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NITROGEN BUDGET FOR A SMALL CONIFEROUS FOREST STREAM[1]

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Abstract. An annual nitrogen budget is presented for a small stream draining Watershed 10, H. J. Andrews Experimental Forest, Oregon. The role of allochthonous debris in the input, flux, and export of nitrogen is emphasized in the material balance budget. All material entering the stream channel was presumed to enter the water sometime during the year. Material estimates are based on total channel area.

The major annual nitrogen input (1974–1975) was subsurface flow (11.06 g/m^2) as dissolved organic nitrogen (10.56 g/m^2) and nitrate (0.50 g/m^2). Biological inputs of nitrogen amounted to 4.19 g/m^2 as direct terrestrial inputs of: litterfall (1.35 g/m^2), lateral movement (1.78 g/m^2), and throughfall (0.30 g/m^2). Nitrogen fixation on fine wood debris contributed an additional 0.76 g/m^2 based on rates from a nearby watershed. Total nitrogen input was 15.25 g/m^2.

The nitrogen pool was dominated by large amounts of particulate organic matter. Coarse wood constituted 32% of the nitrogen pool (3.80 g/m^2) and fine wood fractions 18% (2.18 g/m^2). The coarse wood fraction greatly influenced stream morphology. Fine organic particulates constituted an additional 40% of the nitrogen pool (4.77 g/m^2).

DON (dissolved organic nitrogen) export (8.38 g/m^2) was less than input, presumably due to biological uptake associated with litter mineralization, sorption, and chemical flocculation. Due to effective retention of particulate inputs by debris dams, biological processing in the particulate nitrogen pool, and uptake and sorption of DON, most particulate organic inputs increased in nitrogen concentration prior to export. Particulate organic nitrogen input (3.13 g/m^2) was greater than export (2.53 g/m^2). Total annual nitrogen output was 11.36 g/m^2, resulting in a gain of 3.89 $g \cdot m^{-2} \cdot yr^{-1}$ to the stream. Thus, the stream was not operating on an annual steady state, but on an input-output regime related to the processing of refractory wood debris and resetting by major storms.

Although particulate and dissolved nitrogen loss per hectare was small for the 10-ha watershed, these losses passed through or were accumulated in a pool encompassing <1% of the watershed area. This concentration of N in the stream allowed establishment of a separate ecosystem whose processing efficiency and capabilities for nutrient cycling were related to the retention capacity of the channel and nutrient quality of inputs within the reach.

Key words: allochthonous; decomposition; detritus; ecosystem; nitrogen; streams; watershed.

INTRODUCTION

Small streams draining heavily forested watersheds depend on organic inputs from the adjacent terrestrial environment (allochthonous) as a source of fixed carbon and nutrients for in situ biological processes. This dependence on terrestrial energy sources has been demonstrated for stream reaches where the forest canopy completely covers the stream, e.g., Teal 1957, Minshall 1967, Fisher and Likens 1973, Sedell et al. 1974, Meyer et al. 1981, Triska et al. 1982. In open streams, however, high in-stream (autochthonous) production can reduce the role of allochthonous inputs, e.g., Minshall 1978, Busch and Fisher 1981, Cushing and Wolf 1982. While the role of allochthonous debris as the energy base of small forested streams is well known, the role of such debris in the stream's nutrient balance has only recently been reported. Meyer et al. (1981) found that falling and blown litter contributed 28% of phosphorus input of Bear Brook,

