

Changes in stream stability following forest clearing as indicated by storm nutrient budgets

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With 8 figures and 8 tables in the text

Abstract

This study was designed to examine changes in stream stability following forest disturbance. Two components of stability have been identified in ecological systems. Mechanisms of resistance tend to minimize the effects of disturbance, while mechanisms of resilience tend to promote rapid recovery. We hypothesized that forest clearing would result in a decreased ability of streams to resist the downstream displacement of biologically important materials. Our index of stability was input/output nutrient budgets, constructed for disturbed and reference streams during storms. Thus, a frequently occurring natural phenomenon (storms) was used to evaluate the effects of a large scale disturbance (forest clearing).

Nutrient budgets indicated that disturbed streams were less retentive of nitrogen and phosphorus than reference sites. Nitrogen loss averaged 57 mg/m² streambed/storm from disturbed and 16 mg/m² streambed/storm from reference sites. Phosphorus losses were 34 and 9 mg/m² streambed/storm from disturbed and reference streams respectively. Nitrogen and phosphorus loss was largely accounted for by export of nutrients associated with organic particles. There were no differences in input/output budgets for calcium and potassium, although disturbed streams tended to export more particulate calcium and potassium than reference sites.

Changes in stream stability following forest clearing were attributable to changes in the linkage between streams and forest vegetation. Forest recovery is an autogenic process, determined by the rate of forest regrowth. Stream recovery is largely allogenic, dependent on the return of predisturbance patterns of organic inputs from the surrounding forest. Forest clearing resulted in a complex series of changes in organic inputs and processing rates which decreased the abundance of retention structures in streams. The net effect was a decrease in the ability of streams to resist the downstream transport of nutrients during storms.

Introduction

Ecological disturbance has been defined as "any discrete event characterized by a frequency, intensity or magnitude outside a predictable range" (RESH et al. 1988). The impact of disturbance is generally assessed by examining changes in

population, community, and ecosystem structure or by examining changes in resource availability and utilization (e.g. RESH et al. 1988). The responses of ecological systems to disturbance have also been used to describe their ecological stability. The concept of stability has been defined in a variety of ways – original studies defined stability as the persistence of identifiable communities through time (MAC ARTHUR 1955, PRESTON 1969) or the tendency of biological communities to return to their original state following disturbance (MARGALEF 1968, MAY 1973). More recent studies have linked stability to functional properties of ecosystems (e.g. energy flow, nutrient cycles) and defined stability as the tendency for ecosystems to return to original patterns of energy flow and nutrient cycling following disturbance (WEBSTER et al. 1975, O'NEILL 1976, VAN VORIS et al. 1980, GRIMM & FISHER 1989).

WEBSTER et al. (1975) identified two components of ecological stability which they referred to as resistance and resilience. Ecosystem resistance can be thought of as inertia, i.e. opposition to disturbance or displacement, or the magnitude of disturbance tolerated without degradation of functional integrity (WAIDE 1988). Resistance is often linked to accumulated structure (e.g. community biomass, detrital pools) (WEBSTER et al. 1975, O'NEILL 1976), or empirically has been estimated by examining the changes in state variables over a range of disturbance magnitudes (e.g. GRIMM & FISHER 1989). Resilience is the tendency of ecosystems to return to a reference state following displacement and is often linked to turnover rates of ecosystem components (WEBSTER et al. 1975, O'NEILL 1976). Empirically, resilience has been estimated as the recovery rate of ecosystem parameters displaced during disturbance (e.g. GRIMM & FISHER 1989).

In this study, the concept of ecological stability was used to evaluate the impact of forest disturbance on streams. The effects of disturbance on watershed ecosystems (streams + adjacent forests) have been intensively investigated. Most of the studies treated streams and forests as integrated units (e.g. LIKENS et al. 1970, BORMANN et al. 1974, JOHNSON & SWANK 1973). While there is no question that streams and the areas they drain are closely linked, the study of unit watersheds has resulted in the perception of streams as conduits and perhaps obscured some of the impacts of forest disturbance on stream ecosystems.

The ability of forests to respond to disturbance (i.e. their stability) is linked to two primary components, living forest biomass and dead organic matter stored in forest soils (BORMANN et al. 1969, VITOUSEK & REINERS 1975, GORHAM et al. 1979). Vegetation is an important regulator of nutrient cycling and the physical environment within forest soils (BORMANN et al. 1969). Removal of forest vegetation results in decreased transpiration, increased soil temperature, and increased soil moisture, conditions that generally favor mineralization of stored soil organic matter. Decreased vegetative uptake in combination with increased mineralization rates often results in relatively open nutrient cycles and high rates of nutrient loss from forests following disturbance (LIKENS et al. 1970, BROWN et al. 1973, NEARY

1977, SWANK 1986). However, as vegetation regenerates, forest nutrient cycles rapidly return to predisturbance conditions (MARKS & BORMANN 1972, BORING et al. 1981, 1988).

The second component, soil organic matter and in particular, the litter layer, is an important regulator of erodability of forest soils (BORMANN et al. 1969). Detrital organic matter is a primary factor minimizing erosion and loss of particulate material from forest soils following disturbance. In addition, soil organic matter acts as a long term nutrient reservoir. Together, living vegetation and detrital organic matter confer both resistance to disturbance and resilience following disturbance to forest ecosystems. Rapid regeneration of vegetation promotes the recovery of ecosystem function (i. e. resilience) while the persistence of soil organic matter minimizes the effects of disturbance (i. e. resistance).

The ability of stream ecosystems to respond to disturbance comes from a similar combination of components. However, streams are functionally unique in that the downstream movement of water, especially during spates, can be viewed as a constant source of instability due to scouring and displacement of biologically important material. Mechanisms of response (i. e. resilience) include the short life cycles and rapid recolonization rates of invertebrates (e. g. GRIMM & FISHER 1989, WALLACE 1990), the annual renewal of organic matter (i. e. litter fall) in shaded forest streams (e. g. FISHER & LIKENS 1973), and the rapid regeneration of autotrophic communities in unshaded streams (e. g. POWER & STEWART 1987, GRIMM & FISHER 1989). Mechanisms of resistance include debris dams or other instream retention structures which decrease stream power and minimize downstream loss of material (HEEDE 1972, BILBY & LIKENS 1980, BILBY 1981) and refugia which permit stream biota to avoid potential disturbances (SEDELL et al. 1990, WALLACE 1990).

As a type of disturbance, forest clearing has a great impact on associated streams because of its long-term nature. Cutting or burning are short-term disturbances to forests and in the absence of further disturbance the forest undergoes succession or recovery. Forests recover rapidly because "biomass" is internally generated. In contrast, primary production is minimal in many forest streams and most "biomass" is derived from external sources, i. e. the surrounding forest (e. g. FISHER & LIKENS 1973). Being dependent on imported organic matter means that forest streams cannot fully recover from disturbance until predisturbance patterns of organic input are reestablished. Complete recovery and the return of predisturbance quantity and quality of organic inputs may require 100–400 years depending on the mature forest type of the region (LIKENS & BILBY 1982, SWANSON & LIENKAEMPER 1978).

During forest succession, the most serious impact on stream ecosystems is probably a decrease in the abundance of debris dams or other instream retention structures (BILBY 1981, LIKENS & BILBY 1982, SWANSON & LIENKAEMPER 1978). Our previous studies have indicated that streams draining disturbed areas have

reduced levels of woody debris (GOLLADAY et al. 1989) and typically export more organic matter (GOLLADAY et al. 1987, WEBSTER et al. 1990) than undisturbed streams. We hypothesized that the loss of retention structures causes a gradual displacement of an ecosystem property, i.e. the ability to resist the downstream export of material, and that the effect of displacement would be most pronounced during storms. Thus, forest disturbance reduces stream stability by the reducing their ability to resist the downstream displacement of biologically important material during storms.

In this study, we used input/output nutrient budgets to evaluate the impact of forest clearing on stream ecosystem stability. A similar approach has been used successfully to evaluate the recovery of individual stream reaches from catastrophic flash floods by examining a series of daily budgets during the recovery period (several months) (e.g. GRIMM 1987). Since stream disturbance and subsequent recovery following forest clearing occur over a much longer time, we compared nutrient budgets for streams draining early, intermediate and late successional forest. Our index of stability was nutrient retention, inputs minus outputs, during storms. Thus, we used a frequently occurring natural phenomenon (storms) to evaluate the long-term impacts of a large scale disturbance (forest clearing).

Study site

This work was conducted at Coweeta Hydrologic Laboratory, Macon County, North Carolina, USA. Four sites were selected for study; two streams draining disturbed watersheds were matched with two streams draining reference watersheds of similar size. Big Hurricane Branch (BHB) drains WS (Watershed)-7, a 58.7-ha experimental watershed, which was grazed by cattle from 1941–1952 and cable logged during 1977. Regrowth is dominated by hardwood sprouts, herbs, vines, and seedlings (BORING et al. 1981). Carpenter Branch (CB) drains WS13, a 16.1-ha experimental watershed. Originally mixed hardwoods, all trees and shrubs were cut in 1939–1940 and again in 1962 (SWANK & DOUGLASS 1977). No wood was removed from the site and soil disturbance was minimal (SWANK & DOUGLASS 1977). The watershed is now covered by a young hardwood forest dominated by yellow poplar (*Liriodendron tulipifera*) at lower elevations and mixed oaks (*Quercus* spp.) at higher elevations (LEOPOLD & PARKER 1985). Hugh White Creek (HWC) drains WS-14, a 61.1-ha watershed, and Grady Branch (GB) drains WS-18, a 12.5-ha watershed. Watersheds 14 and 18 are mixed hardwood forests and are long term reference watersheds at Coweeta (SWANK & DOUGLASS 1977). Both sites were selectively logged before 1925 and, except for the chestnut blight, have been undisturbed for 60 years.

