WITHIN-STREAM FACTORS AFFECTING NUTRIENT TRANSPORT FROM FORESTED AND LOGGED WATERSHEDS

J. R. Webster
W. T. Swank

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J. R. Webster¹
W. T. Swank²

ABSTRACT

Nutrient concentrations in stream water are the result not only of inputs from the adjacent forest but also of instream modifications of these inputs. Important instream processes include autotrophic and heterotrophic uptake, macroinvertebrate particle generation, and retention of dissolved and particulate nutrients by woody debris. Major changes in these processes occur following forest logging. As a result of these changes, streams in the southern Appalachian Mountains may have their lowest ability to retain nutrients 20 to 30 years after logging.

INTRODUCTION

Most watershed nutrient budgets are based on samples of exported nutrients taken from the stream at the base of the watershed. However, attempts to compare and explain differences in nutrient budgets are usually based entirely on processes occurring only on the terrestrial part of the watershed (e.g., Vitousek 1977, Bond 1979). Although stream area represents only about 1% of the watershed area, all runoff from the watershed must pass through the stream. Within the stream, significant uptake, mobilization, and transformation of nutrients can occur.

Many of the factors potentially affecting nutrient concentrations in small woodland streams are illustrated in Figure 1. Nutrient inputs come directly as channel interception of throughfall or indirectly as surface or subsurface runoff. Nutrients incorporated in leaves and other material from riparian vegetation also enter streams either directly (litterfall) or by being blown in from the stream bank (lateral movement). In some streams, nitrogen fixation can be significant (e.g., Horne and Carmiggelt 1975, Ward 1984). Major nutrient outputs are dissolved transport and transport of particulates as both bedload and suspended load. Gaseous outputs such as denitrification are also possible.

¹ Biology Department, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.
² Coweeta Hydrologic Laboratory, USDA Forest Service, Ottc, North Carolina 28763.
Figure 1. Factors affecting nutrient dynamics in a forest stream ecosystem.
A number of biotic and abiotic factors affect nutrient concentrations within streams (Fig. 1). Primary production by algae and moss takes dissolved nutrients out of the water column. These nutrients are subsequently returned to the stream by plant secretions, sloughing of particulate matter, and trophic interactions. Fungi and bacteria immobilize dissolved nutrients, but decomposition and nutrient mineralization eventually returns dissolved nutrients back to the water column. Meiofauna (rotifers, copepods, etc) and macroinvertebrates, by feeding on algae, moss, and detritus, play an important part in the comminution of particulate organic matter and also contribute to the mineralization of some nutrients. Important abiotic factors operating within the stream include adsorption onto sediments (e.g., Meyer 1979, Bencala et al. 1984), leaching from organic materials (e.g., Nykvist 1963), formation of particulates from dissolved materials (e.g., Lush and Hynes 1973, Mulholland 1981), and deposition and entrainment of particles.

Our objective in this paper is to discuss processes affecting concentrations of dissolved and particulate nutrients in streams, interactions between nutrients and woody debris, and effects of forest disturbance, particularly logging, on these processes. We will draw heavily on studies conducted at Coweeta Hydrologic Laboratory where we both have been conducting research for many years. Coweeta, a research laboratory operated by the USDA Forest Service, is located in western North Carolina in the southern Appalachian Mountains. Since the 1930's Coweeta has been a site of active hydrologic and forest management research, and, beginning in the 1960's, an interdisciplinary team of researchers has been investigating nutrient cycling in the aquatic and terrestrial ecosystems of the 2184-ha (5395-acre) laboratory.

FACTORS AFFECTING DISSOLVED NUTRIENT CONCENTRATIONS

It has often been observed that instream processes cause a net immobilization of dissolved nutrients (e.g., Kaushik and Robinson 1976, Kaushik et al. 1981). This immobilization is observed as a downstream decrease in concentrations of biologically important nutrients. Data from Big Hurricane Branch (Watershed 7, Coweeta Hydrologic Laboratory) taken before, during, and after logging suggest that for some nutrients instream processes are insignificant (Fig. 2). Na and K concentrations were similar throughout the stream from headwater sites downstream to the weir. Mg concentrations declined downstream during all three years. Since Mg concentrations in low elevation tributaries were lower than mainstream concentrations, we attribute this decline to variations in watershed geochemistry. Ca concentrations were very puzzling; there was a consistent decrease in concentration from the headwaters downstream about 600 m (1970 ft) and a subsequent increase in concentration. This trend cannot be explained by tributary inputs because the lowest elevation tributary had the lowest Ca concentration. We have no ready explanation for this trend; however, we suspect it is geochemical and not due to
Figure 2. Dissolved nutrient concentrations in Big Hurricane Branch (WS7, Coweeta) and its tributaries before, during, and after logging. Each data point is the mean of monthly samples taken for one year. (μg/L = ppb)
instream factors because there was no change in the logitudinal pattern as a result of logging.

