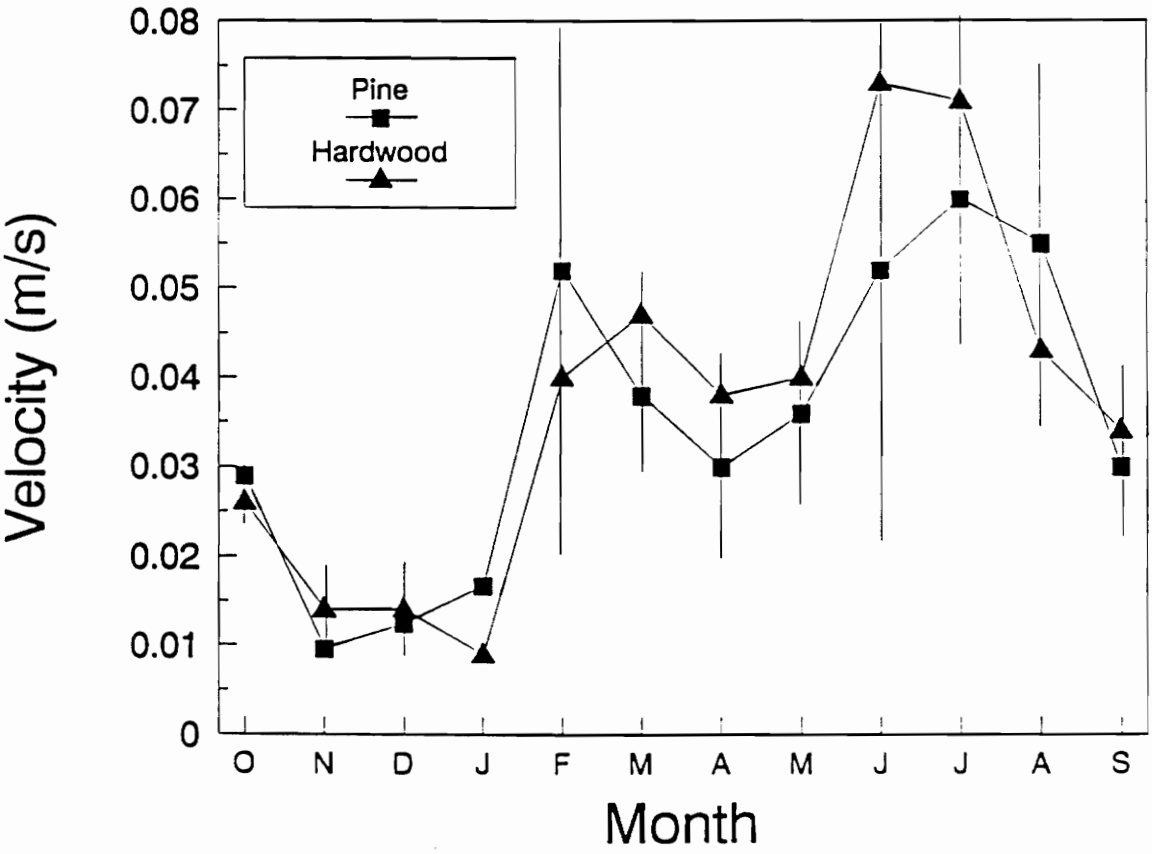

Figure 24. Mean velocity (m/s) in the streams draining pine and hardwood watersheds (n = 3)

Despite attempts to chose watersheds with similar physical characteristics, there were differences in stream temperature and slope of the watersheds. Watersheds on the NW side of the Coweeta basin were signficantly colder (10.1 and 11.5 °C, respectively) and steeper (average slope 18.5 cm/m) than watersheds on the SE side (average slope 16.4 cm/m)(ANOVA, $p < 0.05$). As a result of slope differences, streams on the NW side had faster current velocities (ANOVA, $p < 0.009$) and smaller Manning roughness coefficients, n, where n is obtained from the Manning equation:

$$u = \frac{1.49}{n} R^{2/3} s^{1/2}$$

where: u = velocity, m/s

n = Manning roughness coefficient

R = hydraulic radius, m

s = channel slope, m/m

than streams on the SE side (Tab. 5). In contrast discharge was not significantly different based on aspect (t-test, $p > 0.05$).

Biological parameters

There was no significant difference in annual mean CPOM biomass between streams draining pine and hardwood watersheds (Fig. 25)(t-test, $p > 0.05$). CPOM levels in both stream types were approximately 125 g AFDW/m^2 in October. CPOM in the hardwood watersheds jumped to about 400 g AFDW/m^2, dropped to about 200 gAFDW/m^2 in December and stabilized there until April when CPOM levels dropped to less than 50 g AFDW/m^2. CPOM in the pine watersheds increased gradually between

Table 5. Characteristics of watersheds and streams grouped by basin side.

Aspect	South East			North West		
Watershed	1	2	3	14	17	18
Manning n	0.178	0.120	0.267	0.304	0.295	0.322
CPOM (g/m^2)	328.8	228.3	322.8	207.7	178.9	133.3
FPOM (g/m^2)	116.9	95.0	81.8	94.6	83.1	58.2
CPOM:FPOM	2.81	2.40	3.95	2.19	2.15	2.29

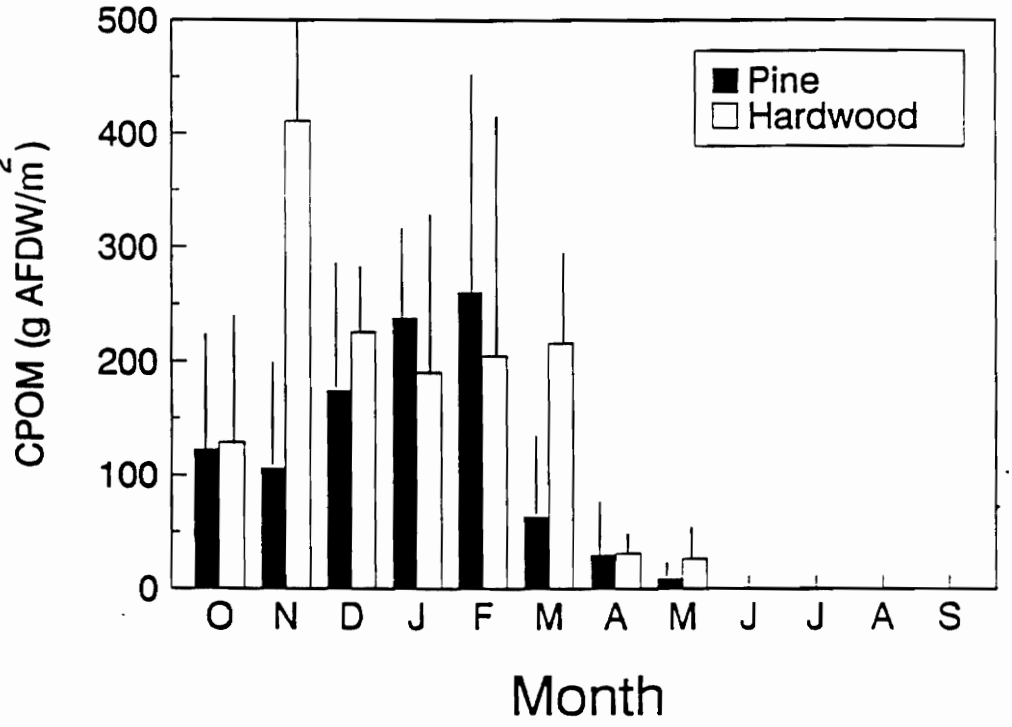

Figure 25. Mean CPOM biomass (g/m^2) in streams draining pine and hardwood watersheds (n = 3)

October and February to about 200 g AFDW/m^2, dropped to about 65 g AFDW/m^2 in March and then began a steady decline to insignificant levels in the summer. Because CPOM levels in the pine streams dropped dramatically in March and CPOM in the hardwood streams didn't decrease markedly until April, pine streams contained significantly more CPOM in March (ANOVA, $p < 0.05$). Although CPOM biomass was the same in both watershed types on an annual basis, significantly more CPOM accumulated on the less steep (SE) side of the basin (Tab. 5). It is possible that higher current velocity in the steeper streams resulted in less CPOM retention.

FBOM was not significantly different between the pine and hardwood streams on either a monthly or annual basis (t-test, $p > 0.05$). Yearly pattern of FBOM biomass accumulations and losses were similar in the two stream types (Fig. 26). FBOM biomass was highest in the autumn, declined in February due to an increase in discharge, accumulated some biomass in the spring when discharge was stable, and then decreased through the summer months when discharge again increased. For all streams combined, FBOM biomass was negatively correlated with both dischage and velocity ($r = -.606$ $p < 0.001$; and $r = -.447$ $p < 0.0002$). Highest biomass of FBOM occurred during the fall when flow was low and and biomass decreased as flow increased during winter and spring. FBOM biomass was not correlated with stream slope. Because FBOM was not slope related and CPOM biomass was lower on the steep side of the basin, the ratio of CPOM to FBOM was smaller on the NW (e.g. steep) side (Tab. 5).

Microbial respiration of FBOM was significantly lower in the pine streams than in the hardwood streams (t-test, $p < 0.005$) but the annual pattern was the same. Microbial respiration as ^{14}C glucose respiration/g AFDW/m^2 on FBOM was lowest in the fall, increased slightly in February when discharge increased, and then increased further between March and June, probably as a result of increasing temperatures. However, respiration declined between June and September (Fig. 27). Because temperature was

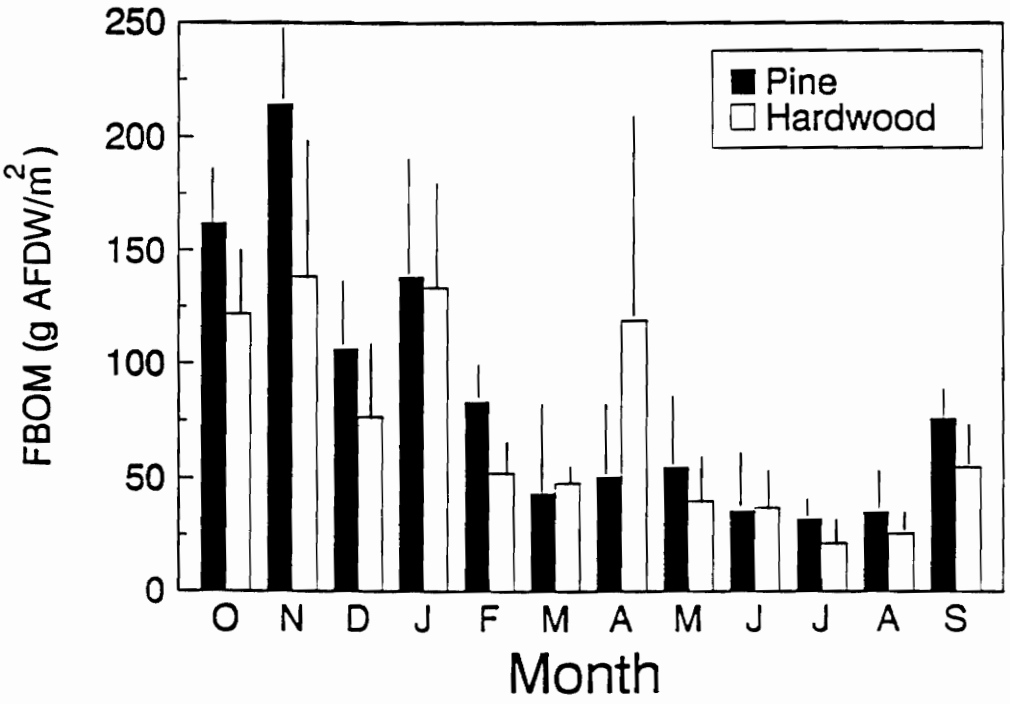

Figure 26. Mean FBOM biomass (g/m^2) in streams draining pine and hardwood watersheds (n = 3)

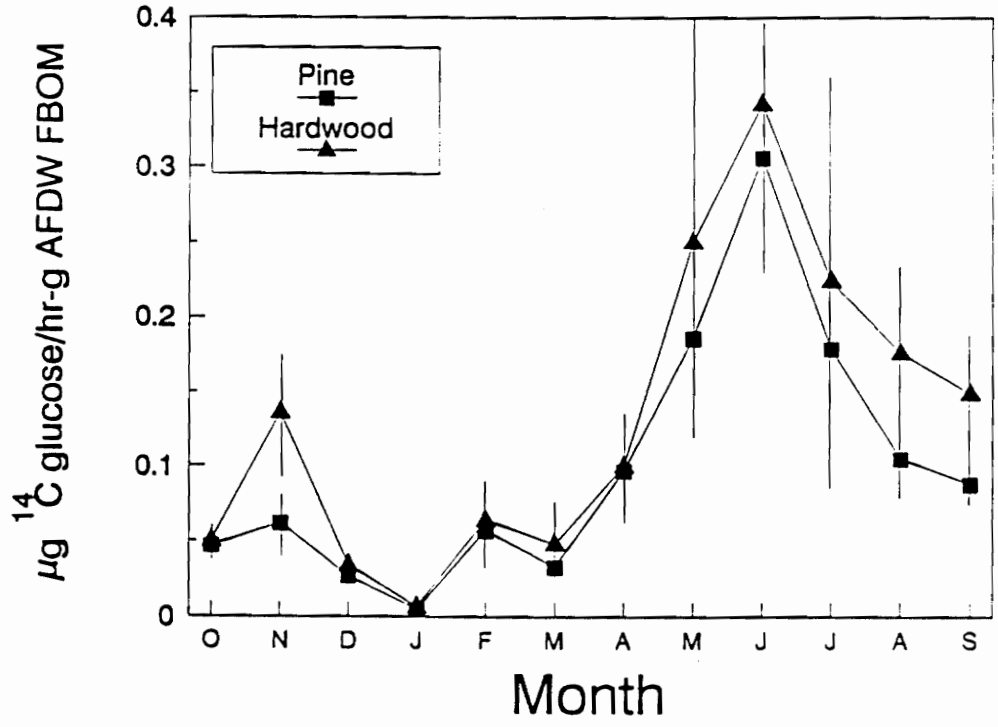

Figure 27. Microbial respiration of FBOM (ug glucose respired/g AFDW)

stable or rising during this time, it appears that respiration declined in reponse to a decline in quality or declining discharges. Respiration was correlated with both temperature (Pearson, $p < 0.05$) and discharge (Pearson, $p < 0.05$). Despite differences in temperature between watersheds on the NW and SE sides of the basin, there was no significant difference in microbial respiration based on basin side.