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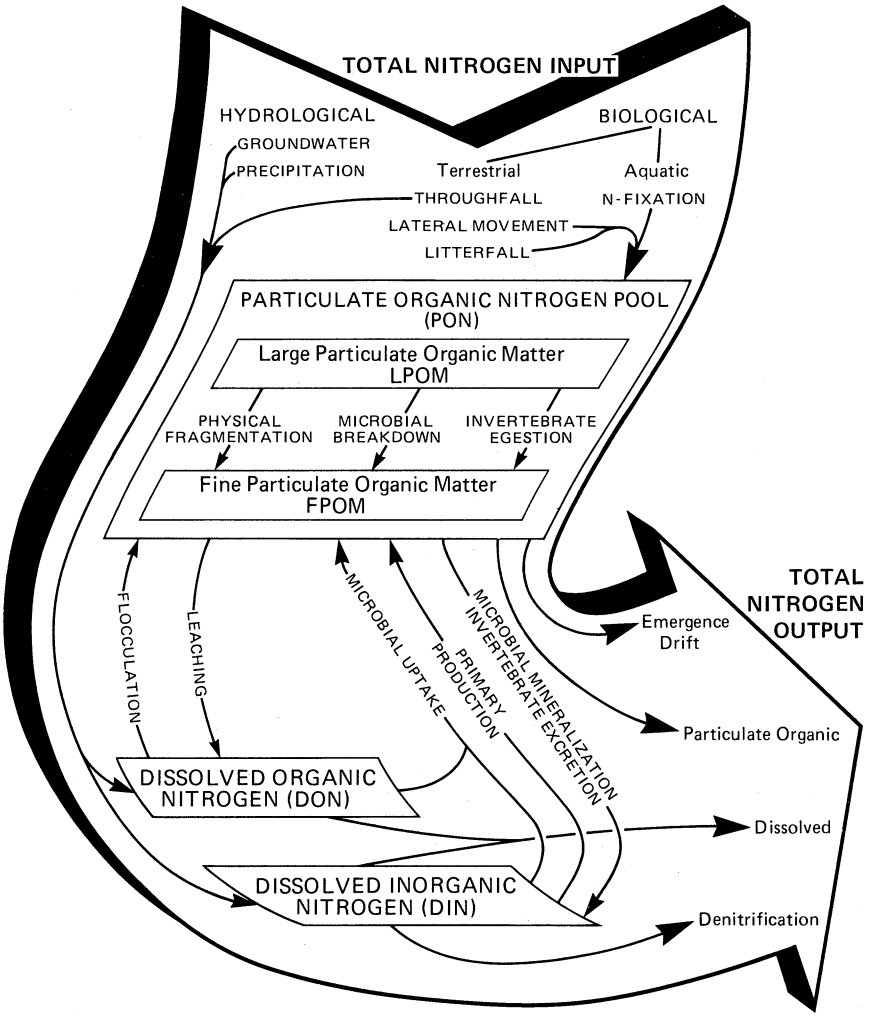

FIG. 1. Schematic drawing of major inputs and pools of nitrogen and nitrogen flux resulting from physical and biological processing of inputs in the watershed stream.

New Hampshire in 1968–1969 and 23% in 1974–1975 (Meyer and Likens 1979). Meyer et al. (1981) also report direct litterfall is ≈11% of the nitrogen budget of the same stream.

In old-growth forests of the Pacific Northwest, nitrogen is an element of interest, since nitrogen concentrations in stream water are often low, and forested watersheds may even exhibit annual net accumulation of nitrogen (Fredriksen 1972, Sollins et al. 1980). Major losses of nitrogen from the forest include leaching and mineralization of organic debris from the litter layer, and direct biological losses such as litterfall. Weathering, an important source of many nutrients, is an insignificant nitrogen source.

Once lost to the stream, nitrogen may be exchanged between the particulate and dissolved components by numerous physical and biological pathways (Fig. 1). For example, dissolved nitrogen can be taken up and immobilized during mineralization of organic carbon by bacteria and fungi. Large particulate organic matter (LPOM) can serve as a nutrient source to detritus-feeding consumers. LPOM can be converted from litter to fine particulate organic matter (FPOM) via invertebrate egestion or physical fragmentation. Particulate organic nitrogen can be converted to dissolved nitrogen via physical leaching or microbial and invertebrate excretion.

The biotic interactions which occur in the particulate organic nitrogen (PON) pool result in an increase in nitrogen concentration and often an increase in absolute levels of nitrogen during decomposition of organic matter (Kaushik and Hynes 1968, 1971, Hynes and Kaushik 1969, Iversen 1973, Hodkinson 1975, Gotto and Taylor 1976, Suberkropp et al. 1976, Triska and Sedell 1976, Davis and Winterbourn 1977, Triska and Buckley 1978, Triska and Cromack 1980, Elwood

et al. 1981, J. Rosset and F. Barlocher, *personal communication*). Since nitrogen-enhancing processes are basically microbial and the C:N ratio of litter is high, it has been hypothesized that microbial colonization is instrumental in the passage of fixed carbon and/or nutrients to higher trophic levels in lotic ecosystems (conditioning) (Triska 1970, Barlocher and Kendrick 1973, Petersen and Cummins 1974, Anderson and Grafius 1975, Suberkropp and Klug 1976, Triska and Buckley 1978, Anderson and Sedell 1979, Martin et al. 1980, Triska et al. 1982). Extensive reviews of conditioning and the invertebrate feeding process are provided in Cummins and Klug (1979) and Barlocher and Kendrick (1981).