Although soluble reactive phosphorus (SRP) concentrations are very low, data prior to logging showed a slight downstream decrease. It has been shown that the uptake length of radioactive SRP in Coweeta streams is very short, 7-25 m (23-82 ft) depending on season (Newbold, Elwood, Webster, and Wallace unpublished data). Thus our sampling of SRP in Big Hurricane Branch may not have been adequate to measure the very rapid instream changes in SRP concentrations. Further evidence for the rapid instream uptake of SRP comes from samples collected with porous cup lysimeters. Groundwater SRP concentration on WS 7 before logging averaged 100 μg/L (ppb) and after logging averaged 364 μg/L (ppb), both well above stream water concentrations. Other studies have also shown a very rapid uptake of dissolved P in streams (e.g., Rigler 1979, Newbold et al. 1983).

Prior to logging there was no evident downstream trend in NO$_3$-N concentration, but during and following logging, NO$_3$-N concentration was significantly higher at the source than downstream. This change may have been the result of either increased autotrophic uptake or denitrification (Swank and Caskey 1982). In general, NO$_3$-N concentrations during logging were as low or lower than prelogging concentrations, but by the following year NO$_3$-N levels were elevated. This increased loss of NO$_3$-N following forest disturbance has been demonstrated in several watershed studies at Coweeta (Swank and Douglass 1977) and other sites (e.g., Bormann and Likens 1979a), though for some sites the loss is fairly small (Vitousek et al. 1979, Vitousek and Melillo 1979). Attempts to explain the differences among sites have been based entirely on forest floor and soil mechanisms (Vitousek et al. 1979, Vitousek and Melillo 1979).

SO$_4$ concentrations (Fig. 2) are enigmatic. During all three years there was evidence of a downstream increase in SO$_4$ concentrations, suggesting instream SO$_4$ sources. However, S cycling in streams has not been well documented, making it difficult to speculate about instream SO$_4$ sources.

### Autotrophic Nutrient Uptake

Uptake of nutrients by primary producers in streams has been demonstrated in several studies (e.g., Grimm et al. 1981, Triska et al. 1983) but has not been directly studied at Coweeta. However, indirect estimates can be made from measurements of algal and moss production. Periphyton primary production is typically low for undisturbed Coweeta streams with estimated rates of 2.9 g dry weight (DW)/m$^2$/y (0.069 lb DW/ft$^2$/y) (Webster et al. 1983). In the first year after logging WS7, periphyton production increased to about 87 g DW/m$^2$/y (2.1 lb DW/ft$^2$/y) in response to canopy removal, increased solar insolation, and increased dissolved nutrients. In the subsequent two years, periphyton production approached baseline conditions.
Using data from WS7 before and after logging, we can estimate the importance of algal nutrient uptake. Based on a streambed area of 4034 m$^2$ (43,380 ft$^2$) (Webster 1983) and an estimate that algae are 0.7% nitrogen (Vallentyne 1974, in Wetzel 1975), algal uptake of N prior to logging would have been about 82 g/y (0.18 lb/y) or 1.8% of the annual N export as nitrate and ammonium. Similar, P uptake (based on algae P content of 0.08%) would have been 9 g (0.02 lb) or 0.2% of annual dissolved P export. In the year after logging, N uptake would increase to 2.4 kg (5.3 lb) and, accounting for the increase in dissolved inorganic N export, could equal 7.8% of N export. P uptake would be 281 g (0.62 lb) or 4.5% of dissolved export.

Hains (1981) found that primary production was highest in stream-areas containing both moss and epiphytic algae. He measured rates of primary production of 40 g DW/m$^2$/y (0.94 lb DW/ft$^2$/y) in moss covered areas of an unlogged stream and 333 g DW/m$^2$/y (7.9 lb/ft$^2$/y) in similar areas of a stream the first year after logging. Gurtz and Wallace (1984) estimated that 11% of the streambed area in Big Hurricane Branch (WS7) is rock face. Since much of this rock face habitat is covered by moss, inclusion of these areas in estimates of autochthonous nutrient uptake would result even greater estimates of autotrophic nutrient immobilization.