Phosphorus retention

Using either uptake length or uptake rate (Fig 28) as as measure of retention, phosphorus retention was similar in the pine and hardwood watersheds (ANOVA, $p > 0.05$). Streams were most retentive of phosphorus in autumn when discharge was low, were less retentive during winter and spring, and then became more retentive during summer. On a monthly basis, retention in pine and hardwood streams alternated between no difference, greater retention by pine streams, and greater retention by hardwood streams. Relative retentiveness of the two stream types appears to be governed by changes in discharge. Discharge and velocity were negatively correlated ($p < 0.05$) with retention. Large storms occurred in February, June, and July. This caused increases in discharge of 2 to 3 L/s. These increases in discharge were accompanied by a decreased retention.

Changes in both discharge and nutrient retention were more pronounced in the pine streams than in the hardwood streams as revealed by calculation of the standard deviation about the mean for uptake length and discharge (Table 6). Furthermore, discharge and nutrient retention recovered more quickly and to a greater degree in the pine watersheds. During low flow months (e.g. October-January, April-May, September), pine watersheds were nearly as retentive or more retentive than hardwood watersheds.

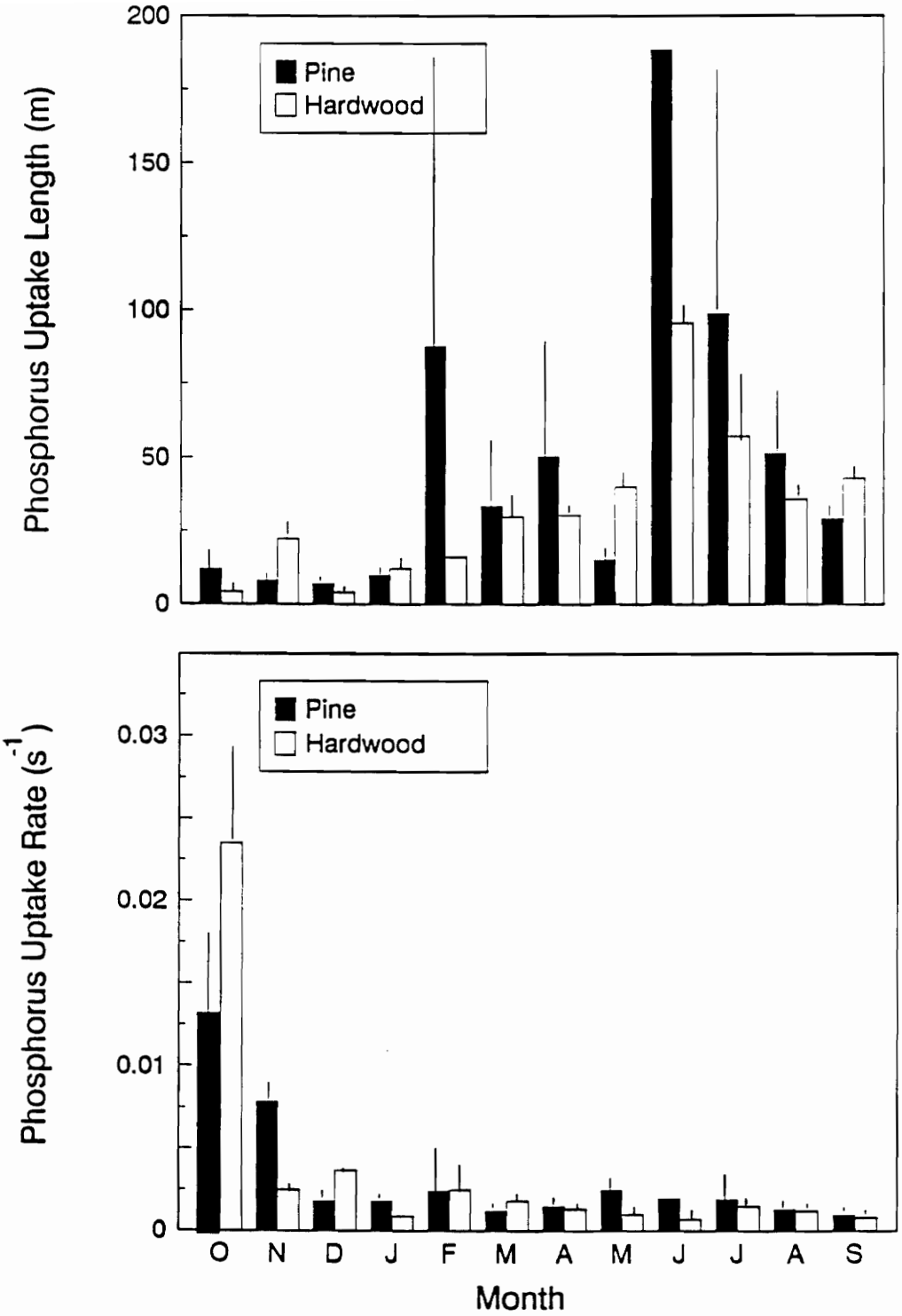

Figure 28. Mean phosphorus uptake length (m) and uptake rate (s) in streams draining pine and hardwood watersheds (n = 3).

Table 6. Standard deviation of uptake length (m) and discharge (L/s) in pine and hardwood streams.

Vegetation Type	Standard Deviation	
	Pine	Hardwood
Uptake length (m)	50.9	25.5
Discharge (L/s)	1.91	1.37
Ratio UL/Discharge	26.6	18.6

During rainy months, pine watersheds were as retentive or less retentive than hardwood watersheds. The ratio of the standard deviation for uptake length to the standard deviation for velocity shows that uptake length in the pine watersheds changed more per unit change in velocity than in the hardwood watersheds (Table 6). This suggests that the pine streams may be less resistant to increases in discharge but more quickly recovered (i.e. were more resiliant).

In addition to watershed type, watershed location (i.e. slope) also affected uptake. Because velocity was faster on the steep side of the basin and less CPOM accumulated in the steeper streams, uptake length was significantly longer (ANOVA, $p < 0.03$). In contrast, uptake rate, which is less dependent on velocity, was not significantly different betweem steep and more gradual streams.

5.5 Discussion

Physical and biological parameters

Few differences were found between streams draining hardwood and 35-yr-old experimental pine watersheds. This concurrs with the findings of Webster and Patten (1979). They used Coweeta Watersheds 17 (pine) and 18 (hardwood) in their study of calcium retention and found that by the early 1970's there were already few functional differences between the watersheds. In this study, physical characteristics such as velocity and temperature were also not significantly different. However, discharge was significantly less ($p < 0.01$) in the pine watersheds than in the hardwood watersheds.

Although average discharge was lower in the pine watersheds, it was more variable than in the hardwood watersheds (Fig. 23, Tab. 6). Storms caused a greater increase in discharge in the pine watersheds and discharge returned to baseflow levels more quickly. It has been suggested that ecosystems with a smaller organic matter pool are less resistant but more resiliant than watersheds with a large organic matter pool (Golley 1974; O'Neill et al. 1975; O'Neill and Reichle 1980). The pine watersheds used in this study may have a smaller terrestrial organic matter layer covering the bedrock due to erosion during logging. A decreased organic matter layer may render these watersheds less able to buffer the stream against increased runoff from storms. This would be especially true during wet years such as this one (1988-89), when the ground was often saturated.

In addition to canopy related differences, physical characteristics of the streams were also influenced by watershed location. Watersheds on the NW side of the basin were steeper than watersheds on the SE side of the basin. Consequently, NW watersheds were more similar in terms of discharge, velocity, and retention of CPOM and phosphorus, than SE watersheds, regardless of canopy type. Although there were no significant differences in discharge as a result of slope, velocity was significantly higher (ANOVA, $p < 0.03$) in the steeper streams (NW), while roughness coefficients and temperature were higher in the more gradually sloping streams (SE).

Biological differences were also more dependent on slope than watershed type. Although CPOM composition differed greatly between the two watershed types (i.e. hardwood watersheds contained a variety of leaves while pine watersheds contained almost exclusively needles), CPOM and FBOM biomass in the different watershed types were not significantly different. Annual respiration regimes, timing of inputs and losses of organic matter were fairly similar for both watershed types. Microbial respiration on FBOM was significantly higher in hardwood streams. In contrast to the similarities between watershed types, there were several differences based on stream slope. Watersheds

with less slope (SE) accumulated significantly (ANOVA, $p < 0.03$) more CPOM than steeper watersheds on the opposite side of the basin (NW). There was no difference in FBOM concentration based on slope, however, this resulted in a CPOM to FBOM ratio that was greater in the gradually sloping watersheds than in the steeper watersheds (3.05 and 2.01 respectively). CPOM accumulation may be more dependent on slope and velocity than is FBOM accumulation because much CPOM retention occurs due to entrainment on rocks and snags that are more exposed and effective during low flow conditions. Additionally, CPOM enters the stream primarily during autumn whereas FBOM is generated throughout the year. Therefore, FBOM may be as dependent upon the rate of generation as the removal rate. Temperature differences between basin sides did not appear to play an important role as there were no differences in microbial respiration based on basin side.

Nutrient Retention

Irrespective of canopy type or slope, uptake length was positively correlated (Pearson's correlation) with discharge ($p < 0.0001$) and velocity ($p < 0.0001$) and negatively correlated with temperature, CPOM, and FBOM ($p < 0.05$). Therefore, canopy and slope related differences in uptake length should be explainable in terms of these variables. Uptake rate was not correlated with discharge or velocity ($p < 0.01$), because discharge and velocity effects are accounted for in the conversion from uptake length to uptake rate.

Both watershed type and stream slope affect the above listed factors and thereby influence retention. As a result of variable discharge regimes, phosphorus retention was more variable in the pine watersheds (Fig. 28) than in the hardwood watersheds. For a

unit change in discharge, changes in uptake length in the pine watersheds was about 1.5 times the change in the hardwood watersheds. That is, phosphorus retention decreased more in the pine watersheds during high flow periods. However, during low flow, phosphorus retention was greater in the pine watersheds. Therefore, even though uptake in the pine watersheds was more variable and losses were greater during storms, average annual retention was not significantly different between the two watershed types. Average annual retention was not different primarily because pine trees transpire more water resulting in a lower stream discharge. If these watersheds had been logged and replanted in mixed-hardwoods that do not reduce baseline streamflow the lack of buffering capacity of the watersheds would likely have resulted in a decreased retentiveness of the disturbed watersheds.

Slope effects on retention were more readily apparent than watershed type effects. Based on ANOVA, there were significant differences in uptake length as a function of basin side slope ($p < 0.03$). With few exceptions, t-test showed that uptake length was most similar in watersheds that had similar slopes (i.e. were on the same side of the basin). Primarily due to lower velocities, uptake lengths were shorter in more gradually sloping streams (SE). In addition to lower velocities, increased retention in the more gradually sloping streams was also aided by higher CPOM biomass and roughness coefficients in these streams indicating that geomorphology may be one of the most important factors determining retention. Water temperatures were also warmer in the SE facing streams (less steep streams) but microbial respiration on FBOM from SE facing streams was lower than on the steeper NW facing slopes. Therefore, temperature differences between the NW and SE facing streams do not appear to be responsible for differences in stream retention. Uptake rate is not dependent on slope because velocity differences only minimally influence uptake rates.

Emphasis of stream ecosystem research is currently being placed on interbiome comparisons with the objective of elucidating fundamental regional differences in nutrient retention mechanisms. The strong impact of watershed stream slope, and possible implications of disturbance history on phosphorus retention characteristics demonstrate the need to carefully choose sites for comparison. Newbold et al. (1981) suggested that in streams with different morphologies, physical factors should dominate nutrient retention rather than biological ones. If the effects of physical characteristics such as slope are not carefully examined, and long-term disturbance or land-use histories taken into account, the risk of attributing random differences in physical or historical features to regional characteristics is taken.