Despite large inputs of litter debris into small streams, litter and its associated biological processes in streams have not been extensively explored as components of a stream nitrogen budget. Two exceptions include an early study by Bormann et al. (1969), which estimated particulate organic nitrogen export at Hubbard Brook, and Meyer et al. (1981), who measured litterfall and fluvial particulate nitrogen in the nitrogen budget of Bear Brook, New Hampshire. More traditionally, watershed budgets assumed that alterations of the stream's water chemistry or processing by the biota of first-order streams were insignificant, although the potential contribution of exported energy and nutrients to downstream food webs has long been recognized (e.g., Bormann et al. 1969). The objective of this study was to estimate terrestrial nitrogen inputs, both dissolved and particulate, the nitrogen pool associated with organic particulates and instream autotrophs, nitrogen fixation, and other associated within-stream biological processes on the nitrogen budget of a first-order Pacific Northwest stream.

Conceptual framework

We modified the conceptual input scheme of Bormann and Likens (1967, 1970) and Fisher and Likens (1973) to highlight the biological inputs and transformations of nitrogen (Fig. 1). Input to the streams was considered hydrological-meteorological or biological (terrestrial and aquatic) (Fig. 1). Bormann and Likens (1967) defined meteorologic inputs as those which result in direct entrance of organic matter into the stream due to wind, rainfall, and other meteorologic vectors. In addition to precipitation, they included lateral movement, litterfall, and throughfall, which we defined as terrestrial biological inputs. The first of these, lateral movement, is equivalent to the blow-in of Fisher and Likens (1973). Due to the high canopy (60–90 m) and steep slopes (30–60%), wind was a minor input vector. Lateral movement inputs resulted instead from the force of gravity on the steep sidewalls, in conjunction with alternate wetting and drying of litter. Although litterfall was intensified by early autumn rains, abscission occurred over an extended period, particularly for coniferous litter, and was considered a biological rather than a meteorological input. The high canopy minimized direct interception of precipitation. Instead precipitation reached the stream indirectly by canopy drip, which resulted in significant nutrient input as throughfall. The only potential aquatic biological input of nitrogen was dinitrogen fixation. Hydrological-meteorological inputs were composed of particulate and dissolved nitrogen from upstream reaches, and direct subsurface flow to the study reach. Since the entire stream constituted our study reach, upstream import was eliminated as a separate factor. The major output was physical export of both particulate and dissolved nitrogen. Litter storage deep in the sediments was not considered an important factor, as loose mineral sediments were not thick. Nitrogen output due to microbial denitrification was not estimated, since most input-output estimates were made prior to general acceptance of the acetylene inhibition technique. Although quantification of flux within the nitrogen pool was not an objective of the study, estimation of budget parameters contributed significant insight into the impact of biological processes on the stream's nitrogen budget. As most of the stream's energy base was allochthonous and most of those inputs were at least partially processed within the reach (Sedell et al. 1974, Triska et al. 1982), biotic impacts on the nitrogen budget were investigated where possible. The approach was to construct a material balance budget by tallying hydrological-meteorological inputs, and terrestrial and aquatic biological inputs, minus hydrological and biological exports and changes in particulate organic storage. A secondary goal was assessing the contribution of associated biological processes on the stream's nitrogen budget.

Study Area

The study was made at Watershed 10 in the H. J. Andrews Experimental Forest, in the western Cascades of Oregon, USA. At the time of the study the vegetation was dominated with seral 450-yr-old Douglas-fir (*Pseudotsuga menziesii*) with a well-developed understory canopy of western hemlock (*Tsuga heterophylla*). Local environmental variation on the watershed resulted in four major plant community types which are described in detail by Grier and Logan (1977). The watershed covers 10.1 ha and rises from 430 m at the outlet stream gauging station to a maximum watershed elevation of 670 m. Mean annual precipitation is 240 cm (Waring et al. 1978*b*). Overall slope of the stream channel is 45%. Side slopes and headwall, however, range up to 60% because of deep incision of the basin into the main ridge.