**Heterotrophic Nutrient Uptake**

Uptake of dissolved nutrients by heterotrophic microorganisms in streams is well documented (e.g., Hynes and Kaushik 1969, Kaushik and Hynes 1971, Triska et al. 1975, Howarth and Fisher 1976, Suberkropp et al. 1976, Gregory 1978, Triska and Buckley 1978, Meyer 1980, Elwood et al. 1981, Killingbeck et al. 1982). Such studies typically show that as leaves decompose, the percent composition of nutrients, especially nitrogen, increases. In a study comparing leaf composition in two streams at Coweeta, Meyer and Johnson (1983) also found this immobilization of N in one case. Because of the large mass of leaves that enter woodland streams, even a small uptake of dissolved nutrients could significantly alter dissolved nutrient concentrations, at least for a short period in autumn. For example, the allochthonous input to Big Hurricane Branch prior to logging was 568 g/m$^2$/y (13.5 lb/ft$^2$/y) (Webster and Waide 1982). Based on a streambed area of 4,034 m$^2$, (43,380 ft$^2$) this would be 2.3 T (2.5 ton) of leaves. If the nitrogen content of these leaves only increased 0.5% (e.g., from 2.0 to 2.5% of the AFDW, Meyer and Johnson 1983), this would cause the immobilization of 11 kg (24.3 lb) of nitrogen, or more than 200% of the annual export of dissolved inorganic N. While some of this N immobilization is temporary, an unknown fraction remains tied with organic matter and is exported in particular or dissolved organic form.

A study by Swank and Caskey (1982) demonstrated the potential influence of heterotrophic denitrifying microorganisms in Coweeta streams. This study was conducted in Big Hurricane Branch following logging on the watershed (WS7). The schedule of
treatments on WS7 and monthly weighted NO$_3$-N concentrations over a 4-year period for the headwater stream and watershed outlet (weir) are illustrated in Figure 3. In response to N leached from roadbank fertilization, NO$_3$-N concentrations increased markedly in the headwater stream, but 650 m (2100 ft) downstream at the weir, concentrations were only slightly elevated. A concentration difference of more than 150 µg/L (ppb) between headwater and weir sites were maintained during two years (1978, 1979) of the treatment period and then declined toward the end of 1980, primarily because of reduced headwater concentrations.

Calculation showed that in the year of road construction and logging, annual within stream NO$_3$-N depletion was 3.3 kg (6.6 lb), which represented 127 percent of the NO$_3$-N exported at the weir (Table 1). In each of the next two years, depletion was 27.9 kg (61.6 lb) N, but because of increased NO$_3$ discharge at the weir, the percentage of the total N export decreased to 99 and 43%. By 1980, stream depletion was 3.9 kg (8.6 lb), which represented only 5% of the total NO$_3$-N discharged at the weir. Other studies of stream N mass balances have implicated denitrification in sediments as a significant mechanism of N disappearance in well oxygenated streams (Kaushik et al. 1975, Hill 1979, 1983).

Direct evidence for denitrification in stream sediments of WS 7 was obtained in the fourth year of the treatment. Rates of denitrification varied substantially between sites, but analyses showed that the mean denitrifying enzyme activity at each site was positively correlated with total Kjaldahl N and organic matter and negatively correlated with sediment NO$_3$ concentrations (Swank and Caskey 1982). Activities measured at each site were projected to monthly rates of denitrification based on volumes of sediment at each site. The potential annual loss of N by denitrification was estimated as 1.7 kg (3.7 lb) N, compared to the mass balance calculation for the same year of 3.9 kg (8.6 lb) N shown

Table 1. Nitrate-N export and within stream depletion (kg/y) following watershed disturbance. Data from Swank and Caskey (1982). Below road estimates are based on N exported from all drainages below the road.