6.0 Analysis of solute dynamics in streams: a modeling approach.

6.1 Abstract

A one-dimensional numerical model of solute transport in streams was developed. The model included advection, dispersion, and uptake kinetics and was verified against an analytical steady-state solution. Solute transport in artificial and natural streams was simulated to determine under what conditions the basic advection-dispersion model would accurately predict field data and when a more complicated model that includes transient storage is required and to evaluate dispersion within the artificial and natural streams under different conditions. Results demonstrated that the basic model could accurately predict solute dynamics in the artificial streams but could only accurately predict solute dyanamics in the natural streams when transient storage was small relative to leading-edge velocity. For both artificial and natural streams, dispersion was positively correlated with velocity ($p < 0.05$). A positive correlation was also obtained between phosphorus uptake rates simulated by the model and those calculated from the field data for the natural streams ($p < 0.003$).

6.2 Introduction

As demonstrated by an increase in research activity (e.g. Meyer et al. 1988; Grimm et al. 1988; Triska et al. 1989) and a recent workshop (Solute Work Group 1990), the study of stream solute dynamics (i.e. the transport and transfer of solutes) is maturing into a major component of stream ecology research. Solutes are defined as materials chemically dissolved in water. They are important because many are present in short supply and consequently they often regulate biological processes. Furthermore, solutes are critical for linkages between terrestrial and aquatic ecosystems and between up-stream and downstream reaches of streams and rivers (Meyer et al. 1988).

Researchers have investigated the impacts of different ambient solute concentrations on processes such as productivity (e.g. Triska et al. 1983; Grimm and Fisher 1986) and decomposition (Triska and Sedell 1976; Elwood et al. 1981). Nutrient additions have also been performed to determine which solutes are limiting under what conditions, and solute dynamics (recycling, transport, and retention) have also begun receiving study. In streams, solutes do not cycle in place but rather are tranported downstream forming spirals as they cycle (Webster and Patten 1979). Spiralling length provides a measure of retention, with more retentive streams having shorter spiralling lengths than less retentive streams. Retention has been studied in light of the effects of temperature, geomorphology (Frissel et al. 1986; Gregory et al. in press), hydrology (Bencala 1983; Bencala and Walters 1983), flora (Grimm and Fisher 1989), fauna (Newbold et al. 1982; Mulholland et al. 1985b), and detritus (Newbold et al 1983; Mulholland et al. 1985). Solute dynamics have been examined in systems ranging from small mesocosms where substrate specific uptake rates can be determined (Bothwell

1985; Grimm and Fisher 1986) to whole watersheds where spiralling techniques are used to determine whole stream retention.

One major deterent to understanding stream solute dynamics has been an inability to separate the intertwined effects of factors on solute transport and retention and the absence of a unifying procedure that allows for comparisons among studies done at different scales or in studies done at the same scale under different physical conditions (Solute Work Group 1990). Solute models provide quantitative information that can be normalized for stream size. Therefore solute models, used in conjunction with carefully controlled experimental studies, can be used to separate effects of different variables and also allow for a direct comparison of results from different studies. To date, few solute models have been developed for this use. Examples include solute models developed by Bencala (1983) and Bencala and Walters (1983) to examine solute-sediment interactions and transient storage mechanisms in small mountain streams and one by Hart et al. (1990) that was used to separate the proportion of phosphorus taken up by the channel sediments from that taken up in storage zones. Newbold et al. (1983) used a similar model to simulate ^{32}P dynamics in streams and allocate phosphorus to different stream compartments.

The model implemented here was designed to determine the conditions under which the simplest tranport equations are sufficient to model solute dynamics and when more complicated versions must be used. The model was also used to compare solute uptake information from different studies and to help identify and understand the transport mechanisms operating in each system.

6.3 Model Development

This model is a modification of a one-dimensional advection-dispersion model (Thomann and Mueller 1987) solved using a central-difference approximation. A detailed discussion of model development and the numerical code was provided by Hann and Young (1971). The model presented here includes advection, dispersion and kinetic reactions (e.g. biological uptake):

$$1)\ \frac{\partial s}{\partial t} = -u\frac{\partial s}{\partial x} + E\frac{\partial^2 s}{\partial x^2} - ks$$

where s is solute concentration, t is time, x is distance, u is velocity, E is a dispersion coefficient, and k is the uptake rate. This equation is valid when discharge (Q) and stream area (A) are constant. The model can be expanded to accomodate changing values of Q, A, and E (Solute Work Group 1990) using values for Q and A obtained from field data:

$$2)\ \frac{\partial s}{\partial t} = -\frac{Q}{A}\frac{\partial s}{\partial x} + \frac{1}{A}\frac{\partial}{\partial x}\left[AD\frac{\partial s}{\partial x}\right].$$

After the model has been parameterized with the appropriate Q's and A's (or u's), dispersion can be determined by curve fitting tracer (e.g. chloride) data with model output. Once values for dispersion have been obtained, the model can be re-run for a non-conservative solute and curve fit to estimate uptake (k). Curve fitting was done subjectively in this study but standard objective techniques (e.g. least squares minimization) are available (Wagner and Gorelick 1986). For the streams modelled in this paper, benthic demands and storage zones were not modeled directly, but the general equation

can be expanded to include benthic demands and storage. Bencala (1983) illustrated that storage zones (e.g. behind rocks or in holes) can be essential to properly model the tail of the solute curve:

$$3)\ \frac{\partial s}{\partial t} = -\frac{Q}{A}\frac{\partial s}{\partial x} + \frac{1}{A}\frac{\partial}{\partial x}[AD\frac{\partial s}{\partial x}] + \alpha(s_s - s)$$

where s_s is the solute concentration in transient storage zones. Equation 4 (from Solute Work Group 1990) models the change in solute concentration of the storgae zones and must be solved simultaneously with equation 3.

$$4)\ \frac{\partial s_s}{\partial t} = \alpha\frac{A}{A_s}(s_s - s)$$

where A_s is the cross-sectional area of the storage zone and α is the coefficient of exchange for the strorage zone area.

Model Verification

The model (eqn 2) can be verified for steady state conditions with constant Q, A, and E by comparing the numerical solution to analytical solutions (Thomann and Mueller 1987). Equation 5 is the analytical solution for a time variable buildup of solute and was used to check the rising limb of the solute curve. Equation 6 is the solution for a rectangular input and was used to solve for the falling limb of the solute curve after input had been stopped.

$$5)\ s(x,t) = \frac{W}{2A\sqrt{\Pi E}}\int_0^t t^{\frac{-1}{2}}\exp[\frac{-(x-ut)^2}{4Et} - kt]dt$$

$$6)\ s(x,t) = \frac{s_o}{2} \exp\left(-\frac{kx}{u}\right)\left[erf\frac{x-u(t-\tau)(1+\eta)}{\sqrt{4E(t-\tau)}} - erf\frac{x-ut(1+\eta)}{\sqrt{4Et}}\right]$$

where: W is a loading term (mass/time), erf is the error function, and η is a dimensionless number defined by equation 7:

$$7)\ \eta = \frac{KE}{U^2}$$

For conditions where the analytical equation is valid, analytical data accompanies field data and model output.

6.4 Methods

The artificial streams were constructed of plastic gutter pipe and were 15 m long, 20 cm wide, and had a slope of 2%. Water depth ranged from 0.5 cm to 3 cm. The bottom of the streams were layered with gravel to a depth of about 2 cm. Several of the artificial streams contained dogwood leaves and several contained oak leaves.

The natural streams located at Coweeta Hydrologic Laboratory, Macon County, North Carolina, are first-order streams with flows ranging from 0.5 L/s to 5.0 L/s during the year-long sampling season. Table 7 summarizes physical information about the streams and their watersheds. We chose 25- to 30-m reaches from the downstream most section of each watershed to conduct solute studies.

Table 7. Physical characteristics of pine and hardwood watersheds used in this study[1].

Vegetation Type	Pine			Hardwood		
Watershed	1	3	17	2	14[2]	18
Aspect	SE	SE	NW	SE	NW	NW
Area (ha)	16	9	13	12	14[3]	13
Watershed Elevation (m)						
Maximum	988	931	1021	1004	992	993
Minimum	755	739	760	709	707	726
Stream slope in study area(cm/m)	16	14	20	18	13	23
Mean Ann. Dischg. (L/s) 88-89	1.91	1.30[4]	2.38	2.65	2.80[4]	2.35
Maximum	4.27	-	5.84	5.22	-	4.41
Minimum	0.52	-	0.29	0.44	-	0.43
mean SRP (ug/L)	< 2.0	< 2.0	< 2.0	< 2.0	< 2.0	< 2.0

[1]Data from this study and Swank and Crossley (1988)
[2]Tributary used
[3]Estimated from topographic map
[4]Estimated from ratio of area to discharge of similar watershed type

Nutrient Uptake Length

To determine nutrient uptake lengths, a nutrient solution containing phosphate (as Na_2HPO_4) and chloride (as NaCl) was released into each stream for a period sufficient to allow the stream nutrient concentration to reach a plateau (10-20 min for the artificial streams, 20-40 min for the natural streams). Nutrient concentrations added were sufficient to raise stream nutrient concentrations to 5-10 x ambient levels (about 30 ug/L SRP and 3 mg/L Cl). Chloride (as NaCl) is conservative in most streams and was used to account for nutrient dilution and dispersion (Bencala et al. 1987).

At the downstream end of the reach, water samples were taken every 1-3 minutes. After 10 min., when nutrient concentrations reached a plateau, water samples were taken at 5 stations (4 m apart) along the stream. Solution input was then stopped and sample collection continued at the downstream end of the reach at 5-10 minute intervals for an additional 30 minutes. Samples were filtered as they were collected (0.45 μGelman A/E glass fiber filters) and then taken to the laboratory and refrigerated (4 °C). Samples were frozen or analyzed within 24 hr for SRP and chloride. These samples were used to determine the rise, plateau, and decline in nutrient concentrations at the downstream site.

Laboratory Analyses

All chemical analysis were performed at Coweeta Hydrologic Laboratory. The protocol for water chemistry analysis used at Coweeta was described in detail by Reynolds and Deal (1986). Phosphorus and chloride were analyzed using a 3-channel Technicon Autoanalyzer-II system. Soluable reactive phosphorus concentrations were

measured using the ammonium-molybdate reaction. Chloride was determined using the ferricyanide method.

Data Analyses

Leading edge velocity in the artificial and natural streams was determined by timing the transport of rhodomine dye. Mean velocity was calculated from the chloride data collected at the site furthest downstream from the nutrient release. Figure 29 is an example of a chloride curve produced from water samples collected at the downstream site. These data were used to calculate mean stream velocity by integrating the area under the curve and determining the time for half of the chloride to pass the downstream station. The difference between the time at which half of the solution was released and the time for half of the chloride to pass the station is the nominal transport time (Triska et al. 1989). Velocity was calculated as distance divided by nominal transport time.

Because chloride is conservative tracer in these streams, the decline in chloride concentration is a result of dilution and dispersion (Fig 30). Therefore, chloride data can be used to adjust phosphorus data to eliminate losses due to dilution and dispersion. In the lower panel, phosphorus concentrations have been corrected for losses due to dilution and dispersion The decline in concentration is expressed as percent of upstream concentration. For this example, about 70% of the phosphorus released into the stream was removed from solution, either biotically or abiotically, in the first 10-15 m. The log of the slope of this decline is phosphorus uptake per meter. The inverse of the slope is the uptake length (m). Uptake rate (s^{-1}) was obtained by multiplying the decline in nu-

trient concentration (i.e. the rate at which a nutrient is removed from the water column) (m^{-1}) by velocity (m/s).

6.5 Results and Discussion

A simple model that included advection and dispersion provided a good fit for the artificial streams. For all runs the numerical and analytical models gave almost identical fits to the data. In November when the artificial streams contained only gravel, dispersion in the streams was negligable. The decline in chloride concentration may have been affected by sampling frequency. If samples had been collected more frequently, the decline in chloride concentration would probably have been even more abrubt. In December, after leaves had been in the streams about 1 month, dispersion increased from about 0 m^2/s for the earlier run without leaves to 0.05 m^2/s (Fig 31). The addition of leaf material increased dispersion because rather than passing down the channel unobstructed, the water now had to weave through the packs of leaf material. By March dispersion increased to about 0.2 m^2/s in the dogwood streams and 0.1 m^2/s in the oak streams (Fig 32) probably due to further compaction of leaf material into dams. Although velocity in the oak streams was typically higher than in the dogwood streams (Fig 33) and, as previously illustrated by Elder (1959), dispersion was positively correlated with velocity (Fig 34; $p < 0.05$), dispersion in the dogwood streams was almost always higher than in the oak streams. Dispersion was probably higher in the dogwood streams because the dogwood leaves were softer and tended to form packs more readily than the oak leaves which remained flat against the stream-bed for a longer period of time.