A complicating factor in comparing these disturbed and reference streams is differences in bedrock composition beneath their basins. However, the use of inputs/output budgets permits identification of differences in nutrient inputs attributable to geologic factors. Results of preliminary surveys indicate two principal lithostratigraphic units underlying Coweeta Hydrologic Laboratory, the Tallulah Falls formation and the Coweeta Group (VELBEL 1985 a, 1985 b). Of these formations, the Tallulah Falls group is more weatherable. Thus, streams draining Tallulah Falls bedrock receive higher soil water solute concentrations than those draining Coweeta group bedrock (VELBEL 1985 a, 1985 b). Big Hurricane Branch (disturbed) and Grady Branch (reference) drain watersheds entirely on the Tallulah Falls

formation. Hugh White Creek (reference) drains a watershed with upper slopes on the relatively resistant Coweeta group and lower areas on the Tallulah Falls formation. Carpenter Branch (disturbed) drains an area entirely on Coweeta group (VELBEL 1985 a, 1985 b).

At Coweeta, reference streams are densely shaded by streamside vegetation, instream primary production is low, and autumn leaf fall provides a majority of the annual energy input (WEBSTER et al. 1983). Coweeta streams support a diverse invertebrate fauna dominated by detritivores (WOODALL & WALLACE 1972, HAEFNER & WALLACE 1981). Geological differences aside, many of the measurements made are influenced by stream size, thus streams were paired based on similarities in average annual discharge and watershed area (Table 1).

Table 1. Physical features of the study sites. Values in parentheses are 95% confidence intervals about the mean.

	Big Hurricane Branch	Carpenter Branch	Hugh White Creek	Grady Branch
Watershed #	7	13	14	18
Treatment	Disturbed	Disturbed	Reference	Reference
Area (ha)	58.7	16.1	61.1	12.5
Main Channel Length (m)	1225	604	1125	345
Gradient (m/m)	0.19	0.19	0.15	0.20
Streambed Area (m ²)	3274	1330	8085	1116
Average Annual Discharge (L/sec) ^a	18.52 (1.85)	5.39 (0.32)	19.37 (1.45)	4.06 (0.31)

^a Based on a minimum of 35 years of Forest Service records

Hugh White Creek was selected as a reference stream for Big Hurricane Branch, and Grady Branch was selected as a reference stream for Carpenter Branch. All streams are located within two kilometers of each other. They are equipped with V-notch weirs, and continuous records of streamflow are maintained by the Forest Service. Further characteristics of the study sites are presented in Table 1.

Methods

From June 1984 – May 1985, major sources and downstream transport of nutrients were measured in each stream during 8 storms. There were 72 storms during the year, so our sampling represented 11% of the total number (W. T. SWANK, unpubl. data). Storms were sampled during each season of the year. Additional stream water and soil water samples were collected seasonally during baseflows to determine background nutrient concentrations at each site. The major sources of nutrients to streams during storms were in throughfall and in soil water, during baseflows the major source of nutrients was soil water.

Throughfall collectors (10 × 400 cm PVC troughs draining into 20-L buckets) were placed at intervals over the length of each stream to estimate inputs of nutrients from precipitation and the forest canopy during storms. The samplers, located above the stream channel, were allowed to fill during storms. Immediately following storms, throughfall volumes were recorded and subsamples (ca. 250 ml) were taken to the laboratory for chemical

analysis. Throughfall collectors permitted estimation of nutrients entering streams in dissolved inorganic, dissolved organic, and fine particulate organic form (< 1 mm). Inputs of coarse particulate organic matter (i. e. litterfall > 1 mm) were minimal during most storms (GOLLADAY, pers. observ.). Thus, nutrient inputs in coarse organic form were not included as an input during storms.

Porous cup lysimeters were placed on each watershed to measure nutrient concentrations in soil water entering each stream. Lysimeters, 200×5 cm diameter PVC pipe with a ceramic cup on the bottom, were installed to a depth of 30–50 cm in the soil adjacent to the stream bank. Lysimeters were emptied once weekly for six months prior to being sampled during storms. When storms seemed likely, lysimeters were emptied, set at 0.1 bar vacuum, and allowed to fill over the duration of the storm. Following the storm, water was collected from each lysimeter (ca. 250 ml), taken to the laboratory, and analyzed. Lysimeters permitted estimation of nutrients entering streams in dissolved inorganic and dissolved organic form, particulate materials were negligible in soil water samples (WEBSTER & GOLLADAY 1984, GOLLADAY pers. observ.).

Stream water samples (ca. 500 ml) were collected by ISCO Model 2100 automated water samplers. Intake hoses were positioned above the streambed in well-mixed riffles just upstream from the gauging station on each stream. Samplers were manually turned on when there appeared to be a possibility of rain. Streams were sampled during storms at a frequency that varied depending on how fast streamflow was changing. Sampling frequency was greatest during rising flows and continued less frequently following storms until streamflow returned to within 5–10% of original baseflow. Sampling frequency varied from 5 minutes during intense thunderstorms to several hours during less intense steady rains. Fifteen to 25 samples were collected from each stream during each storm. Stream water samples permitted estimation of nutrient outputs in an dissolved inorganic, dissolved organic, and fine particulate organic (< 1 mm) form. Since extensive transport of coarse particulate organic matter (> 1 mm) was not observed during storms (GOLLADAY, pers. observ.) and coarse material tends to have relatively short travel distances in streams (e. g. WEBSTER et al. 1987), nutrient export in coarse organic form was assumed minimal.

Following collection, water samples were taken to the laboratory, refrigerated, and subsamples were filtered (Gelman type A/E glass fiber filters) within 48 hr of collection. An additional subsample was taken from the filtered fractions and acidified to pH 2, then the three fractions (unfiltered, filtered, filtered and acidified) from each original water sample were frozen. Samples were subsequently analyzed for the following: acidified – ammonium (NH_4^+); filtered – total Kjeldahl nitrogen (TKN), nitrate (NO_3^-), total phosphorus (TP), soluble reactive phosphorus (SRP), K^+ , Ca^{+2} ; unfiltered – TKN, TP, total potassium (TK), total calcium (TCa). Samples collected from lysimeters were analyzed as filtered samples (particulate materials in lysimeters were negligible).

All chemical analyses were performed at Coweeta Hydrologic Laboratory using a water chemistry protocol described in detail by REYNOLDS & DEAL (1987) based on procedures outlined in Standard Methods (Anonymous 1985). Phosphorus, nitrogen and sulfate were analyzed using a Technicon Autoanalyzer-II system. Samples used in TKN determinations were digested in H_2SO_4 , then the cyanurate-salicylate reaction was used to determine TKN as NH_4^+ . NO_3^- concentrations were determined using Cd/Cu reduction to NO_2^- followed by a sulfamide color reaction. At Coweeta, NO_2^- concentrations are undetectable (REYNOLDS & DEAL 1987), so no separate analyses for NO_2^- were performed. NH_4^+ analyses were performed using the colorimetric Berthelot reaction. Potassium-sodium tartrate was added to NH_4^+ samples to prevent metal hydroxide interferences. An H_2SO_4 digestion was used in TP determinations with TP determined as orthophosphate. SRP concentrations were measured using the ammonium-molybdate reaction. Samples were digested in H_2SO_4 to hydrolyze

condensed phosphates to SRP. An $\text{H}_2\text{SO}_4/\text{HNO}_3$ digestion was used to convert TK and TCa into K^+ and Ca^{+2} . All cation concentrations were determined using a Perkin Elmer Model 372 atomic absorption spectrophotometer.

This sampling program permitted the estimation of nutrient inputs and outputs during storms. Major sources of nutrients to Coweeta streams during storms are in channel interception and soil water. Soils at Coweeta are highly permeable, with infiltration rates often exceeding 125 cm/hr, thus overland flow is negligible (DOUGLASS & SWANK 1975) and the major input of nutrients from soils is in subsurface runoff. Rainwater does not rapidly move through soils but instead tends to displace stored water from the bottom of the soil profile (HEWLETT et al. 1977). Thus, soil water solute concentrations entering streams tend to be stable during storms (JOHNSON & SWANK 1973, VELBEL 1985a).

In order to test the assumption that the chemistry of water collected in lysimeters was representative of soil water entering the streams, chloride (Cl^-) concentrations in stream and soil water were compared at each site. Chloride has been used to measure the reliability of budget estimates at Coweeta since biological accumulation of this ion tends to be small (e. g. SWANK & WAIDE 1988). No significant differences in Cl^- concentrations were detected in soil and stream water at any site (2-sample t-test by site, $p > 0.10$) and we concluded that our lysimeter arrays provided reasonable estimates of soil water chemistry entering streams.

Channel interception was estimated from the volume of water in throughfall collectors and bank-full channel area. Soil water volume was estimated as the difference between streamflow and water entering as stream channel interception. The total amounts of dissolved and particulate nutrients entering the stream during each storm were calculated as the product of nutrient concentration and volume of water for each input. The net loss or gain of a nutrient during a storm was the difference between nutrient transport in streamflow and inputs as channel interception and soil water. The total loss of nutrients was calculated by multiplying stream nutrient concentration times the volume of streamflow represented by each sample and summing over the duration of the storm. Storms were defined as beginning with the onset of precipitation and continuing until streams returned to within 5–10% of original baseflow.