Stream discharge typically ranges from ≈0.23 L/s in the summer to peak flows of 140 L/s during the highest winter freshets. Mean discharge over approximately triweekly intervals between 5 March 1974 and 18 March 1975 is presented in Table 9. The uppermost forks are intermittent during summer. Width of the stream chan-

TABLE 1. Mean annual element concentrations in discharge water collected from the weir at Watershed 10. Estimates are from a composite, discharge-proportional water sample analyzed at ≈3-wk intervals.

Source	Nutrient	Mean concentration (mg/L)
R. L. Fredriksen, *personal communication**	NO_3-N	0.006
	Kjeldahl N	0.027
	Total dissolved P	0.101
	Ortho-P	0.042
R. L. Fredriksen (1975)†	Na	1.96
	K	0.339
	Mg	0.834
	Ca	3.20
	Alkalinity (HCO_3^-)	4.17

* 5 March 1974–18 March 1975.
† May 1972–May 1975.

nel ranges from 0.25 m in the upper reaches to 1.0–1.5 m at the watershed's base. Streambed morphology is a "stairstep" series of small pools connected by free-fall zones or riffles running on bedrock. Pools are formed mainly behind accumulations of wood debris. The substrate consists of loose rocks and gravel from weathered tuff and breccia material and bedrock of unweathered tuff and breccia. As the stream was gauged at bedrock, little water was lost due to deep seepage. Water temperature typically ranges between 1° and 15°C (Sedell et al. 1975).

During the year of the study the pH of stream water ranged between 6.4 and 7.4, and bicarbonate alkalinity between 4.1 and 7.34 mg/L (Table 1). Nitrogen concentration was typically low in all forms, and dissolved phosphorus was high relative to nitrogen. Mean dissolved Kjeldahl nitrogen was 0.027 mg/L, and nitrate-nitrogen, 0.006 mg/L. Nitrite and ammonium were mostly undetectable. The nitrate concentration was historically high, due to a large pulse of nitrate of unknown origin, whose maximum concentration was discharged between 14 January and 11 February 1974. Between 28 May 1974 and 26 February 1975, mean nitrate concentration in continuously collected composite samples was 0.001 mg/L (14 samples). Dissolved total phosphate had a mean annual concentration of 0.10 mg/L and orthophosphate a mean annual concentration of 0.04 mg/L. Typical concentrations of other major cations and anions are provided in Table 1.

All inputs which entered the bank-full channel were assumed to enter the water sometime during the year. Total area of stream channel, determined by measuring bank-full width every 10 m, was calculated at 767 m^2. Lateral inputs were a function of total bank length, which was estimated at 1500 m.

Between 1972 and 1975, numerous input-export characteristics were measured: litterfall, lateral movement, standing crop, litter decomposition, seep chemistry, stream chemistry, particulate export, moss cover, insect biomass, and insect emergence. In addition, nitrogen fixation was measured in the stream at Watershed 2, a larger but chemically similar second-order stream in the same forest.

MATERIALS AND METHODS

Terrestrial biological inputs

Nitrogen input by litterfall was estimated with 11 randomly placed 1.0-m^2 litter boxes which sampled 1.5% of channel area. Trap height was 0.5 m above the water. Traps were 15 cm deep and had a removable nylon insert with a mesh opening of 500–800 μm. Litterfall was sampled approximately monthly between March 1972 and March 1975. Data from two full years, May 1972–May 1974, are reported here. Samples were returned to the laboratory, air dried, and sorted into four categories: leaves, needles, CTBW (cones, twigs, bark, wood), and miscellaneous (frass, flower parts, seeds, fruit, etc.). After fractionation, each category was dried at 50°C and weighed. Nitrogen concentration was determined on composite samples by micro-Kjeldahl analysis. Where possible, samples were composited both by year and season.

Lateral movement was sampled by 30 randomly placed rectangular boxes (0.1 m high by 0.3 m deep by 0.5 m wide) with aluminum tray inserts. Traps were placed on the forest floor adjacent to the streambed with the open end (0.5 m) parallel to the stream and facing upslope. Lateral-movement boxes sampled 1% of bankside inputs. Samples were collected monthly and sorted into the five categories described above, dried, and weighed. Seasonally composited samples of each category were analyzed for nitrogen by the micro-Kjeldahl technique. Trays were collected, sorted, and composited for nutrient analysis between March 1973 and May 1975. Two years of data, May 1973–May 1975, are reported.