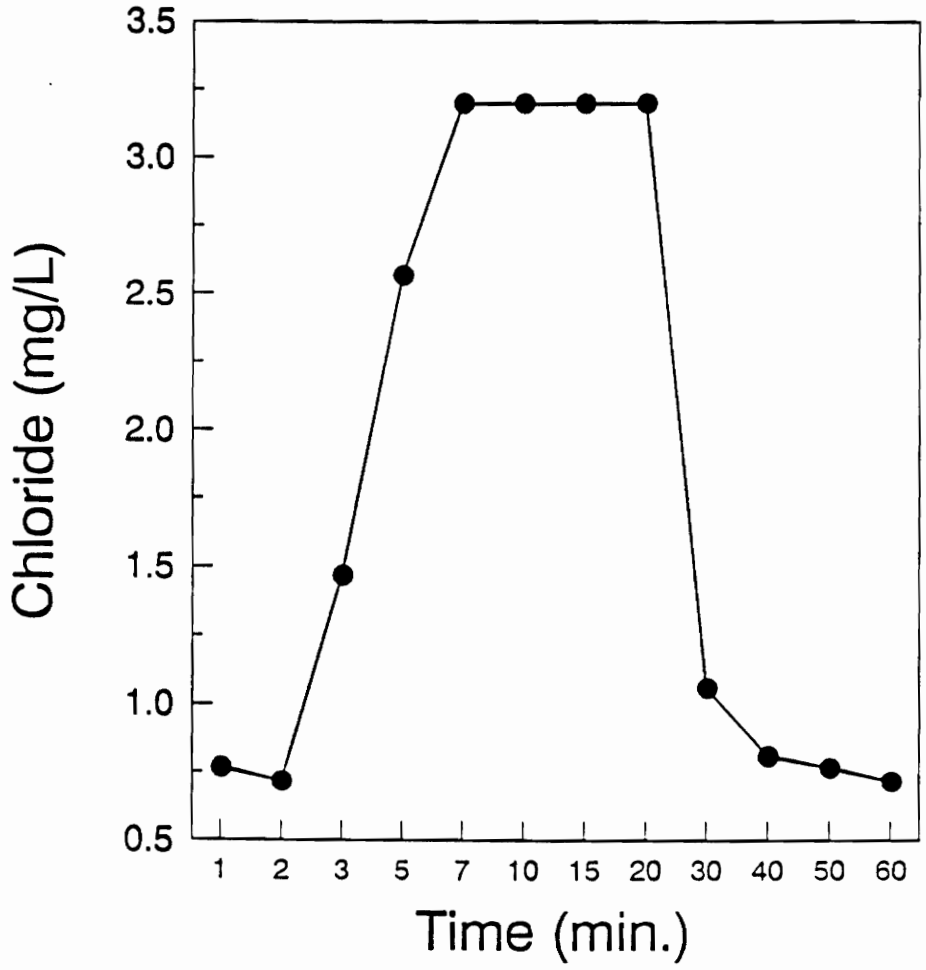

Figure 29. Example chloride curve produced from samples collected at a downstream site

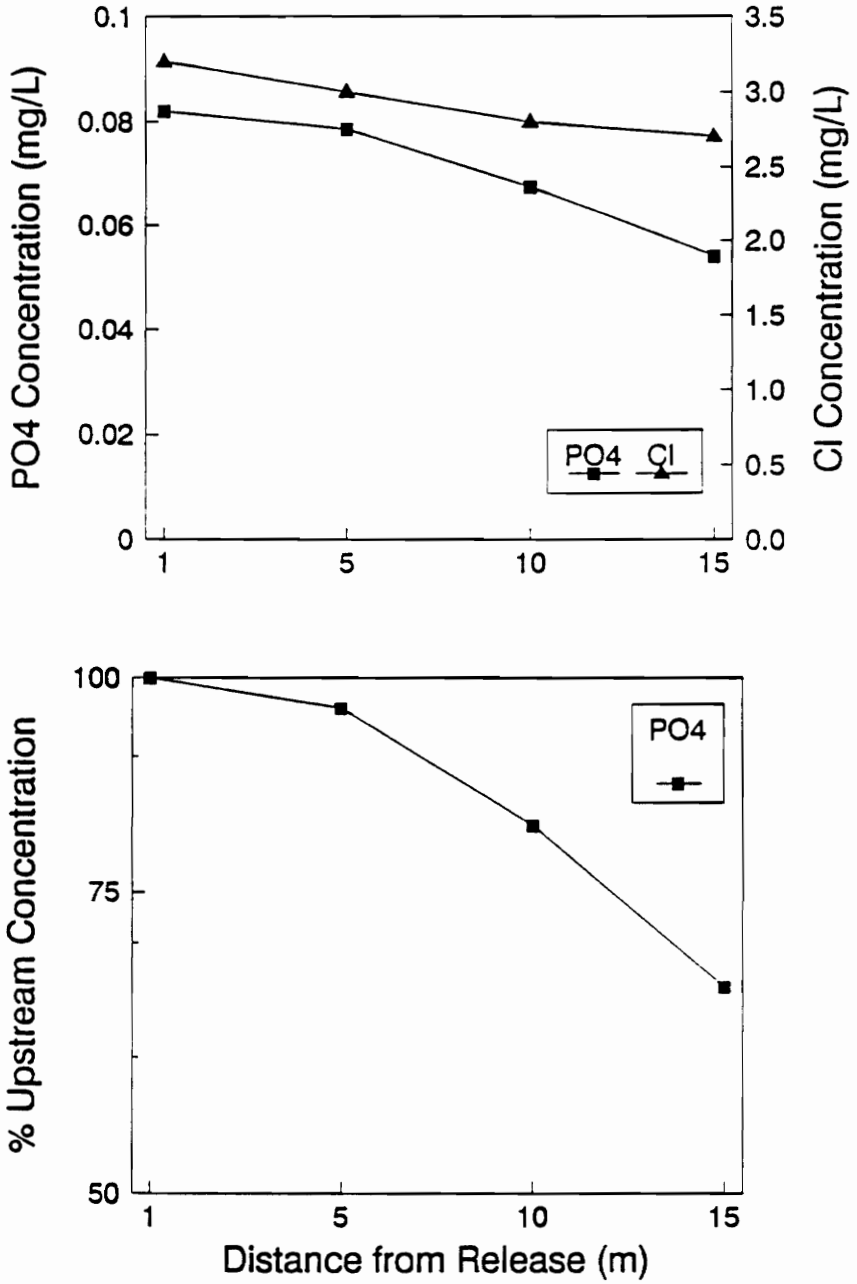

Figure 30. Example chloride and phosphorus curve from samples collected along the length of the stream: The upper panel shows the downstream decline in phosphorus and chloride concentrations. The lower panel shows the phosphorus data corrected for losses due to dilution and dispersion and expressed as a percent of upstream concentration.

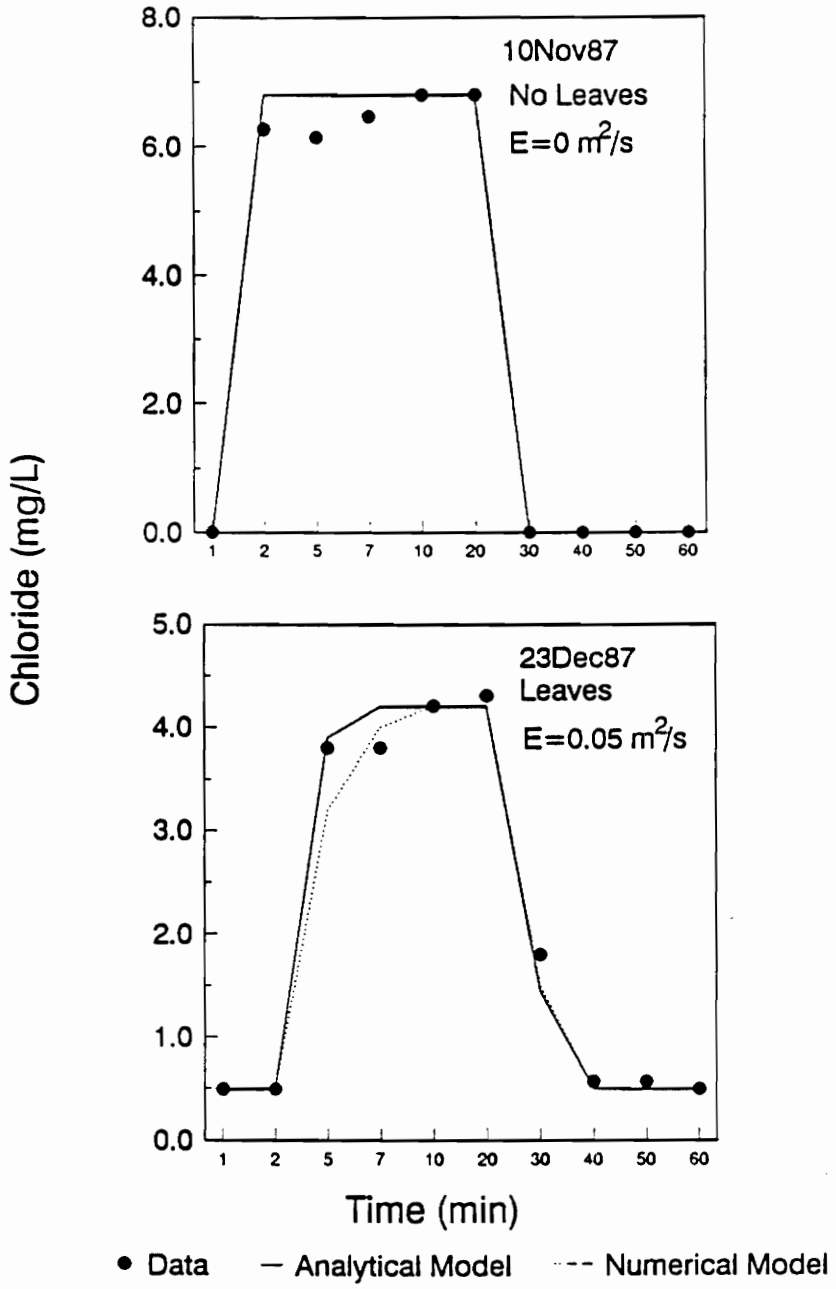

Figure 31. **Example chloride curve for the articial streams in November and December:** In November the streams contained only gravel. In December, leaves had been in the streams for about one month. E is dispersion in m^2/sec.

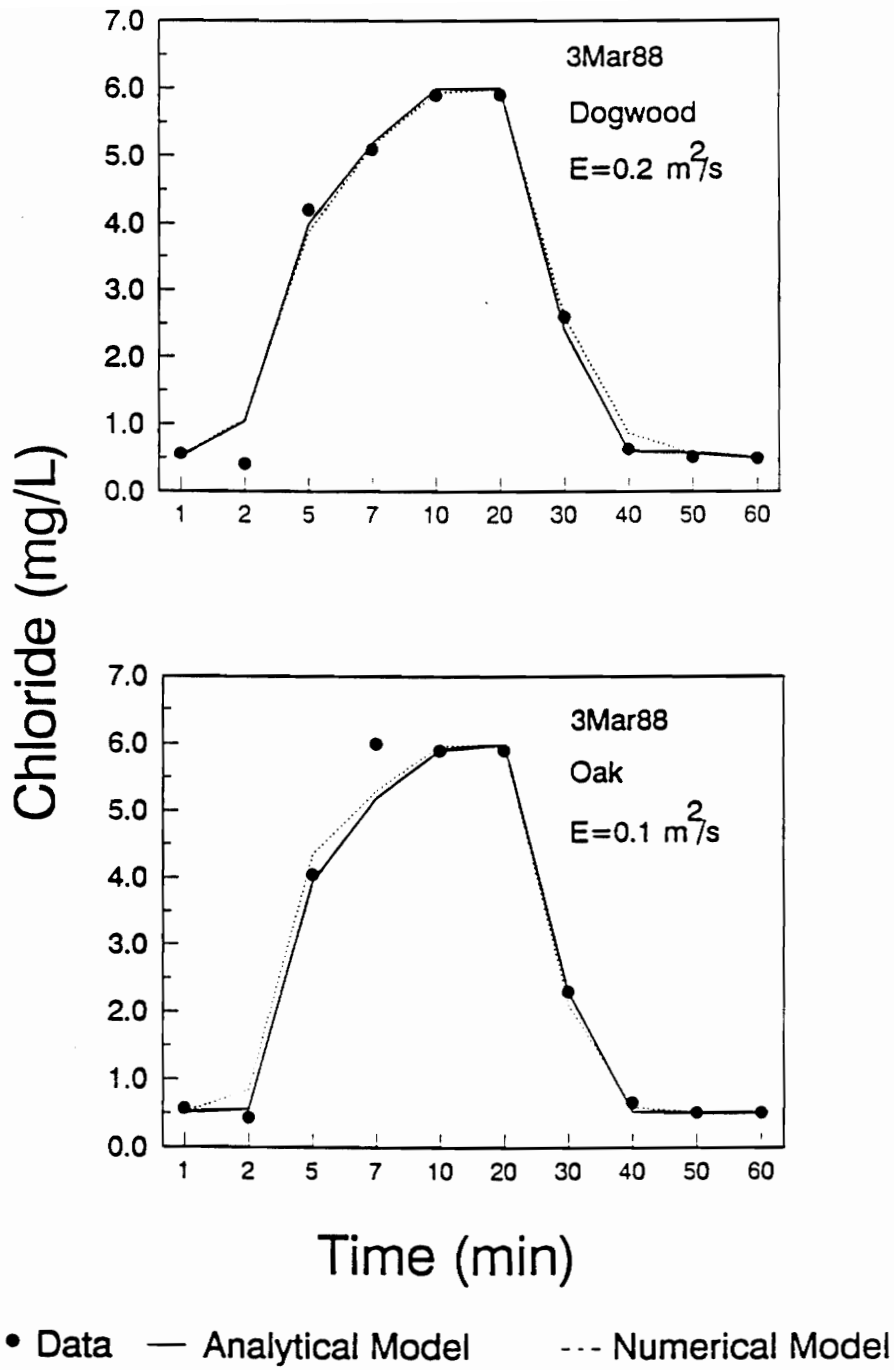

Figure 32. Example chloride curve from a Dogwood and an Oak stream in March.: Dispersion (E) for both dogwood and oak streams increased between December and March. Dispersion was typically higher in the dogwood streams during all months.