Our goal was to sample storms during each season of the year. However, an extended dry period prevented sampling from July–October 1984. Rainfall during the 8 storms sampled ranged from 0.5 to 7.0 cm and average rainfall intensities ranged from 0.5 to 1.05 cm/hr (Table 2). Late autumn and winter storms were long duration (up to 40 hours) and moderate intensity. Spring and summer storms were generally shorter (1–6 hrs) and

Table 2. Total rainfall and average intensity of storms sampled. Intensity was calculated by dividing total rainfall amount by the duration of a storm. Values represent averages of all sites.

Storm Date	Total Rainfall (cm)	Intensity (cm/hr)
15 Jun 84	0.50	0.15
20 Jun 84	1.57	1.05
10 Nov 84	3.27	0.55
4 Dec 84	4.04	0.23
11 Feb 85	6.30	0.48
21 Mar 85	2.10	0.06
1 May 85	1.24	0.08
7 May 85	4.19	0.10

more variable in intensity but often characterized by periods of relatively intense rainfall. Rainfall amounts and intensities were very similar between watersheds. Based on Forest Service records, there was 149.6 cm of precipitation during the period from May 1984 – April 1985. The 52-year average for Coweeta is 180.3 cm (range 122.9–224.5), and the period sampled was the 6th driest year on record (W. T. SWANK, unpubl. data).

Results

Baseflow nutrient concentrations

Nutrient concentrations in soil and stream water were measured seasonally during stable baseflows (June 1984, November 1984, February 1985, May 1985), and averaged over the entire year (Table 3). Soil water $\text{NO}_3\text{-N}$ concentrations tended to be greater on disturbed (BHB, CB) than reference sites (HWC, GB). Concentrations of the other nitrogen species in both stream and soil water were similar at disturbed and reference sites. In both soil and stream water, phosphorus species concentrations were near detection limits, being similarly low at disturbed and reference sites. Cation concentrations were variable, reflecting differences in geology and disturbance histories at the sites (see discussion). Greatest cation concentrations (K^+ and Ca^{+2}) in soil water and stream water were measured at BHB (recently disturbed). For PK, greatest concentrations were measured in disturbed streams (BHB, CB). Greatest concentrations of PCa were measured in the most recently disturbed site (BHB) and one of the reference sites (GB).

Nitrogen

Sources of nitrogen during storms – Inputs of nutrients to streams are influenced by both concentrations and absolute volumes of water entering the stream channel from its sources. In this study, concentrations of nutrients were often greater in throughfall than soil water. However, the volume of water entering streams from soils was usually much greater than throughfall, the result was large amounts of nutrients entering streams from forest soils.

Concentrations of nitrogen species in throughfall were generally an order-of-magnitude greater than in soil water (Table 4). Average throughfall $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ concentrations were similar in disturbed and reference streams, while PON (particulate organic nitrogen) and DON (dissolved organic nitrogen) concentrations tended to be greater in the reference sites. Soil water nitrogen species were more variable. $\text{NO}_3\text{-N}$ concentrations in soil water entering the disturbed sites were significantly greater than reference levels ($\text{CB} > \text{BHB} > \text{HWC}$ and GB , ANOVA followed by multiple comparisons, $P < 0.05$). There were no significant differences in the concentrations of the other nitrogen species ($\text{NH}_4\text{-N}$ and DON) entering the streams in soil water (ANOVA, $P > 0.10$). Concentrations of all nitrogen species in soil water were similar during baseflows and stormflows (Tables 3 and 4).

Table 3. Concentrations (mg/L) of nutrient species in soil water and streamwater during baseflows. Values are means with 95% confidence intervals and sample sizes in parentheses.

	Big Hurricane Branch		Carpenter Branch		Hugh White Branch		Grady Branch	
	Soil	Stream	Soil	Stream	Soil	Stream	Soil	Stream
NO ₃	0.026 (0.012,24)	0.053 (0.018,10)	0.059 (0.013,15)	0.040 (0.018,10)	0.005 (0.002,26)	0.013 (0.005,10)	0.004 (0.002,15)	0.013 (0.002,10)
NH ₄	0.011 (0.006,25)	0.011 (0.002,10)	0.009 (0.004,15)	0.015 (0.009,10)	0.013 (0.010,26)	0.012 (0.005,10)	0.010 (0.004,15)	0.014 (0.005,10)
DON	0.026 (0.012,25)	0.032 (0.009,10)	0.026 (0.015,15)	0.033 (0.023,10)	0.018 (0.010,26)	0.043 (0.032,10)	0.020 (0.015,15)	0.018 (0.014,10)
PON	—	0.018 (0.018,10)	—	0.033 (0.034,10)	—	0.024 (0.023,10)	—	0.030 (0.025,10)
SRP	0.004 (0.002,25)	0.002 (0.002,10)	0.002 (0.001,15)	0.003 (0.002,10)	0.006 (0.004,26)	0.002 (0.002,10)	0.005 (0.004,15)	0.004 (0.002,10)
DOP	0.009 (0.008,25)	0.006 (0.005,10)	0.013 (0.011,15)	0.005 (0.005,10)	0.016 (0.010,26)	0.002 (0.002,10)	0.004 (0.004,15)	0.006 (0.007,10)
POP	—	0.021 (0.016,10)	—	0.026 (0.023,10)	—	0.016 (0.009,10)	—	0.006 (0.007,10)
K ⁺	0.639 (0.151,25)	0.497 (0.038,10)	0.357 (0.034,15)	0.346 (0.027,10)	0.250 (0.029,25)	0.338 (0.034,10)	0.315 (0.051,15)	0.413 (0.041,10)
PK	—	0.080 (0.045,10)	—	0.057 (0.018,10)	—	0.028 (0.020,10)	—	0.034 (0.027,10)
Ca ⁺²	0.919 (0.369,25)	0.835 (0.061,10)	0.432 (0.090,15)	0.379 (0.025,10)	0.502 (0.272,25)	0.386 (0.032,10)	0.539 (0.236,15)	0.535 (0.054,10)
PCa	—	0.110 (0.059,10)	—	0.047 (0.023,10)	—	0.059 (0.027,10)	—	0.093 (0.048,10)

Table 4. Concentrations (mg/L as nitrogen) of nitrogen species in throughfall, soil water, and streamwater during storms averaged over the entire study. Values are means with 95% confidence intervals and sample sizes in parentheses.

	BHB (disturbed)	CB (disturbed)	HWC (reference)	GB (reference)
Throughfall				
NO ₃ -N	0.250 (0.048,40)	0.235 (0.053,37)	0.208 (0.048,39)	0.330 (0.135,40)
NH ₄ -N	0.112 (0.030,40)	0.134 (0.032,37)	0.068 (0.018,39)	0.123 (0.036,40)
DON	0.449 (0.228,40)	0.438 (0.230,37)	0.599 (0.236,39)	0.589 (0.273,40)
PON	0.541 (0.244,40)	0.468 (0.176,39)	0.815 (0.426,39)	0.741 (0.275,40)
Soil water				
NO ₃ -N	0.023 (0.008,58)	0.049 (0.016,31)	0.005 (0.001,59)	0.004 (0.001,34)
NH ₄ -N	0.011 (0.004,58)	0.009 (0.002,31)	0.012 (0.005,59)	0.011 (0.004,34)
DON	0.043 (0.014,58)	0.026 (0.014,31)	0.026 (0.010,59)	0.026 (0.016,34)
Streamwater				
NO ₃ -N	0.059 (0.003,173)	0.053 (0.004,174)	0.012 (0.001,166)	0.025 (0.005,168)
NH ₄ -N	0.011 (0.001,173)	0.013 (0.001,174)	0.013 (0.002,166)	0.012 (0.001,168)
DON	0.040 (0.006,173)	0.040 (0.005,174)	0.038 (0.005,166)	0.035 (0.005,168)
PON	0.190 (0.045,173)	0.123 (0.024,174)	0.097 (0.018,166)	0.103 (0.018,170)

When averaged over all storms, soil water inputs represented 67% and 61% of the nitrogen entering disturbed streams (BHB and CB, respectively) and 36% and 39% of the nitrogen entering reference sites (HWC and GB, respectively). Both disturbed streams received significantly greater quantities of soil nitrogen than reference sites (BHB > HWC, CB > GB; paired t-test by storm $P < 0.05$), differences were most pronounced during winter storms (Fig. 1). There were no differences in throughfall inputs to disturbed and reference sites (paired t-test by storm, $P > 0.10$). This analysis indicates that a primary difference between streams is a large amount of nitrogen (primarily DIN, i.e. NO₃-N + NH₄-N) entering streams draining disturbed forests.