<table>
<thead>
<tr>
<th>Year (June-May)</th>
<th>NO$_3$-N exported</th>
<th>NO$_3$-N depletion</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Below road</td>
<td>Watershed outlet (weir)</td>
</tr>
<tr>
<td>1976-1977</td>
<td>5.9</td>
<td>2.6</td>
</tr>
<tr>
<td>1977-1978</td>
<td>55.9</td>
<td>28.0</td>
</tr>
<tr>
<td>1978-1979</td>
<td>108.7</td>
<td>76.3</td>
</tr>
<tr>
<td>1979-1980</td>
<td>83.9</td>
<td>80.0</td>
</tr>
</tbody>
</table>
Figure 3: Flow-weighted NO₃-N concentrations in Big Hurricane

From Swank and Caskey (1982), UN = \( \frac{1}{5} \) ppb
in Table 1. Concurrent measurements of denitrifying activity and depletion were made in only 1979-1980, but results suggest that sediment denitrification can be a major mechanism of N loss even in streams where NO\textsubscript{3}-N concentrations are quite low. Studies of NO\textsubscript{3} transformations in stream sediments of other ecosystems support this conclusion (Wyer and Hill, 1984).

**FACTORS AFFECTING PARTICULATE TRANSPORT IN STREAMS**

Likens et al. (1977) compared the relative importance of particulate and dissolved export from Hubbard Brook Watersheds. Their data indicate that particulate export is rather small for most nutrients except P and K. More extensive study of P export by Meyer and Likens (1979) showed that 81% of P was exported as particulates, with most of this particulate export occurring during storms. Studies at Coweeta have shown that particulate export of cations is small relative to dissolved export (Johnson and Swank 1975, Monk 1975, Webster and Patten 1979), though more recent measurements suggest that particulate transport of Ca and K may be as much as 10-20% of annual export (Golladay, unpublished data). Of greater importance is the particulate transport of P and N. At all times, particulate transport of P greatly exceeds dissolved transport. Also, Swank and Swank (1981) estimated that sediment export of N (suspended and bed load particles) may be more than ten times the dissolved N export from undisturbed Coweeta watersheds.

The importance of particulate transport during storms is illustrated in Table 2. For the three storms, particulate N and P averaged 72 and 88% of total transport respectively, while particles of potassium and calcium accounted for 22 and 21% of the total transport.

There are several potential sources of particulates transported from watersheds. These include terrestrial sources such as particles in surface and subsurface runoff and particles washed off the canopy and received by the stream as channel interception. However, both of these terrestrial sources are small in undisturbed streams. Surface runoff is rare in forested watersheds, though it can be an important source of particles following watershed disturbance such as commercial logging (e.g. Lieberman and Hoover 1948, Tebo 1955). Subsurface inputs to streams at Coweeta contain very low concentrations of particles (Webster and Golladay 1984). Also, recent measurements show that particulate nutrients in throughfall are much less important than dissolved nutrients (Golladay, unpublished data). These observations suggest that instream factors are the major sources of particle transport, and other evidence from studies of Coweeta streams suggests that biological sources are often more important than physical erosion and entrainment.

The Role of Macroinvertebrates in Particle Transport

Based on radioactive tracer studies of cations, Webster and Patten (1979) estimated that macroinvertebrates annually ingest
Table 2. Nutrient transport from WS 18 (Coweeta Hydrologic Laboratory) during three summer storms. Twenty to 25 samples were collected and analyzed during each storm and subsequently integrated with discharge data. TKN (total Kjeldahl nitrogen) includes NH$_4$-N and TP (total phosphorus) includes SRP (soluble reactive phosphorus). If SRP > TP, then total dissolved phosphorus = SRP. All numbers are g per storm or percent. Data from Golladay (unpublished).