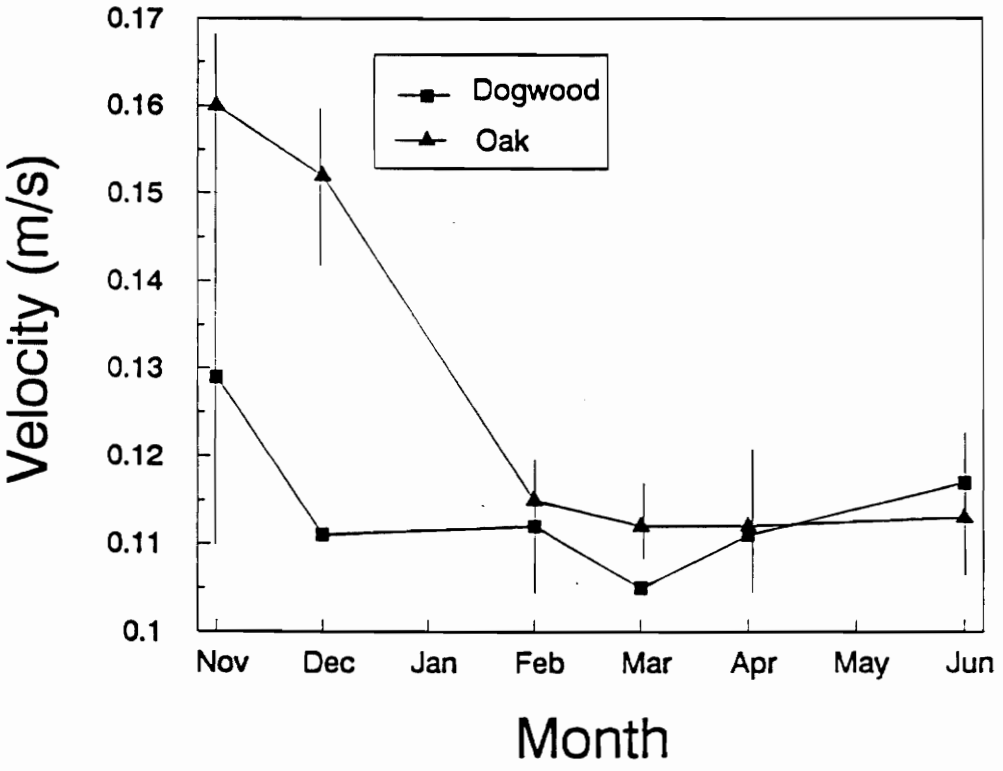

Figure 33. Velocity in the dogwood and oak streams from December to March.

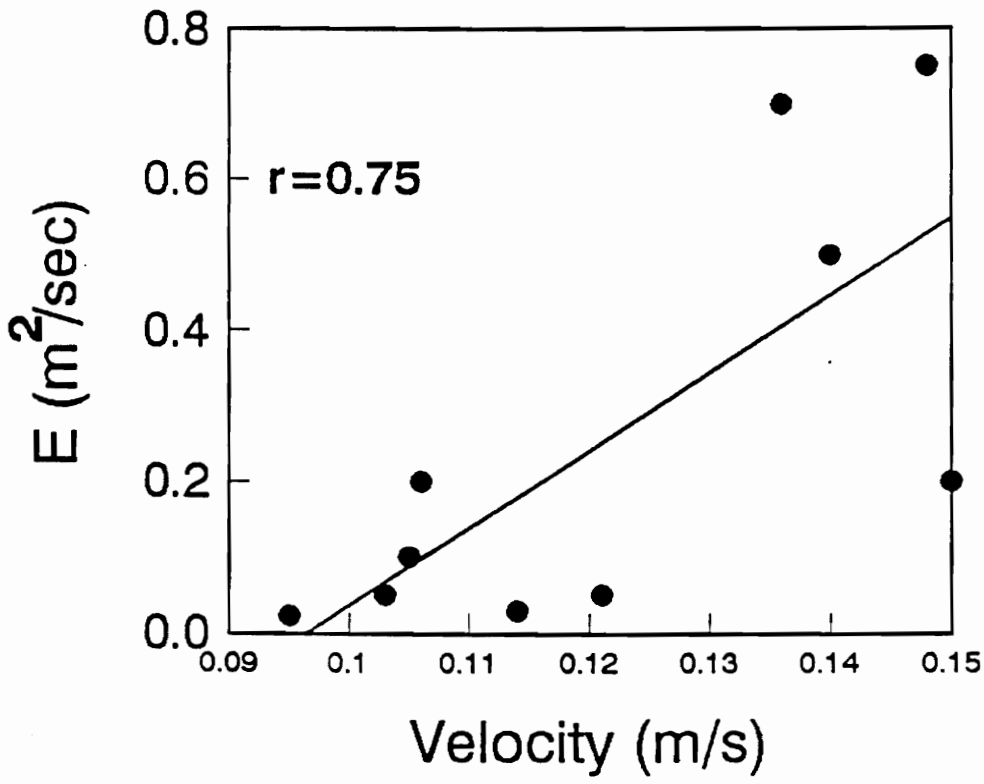

Figure 34. Regression of dispersion (E) versus velocity for the artificial streams ($p < 0.05$; ANOVA).

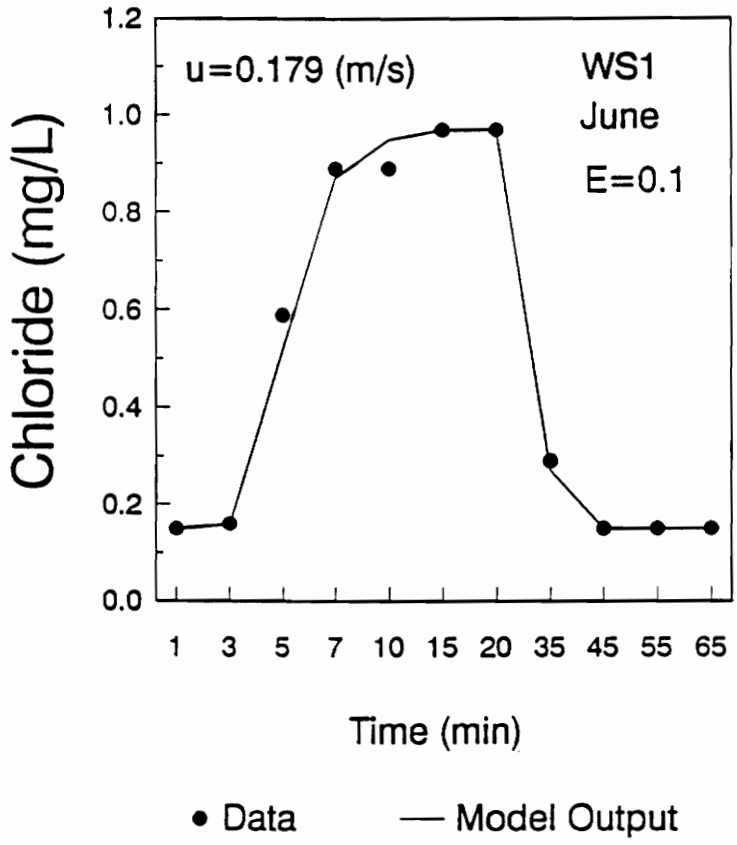

Figure 35. **Example chloride curve for a natural stream in June.:** u = velocity (m/s) and E = dispersion (m^2/sec).

For the natural streams, the simple model (using leading edge velocity) without transient storage provided a good fit for some data sets. During June, the simple model fit all streams well (Fig 35). The leading edge velocity was 0.179 m/s, which means that with no dispersion or storage the slug of solute should have reached the downstream station after about 3 min. Because of dispersion, most of the solute does not reach the downstream station until after 5 to 7 min. After the solute input stopped at 25 min., the solute concentration quickly dropped indicating that there is little retention by transient storage mechanisms. The model does not provide a good fit for the September data (Fig 36). Using the leading edge velocity, the rising limb of the curve was too low indicating that the leading edge velocity was too slow, but the falling limb of the curve dropped too rapidly indicating the velocity was too fast. The September data were modeled more effectively when the leading edge velocity was used for the rising limb and the nominal transport velocity was used for the falling limb (Fig 36). An even better fit could be obtained if the leading edge velocity were increased somewhat from the measured value. This indicates that during September, transient storage mechanisms were more important than in June. Others (Stanford and Ward 1988; Triska et al. 1989) have also found that transient storage of nutrients is important especially if the hyporheic zone in large and complex. Whether and under what conditions the size and retention time of the transient storage zone changes has not been addressed.

Because the leading edge velocity best describes when the solute pulse will arive and the mean velocity best describes the importance of storage, the difference between these two values should provide information about the relative importance of each measure. A regression of the leading edge velocity and the average velocity revealed that as the leading edge velocity increases the difference between the leading edge velocity and the nominal transport time also increases (Fig 37). This suggests that the nominal transport time is more buffered to changes in discharge than the leading edge velocity. This re-

lationship may indicate that storage zones may be responsible for a greater proportion of uptake during low flows than during high flow conditions. Dispersion in the natural streams was positively correlated with both leading edge velocity ($p < 0.05$) and mean velocity ($p < 0.05$) but the relationship was stronger between dispersion and mean velocity (Fig. 38).

Dispersion values for streams draining the pine watersheds were typcially lower than values obtained for the hardwood streams (Table 8). Dispersion may have been higher in the hardwood streams because these streams have a wider cross sectional area and meander more through the streambed.

Dynamics of a non-conservative solute, phosphorus, were also simulated for the natural streams to determine phosphorus uptake rate (s^{-1}). Uptake rate (k) ranged from 0.0001 to 0.0027 (s^{-1}) and model uptake rates were significantly correlated ($p < 0.01$) with uptake rates calculateed from field data (Fig 39). Although k values were not directly correlated with dispersion (Fig 40; Thomann 1973), a very high dispersion, which results in a lower peak downstream concentration, will result in a lower k value being obtained. Therefore, when transient storage is included in the model and more accurate dispersion values are obtained, the fit of model k values to field k values should improve.

6.6 Conclusions

Model results indicate that the numerical model provides a good approximation of the analytical solution and is appropriate for artificial streams or natural streams with very little transient storage. Streams with a fast leading-edge velocity and a gradually

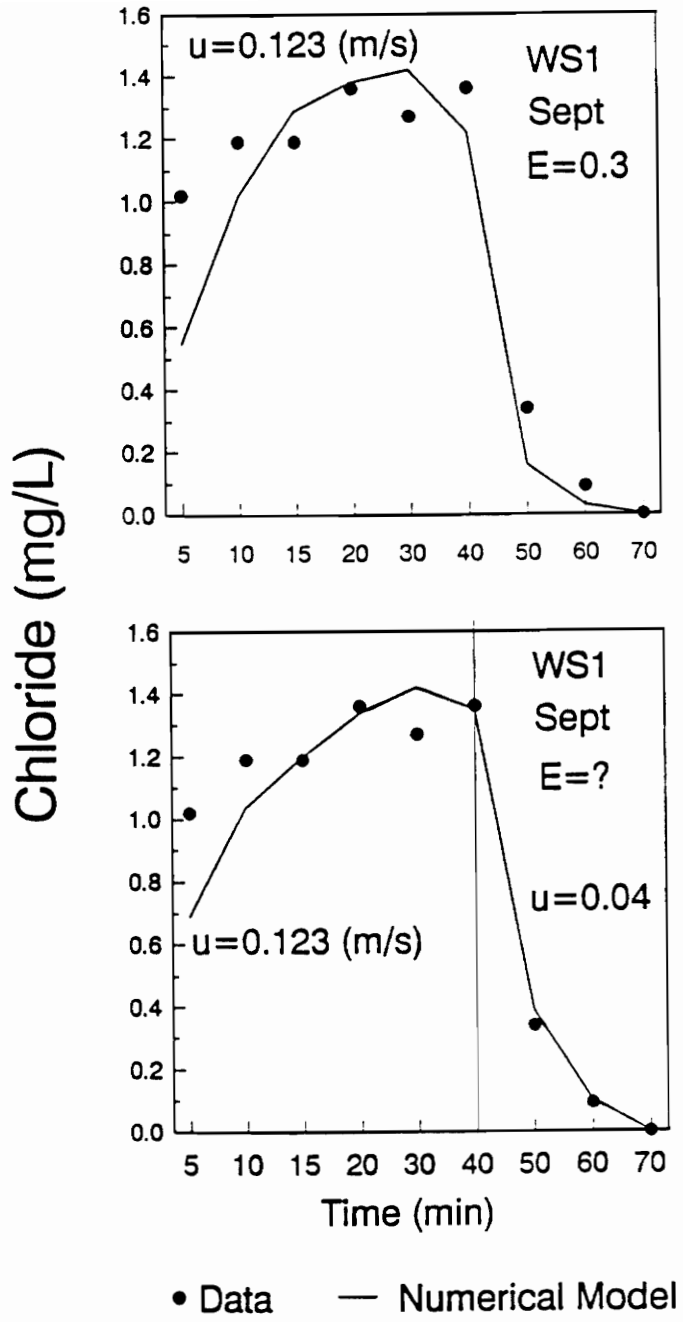

Figure 36. **Example chloride curves for a natural stream in September.:** u = velocity (m/s) and E = dispersion (m&sup2/s). The upper panel shows the fit between data and model output when a leading edge velocity (u) of 0.123 m/s was used in the model. The lower panel shows the fit between data and model output when a leading edge velocity of 0.123 m/s was used to model the rise in chloride concentration and an average velocity of 0.04 m/s was used to model the decline in concentration.