Forms of nitrogen loss during storms – Concentrations of NH₄-N, NO₃-N, and DON were similar during base and stormflows at all sites (Tables 3 and 4). PON concentrations increased rapidly with the onset of precipitation and at all sites average storm concentrations were substantially greater than baseflow concentrations. Storm PON concentrations measured in BHB (disturbed) were signi-

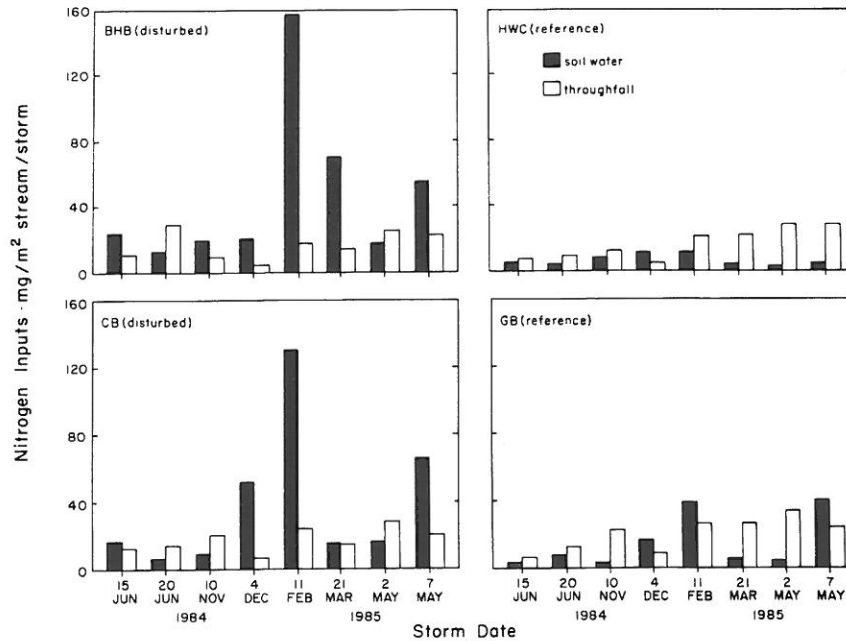


Fig. 1. Nitrogen inputs (mg/m^2 stream/storm) to Coweeta streams during 8 storms sampled 1984–1985.

ificantly greater than those observed in the other streams (ANOVA, followed by multiple comparisons, $P < 0.05$) (Table 5). Storm concentrations of $\text{NO}_3\text{-N}$ were also significantly greater in disturbed streams compared to reference sites ($\text{BHB} > \text{CB} > \text{GB} > \text{HWC}$; ANOVA, followed by multiple comparisons, $p < 0.05$). There were no differences in the average concentrations of either $\text{NH}_4\text{-N}$ or DON among the four streams during storms.

PON was the dominant form of nitrogen output from all streams during storms, averaging 46% of the total in disturbed and 52% in reference streams. DIN was the second most important form of nitrogen output averaging 42% of the total in disturbed and 31% in the reference streams. DON outputs averaged less than 20% in all streams (Table 5).

Storm nitrogen budgets – There were generally no significant differences between inputs and outputs of DIN or DON in any stream (Table 5) suggesting that no net transformations occurred during storms. One exception to this pattern was a reference stream (HWC) which tended to accumulate DIN during storms. All streams lost PON during storms (Table 5). In general, disturbed streams lost more PON than reference sites.

Total nitrogen budgets ($\text{DIN} + \text{DON} + \text{PON}$) were strongly influenced by PON fluxes and all streams generally lost nitrogen during storms (Fig. 2). During

Table 5. Average inputs (I) and outputs (O) of nutrient species during 8 storms sampled in 1984–1985. Values are mg/m² streambed/storm. Net difference is the difference between inputs and outputs of a particular species averaged over all storms. Positive values indicate a net accumulation of a nitrogen species; negative values indicate a net loss. Astericks indicate whether differences are significant (paired t-test by storm, * p<0.10, ** p<0.05).

	BHB (disturbed)			CB (disturbed)			HWC (reference)			GB (reference)		
	I	O	net	I	O	net	I	O	net	I	O	net
DIN	31	55	-24	42	42	0	10	7	3**	14	23	-9
DON	26	17	9	9	12	-3	6	7	-1	13	8	5
PON	7	73	-66**	7	38	-31**	8	21	-13**	9	25	-14**
SRP	8	3	5	2	1	1	1	1	0	2	1	1
DOP	4	6	-2	2	3	-1	2	1	1	2	2	0
POP	3	52	-49**	2	25	-23**	3	12	-9*	3	13	-10**
K ⁺	432	353	79**	208	191	17**	109	105	4	162	184	-22**
PK	2	132	-130**	3	60	-57**	4	27	-23**	3	42	-39**
Ca ⁺²	570	576	-6	189	229	-40*	100	127	-27**	155	233	-78**
PCa	3	83	-80**	3	47	-44**	3	30	-27**	3	69	-66**

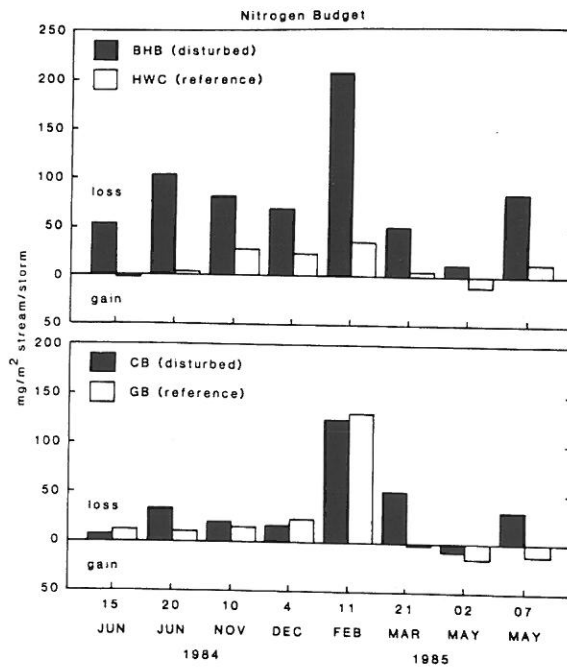


Fig. 2. Nitrogen budgets, net loss or gain (mg/m² stream/storm) of nitrogen from Coweeta streams during 8 storms sampled in 1984–1985.

several storms (15 Jun 84, 21 Mar 85, 2 May 85) however, nitrogen gains were observed. Nitrogen accumulation occurred most frequently in the reference streams (HWC and GB) and tended to be greater than that observed in CB. Nitrogen accumulation was never observed in BHB, the recently disturbed stream. Nitrogen loss from disturbed streams averaged 57 mg/m² streambed/storm and from reference streams averaged 16 mg/m² streambed/storm. When comparisons were made between streams of similar size, BHB (disturbed) lost more nitrogen than HWC (reference) (paired t-test by storm, $p < 0.05$) however, there was no difference in nitrogen loss from CB and GB ($P > 0.10$).

Phosphorus

Sources of phosphorus during storms – POP (particulate organic phosphorus) was the dominant phosphorus species in throughfall at all sites (Table 6). Average phosphorus species concentrations were similar at all sites (ANOVA, $P > 0.10$). Soil water phosphorus concentrations were generally an order-of-magnitude lower than in throughfall (Table 6). Average concentrations of SRP entering BHB (disturbed) were significantly greater than reference levels, while concentrations entering CB, the other disturbed stream, were intermediate (ANOVA, followed by multiple comparisons, $P < 0.05$). There were no significant differences in con-

Table 6. Concentrations (mg/L as PO₄) of phosphorus species in throughfall, soil water, and streamwater during storms, averaged over the entire study. Values are means and in parentheses 95% confidence limits and sample sizes.

	BHB (disturbed)	CB (disturbed)	HWC (reference)	GB (reference)
Throughfall				
SRP	0.095 (0.046,40)	0.051 (0.051,39)	0.096 (0.048,39)	0.077 (0.048,40)
DOP	0.079 (0.034,40)	0.073 (0.038,39)	0.131 (0.077,39)	0.100 (0.046,40)
POP	0.343 (0.099,40)	0.158 (0.069,39)	0.300 (0.158,39)	0.278 (0.103,40)
Soil water				
SRP	0.008 (0.002,59)	0.006 (0.003,32)	0.004 (0.001,59)	0.005 (0.001,36)
DOP	0.008 (0.004,59)	0.007 (0.005,32)	0.012 (0.005,59)	0.012 (0.005,36)
Streamwater				
SRP	0.005 (0.009,173)	0.005 (0.001,174)	0.005 (0.003,166)	0.004 (0.001,169)
DOP	0.008 (0.002,173)	0.011 (0.003,174)	0.009 (0.002,166)	0.008 (0.002,169)
POP	0.122 (0.024,173)	0.083 (0.012,174)	0.082 (0.022,166)	0.083 (0.018,170)

centrations of DOP (dissolved organic phosphorus) entering the streams in soil water (ANOVA, $P > 0.10$). At all sites, soil water phosphorus concentrations were similar during base and storm flows (Tables 3 and 6).

When averaged over all storms, throughfall inputs represented 67% and 57% of the phosphorus entering reference streams (HWC and GB, respectively). Soil water was the major phosphorus input to BHB (disturbed) averaging 69% of total. Phosphorus inputs to CB (disturbed) were evenly distributed between throughfall and soil water. There were no significant differences in phosphorus inputs to disturbed and reference streams in either throughfall or soil water (paired t-test by storm, $p > 0.10$), nor were there consistent seasonal patterns apparent in phosphorus inputs to the streams (Fig. 3). It would appear from this analysis that forest disturbance that has had little impact on the amount of phosphorus entering Coweeta streams.

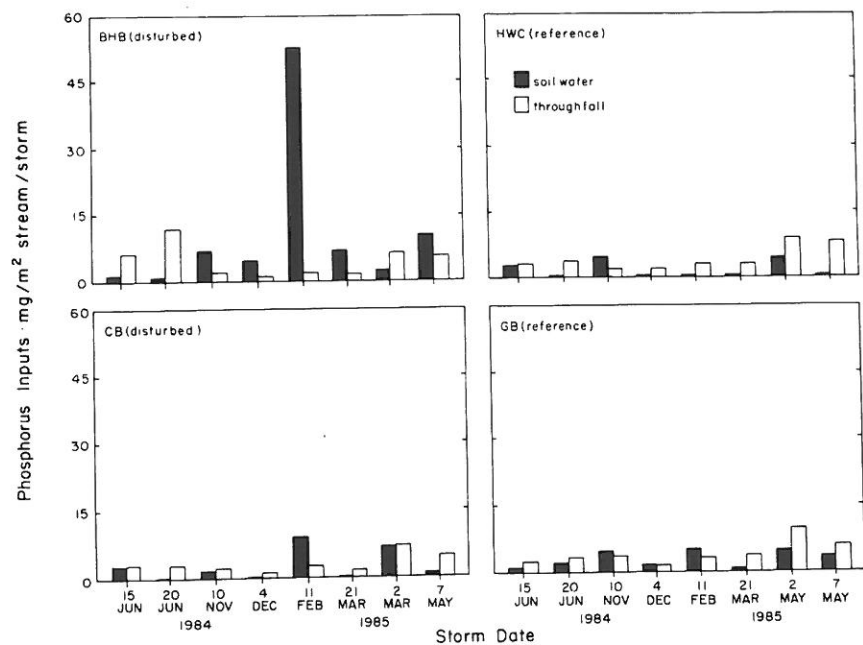


Fig. 3. Phosphorus inputs (mg/m^2 stream/storm) to Coweeta streams during 8 storms sampled 1984–1985.