Throughfall or canopy drip was measured by continuous collection into 20-L polyethylene containers equipped with funnels and strainers of 0.8–1.0 mm mesh (Grier and Logan 1977, L. E. Glenn, *personal communication*), or in precipitation gauges equipped with funnels and glass wool stoppers (Abee and Lavender 1972). Collectors were dispersed both along the stream and in the forest. Samples were taken approximately monthly, filtered (0.8-μm glass fiber filter) and analyzed for total nitrogen (macro-Kjeldahl).

Hydrological-meteorological inputs

The largest nitrogen input to the stream was subsurface runoff of precipitation modified by passing through the litter layer and soil profile. Subsurface runoff was estimated at five seeps, two of which were perennial (Fig. 2). Each seep represented a subbasin based on surface topography, and on the basis of area

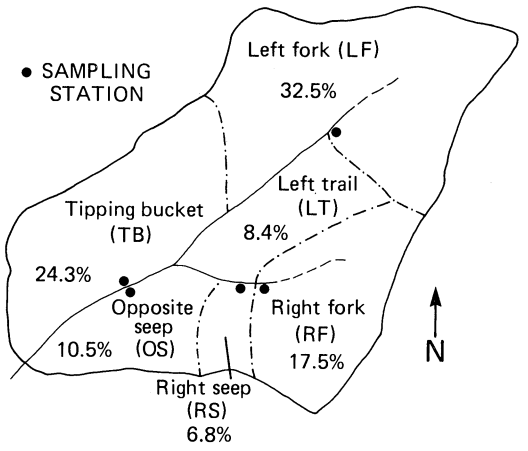

FIG. 2. Map of Watershed 10, indicating the location of major seeps and their estimated contributing areas.

was assigned a proportional contribution of discharge. Subbasin Left Trail (LT) is included with Right Fork (RF) because seepage at LT was partially contaminated by stream water diverted underground by an upstream debris dam, and because the vegetative community (*Rhododendron macrophyllum–Berberis nervosa* type [Grier and Logan 1977]) is similar to RF. Each seep was tapped with a stainless steel pipe to facilitate sampling and minimize biological uptake of nutrients at the seep's surface. Sampling by on-site personnel was approximately biweekly, with intensive sampling during major storms. Most sampling occurred between November and March, the period of greatest precipitation. Seep samples were filtered at a laboratory near the site, then frozen for later analysis of nitrate and total nitrogen (organic nitrogen + ammonium). Total nitrogen was determined by the macro-Kjeldahl method (Jackson 1958), and nitrate by the copper-cadmium reduction method (Noonan and Holcombe 1975, Rand 1976). Extrapolation to N discharge was based on water records from a gauging station at the watershed's base (R. Fredriksen, *personal communication*).

Intermittent seeps were on the stream's right fork. When these seeps ceased flowing, their proportional contribution was determined using the dissolved nitrogen concentrations from seep RF; when all right fork seeps were dry, the most upstream seep (LF, left fork) was used to estimate nitrogen input for the contributing area. These inputs are listed on the data tables as "combined." The most upstream (LF) seep was chosen because it flowed all year, provided the largest contributing area, and had both a north- and south-facing component (Fig. 2). Because nitrate was almost always at or below the limit of detection, fewer samples were analyzed for nitrate than for total nitrogen. To determine inorganic input, samples from two years (1974–1975) were used to enlarge the data base.

Aquatic biological input

The only aquatic biological input of nitrogen was by fixation on various biological substrates, particularly by bacteria associated with wood and moss. Fixation rates were determined on four wood types from Douglas-fir: heartwood blocks, twigs, bark, and wood chips. Wood substrates were dried (50°), weighed, and placed into litter bags (800-μm mesh nylon). Bags were incubated in the stream at Watershed 2, H. J. Andrews Experimental Forest, and removed seasonally for a period of 2 yr, as the study could not be completed at Watershed 10 prior to clearcutting. Upon collection, the sample was divided in half and placed in jars fitted with serum stoppers. Part of the gaseous contents (10 kPa) of the treatment jar was replaced with acetylene generated in the field from calcium carbide. The second jar served as a control. Acetylene gas samples were also checked for potential ethylene contamination. Samples were either incubated in the stream for 24 h or returned to the lab in a cooler filled with stream water and incubated for 24 h at stream temperature. Following incubation, a gas sample was transferred to a nonsterile Vacutainer for analysis by gas chromatography.