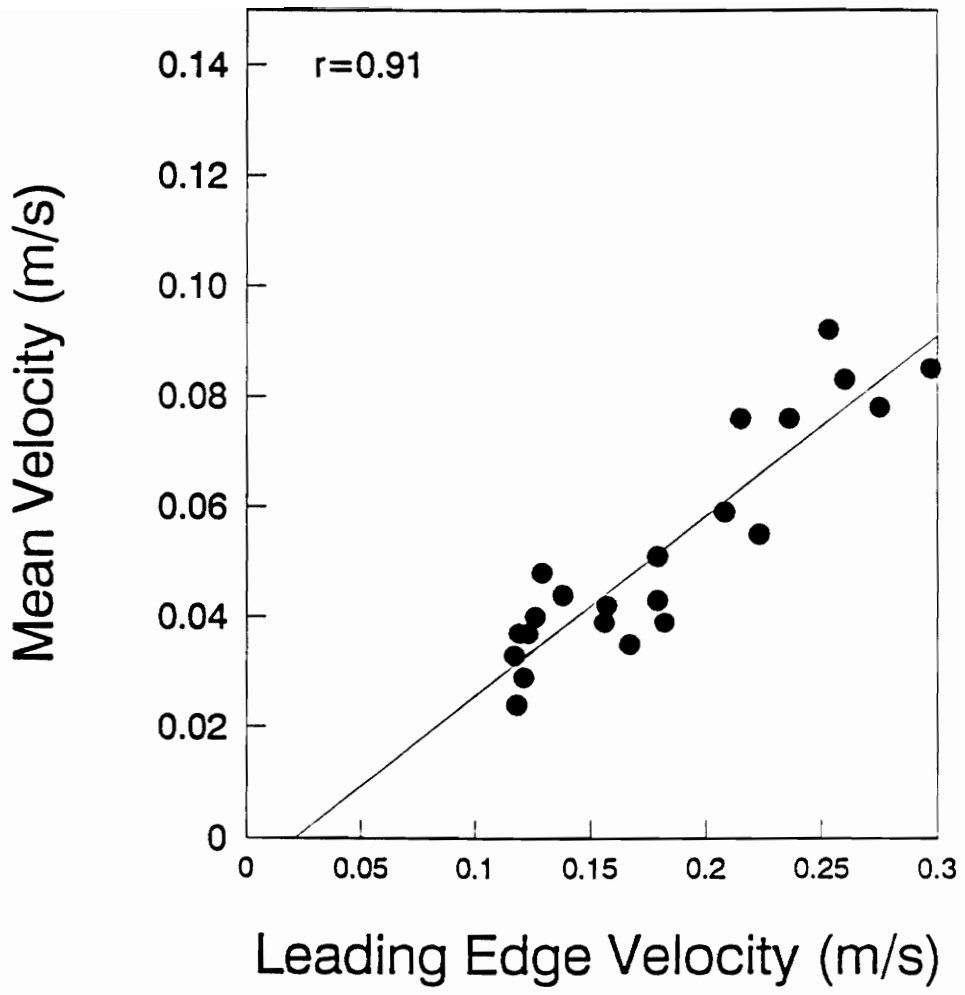

Figure 37. Leading edge velocity versus mean velocity for natural streams

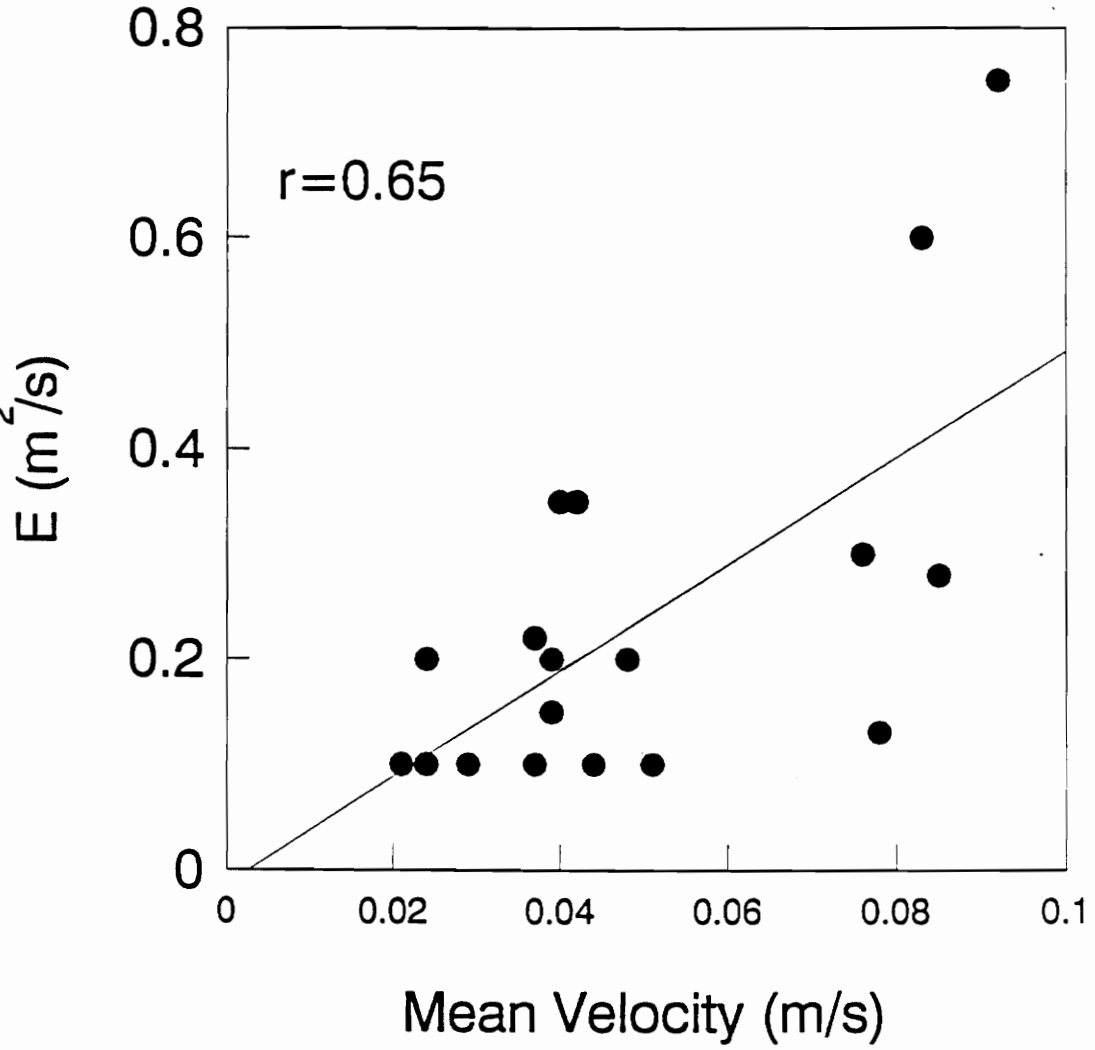

Figure 38. Dispersion (E) as a function of mean velocity for natural streams

Table 8. Dispersion in pine and hardwood watersheds

Mean Dispersion (m^2/scc) Vegetation Type	Pine (n = 3)	Hardwood (n = 3)
May	0.1	0.23
June	0.15	0.38
July	0.085	0.45
September	.14	0.22

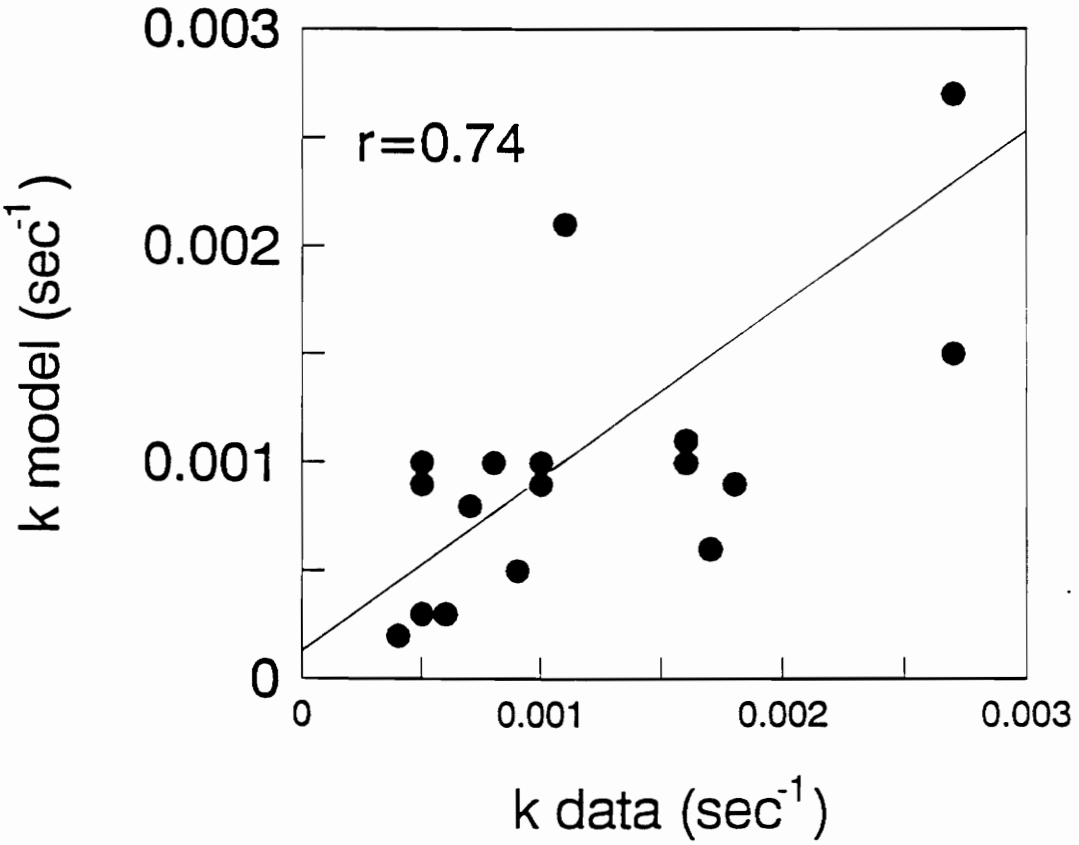

Figure 39. Regression of uptake rates from the model versus rates from natural streams field data ($p < 0.05$; Pearson).

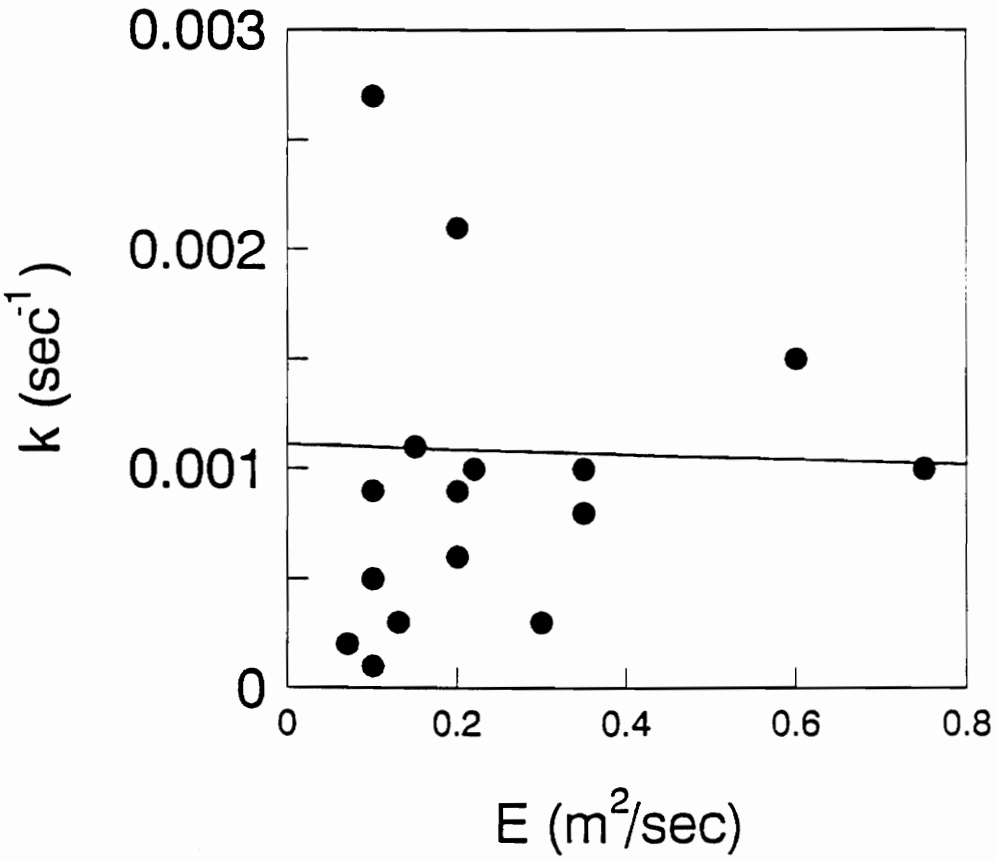

Figure 40. Regression of uptake rates (k) versus dispersion (E) in the natural streams.

sloping falling limb of the chloride curve require that a transient storage component be included in the model.