Forms of phosphorus loss during storms – POP was the only phosphorus species affected by storms, and at all sites, storm concentrations were substantially greater than baseflow concentrations (Tables 3 and 6). Storm POP concentrations measured in BHB (disturbed) were significantly greater than those observed in the other streams (ANOVA, followed by multiple comparisons, $p < 0.05$) (Table 6).

Concentrations of SRP and DOP in stream water were almost always near analytical detection limits, and there were no differences among streams in SRP or DOP concentrations (ANOVA, $P > 0.10$). POP averaged 84% of total output in both reference and disturbed sites during storms. The other species were a minor component of transport. DOP averaged 10% of total output and SRP averaged 6% of total output in both disturbed and reference sites (Table 5).

Storm phosphorus budgets – There were no significant differences in inputs and outputs of SRP and DOP in any of the streams (Table 5). Thus, no net transformations of dissolved phosphorus occurred in Coweeta streams during storms. Both disturbed streams and GB (reference) lost POP during storms (Table 5). HWC (reference) also tended to lose POP during storms. In general, the disturbed streams lost more POP than the reference streams. Forest disturbance appears to have reduced the ability of Coweeta streams to retain phosphorus associated with particles.

Total phosphorus budgets (SRP+DOP+POP) were strongly influenced by POP dynamics. Both disturbed and reference streams generally lost phosphorus during storms. During several storms (15 Jun 1984, 2 May 1984) small gains of phosphorus occurred (Fig. 4). Phosphorus accumulation occurred most frequently in the reference streams (HWC and GB) and tended to be larger than the one storm where a gain of phosphorus was observed in a disturbed stream (CB). Net gains of

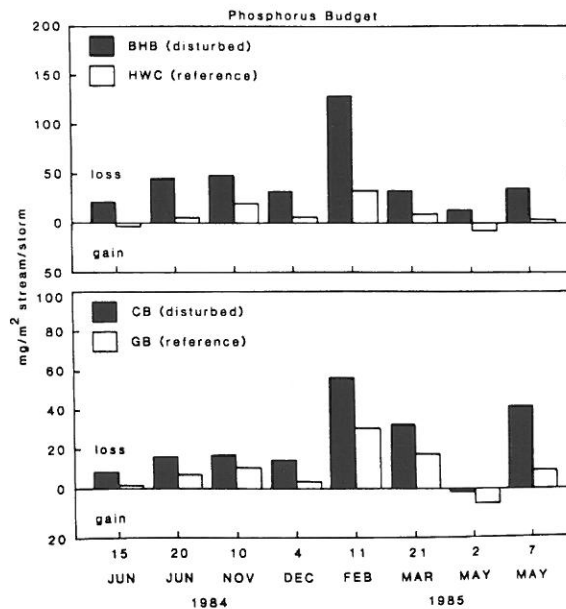


Fig. 4. Phosphorus budgets, net loss or gain (mg/m^2 stream/storm) of phosphorus from Coweeta streams during 8 storms sampled in 1984–1985.

phosphorus were never observed in BHB (disturbed). Phosphorus loss from the disturbed streams averaged 34 mg/m² streambed/storm and from the reference streams averaged 9 mg/m² streambed/storm. In comparisons of the paired streams, both disturbed streams lost more phosphorus than reference sites (paired t-tests, by storm, $p < 0.05$).

Potassium

Sources of potassium during storms – K⁺ was the most abundant form of potassium measured in throughfall at all sites (Table 7). There were no significant

Table 7. Concentrations (mg/L as K) of potassium species in throughfall, soil water, and streamwater during storms, averaged over the entire study. Values are means and in parentheses 95% confidence intervals and sample sizes.

	BHB (disturbed)	CB (disturbed)	HWC (reference)	GB (reference)
Throughfall				
K ⁺	2.028 (0.935,40)	1.888 (0.931,39)	4.085 (2.028,39)	3.211 (1.566,40)
PK	0.137 (0.059,40)	0.203 (0.131,39)	0.517 (0.279,39)	0.335 (0.188,40)
Soil water				
K ⁺	0.621 (0.098,59)	0.377 (0.020,33)	0.262 (0.018,59)	0.322 (0.026,36)
Streamwater				
K ⁺	0.536 (0.012,173)	0.384 (0.008,174)	0.358 (0.008,166)	0.439 (0.012,169)
PK	0.278 (0.057,173)	0.187 (0.033,174)	0.119 (0.016,166)	0.122 (0.018,170)

differences between streams in either throughfall K⁺ or PK (particulate potassium) concentrations (ANOVA, $P > 0.1$). At all sites, concentrations of K⁺ in soil water were lower than those measured in throughfall. Average concentrations of K⁺ entering BHB (disturbed) from soil water were greater than the other streams (ANOVA, followed by multiple comparisons, $P < 0.05$). Soil water K⁺ concentrations were similar during base and stormflows at all sites (Tables 3 and 7).

The primary potassium source during storms was soil water, averaging 76% of total input to reference and 90% of total input to disturbed streams (Table 5). Both disturbed streams received significantly more potassium in soil water than their reference sites (BHB > HWC, CB > GB, paired t-tests by storm, $P < 0.05$), and differences were most pronounced during winter storms (Fig. 5). There were no differences in throughfall potassium inputs to disturbed and reference sites nor any strong seasonal pattern of throughfall inputs. These analyses suggest that forest

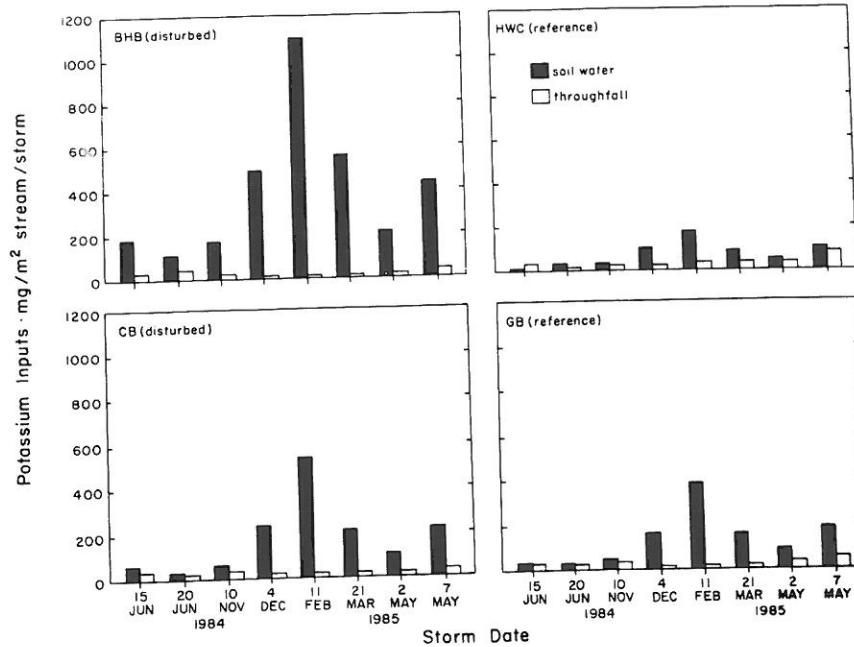


Fig. 5. Potassium inputs (mg/m^2 stream/storm) to Coweeta streams during 8 storms sampled 1984–1985.

clearing resulted in increased movement of potassium from disturbed soils to streams.

Forms of potassium loss during storms – K^+ was the dominant potassium species measured in stream water at all sites during storms, and average concentrations were approximately 2-fold greater than PK in each stream (Table 7). K^+ concentrations were not influenced by storms, and storm concentrations were similar to baseflow concentrations at all sites (Tables 3 and 7). Greatest storm K^+ concentrations were measured in the most recently disturbed stream ($\text{BHB} > \text{GB} > \text{CB} > \text{HWC}$, ANOVA followed by multiple comparisons, $P < 0.05$). Differences in stream water K^+ concentrations reflect the combined effects of forest disturbance as well as geological differences between the sites (see Discussion). Averaged over all storms, K^+ represented 74% of total potassium output from disturbed streams and 80% of total outputs from reference sites (Table 5).

Streamwater PK concentrations were elevated in both disturbed and reference streams during storms (Tables 3 and 7). Greatest storm PK concentrations were observed in disturbed streams ($\text{BHB} > \text{CB} > \text{GB}$ or HWC , ANOVA followed by multiple comparisons, $P < 0.05$).

Storm potassium budgets – All streams lost PK during storms (Table 5). In general, the disturbed streams lost more PK than the reference streams. K^+

dynamics were different in disturbed and reference streams. K^+ inputs and outputs were approximately balanced in HWC (reference) while a net loss was observed in GB (reference). Both disturbed streams tended to accumulate K^+ , and K^+ fluxes tended to be greater than reference sites. Thus, while forest disturbance has reduced retention of PK its effects on K^+ dynamics are more difficult to interpret.