To determine nitrogen fixation rates associated with moss, samples were removed from mineral substrates submerged by stream water. Incubation time, temperatures, and gas sampling procedures were identical for both substrates. Gas analysis was undertaken on a gas chromatograph at ambient temperature using a Porpak R 1.8-m (six-foot) column. The theoretical ratio of three moles acetylene reduced to one mole nitrogen fixed was used as a conversion factor (Bergersen 1970). Recent estimates of nitrogen fixation on wood debris from forested environments (Silvester et al. 1982) indicate a ratio of 5:1 may be a more realistic conversion factor for incubations. Thus our results may be an overestimate of actual fixation rates. After incubation, tissue samples were dried at 50°, then weighed. Fixation was calculated per gram dry mass, and the result extrapolated to the known standing crop.

Terrestrial biological exports

Terrestrial biological exports were measured during a dry year, 1972–1973 (167 cm precipitation), a wet year, 1973–1974 (305 cm precipitation), and continued through spring 1975. During the dry year an 80-μm mesh nylon net was placed at the watershed's base (Fig. 2), and organic particles in excess of that size were collected. The net, $\approx$3 m long, continually sampled the entire discharge. During the wet year (1974) increased water volume necessitated a mesh size of 1000 μm to keep fine organic debris from clogging the net. The net was emptied when filled and samples were refrigerated prior to processing. Samples were separated into coarse particulate organic matter (CPOM) by litter type and fine particulate organic matter

(FPOM) by size class using a Tyler sieve series. Size classes of FPOM were either: large (LFPOM, 1 mm to 250 μm) or medium (MFPOM, 250 μm to 80 μm). As only CPOM was collected during 1974–1975, the year of the budget, FPOM estimates were determined as a proportion of the previous year's export. After sieving, samples were dried (50°) and weighed. Selected storm samples representing a diversity of seasons and discharge volumes were sorted into the four substrate categories used for litterfall and lateral movement. Composited samples were analyzed for nitrogen content using the micro-Kjeldahl determination.

Hydrological-meteorological exports

Hydrological-meteorological output was estimated from grab samples taken at the gauging station each time the seeps were sampled. The samples were filtered and analyzed using identical methods. Additional water samples were collected by a discharge proportional water sampler located at the gauging station (R. Fredriksen, *personal communication*). Continuous samples were composited into a single 20-L polyethylene bottle. Samples were returned to the laboratory, filtered (0.8-μm glass fiber) and analyzed at approximately triweekly intervals. Nitrate and nitrite were determined by the copper-cadmium reduction method, and ammonia and total nitrogen by the macro-Kjeldahl method. Orthophosphate was determined by the molybdate blue method and total phosphorus by the molybdate blue method with ascorbic acid following digestion with persulfate and sulfuric acid (Rand 1976). For both continuous and grab samples, the sum of nitrate, nitrite, and ammonia was subtracted from total nitrogen to estimate dissolved organic nitrogen (DON). Measurements of dissolved export were determined from 5 March 1974 to 18 March 1975, a period of simultaneous intensive sampling, for both grab and continuous samples.

Particulate organic nitrogen pool

Standing crop of particulate organic nitrogen was estimated by taking 15.25 cm diameter (0.018 m^2) cores from the stream bottom. Samples were collected monthly for 18 mo and four times per year for an additional year. Five samples each were removed from riffles and pools on each date. One year's data, May 1973–May 1974, are reported here.

CPOM was removed to a depth of 10 cm by hand and placed in a clean 4-L polyethylene bottle. FPOM was pumped from the bottom of the sampler with a hand-operated pump. Samples were returned to the laboratory, washed through a Tyler sieve series, and sorted to the following size classes: large (LFPOM, 1 mm–250 μm), medium (MFPOM, 250–75 μm), and small (SFPOM, 75–0.45 μm). The smallest size class was determined seasonally. Invertebrates were removed from samples by hand using a dissecting microscope. Coarse particulate organic matter >1 mm was dried, and then sorted into leaves, needles, CTBW, and miscellaneous. Samples of each litter type were analyzed for organic nitrogen content by micro-Kjeldahl technique seasonally. Standing crop of large debris, tree limbs, branches, and boles was determined by Froehlich (1973) using a line transect method.