<table>
<thead>
<tr>
<th></th>
<th>15 Jun 84</th>
<th>20 Jun 84</th>
<th>28 Aug 84</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NO$_3$-N</td>
<td>0.91</td>
<td>0.22</td>
<td>1.02</td>
</tr>
<tr>
<td>NH$_4$-N</td>
<td>1.80</td>
<td>1.52</td>
<td>0.34</td>
</tr>
<tr>
<td>TKN</td>
<td>4.67</td>
<td>10.27</td>
<td>2.05</td>
</tr>
<tr>
<td>Total dissolved N</td>
<td>5.58</td>
<td>10.49</td>
<td>3.07</td>
</tr>
<tr>
<td>Particulate TKN</td>
<td>20.80</td>
<td>24.00</td>
<td>6.90</td>
</tr>
<tr>
<td>Percent particulate</td>
<td>78.8%</td>
<td>69.6%</td>
<td>69.2%</td>
</tr>
<tr>
<td>Phosphorus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRP</td>
<td>0.18</td>
<td>0.13</td>
<td>0.01</td>
</tr>
<tr>
<td>TP</td>
<td>0.15</td>
<td>1.14</td>
<td>0.01</td>
</tr>
<tr>
<td>Total dissolved P</td>
<td>0.19</td>
<td>1.14</td>
<td>0.01</td>
</tr>
<tr>
<td>Particulate TP</td>
<td>1.43</td>
<td>3.59</td>
<td>1.27</td>
</tr>
<tr>
<td>Percent particulate</td>
<td>88.3%</td>
<td>75.9%</td>
<td>99.2%</td>
</tr>
<tr>
<td>Potassium</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dissolved</td>
<td>67.0</td>
<td>61.2</td>
<td>20.0</td>
</tr>
<tr>
<td>Particulate</td>
<td>16.0</td>
<td>24.2</td>
<td>5.0</td>
</tr>
<tr>
<td>Percent particulate</td>
<td>19.3%</td>
<td>28.3%</td>
<td>19.4%</td>
</tr>
<tr>
<td>Calcium</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dissolved</td>
<td>88.8</td>
<td>76.0</td>
<td>30.5</td>
</tr>
<tr>
<td>Particulate</td>
<td>11.2</td>
<td>40.5</td>
<td>6.2</td>
</tr>
<tr>
<td>Percent particulate</td>
<td>11.2%</td>
<td>34.7%</td>
<td>16.7%</td>
</tr>
</tbody>
</table>

as much as 80% of the leaf litter input to a small forest stream at Coweeta. Because of their low assimilation efficiencies, much of this detritus is returned to the stream as small particles. Webster (1983) developed a computer model to simulate the functional role of macroinvertebrates in streams and to integrate a variety of Coweeta stream studies. Simulations of particle transport in a second-order stream, Big Hurricane Branch, indicated that macroinvertebrates were responsible for 27% of annual particle transport. However, the importance of macroinvertebrate particle generation is much greater when only base flow is considered. During winter, macroinvertebrates produce 32% of baseflow particle transport, and during summer this fraction can be as great as 83%.
Webster's (1983) model suggested that macroinvertebrates become even more important in small headwater streams where nearly all baseflow particle transport can be attributed to their egestion. This model result is supported by an experimental study also conducted at Coweeta. Application of insecticide to a small stream reduced aquatic insect densities to < 10 percent of an untreated reference stream (Wallace et al. 1982a, Cuffney et al. 1985). Following reduction of macroinvertebrates, detrital processing rates were significantly reduced, leading to an accumulation of benthic organic matter and a significant reduction of transported particle concentrations (Table 3).

Table 3. Mean particulate organic matter concentrations (mg/L) in a insecticide treated and reference stream. Standard errors are in parenthesis. Data from Wallace et al. (1982a and unpublished). Asterisks indicate significant differences between treated and reference streams (t-test, α=0.05).

<table>
<thead>
<tr>
<th>Date</th>
<th>Treated Stream</th>
<th>Reference Stream</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pretreatment</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13 Oct 1979</td>
<td>1.95 (0.17)</td>
<td>*</td>
</tr>
<tr>
<td>1 Dec 1979</td>
<td>0.82 (0.02)</td>
<td>*</td>
</tr>
<tr>
<td>14 Feb 1980</td>
<td>0.57 (0.06)</td>
<td></td>
</tr>
<tr>
<td><strong>Following treatment</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 May 1980</td>
<td>0.45 (0.07)</td>
<td>*</td>
</tr>
<tr>
<td>13 Jun 1980</td>
<td>0.31 (0.03)</td>
<td>*</td>
</tr>
<tr>
<td>24 Jul 1980</td>
<td>0.10 (0.01)</td>
<td>*</td>
</tr>
<tr>
<td>3 Sep 1980</td>
<td>0.05 (0.02)</td>
<td>*</td>
</tr>
<tr>
<td>4 Oct 1980</td>
<td>0.05 (0.02)</td>
<td>*</td>
</tr>
<tr>
<td>7 Nov 1980</td>
<td>0.10 (0.01)</td>
<td>*</td>
</tr>
<tr>
<td>22 Nov 1980</td>
<td>0.05 (0.01)</td>
<td>*</td>
</tr>
<tr>
<td>3 Jan 1981</td>
<td>0.03 (0.01)</td>
<td>*</td>
</tr>
<tr>
<td>18 Feb 1981</td>
<td>0.61 (0.06)</td>
<td>*</td>
</tr>
<tr>
<td>9 May 1981</td>
<td>0.09 (0.01)</td>
<td>*</td>
</tr>
<tr>
<td>29 Apr 1982</td>
<td>0.35 (0.11)</td>
<td>*</td>
</tr>
<tr>
<td>20 Jun 1982</td>
<td>0.78 (0.15)</td>
<td>*</td>
</tr>
<tr>
<td>12 Jul 1982</td>
<td>1.68 (0.79)</td>
<td>*</td>
</tr>
<tr>
<td>25 Aug 1982</td>
<td>1.01 (0.32)</td>
<td>*</td>
</tr>
<tr>
<td>3 Oct 1982</td>
<td>0.63 (0.14)</td>
<td>*</td>
</tr>
<tr>
<td>23 Oct 1982</td>
<td>1.50 (0.54)</td>
<td></td>
</tr>
<tr>
<td>13 Dec 1982</td>
<td>0.38 (0.10)</td>
<td>*</td>
</tr>
</tbody>
</table>
THE ROLE OF WOODY DEBRIS IN STREAMS