Total potassium budgets ($K^+ + PK$) indicated that both disturbed and reference streams lost potassium during storms (Fig. 6). However, in comparisons of disturbed and reference streams, there were no consistent differences in potassium loss (paired t-tests, $p > 0.10$).

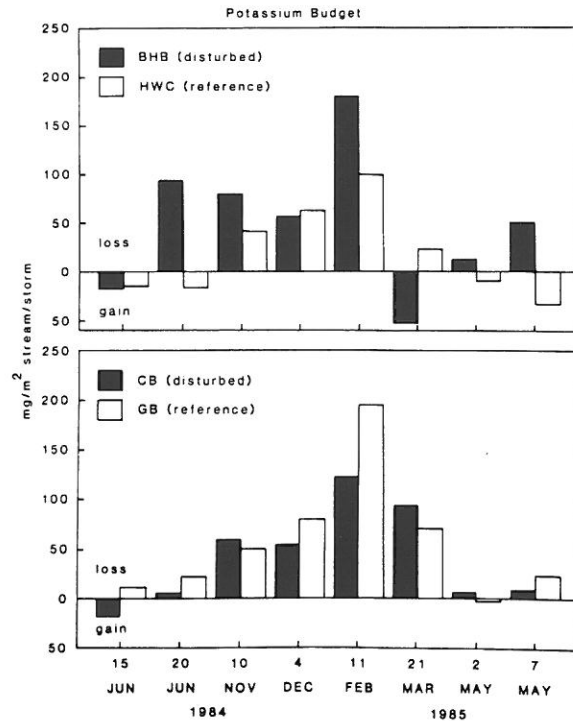


Fig. 6. Potassium budgets, net loss or gain (mg/m^2 stream/storm) of potassium from Coweeta streams during 8 storms sampled in 1984–1985.

Calcium

Sources of calcium during storms – Ca^{+2} was the dominant calcium species in throughfall entering all streams (Table 8), and there were no significant differences between disturbed and reference streams for throughfall Ca^{+2} or PCa (particulate calcium) concentrations (ANOVA, $p > 0.10$). In BHB (disturbed), soil water Ca^{+2}

Table 8. Concentrations (mg/L as Ca) of calcium species in throughfall, soil water, and stream-water during storms, averaged over the study. Values are means and in parentheses 95% confidence limits and sample sizes.

	Big Hurricane Branch	Carpenter Branch	Hugh White Creek	Grady Branch
Throughfall				
Ca ⁺²	0.869 (0.303,40)	0.916 (0.295,39)	1.239 (0.378,39)	1.138 (0.378,40)
PCa	0.149 (0.042,40)	0.130 (0.049,39)	0.190 (0.065,39)	0.161 (0.065,40)
Soil water				
Ca ⁺²	0.950 (0.202,59)	0.390 (0.049,33)	0.427 (0.114,59)	0.466 (0.110,36)
Streamwater				
Ca ⁺²	0.879 (0.013,173)	0.441 (0.006,174)	0.438 (0.009,166)	0.566 (0.015,169)
PCa	0.153 (0.033,173)	0.106 (0.014,174)	0.102 (0.012,166)	0.137 (0.018,170)

concentrations were similar to those measured in throughfall. At the other sites, soil water Ca⁺² concentrations were generally much less than throughfall Ca⁺². Soil water Ca⁺² concentrations entering BHB were significantly greater than those at any of the other sites (BHB > CB or HWC or GB, ANOVA followed by multiple comparisons, $P < 0.05$). At all sites, soil water Ca⁺² concentrations were similar during base and stormflows (Tables 3 and 8).

Soil water was the primary source of calcium to all streams and when averaged over all storms contributed 95% of total inputs to disturbed streams and 86% of total inputs to reference streams (Table 3). Both disturbed streams received significantly more calcium in soil water than their reference sites (BHB > HWC, CB > GB, paired t-tests by storm, $P < 0.05$), and differences were most pronounced during winter storms (Fig. 7). There were no differences in throughfall calcium inputs to disturbed and reference streams nor any strong seasonal pattern of inputs. As with potassium, it appears that forest clearing has resulted in increased movement calcium from disturbed soils to streams.

Forms of calcium loss during storms – Ca⁺² was the dominant calcium species measured in streamwater during storms and average concentrations ranged 4 to 6 fold greater than PCa (Table 8). Ca⁺² concentrations were consistently slightly greater during storms than baseflows at all sites (Tables 3 and 8). Storm Ca⁺² concentrations in BHB, the most recently disturbed stream, were significantly greater than the other streams, while GB (reference) was intermediate between BHB and the other sites (BHB > GB > CB or HWC, ANOVA followed by multiple comparisons, $P < 0.05$). Like potassium, stream water calcium concentrations reflected the combined effects of forest disturbance and geological differences

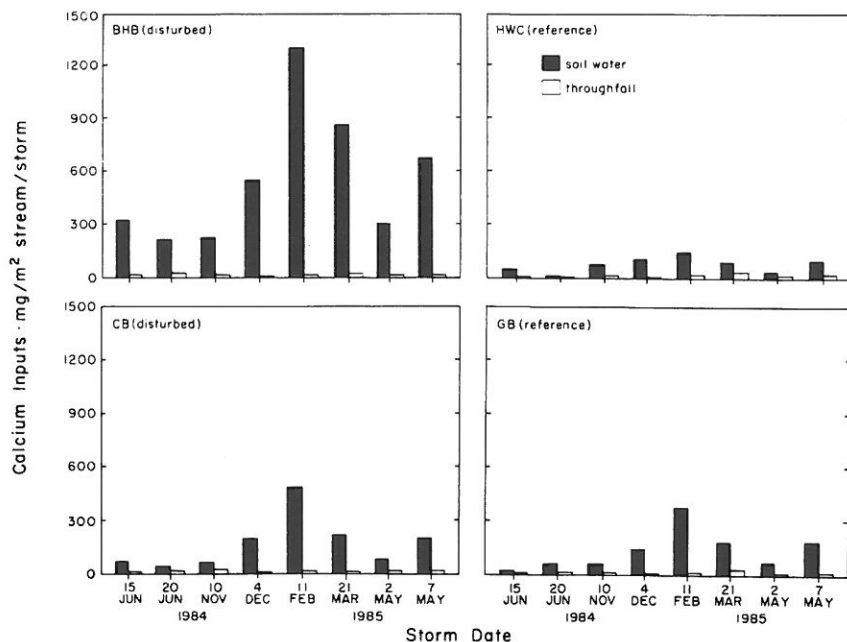


Fig. 7. Calcium inputs (mg/m^2 stream/storm) to Coweeta streams during 8 storms sampled 1984–1985.

between the sites (see Discussion). Stream water PCa concentrations in BHB (disturbed) were significantly greater than those in CB (disturbed) or HWC (reference), average concentrations in GB (reference) were intermediate (ANOVA, followed by multiple comparisons, $P < 0.05$). Averaged over all storms, Ca^{+2} represented 79% of total calcium outputs from the reference sites and 89% of total outputs from the disturbed sites.

In all streams, PCa concentrations were elevated during storms (Tables 3 and 8). Storm PCa concentrations in BHB (disturbed) were significantly greater than those in CB (disturbed) or HWC (reference), average concentrations in GB (reference) were intermediate (ANOVA, $P < 0.05$).

Storm calcium budgets – All streams lost PCa during storms (Table 4). Largest losses were observed from BHB, the most recently disturbed site. Losses of Ca^{+2} were observed in the reference sites (HWC and GB) and in one of the disturbed streams (CB). In BHB, the most recently disturbed site, Ca^{+2} inputs and outputs were balanced (Table 5).

Total calcium budgets ($\text{Ca}^{+2} + \text{TCa}$) indicated that both disturbed and reference streams lost calcium during storms (Fig. 8). Losses were greatest from all streams during winter storms. Net gains of calcium were observed in 3 streams (BHB and CB-disturbed, HWC-reference) and were greatest during spring or early

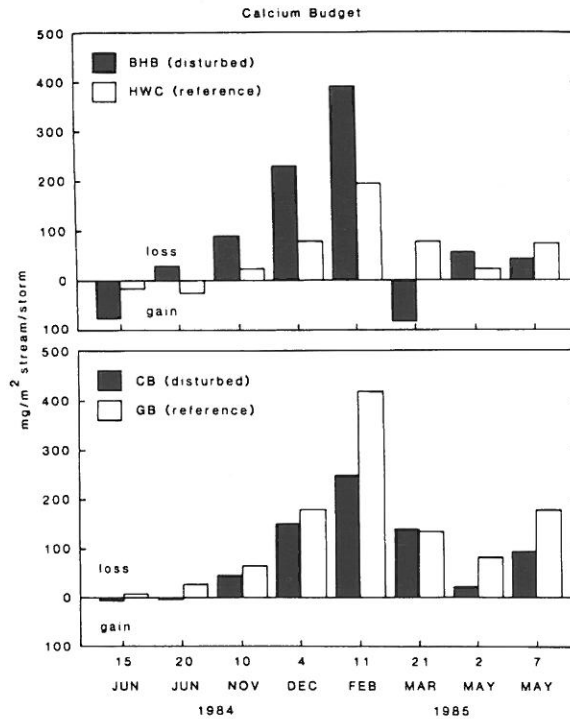


Fig. 8. Calcium budgets, net loss or gain (mg/m^2 stream/storm) of calcium from Coweeta streams during 8 storms sampled in 1984–1985.

summer storms. When streams of similar size were compared, there was no difference in calcium loss between BHB (disturbed) and HWC (reference), however GB (reference) consistently lost more calcium than CB (disturbed) (paired t-test by storm, $P < 0.05$).