Mosses

Approximately 20% of the stream bottom was bedrock colonized by mosses. Moss cover was determined using a gridded metre frame to estimate percent cover. Density was determined by random sampling of 1.0-cm squares of moss along the watercourse (J. Lyford, *personal communication*). Moss was analyzed for nitrogen by the micro-Kjeldahl method and for fixation as described previously. Estimates of cover, density, and moss standing crop were normalized to the total channel area.

Other associated biological processes

Change in nitrogen concentration of litter was monitored by a leaf pack assay (Petersen and Cummins 1974). Disappearance rates were determined for needles of Douglas-fir (*Pseudotsuga menziesii*), the most common litter input, and for deciduous litter of big-leaf maple (*Acer macrophyllum*), vine maple (*Acer circinatum*), and alder (*Alnus rubra*).

Leaf litter was collected at abscission, air dried, and strung on monofilament line to produce a 5–15 g leaf pack. Leaf packs were oven dried (50°), weighed, and anchored in the stream using bricks. Packs were oriented upstream with current holding the pack against the face of the brick. Leaf packs were therefore accessible to both biotic and abiotic processes. The result was a large variation in loss of mass due to physical abrasion, decomposition, and shredding by invertebrates.

Three packs were collected monthly from the stream. Leaf packs and bags were washed and insects and ancillary debris were removed by hand. Contents were dried at 50° and reweighed to calculate loss of mass. Dried samples were combined by date and ground through a 0.42-mm (40-mesh) screen for nitrogen and lignin analysis. Nitrogen analysis was undertaken by the micro-Kjeldahl technique. Lignin analysis was determined by the Van Soest (1963, 1965) technique. To obtain some index of humification, nitrogen content complexed to lignin was also determined by Kjeldahl analysis of lignin prepared by the Van Soest technique. To estimate total phosphorus, tissue samples were digested with nitric acid and perchloric acid, then analyzed using essentially the same method as the water samples.

RESULTS

Terrestrial biological inputs

Big-leaf maple and vine maple litter was the major deciduous leaf input to the stream. Although vine maple decomposed faster than big-leaf maple, the two

TABLE 2. Input of nitrogen introduced by litterfall to the stream channel at Watershed 10, H. J. Andrews Experimental Forest. The contribution of coarse wood debris (CWD) and microparticulate nitrogen is excluded.

	Needle		Leaf		CTBW*		Miscellaneous	
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
	Litterfall N input ($mg \cdot m^{-2} \cdot mo^{-1}$)							
May	15.41	37.20	0.22	0.22	18.41	3.13	1.63	4.42
Jun	48.63	64.89	0	3.13	8.10	17.40	5.67	1.08
Jul	73.04	50.39	1.34	1.56	12.97	6.72	21.20	1.67
Aug	84.89	87.48	2.23	6.46	18.73	5.96	3.06	0.56
Sep	89.97	92.73	1.89	5.48	22.22	7.07	3.23	0.59
Oct	116.65	78.40	9.76	46.67	5.18	15.31	3.65	0.91
Nov	122.12	108.71	119.07	84.09	4.56	57.11	4.12	23.52
Dec	39.33	20.59	10.41	1.30	6.32	9.49	2.97	10.13
Jan	50.56	9.71	2.60	0.38	34.89	13.38	15.76	14.88
Feb	14.82	8.92	0.17	0.17	4.00	6.56	1.88	12.90
Mar	21.56	43.13	0.22	3.26	4.69	34.81	1.62	13.95
Apr	15.33	25.35	0.21	0.21	9.93	7.77	2.26	6.51
	Annual input (g/m^2)							
	0.69	0.63	0.15	0.15	0.15	0.19	0.07	0.09
	Year 1 (May 1972–Apr 1973)				Year 2 (May 1973–Apr 1974)			
	Total annual input		811.16 g		Total annual input		810.65 g	
	Total annual input		1.06 g/m^2		Total annual input		1.06 g/m^2	

* Cones, twigs, bark, wood.

species were combined to estimate nitrogen input. Both were processed faster than coniferous needles (Sedell et al. 1975). Deciduous leaf input was 11% of litterfall nitrogen. Seasonally, most nitrogen input (68%; 80% 1972–1973, 55% 1973–1974) occurred during autumn, particularly November (Table 2). Leaf litter input was intermittent from February through August as leaves entrained by the canopy were slowly released. Partial decomposition in the canopy apparently increased nitrogen concentration, since nitrogen concentration of litter was lower at abscission (Table 3). This factor was considered in calculating nitrogen input. Estimated annual nitrogen input by leaf litter was 0.15 g/m^2 in both years.