The amount of woody debris in streams is highly variable, ranging from 4 to 140 kg/m² (95-3300 lb/ft²) (Anderson et al. 1978, Naiman and Sedell 1979, Triska and Cromack 1980, Swanson et al. 1982). Natural sources of wood include tree death, wind, fire, icing, bank cutting, and debris avalanches (Keller and Swanson 1979). Of these, the ones most important in small Coweeta streams are tree death (especially chestnut blight in the 1930's) and wind. Additionally, large amounts of wood debris may be added to streams by logging. Losses of wood result from decomposition, invertebrate consumption, abrasion, leaching, flotation, and debris torrents. In small streams, losses occur very slowly and residence times of large Douglas fir logs may be up to 500 years (Swanson et al. 1976, Anderson et al. 1978, Anderson and Sedell 1979, Triska and Cromack 1980). At Coweeta, residence times are probably much shorter, as most hardwood logs decay much faster than Douglas fir logs (MacMillan 1981, Molles 1982). However, corduroy road material from logging prior to 1920 and chestnut logs dating from the chestnut blight are still present in some Coweeta streams. A survey of debris dams in Coweeta streams showed that first-order streams draining undisturbed watersheds have about 28 debris dams per 100 m (330 ft). Bilby and Likens (1980) found an average of 34 debris dams per 100 m in first-order Hubbard Brook streams and 14 per 100 m in second-order streams. In general, debris accumulations are greatest in headwater streams and decrease downstream (Anderson et al. 1978, Naiman and Sedell 1979, Bilby and Likens 1980, Wallace et al. 1982b, Triska et al. 1982).

Effects of woody debris on sediment transport and sediment routing have been widely studied. There appear to be at least four ways in which logs reduce sediment transport. The stepped profile caused by logs reduces the gradient over most of the stream, effectively reducing stream power and therefore the ability of streams to carry sediment (Heede 1972, Keller and Swanson 1979, Swanson et al. 1982). Logs also form pools in which sediments settle (Swanson and Lienkaemper 1978, Keller and Swanson 1979, Mosley 1981). Branches, leaves, and small organic particles that accumulate behind logs filter finer particulate material from the stream (Swanson and Lienkaemper 1978, Triska et al. 1982). Logs also affect the rate at which sediment is added to streams by hillslope processes. While in some cases logs may accelerate sediment inputs from bank cutting and lateral channel migration, in general, large woody debris stabilizes sediment transport (Swanson et al. 1982).

Bilby and Likens (1980) and Bilby (1981) clearly demonstrated the stabilizing influence of debris dams in low-order Hubbard Brook streams. When woody debris was removed from a second-order stream, export of particulate material increased more than 500%. Debris dam removal caused a 13% increase in the annual transport of dissolved organic carbon (Bilby and Likens 1980); however, there was no discernable effect on nonstorm concentrations of dissolved inorganic nutrients (Bilby 1981). Changes
In annual nutrient budgets were attributed entirely to the increase in particulate transport.