Discussion

Effects of forest disturbance on nutrient inputs to streams

Soil water – Changes in nutrient inputs to streams following forest clearing reflect disruptions of nutrient cycling in forest canopies and soils. In this study, nitrogen availability in forest soils was very sensitive to forest disturbance. Concentrations of DIN in soil water entering reference streams were relatively low, ($\text{NO}_3\text{-N} < 0.005$ mg/L, $\text{NH}_4\text{-N} < 0.013$ mg/L) and the dominant form of DIN was $\text{NH}_4\text{-N}$ (Tables 3 and 4). In disturbed sites, soil water concentrations of $\text{NO}_3\text{-N}$ were elevated above reference levels ($\text{NO}_3\text{-N} > 0.020$ mg/L). Differences in nitrogen inputs to disturbed and reference streams were most pronounced

during large, long-duration storms when substantial quantities of $\text{NO}_3\text{-N}$ were flushed from forest soils to streams (Fig. 1).

There are many factors associated with forest clearing that alter nitrogen inputs to streams. The magnitude and timing of nitrogen losses from disturbed forest soils is site specific, determined by the degree to which soil microclimate is altered and the rate at which vegetation regenerates. At Coweeta, extensive studies of disturbed forest soils have been conducted on WS-7, the site surrounding BHB (clearcut 1977). Increased soil temperatures (WAIDE et al. 1988), decreased evapotranspiration and increased soil moisture (SWANK & VOSE 1988), decreased microbial activity (WAIDE et al. 1988), and decreased microarthropod densities (SEASTEDT & CROSSLEY 1981) were all observed immediately following logging. However, forest regeneration is rapid in the southern Appalachians, within 3 years of clearing, the leaf area index on WS-7 was 68% of predisturbance levels (BORING et al. 1988). Within 5 years of clearing, soil temperatures, soil moisture, and microbial activity on WS-7 had recovered to predisturbance levels (SWANK & VOSE 1988, WAIDE et al. 1988).

Although changes in soil microclimate in the southern Appalachians are relatively short-lived, modest changes in standing stocks and cycling of nitrogen in disturbed forests have been reported. WAIDE et al. (1988) observed increased concentrations of organic matter (primarily logging residue) and total nitrogen in surface and subsurface layers of soils on WS-7 for at least 7 years following disturbance. They attributed increased concentrations to slight increases in nitrogen mineralization rates, substantial increases in nitrification rates, and short-lived reductions in nitrogen immobilization rates. Increases in both symbiotic and free-living nitrogen-fixing bacteria may also have contributed to increases in observed soil nitrogen pools (BORING et al. 1984, 1988, WAIDE et al. 1988). Most of the nitrogen released by mineralization appears to be recovered by the rapidly regenerating forest, however elevated $\text{NO}_3\text{-N}$ concentrations have been reported in streams draining disturbed watersheds for at least 20 years (SWANK 1988, WAIDE et al. 1988). The nitrogen measurements made for this study generally support the observation that nitrogen cycling is extremely sensitive to disturbance and even slight increases in the rate of nitrogen loss from forests can result in substantial increases in nitrogen inputs to streams.

Phosphorus inputs to Coweeta streams appear to be relatively insensitive to forest disturbance. Slight but significant increases in SRP concentration entering BHB (recently disturbed) were observed during storms, but there were no differences in inputs of phosphorus to disturbed and reference sites. SRP is immobilized by a variety of physical and biological processes (e.g. WOOD et al. 1984) and does not appear to be readily flushed from forest soils to streams following disturbance.

Inputs of cations (K^+ and Ca^{+2}) were moderately affected by forest disturbance. The predominant source of K^+ and Ca^{+2} in soil solution at Coweeta is

bedrock weathering (VELBEL 1985a, 1985b). Cation availability is determined by the weatherability of bedrock and the rate at which water moves through forest soils (VELBEL 1985a, 1985b). However, K^+ and Ca^{+2} are also required for plant growth, and thus a portion of the total cation pool is tied up in living and dead forest biomass (LIKENS et al. 1970, COVINGTON 1981, BORING et al. 1981). Therefore, the yield of cations to streams is determined not only by bedrock weathering but also by the balance between immobilization and mineralization. In this study, even with geological differences between watersheds, streams draining disturbed sites received more K^+ and Ca^{+2} than reference sites. At all sites, largest cation inputs were observed during large, long-duration storms, when substantial quantities of water entered streams from soil solution (Figs. 5 and 7).

Similarly elevated concentrations of cations in soil solution and increased inputs to streams draining disturbed sites have been widely reported (e.g. LIKENS et al. 1970, BROWN et al. 1973, NEARY 1977). Increased cation concentrations have been linked to increased mineralization rates in disturbed soils (LIKENS et al. 1970). Also increased nitrification, typical of disturbed soils, produces hydrogen ions. H^+ tends to displace cations from exchange sites resulting in elevated cation concentrations in soil solution and stream water (LIKENS et al. 1970). At Coweeta, increases in mineralization and nitrification rates have been observed in disturbed soils (WAIDE et al. 1988) and may contribute to increased cation inputs to streams draining disturbed areas.

It is not clear whether weathering rates are affected by forest disturbance and contribute to increased concentrations of cations in soil solutions. Total cation flux from watersheds to streams is determined not only by concentrations in soil solution but also by the volume of water moving through soils (VELBEL 1985a, 1985b). Increased water storage in disturbed sites caused by decreased interception or transpiration could result in increased weathering simply because a greater volume of water moves through soils. At Coweeta, rapid regeneration of vegetation (BORING et al. 1988) results in a rapid return of soil moisture levels to predisturbance conditions (SWANK & VOSE 1988). Water yields to streams appear to recover within 10–20 years (SWIFT & SWANK 1981). Together these studies suggest that forest hydrology recovers rapidly following clearing and long term impacts on weathering rates are probably minimal.

A final factor complicating the pattern of cation inputs observed in this study is geological differences between the watersheds. Concentrations of soil water cations entering HWC (resistant Coweeta Group) are lower than those entering the other reference stream (GB) and reflect the relatively lower weatherability of the bedrock beneath a portion of its basin (Tables 7 and 8). Cation concentrations entering CB (disturbed), whose basin is entirely underlain by the relatively resistant Coweeta Group, are similar to reference levels, being slightly higher in K^+ and lower in Ca^{+2} concentration. BHB (recently disturbed) receives the greatest concentrations of cations but drains an area underlain by the more weatherable

bedrock. Overall, the effects of disturbance are partially obscured by geological differences between basins. Our results indicate that forest disturbance alters cation inputs to streams but the actual effect is the result of combined biological and geochemical processes.

To summarize, our measurements of soil chemistry indicate that even the slight increases in nutrient availability observed in disturbed forest soils at Coweeta can result in elevated nutrient inputs to streams. Nutrients that undergo a number of transformations (e.g. nitrogen) appear to be most sensitive to forest clearing. Nutrients with substantial geological and biological pools (e.g. calcium and potassium) appear to be less strongly affected by forest clearing, and the resulting changes in nutrient inputs to streams are relatively modest. Elements that are normally strongly retained in forest soils (e.g. phosphorus) appear to be little affected and their inputs to streams do not appear to be altered by forest clearing.

Throughfall – Nutrient concentrations in throughfall are determined by background concentrations in precipitation and are modified by any net uptake or release of material as rainwater penetrates the forest canopy. Generally, nutrient concentrations increase as water travels through forest canopies. Increases result from foliar leaching and rainfall scavenging of material deposited between storms (SWANK 1984). Complete removal of the forest canopy should reduce nutrient inputs to streams since foliar leaching and rainfall scavenging would be eliminated. However, with rapid regrowth of vegetation (e.g. MARKS & BORMANN 1972, BORING et al. 1981, BORING & SWANK 1984) canopy contributions to throughfall should return to redisturbance levels within a few years.

Data from this study show that there were no differences in throughfall inputs to disturbed and reference streams and suggest a rapid recovery of canopy contributions following disturbance. However, forest clearing may have a subtle effect on timing of throughfall contributions to streams. At reference sites, concentrations of many nutrient species (especially PON, K^+ , PK, Ca^{+2} , and PCa) were greater (Tables 4, 6–8) while throughfall volumes were lower than disturbed sites. This suggests greater rainfall interception in undisturbed forest. Thus, throughfall contributions to reference streams appear to be a smaller volume, more concentrated solution than those entering disturbed streams.

Effects of forest disturbance on nutrient retention in streams

While changes in nutrient inputs to streams following forest clearing reflect disruptions of forest nutrient cycles, changes in nutrient outputs reflect both disruptions of forest nutrient cycling and also disruptions of instream mechanisms of nutrient retention. Changes in retention were apparent during storms as a decreased ability to resist the downstream displacement of nutrients. Our storm nutrient budgets suggest that mechanisms of nitrogen and phosphorus retention

may be very sensitive to forest disturbance since losses of both elements were elevated in disturbed sites.

The primary form of nitrogen loss during storms was PON. Since PON was a minor component of total N-inputs, most PON must be present in stream channels prior to storms. In our study, decreased retention of PON is indicated by greater streamwater concentrations (Table 4), total outputs (Table 5), and greater net losses (Table 5) from disturbed streams. Although outputs of DIN were also greater from disturbed sites (Table 5), these losses were the result of large $\text{NO}_3\text{-N}$ inputs from disturbed soils. Forest disturbance affects the availability of DIN in soils, but this material appears to flush through Coweeta streams during storms without undergoing any net transformations.