For both artificial and natural streams, dispersion was correlated with velocity. Dispersion was greater in the artificial streams with dogwood leaves than streams with oak leaves probably because the dogwood leaves more readily formed packs that dispersed the water. In the natural streams, dispersion was greater in the hardwood streams because the wider more meandering channels and hardwood leaf species provided more obstacles to get around than the narrower more deeply encised pine streams that contained mostly mats of pine needles that should be more porus.

Quantitative analyses of solute data, even with these simplistic mathematical models, provided information that could not be obtained from direct analysis or manipulation of field data. Model output showed that factors such as leaf type and stream bed morphology alter velocity and dispersion. Leaf type and stream bed geomorphology can then be quantitatively accounted for when comparing streams of different sizes and from different biomes. Quantification then sets the stage to determine if physical factors such as debris dams and channel morphology are fundamental properties of streams that govern solute dyanamics, or whether they just add variability that is masking the inherent biological properties that produce stream specific or biome specific stream solute dynamics.

This model will ultimately be used to compare transport and retention in stream of different size and morphology and in streams in different biomes. Here I have begun a systematic use and verification of the model by analyzing transport, dispersion, and uptake kinetics in an artificial stream system with constant area, discharge, and velocity and progressed to examining these processes in natural streams draining white-pine and mixed-hardwood watersheds. The model used to simulate solute transport is not entirely effective because it does not include transient storage. However, running the model

without transient storage allowed me to determine what streams (and under what conditions) could be modeled effectively without taking transient storage into account and what streams and under what conditions transient storage was required to provide a good fit. Transient storage components can then be added to the model to provide a more complete analysis of retention mechanisms.

7.0 Literature Cited

Ball, R.C., and F.F. Hooper. 1961. Translocation of phophorus in a trout stream ecosystem. Pages 217-228. *in* V. Schultz and A.V. Klement, Jr., eds. Radioecology. Reinhold, New York, NY USA.

Barlocher, F., 1985. The role of fungi in the nutrition of stream invertebrates. Botanical Journal of the Linnean Society 91:83-94.

Barlocher, F., and B. Kendrick. 1974. Dynamics of the fungal populations on leaves in a stream. Journal of Ecology 62:761-791.

Bencala, K.E. 1983. Simulation of solute transport in a mountain pool-and-riffle stream with a kinetic mass transfer model for sorption. Water Resour. Res. 19(3):732-738.

Bencala, K.E. and R.A. Walters. 1983. Simulation of solute transport in a mountain pool-and-riffle stream: a transient storage model. Water Resour. Res. 19:718-724.

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

Benfield, E.F., R.W. Paul, J.R. Webster. 1979. Influence of exposure technique on leaf breakdown rates in streams. Oikos 33:386-91.

Benfield, E. F., and J. R. Webster. 1985. Shredder abundance and leaf breakdown in an Appalachian Mountain stream. Freshwater Biology 15:113-120.

Bond, H.W.. 1979. Nutrient concentration patterns in a stream draining a montane ecosystem in Utah. Ecology 60:1184-1196.

Bothwell, M.L. 1985. Phosphorus limitation of lotic periphyton growth rates: An inter-site comparison using continuous-flow troughs (Thompson River system, British Columbia). Limnology and Oceanography 30:527-542.

Bormann, F.H., G.E. Likens, T.G. Siccama, R.S. Pierce, and J.S. Elton. 1974. The export of nutrients and recovery of stable conditions following deforestation at Hubbard Brook. Ecological Monographs. 44:255-277.

Brock, T.C. M., C.A.M. Huijbregts, M.J.H.A. Van de Steeg-Huberts, M.A. Vlassak. 1982. In situ studies on the breakdown of *Nymphoides peltata* (Gmel.) O. Kumtze (Menyanthaceae); some methodological aspects of the litter bag technique. Hydrobiol. Bull. 16:35-49.

Brock, T.C.M., M.J.H. DeLyon, E.M.J.M. VanLaar, and E.M.M. VanLoon. 1985. Field studies on the breakdown of *Nuphar lutea* (L.)SM. (Nymphaeaceae), and a comparison of three mathematical models for organic weight loss. Aquatic Botany 21:1-22.

Brown,G.W. and J.T. Krygier. 1971. Clearcut logging and sediment production in the Oregon Coast Range. Water Resour. Res. 7:1189-1199.

Chamier, A.C., and P.A. Dixon. 1982. Pectinases in leaf decomposition by aquatic hyphomycetes I: the field study the colonization-pattern of aquatic hyphomycetes on leaf packs in a survey stream. Oecologia 52:109-115.

Chen, M.. 1974. Kinetics of phosphorus absorption by *Corynebacterium bovis.* Microbial Ecol. 1:164-175.

Chergui, H and E. Pattee. 1988. The effects of water current on decomposition of dead leaves and needles. Verh. Internat. Verein. Limnol. 23:1294-1298.

Corning, K.E., H.C. Duthie, B.J. Paul. 1989. Phosphorus and glucose uptake by seston and spilithon in boreal forest streams. J. N. Amer. Benthol. Soc. 8(2):123-133.

Cromack, K. Jr, and C.D. Monk. 1975. Litter production, decomposition, and nutrient cycling in a mixed hardwood watershed and a white pine watershed. Pages 609-624. *in* F.G. Howell, J.B. Gentry, M.H. Smith. (eds) Mineral Cycling in Southeastern Ecosystems.

Cuffney, T.F., J.B. Wallace, and J.R. Webster. 1984. Pesticide manipulation of a headwater stream: invertebrate responses and their significance for ecosystem processes. Freshwater Invertebrate Biology 3:153-171.

Cummins, K.W. 1974. Structure and function of stream ecosystems. Bioscience 24:631-41.

Cummins, K.W. 1989. Shredders and Riparian Vegetation. Bioscience. 39(1):24-30.

Cummins, K.W., R.C. Peterson, F.O. Howard, J.C. Wuycheck, V.I. Holt. 1973. The utilization of leaf litter by stream detritivores. Ecology 54:336-45.

Cummins, K.W., G.L., Spengler, G.M. Ward, R.M. Speaker, R.W. Ovink. 1980. Processing of confined and naturally entrined leaf litter in a woodland stream ecosystem. Limnol. Oceanogr. 25:952-957.

Douglass, J.E. and W.T. Swank. 1975. Effects of management practices on water quality and quantity: Coweeta Hydrologic Laboratory, North Carolina. Northeastern Experiement Station (USDA Forest Service Gen. Tech. Rep. NE-13).

Elder, J.W. 1959. The dispersion of marked fluid in turbulend shear flow. Journal of Fluid Mechanics. 5:544-560.

Elwood, J.W., J.D. Newbold, R.V. O'Neill, R.W. Stark, and P.T. Singley. 1981. The role of microbes associated with organic and inorganic substrates in phosphorus spiralling in a woodland stream. Verh. Internat. Verein. Limnol. 21:850-856.

Elwood, J.W., J.D. Newbold, R.V. O'Neill, and W. VanWinkle. 1983. Resource spiralling: an operational paradigm for analyzing lake ecosystems. *in* Fontaine, T.,

and S. Bartell, eds. Dynamics of Lotic Ecosystems, Ann Arbor Science Publ., Ann Arbor, Michigan.

Fairchild, J. F., T. P. Boyle, E. Robinson-Wilson, and J. R. Jones, 1984. Effects of inorganic nutrients on microbial leaf decomposition and mitigation of chemical pertubation. Journal of Freshwater Ecology 2:405-416.

Feeny,P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of Spring feeding by winter moth caterpillars. Ecology 51:565-581.

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.

Fisher, S.G., 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. Int. Revue ges. Hydrobiol. 62:701-727.

Frissel, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchial framework for stream habitat classification: viewing streams in a watershed context. Environ. Management 10:199-212.

Godshalk, G.L., and R.G. Wetzel, 1978. Decomposition of aquatic angiosperms. II. Particulate components. Aquatic Botany 5:301-327.

Golladay, S.W., J.R. Webster, and E.F. Benfield. 1989. Changes in stream benthic organic matter following watershed disturbance. Holartic Ecology. 12(2):96-105.

Golley,F.B. 1974. Structural and functional properties as they influence ecosystem stability. pages 97-102. *in* Proceedings of the First International Congress of Ecology. The Hague, Netherlands.

Gregory, S.V. 1978. Phosphorus dynamics on organic and inorganic substrates in streams. Verh. Internat. Verein. Limnol. 20:1340-1346.

Gregory, S.V., F.J. Swanson, W.A. Mckee. An ecosystem perspective of riparian zones. BioScience (in press).

Grimm, N.B. and S.G. Fisher. 1986. Nitrogen limitation in a Sonoran Desert stream. Journal of the North American Benthological Society 5:2-15.

Grimm, N.B. and S.G. Fisher. 1988. Role of macroinvertebrates in nitrogen dynamics of a desert stream. Ecology 69:1884-1893.

Hann, Roy W., Jr. and P.J. Young. 1971. Mathematical models of water quality parameters for rivers and estuaries. Tech. Report # 45. Water Resources Institute. Texas A&M University. 424p.

Hains, J.J. 1981. Response of stream flora to watershed perturbation. M.S. Thesis, Clemson University, Clemson.

Hart, B.T., P. Freeman, I.D. McKelvie, S. Pearse and D.G. Ross. in press. Phosphorus Spiralling in Myrtle Creek, Victoria, Australia. Verh. Internat. Verein. Limnol. 24:(in press).

Hauer, F.R., N.C. Poff, P.L. Firth. 1986. Leaf litter decomposition across broad thermal gradients in southeastern coastal plain streams and swanps. J. Freshwat. Ecol. 3:545-552.

Helvey, J.D. 1967. Interception by Eastern White Pine. Water Resour. Res. 3(3):723-729.

Hewlett, J.D. 1950. Pine and Hardwood Forest Water Yield. J. Soil and Water Conserv. 13:106-109.

Hobbie, J.E. and C.C. Crawford. 1969. Respiration corrections for bacterial uptake of dissolved organic compounds in natural waters. Limnol. Oceanogr. 14:528-519.

Howarth, R.W., and S.G. Fisher. 1976. Carbon, nitrogen, and phosphorus dynamics during leaf decay in nutrient enriched stream microecosystems. Freshwater Biology 6:221-228.

Iverson, T.M., J. Thorup, J. Skriver. 1982. Inputs and transformations of allochtnonous particulate organic matter in a headwater stream. Holarct. Ecol. 5:10-19.

King,G.M. and T.Berhman. 1984. Potential effects of isotopic dilution on apparent respiration in 14C heterotrophy experiments. Marine Ecology. 19:175-180.

Hynes, H.B.N. 1970. The Ecology of Running Waters. University of Toronto Press, Ontario, CANADA, 555 p.

Kaushik, W.K., and H.B.N. Hynes. 1968. Experimental study on the role of autumn shed leaves in aquatic environments. Journal of Ecology 56:229-245.

Kaushik, N.K., and H.B.N. Hynes, 1971. The fate of the dead leaves that fall into streams. Archiv fur Hydrobiologie 68:465-515.

Kirby, J.M., J.R. Webster, and E.F. Benfield. 1983. The role of shredders in detrital dynamics of permanent and temporary streams. Pages 425-435 *in* T.D.Fontaine, III, and S.M.Bartell, eds. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan.

Lieberman, J.A. and M.D. Hoover. 1948. The effect of uncontrolled logging on stream turbidity. Wat. and Sewage Works. 95:255-258.

Lock, M.A., and P.H. John, 1979. The effect of flow patterns on uptake of phosphorus by river phytoplankton. Limnology and Oceanography 29:376-382.

McColl, R.H.S. 1974. Self-purification of small freshwater streams: phosphate, nitrate and ammonia removal. N.Z. J. Marine and Freshwater Res. 8(2):375-388.

McIntire, C.D. 1966. Some effects of current velocity on periphyton communities in laboratory streams. Hydrobiol. 27:559-570.

Melillo, J.M., J.D. Aber, and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621-626.

Meyer, J.L.. 1979. The role of sediments and bryophytes in phosphorus dynamics in a headwater stream ecosystem. Limnology and Oceanography 24:365-376.

Meyer, J.L.. 1980. Dynamics of phosphorus and organic matter during leaf decomposition in a forest stream. Oikos 34:44-53.

Meyer, J.L., and G.E. Likens. 1979. Transport and transformation of phosphorus in a forest stream ecosystem. Ecology 60(6):1255-1269.

Meyer, J.L., G.E. Likens, and J. Sloane. 1981. Phosphorus, nitrogen, and organic carbon flux in a headwater stream. Arch. Hydrobiol. 91:28-44.