There are other possible effects of woody material on stream nutrients. Anderson et al. (1978) suggested that logs provide a long term nutrient source. As has been found for logs on the forest floor (e.g., Cornaby and Waide 1973), wood in streams may be an important site of nitrogen fixation (Buckley and Triska 1978, Triska et al. 1984). Logs are also a direct food resource for many microorganisms and invertebrates (Anderson et al. 1978, Anderson and Sedell 1979, Triska and Cromack 1980, Triska et al. 1982) and may buffer the energy base when other foods are unavailable (Swanson et al. 1982). Probably more important than its role as a carbon resource, however, is the importance of wood as a habitat for invertebrates and fish (Swanson et al. 1976, Anderson and Sedell 1979, Triska and Cromack 1980) and the interactions between wood and nutrient dynamics (e.g., Triska et al. 1984).

**SUCCESSION AND NUTRIENT DYNAMICS IN STREAMS**

Odum (1969) defined ecological succession as an orderly process of community development resulting in modification of the physical environment. As succession proceeds, community production and respiration tend to become balanced, net import and export of materials decreases, and there is often a shift in trophic structure from simple herbivore based food chains to complex detritus based food webs. These factors lead to a greater capacity to entrap and retain nutrients and thus mature ecosystems have been characterized as having very tight nutrient cycles (Odum 1969).

Secondary succession, especially as a response to logging, has been extensively studied in eastern deciduous forests. Following logging, forests may lose large quantities of organic materials and nutrients (e.g., Bormann and Likens 1979a). As vegetation becomes reestablished, nutrient losses decline. During intermediate stages of succession (20-60 years following logging in eastern deciduous forests), forest ecosystems are typically very productive and begin to accumulate organic material and inorganic nutrients (Bormann and Likens 1979a). Marks and Bormann (1972), Johnson and Swank (1973), Vitousek and Reiners (1975), and Vitousek (1977) reported that concentrations of some nutrient in streams draining intermediate age forests were lower than in mature forests due to greater nutrient uptake by the rapidly growing stands. In contrast to the generality proposed by Odum (1969), Vitousek (1977) and Vitousek and Reiners (1975) suggested that tightest nutrient cycles exist during intermediate stages of forest succession.

Successional Response of Streams to Forest Logging

During succession following logging, stream ecosystems are hypothesized to exhibit a very different pattern of nutrient retention than surrounding terrestrial ecosystems: nutrient retention in streams is high prior to logging, decreases slightly
following logging, decreases further during intermediate stages of forest succession, and then increases as the forest matures (Golladay and Webster, unpublished). The basis of this postulate is the importance of woody debris in streams and the changes in woody debris accumulations that occur following logging.

Likens and Bilby (1982), Molles (1982), and Swanson et al. (1982) proposed the relationships between forest succession and accumulation of detritus in streams illustrated in Figure 4. When the forest is cut, allochthonous leaf inputs are greatly reduced initially (Webster and Waide 1982), and autochthonous production increases due to absence of shading and increased stream nutrient concentrations (Gregory 1979, Hains 1981). The pulse of primary production lasts only a few years as rapid regrowth of riparian vegetation returns the stream to a detritus base (Likens and Bilby 1979, Swanson et al. 1982).

As a result of changes in leaf input, there is a rapid initial decline in the standing crop of non-woody detritus. As leaf input increases, the standing crop of detritus slowly increases. The slow increase of detritus standing crop (LPOM in Fig. 4) is the result of several factors. Webster and Waide (1982) showed that conditions two years after logging resulted in accelerated leaf breakdown, and the species composition of leaf inputs was shifted toward species with more rapid breakdown. Also, Webster et al. (1985) documented continued high loss of particulate organic matter from streams for 15 or more years following logging.

Depending on logging practices, there may be a substantial input of wood debris from logging slash. This input may last for several years as the residue above the stream rots, breaks, and falls into the channel. For the next 5-20 years the watershed is dominated by rapidly growing successional vegetation, and there is little wood input to the stream (Likens and Bilby 1982, Swanson et al. 1982). In the ensuing years there may be some death of successional vegetation adjacent to the stream. Likens and Bilby (1982) suggested that in the White Mountains of New Hampshire pin cherry death would be a significant wood input, and Swanson et al. (1982) hypothesized that a similar wood input would occur in Oregon after 30-60 years when upslope conifers shade out deciduous riparian species. In the southern Appalachians, black locust (Robinia pseudoacacia) often dominates watersheds following logging (Boring et al. 1981), and many black locusts die after 15-20 years, due to infection by locust stem borers and other insects (Schowalter 1981).