Phosphorus outputs were also dominated by POP. Although inputs of POP were substantial at all sites, significant net losses (Table 5) suggest an instream origin for a portion of this material. Decreased retention following forest clearing is indicated by greater outputs and larger net losses of POP from disturbed streams compared to reference sites. Forest disturbance appeared to have little impact on the ability of streams to retain either SRP or DOP. Although losses of SRP and DOP were greater from BHB (recently disturbed) compared to the other streams, they probably reflect a somewhat greater availability of phosphorus in recently disturbed soils. Concentrations of SRP and DOP were near detection limits in both soil solution and stream water suggesting that there were seldom substantial quantities available in either form.

Storm nutrient budgets suggest that forest clearing has had little impact on the ability of streams to retain calcium and potassium. The primary output of each element was in ionic form. BHB (recently disturbed) had higher streamwater concentrations and greater outputs of K^+ and Ca^{+2} but also received more of each cation from soil solution than the other sites. Large outputs of cations from BHB are probably attributable to the combined effects of greater bedrock weatherability beneath its watershed and increased cation yields from disturbed soils rather than a reduction in instream mechanisms of cation retention.

Although a small component of total outputs, net losses of PK and PCa were generally observed from both disturbed and reference streams (Table 5). For PK, net losses were greatest from disturbed sites and for PCa, BHB (recently disturbed) had greater net losses than the other streams. It appears that the greatest impact on calcium and potassium retention in streams is a decreased ability to retain PK and PCa.

Causes of altered stream stability following forest clearing

Clearly, this study indicates that disturbed streams exhibit a decreased ability to resist downstream displacement of nutrients during storms. In forests, disturbance appears to interfere primarily with biological uptake and accumulation

of nutrients. In streams, the same disturbance results in a reduction in the ability to retain nutrients already associated with particles. As a result, disturbed streams lose substantial quantities of nutrient-containing particles during storm flows. Elements with whose inputs and outputs have a substantial particulate fraction (i.e. nitrogen and phosphorus) are most affected by forest clearing. However, even elements with budgets dominated by inputs and outputs of dissolved species may be affected by disturbance, especially where dissolved species are moving through stream ecosystems without undergoing net transformations.

Our nutrient budgets indicate that both disturbed and reference streams are exporters of particulate nutrients without incorporating either a possible source for that material or an explanation of decreased retention (i.e. resistance). The origins of particles in headwater streams are somewhat obscure although WOTTON (1984) discussed mechanisms that result in the generation of microfine particles (0.5–1.0 μm) in aquatic systems and can probably be applied to larger particles as well. There are two categories of particles generated in streams. Primary particles result from the comminution of larger organic matter (WOTTON 1984), usually the result of sequential processing of allochthonous inputs by stream biota (CUMMINS 1974, BOLING et al. 1975). The second category, secondary particles, results from a combination of physical and biological processes, including ingestion, aggregation, and subsequent egestion of primary particles by organisms; flocculation of dissolved organic matter; bubble scavenging of dissolved and particulate organic matter (BOWEN 1984, WOTTON 1984).

Because net losses of particulate nutrients are elevated in disturbed streams, forest clearing must affect the rate at which nutrient containing particles are generated or the efficiency with which they are retained, or both. Particle generation rates in streams are determined by the availability of organic matter to be processed, the presence of consumer organisms, and the physical-chemical environment (i.e. nutrient levels, temperature). Following forest disturbance, a number of factors interact, all potentially influencing particle generation rates.

Physically, with the removal of forest vegetation, stream temperature and nutrient levels often increase, creating conditions that favor accelerated organic matter processing (e.g. LIKENS et al. 1970, SWIFT & MESSER 1971, SWANK 1988). Concurrently, the availability of organic matter may be greatly reduced due to decreased litter inputs (e.g. SWANSON et al. 1982, WEBSTER et al. 1983, 1990). With the regrowth of forest vegetation, physical conditions and litter inputs recover, conferring resilience to stream ecosystems. At Coweeta, leaf inputs to disturbed streams return to 80–90% of predisturbance levels within 10 years (GOLLADAY et al. 1989, WEBSTER et al. 1990). Perhaps of greater significance, the composition of litter inputs may change considerably from late successional, chemically recalcitrant species (e.g. oaks) to chemically labile, early successional species (e.g. dogwood and birch) (WEBSTER et al. 1990).

The invertebrate community, while strongly affected by forest clearing, appears capable of maintaining its functional role in streams. At Coweeta, total shredder abundance in BHB remained relatively constant following forest removal even though significant shifts in community structure, including the near elimination of the dominant shredder, occurred (WEBSTER et al. 1983, GURTZ & WALLACE 1984). In the absence of leaf litter, their preferred food resource, shredders colonized alternate habitats (GURTZ & WALLACE 1984). However, when leaf litter was introduced into BHB it was rapidly colonized and processed by stream detritivores (e. g. WEBSTER & WAIDE 1982). Flexibility in invertebrate food habits permits rapid recovery (i. e. resilience) of organic matter processing as forests regrow and litter inputs are restored.

Thus, alterations in litter quantity and quality, combined with detritivore flexibility, and altered physical factors (increased nutrient levels, increased temperature), result in conditions that favor rapid leaf decay. Studies of leaf processing at Coweeta have generally shown more rapid breakdown rates in streams draining disturbed sites (WEBSTER & WAIDE 1982, GOLLADAY & WEBSTER 1988, BENFIELD et al. 1991). Following forest clearing, particle generation rates in streams may be initially reduced, but appear recover rapidly and may even exceed predisturbance rates as forests regenerate.

The retention efficiency of streams is probably greatly diminished following forest clearing due to a gradual loss of wood debris in stream channels. The structural role of wood debris in stream ecosystems has been well documented. Organic matter tends to accumulate into debris dams large enough to span stream channels and not be displaced by stream flow (BORMANN et al. 1969, SWANSON & LIENKAEMPER 1978, LIKENS & BILBY 1982). Aggregation promotes within reach processing and retention of organic matter (BILBY & LIKENS 1980, TRISKA & CROMACK 1980, BILBY 1981), and causes a stepped pattern of streambed morphology, reducing stream power, erosiveness, and particle transport (HEEDE 1972, FISHER & LIKENS 1973, KELLER & SWANSON 1979).

During the early stages of stream recovery, wood debris may also be an important site of nutrient immobilization and retention. COVINGTON (1981) reported that logging slash tends to accumulate and retain nutrients released from disturbed forest soils. Similar mechanisms could operate in streams as wood surfaces have been reported to immobilize and accumulate nitrogen (BUCKLEY & TRISKA 1978, AUMEN et al. 1983, 1985a, 1985b, BAKER et al. 1983, MELLILLO et al. 1983). However, as wood decays it becomes increasingly susceptible to abrasion, resulting in the production of nutrient-containing fine particles (GOLLADAY & SINSABAUGH 1991). WARD & AUMEN (1986) estimated that abrasion of decomposing wood contributed substantial quantities of fine organic particles to western Cascade Mountain streams. It seems clear that wood debris has the potential to be an important source of fine, nutrient containing particles as well as an important structural element of streams. Also, over the course of decay, nutrient uptake by

coarse wood debris followed by abrasion represents a net conversion of nutrients from dissolved to particulate form. No information on rates of particle generation is available for wood debris in Coweeta streams however, breakdown rates appear to be accelerated following logging (GOLLADAY & WEBSTER 1988).

The abundance of wood in forest streams is determined by the input rate watersheds and breakdown by instream processes. Following logging, wood standing stocks may initially increase due to inputs of logging slash (LIKENS & BILBY 1982, GURTZ & WALLACE 1984, DUNCAN & BRUSVEN 1985). However, during forest regrowth, wood litterfall is reduced until predisturbance patterns of vegetation are restored (SWANSON & LIENKAEMPER 1978, LIKENS & BILBY 1982, HEDIN et al. 1988). The abundance of wood in Coweeta streams decreases following forest clearing and is attributable to reduced inputs and accelerated breakdown rates (GOLLADAY & WEBSTER 1988, GOLLADAY et al. 1989). Similar declines in wood abundance have been reported in streams draining other disturbed areas (e. g. LIKENS & BILBY 1982, SWANSON & LIENKAEMPER 1978, HEDIN et al. 1988).

Clearly, forest disturbance has caused a complex series of changes in Coweeta streams resulting in decreased stability. Leaf processing rates are accelerated in disturbed streams and annual litter inputs are rapidly converted from a form that is efficiently retained (CPOM) to nutrient-containing fine particles which are readily transported (GOLLADAY et al. 1987, 1989). Much of this transformation occurs in late autumn, and substantial quantities of nutrient containing particles are lost from disturbed streams during large, long-duration winter storms. Decreases in wood abundance have led to a decline in the frequency of stream retention structures (GOLLADAY et al. 1987, 1989). In disturbed Coweeta streams, average velocities are greater and channel roughness (Mannings n) is lower than reference sites, reflecting a decreased ability to resist the downstream movement of water and nutrients in transport (GOLLADAY et al. 1987).

Thus, stream recovery provides an interesting contrast to forest recovery. Forest recovery is characterized by a brief period of degradation (relatively high net nutrient loss) followed by a period of rapid recovery (nutrient accumulation). The reestablishment of nutrient cycles is largely autogenic, i. e. regulated by the regrowth of forest biomass. In contrast, the degradation of forest stream ecosystems is prolonged and the recovery period more gradual. Recovery of forest streams is largely allogenic, lagging behind and dependent upon the rate at which predisturbance patterns of allochthonous inputs (especially woody debris) are restored. During the recovery period following forest clearing, stream stability is reduced, reflected in a decreased ability to respond to a frequently occurring natural phenomenon, i. e. the ability to resist the downstream transport of nutrients during storms.

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