Meyer, J.L., and C. Johnson. 1983. The influence of elevated nitrate concentration on rate of leaf decomposition in a stream. Freshwater Biology 13:177-183.

Meyer, J.L., W.H. McDowell, T.L. Bott, J.W. Elwood, C. Ishizaki, J.M. Melack, B.L. Peckarsky, B.J. Peterson, and P.A. Rublee. 1988. Elemental dynamics in streams. N. Amer. Benthol. Soc. 7:410-432.

Minshall, G.W. 1967. Role of allochthanous detritus in the trophic structure of a woodland springbrood community. Ecology 48:139-49.

Monk, C.D., D.A. Crossley, W.T. Swank, R.L. Todd, J.B. Waide, J.R. Webster. 1977. An overview of nutrient cycling research at Coweeta Hydrologic Laboratory. pages 505-526. *In* D.L. Correll (ed.) Watershed Reserach in Eastern North America, Smithsonian, Washington, D.C.

Mulholland, P.J., J.W. Elwood, J.D. Newbold, J.R. Webster, L.A. Ferren and R.E. Perkins. 1984. Phosphorus uptake by decomposing leaf detritus: Effect of microbial biomass and activity. Verh. Internat. Verein. Limnol. 22:1899-1905.

Mulholland, P.J., J.W. Elwood, J.D. Newbold, and L.E. Ferren. 1985a. Effect of a leaf-shredding invertebrate on organic matter dynamics and phosphorus spiralling in heterotrophic laboratory streams. Oecologia 66:199-206.

Mulholland, P.J., J.D. Newbold, J.W. Elwood, and L.E. Ferren and J.R. Webster, 1985b. Phosphorus spiralling in a woodland stream: seasonal variations. Ecology 66:1012-1023.

Mutch, R.A., and R.W. Davies. 1984. Processing of willow leaves in two Alberta Rocky Mountain streams. Holarctic Ecology 7:171-176.

Mutch, R.A., R.J. Steedman, S.B. Berte, and G. Pritchard. 1983. Leaf breakdown in a mountain stream: a comparison of methods. Hydrobiologia 97:89-108.

Naiman,R.J. and J.M. Melillo. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). Oecologia 62:150-155.

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

Newbold, J.D., P.J. Mulholland, J.W. Elwood, and R.V. O'Neill. 1982a. Organic carbon spiralling in stream ecosystems. Oikos. 38:266-272.

Newbold, J.D., P.J. Mulholland, J.W. Elwood, and R.V. O'Neill. 1982b. Nutrient spiralling in streams: implications for nutrient limitation and invertebrate activity. American Naturalist 120:628-652.

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 spiralling. Ecology 64:1249-1265.

Nykvist, N.. 1963. Leaching and decomposition of water-soluble organic substances from different types of leaf and needle litter. Studia Forestalia Suecica 3:1-29.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164: 262-270.

O'Neill,R.V., W.F. Harris, B.S. Ausmus, and D.E. Reichle. 1975. A theoretical basis for ecosystem analysis with particular reference to elemental cycling. *In* F.G. Howell, J.B. Gentry, and M.H. Smith (eds.) Mineral cycling in Southeastern ecosystems. ERDA Symposium Series, Washington, D.C.

O'Neill, R.V. and D.E. Reichle. 1980. Dimensions of ecosystem theory. pages 11-26 *In* R.H. Waring (ed.), Rorests: fresh perspectives from ecosystem analysis. Oregon St. Univ. Press, Corvallis.

Paul, R.W.,Jr, E.F. Benfield, and J. Cairns Jr. 1983. Dynamics of leaf processing in a medium-sized river. Pages 403-423 *in* T.D. Fontaine III and S.M. Bartell, eds. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, MI.

Peters, G.T., E.F. Benfield, and J.R. Webster. 1989. Chemical composition and microbial activity of seston in a southern Appalachian headwater stream. J. N. Am. Benthol. Soc. 8(1):74-84.

Petersen, R.C., and K.W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biology 4:345-368.

Reynolds, B.C., and J.M. Deal. 1986. Procedures for chemical analysis at the Coweeta Hydraulic Laboratory.

Rosset, J., F. Barlocher, and J.J. Oertli. 1982. Decomposition of conifer needles and deciduous leaves in two black forest and two Swiss jura streams. Intern. revue gesonten Hydrobiologie 67:695-711.

Rounick, J.S., and M.J. Winterbourn. 1983. Leaf processing in two contrasting beech forest streams: Effects of physical and biotic factors on litter breakdown. Arch. Hydrobiol 96:448-74.

Sedell, J.R., F.J. Triska, and N.S. Triska. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams: I weight loss and associated invertebrates. Verh. Internat. Verein. Limnol. 19:1617-1627.

Simmons, B.L. and D.M.H. Cheng. 1985. Rate and pathways of phosphorus assimilation in the Nepean River at Camden, New South Wales. Water Res. 19:1089-95.

Smith, D.L. 1986. Leaf litter processing and the associated invertebrate fauna in a tallgrass prairie stream. Amer. Midl. Nat. 116:78-86.

Solute Working Group. in press. Solute dynamics in stream. N. Amer. Benthol. Soc. (in press).

Stanford, J.A. and J.V. Ward. 1988. The hyporheic of river ecosystems. Nature 335: 64-66.

Suberkropp, K., and M.J. Klug. 1976. Fungi and bacteria associated with leaves during processing in a woodland stream. Ecology 57:707-719.

Suberkropp, K., and M.J. Klug. 1980. The maceration of deciduous leaf litter by aquatic hyphomycetes. Canadian Journal of Botany 58:1025-1031.

Suberkropp, K, G.L. Godshalk, and M.J. Klug. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. Ecology 57:720-727.

Suberkropp, K., G.L. Godshalk, and M.J. Klug. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. Ecology 57:720-727.

Suberkropp, K., and M.J. Klug. 1981. Degredation of leaf litter by aquatic hyphomycetes. pages 761-766 *in* D.T. Wicklow and G.C. Carroll (eds.). The fungal community. Marcel Dekker Inc. NY.

Suberkropp, K., T.L. Arsuffi, and J.P. Anderson, 1983. Comparison of degrative ability, enzymatic ability, and palatability of aquatic hyphomycetes grown on leaf litter. Applied Environ. Micro. 46:237-244.

Superkropp, K., T.L. Arsuffi, and J.P. Anderson. 1983. Comparison of degradative ability, enzymatic activity, and palatability of aquatic hyphomycetes grown on leaf litter. Appl. Environ. Micro. 46(1):237-244.

Swank, W.T. and D.A. Crossley. 1988. Introduction and site description. pages 3-16 *in* W.T. Swank and D.A. Crossley (eds.). Ecological Studies, Vol 66: Forest Hydrology and Ecology at Coweeta. Springer-Verlag. New York. pp469

Swank, W.T. and N.H. Miner. 1968. Conversion of Hardwood-Covered watersheds to white pine reduces water yield. Water Resources Research 4(5):947-954.

Swank, W.T. and J.E. Douglass. 1974. Streamflow greatly reduced by converting deciduous hardwood stands to pine. Science. 185:857-859.

Swank, W.T. and J.E. Douglass. 1977. Nutrient budgets for undisturbed and manipulated hardwood forest ecosysems in the mountains of North Carolina pages 343-362 *in* D.L. Correll (ed.). Watershed Research in Eastern North America. Workshop to compare results. Smithsonian Institute, Edgewater, NJ.

Swank,W.T.,L.W. Swift Jr., and J.E. Douglass. 1988. Streamflow changes associated with forest clearcutting, species conversions, and natural disturbances pages 297-312 *in* W.T. Swank and D.A. Crossley (eds.). Ecological Studies, Vol 66: Forest Hydrology and Ecology at Coweeta. Springer-Verlag. New York. pp469

Swank, W.T. 1988. Stream chemistry responses to disturbance. pages 339-357 *in* W.T. Swank and D.A. Crossley (eds.). Ecological Studies, Vol 66: Forest Hydrology and Ecology at Coweeta. Springer-Verlag. New York. pp469

Swift, L.W. Jr. 1982. Duration of stream temperature increases following forest cutting in the southern Applachian mountains. Proc. Int. Symp. Hydrometeorol. 273-275.

Swift, L.W. Jr. and J.B. Messer. 1971. Forest cuttings raise temperatures of small streams in the southern Applachians. J. Soil Water Conserv. 26:111-116.

Thomas, W.A.. 1970. Weight and calcium losses from decomposing tree leaves on land and in water. The Journal of Applied Ecology 7:237-242.

Thomann, R.V. 1973. Effect of longitudinal dispersion on dynamic water quality response of streams and rivers. Water Resources Research. 9:355-366.

Thomann, R.V. and J.A. Mueller. 1987. Principles of Water Quality Modeling and Control. Harper and Row, Publishers, NY. 644p.

Triska, F.J.. 1970. Seasonal distribution of aquatic hyphomycetes in relation to the disappearance of leaf litter from a woodland stream. Doctoral Dissertation. University of Pittsburg. 189p.

Triska, F.J., and J.R. Sedell. 1976. Decomposition of four species of leaf litter in response to nitrate manipulation. Ecology 57:783-792.

Triska, F.J., J.R. Sedell, and S.V. Gregory. 1982. Coniferous forest streams. pages 292-332. *in* R.L. Edmonds (ed.). Analysis of coniferous forest ecosystems in the Western United States. Hutchinson Ross Publ. Co. Stroudsburg, PA.

Triska, F.J., V.C. Kennedy, R.J. Avanzino, and B.N. Reilly. 1983. Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton comminities. Pages 129-159 *in* T.D. Fontaine and S.M. Bartell (eds). Dynamics of Lotic Ecosystems. Ann Arbor Science, USA.

Triska, F.J., V.C. Kennedy, R.J. Avanzino, G.W. Zellweger, and K.E. Bencala. 1989. Retention and transport of nutrients in a third-order stream: channel process. Ecology 70(6):1877-1892.

Van Voris, P., R.V. O'Neill, W.R. Emanuel and H.H. Shugart Jr. 1980. Functional complexity and ecosystem stability. Ecology 61(6):1352-1360.

Vitousek, P.M. and W.A. Reiner. 1975. Ecosystem succession and nutrient retention: A hypothesis. Bioscience 25(6): 376-381.

Vincent, W.F., and M.T. Downs. 1980. Variation in nutrient removal from a stream by watercress (*Nasturtium officinale* R. Br.). Aquatic Botany 9:221-35.

Wagner, B.J. and S.M. Gorelick. 1986. A statistical methodology for estimating transport parameters: theory and applications to one-dimensional advective-dispersive systems. Water Resources Research 22:1303-1315.

Wallace, J.B., J.R. Webster, and T.F. Cuffney. 1982. Stream detritus dynamics: regulation by invertebrate consumers. Oecologia (Berl.) 53:197-200.

Webster, J.R.. 1975. Analysis of potassium and calcium dynamics in stream ecosystems on three southern Appalachian watersheds of contrasting vegetation. Doctoral dissertation. University of Georgia, Athens, Georgia, USA.

Webster, J.R., and B.C. Patten. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. Ecological Monographs 49:51-72.

Webster, J.R., and J.B. Waide. 1982. Effects of forest clear cutting and leaf breakdown in a southern Appalachian stream. Freshwater Biology. 12:331-334.

Webster, J.R. and W.T. Swank. 1985. Within-stream factors affecting nutrient transport from forested and logged watershed. pages 18-41. *in* Blackman (ed). Proceedings

of Forestry and Water Quality: A mid-South Symposium. University of Arkansas, Monticello, Arkansas.

Webster, J.R. and E.F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Amm. Rev. Ecol. Syst. 17:567-594.

Wetzel, R.G. 1983. Limnology. Saunders College Publishing. Philadelphia, PA. 753p.

Whitford, L.A., and G.J. Schumacher. 1964. Effect of a current on respiration and mineral uptake in *Spirogyra* and *Oedogonium*. Ecology 45:168-170.

Williams, P.J. and C. Askew. 1968. A method of measuring the mineralization by micro-organisms of organic compounds in seawater. Deep-Sea Research 15:365-375.

8.0 CURRICULUM VITAE

Donna J. D'Angelo
April, 1990

Personal Data: Date of Birth: 22 November 1962
Place of Birth: Steubenville, Ohio

Education:

1980-84	Wittenberg University, B.A.
1984-86	Michigan Technological University, M.S. Thesis title: Density-dependent growth fecundity and maturation in Lake Superior lake herring. Major Advisor: Dr. S.H. Bowen.
1986-90	Virginia Polytechnic Inst. and State University, Ph.D. Dissertation topic: Effects of watershed use on phosphorus retention in streams. Major Advisor: Dr. J.R. Webster.

Professional Experience:

1983	Summer Internship, Ecological Modeling, Savannah River Ecology Laboratory, Aiken, SC
1985-86	Research Assistant, Michigan Technological University
1986	Teaching Assistant, Developmental Biology, Michigan Technological University
1986	Physical Scientist (Modeling), NOAA, Great Lakes Environmental Research Laboratory, Ann Arbor, MI
1986-88	Teaching Assistant, General Biology, Aquatic Ecology, Field and Lab Ecology, Ecosystem Dynamics, VPI&SU
1988-90	Research Assistant, VPI&SU

Current Research Interests:

Nutrient and energy dynamics in stream ecosystems
Ecological modelling
Fish population dynamics
Macroinvertebrate community structure and function in streams