Following this period of wood input from the death of successional vegetation, there may be a period of lower wood input until the forest matures. In northern hardwoods this may require about 200 years (Bormann and Likens 1979b), and in Douglas fir forests of Oregon it may require as much as 400 years (Swanson et al. 1982). In the southern Appalachians the time until significant tree mortality begins may be less than 100 years, and in some cases a period of reduced wood input may not occur.
Figure 4. Hypothetical trends in organic matter inputs and standing crops following logging. Modified from Likens and Bilby (1982), Molles (1982), and Swanson et al. (1982). Data points are from various Coweeta studies. LPOM is large particulate organic matter.
The standing crop of woody debris in streams may reflect the pattern of inputs shown in Figure 4. However, Swanson et al. (1982) suggested that slow decomposition rates enable Douglas fir logs to remain in streams long enough to continue controlling stream environments until post-disturbance stands begin to contribute woody material. However, this may not be the case in deciduous forests because of the faster decompostion of hardwood logs. Eleven years after deforestation (without timber removal) of WS 2 at Hubbard Brook, the number of debris dams was approximately 50% that of similar but undisturbed streams (Bilby 1981, Likens and Bilby 1982). Data from Coweeta streams show a similar decrease in debris dams during succession (Table 4). However, the pattern is highly dependent on logging practices -- how much slash fell in the stream, was slash removed from the stream, and how large was the material left in the stream. If the treatments to Coweeta watersheds represent what would happen following commercial logging, then the minimum standing crop of woody debris probably occurs 20-30 years after logging. The decrease in woody debris and its subsequent slow accumulation would also delay accumulation of non-woody detritus.

Based on the trends shown in Figure 4, streams draining successional forests should have the least ability to retain nutrients. Canopy shading is by this time sufficient to limit instream primary production and associated nutrient uptake. Because of the absence of woody debris, few of the leaves that fall in the stream are retained, thus reducing heterotrophic nutrient uptake. Finally, without the stabilizing effect of woody debris, losses of particulates from the stream bed are high, especially during storms. Investigation of these trends is one of the objectives of current long-term research at Coweeta.

SUMMARY

We have discussed a variety of instream factors that affect nutrient concentrations in streams draining undisturbed forested watersheds. There is evidence that, because of these factors, concentrations of some nutrients may be quite different than when they first left the terrestrial part of the watershed. Logging may affect stream nutrient transport in two ways -- by altering input of nutrients to the stream or by altering instream nutrient processes. Most studies have concentrated on changes in terrestrial systems and thus on inputs to streams. In this paper we have discussed effects of logging and subsequent forest succession on instream processes. Due to a variety of factors including decreases in canopy shading, rates of allochthonous inputs, and accumulation of woody debris, streams draining successional watersheds are least retentive of nutrients.
Table 4. Frequency of woody debris dams in Coweeta streams. In this survey a debris dam was defined as an aggregation of organic material spanning the stream that included woody material with a diameter greater than 2.5 cm (1 in.). At least 150 m (392 ft) of each stream were surveyed. Data from Webster et al. (1985).

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Treatment History</th>
<th>Frequency of Debris Dams, No./100 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>Clearcut, 1958, slash burned; converted to grass, 1959; succession since 1967</td>
<td>1.3</td>
</tr>
<tr>
<td>7</td>
<td>Commercial clearcut, 1977</td>
<td>25.4</td>
</tr>
<tr>
<td>13</td>
<td>Clearcut but no products removed, 1939 and 1962</td>
<td>12.0</td>
</tr>
<tr>
<td>17</td>
<td>Clearcut but no products removed, 1940; recut annually; white pine planted, 1956</td>
<td>11.3</td>
</tr>
<tr>
<td>19</td>
<td>Understory vegetation cut, 1948-1949, 22% of basal area</td>
<td>20.3</td>
</tr>
<tr>
<td>22</td>
<td>Alternate 10-m strips cut without removal, 1955</td>
<td>21.3</td>
</tr>
<tr>
<td>2</td>
<td>Reference -- selective logging prior to 1930; chestnut blight, 1930's</td>
<td>30.0</td>
</tr>
<tr>
<td>14</td>
<td>Reference</td>
<td>23.1</td>
</tr>
<tr>
<td>18</td>
<td>Reference</td>
<td>28.7</td>
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<tr>
<td>21</td>
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<tr>
<td>34</td>
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</table>

1 31% of these logs were slash from recent logging; slash was removed from lower sections of the stream.

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