Needles were the major nitrogen component (49%) in litterfall (Table 2). Needlefall input began in June with the onset of moisture stress and continued with increasing intensity through November. Input during June and July consisted primarily of hemlock with increasing amounts of Douglas-fir in succeeding months.

Needle litterfall during summer and fall was lowest in nitrogen concentration (Table 3). Presumably most nitrogen was reabsorbed prior to natural abscission (Whittaker et al. 1979). During winter and spring, green needles were a smaller but more concentrated input. Winter input was often storm generated, when wind or wet snow in the canopy removed fine twigs with attached live needles. Annual nitrogen input by needle litterfall was 0.66 g/m^2.

Cones, twigs, bark, and wood (CTBW) accounted for 13% of litterfall nitrogen input (Table 2). Monthly nitrogen input ranged from 3 to 57 $mg \cdot m^{-2} \cdot mo^{-1}$, mostly as a continuous shedding of small twigs. Occasionally more catastrophic events, such as a major limb or bole falling in the vicinity of a litter trap (November 1973), resulted in a large nitrogen input. Nitrogen concentration of twigs, the primary CTBW component, remained nearly constant seasonally (Table 3). Mean annual nitrogen input of CTBW was 0.17 g/m^2.

TABLE 3. Nitrogen concentration (percent) by season, for selected biological substrates from Watershed 10, H. J. Andrews Experimental Forest.

	Needle	Leaf	CTBW*	Miscellaneous
Litterfall				
Winter (Dec–Feb)	0.54	0.60	0.34	0.96
Spring (Mar–May)	0.71	0.70	0.36	0.75
Summer (Jun–Aug)	0.42	0.72	0.31	0.90
Fall (Sep–Nov)	0.46	0.63	0.38	0.98
Lateral movement				
Winter (Jan–Mar)	0.54	0.76	0.30	1.10
Spring (Apr–Jun)	0.77	0.58	0.36	1.05
Summer (Jul–Sep)	0.66	0.65	0.39	1.03
Fall (Oct–Dec)	0.48	0.60	0.29	1.00
Particulate nitrogen pool				
Winter (Dec–Feb)	0.66	0.87	0.29	0.62
Spring (Mar–May)	0.74	0.86	0.24	0.66
Summer (Jun–Aug)	0.53	1.11	0.31	0.80
Fall (Sep–Nov)	0.52	1.16	0.29	1.00
Fine particulate nitrogen pool	Large	Medium		Small
All seasons	0.71	0.75		1.44
Export				
Winter (Dec–Feb)	0.63	0.98	0.48	1.11
Fall (Oct–Dec)	0.56	1.04	0.37	1.47

* Cones, twigs, bark, wood.

TABLE 4. Nitrogen introduced by lateral movement of organic material to the stream channel at Watershed 10, H. J. Andrews Experimental Forest.

	Needle		Leaf		CTBW*		Miscellaneous	
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
	Lateral-movement N input ($mg \cdot m^{-2} \cdot mo^{-1}$)							
May	16.46	22.19	11.33	9.88	19.53	331.55	10.74	35.15
Jun	38.33	20.73	8.88	6.61	91.58	19.44	52.28	17.20
Jul	33.14	18.40	21.36	7.65	38.20	21.76	26.18	17.56
Aug	14.12	22.50	7.05	8.87	31.19	33.25	11.81	23.63
Sep	25.93	23.56	13.70	17.21	47.72	75.23	40.47	9.57
Oct	38.68	25.89	20.45	46.51	50.43	91.24	17.67	25.11
Nov	48.95	28.94	119.66	77.58	101.53	29.66	37.81	20.10
Dec	30.65	30.05	26.59	29.01	29.94	123.61	36.27	34.41
Jan	29.79	23.77	25.92	16.96	41.57	61.75	30.29	20.12
Feb	21.93	21.46	21.43	15.32	26.79	55.78	43.99	18.18
Mar	19.41	15.23	17.43	20.97	176.60	91.14	37.51	22.84
Apr	28.19	11.08	13.74	11.30	43.52	55.62	44.72	21.11
	Annual input (g/m^2)							
	0.35	0.26	0.31	0.27	0.70	0.99	0.39	0.27
	Year 1 (May 1973–Apr 1974)				Year 2 (May 1974–Apr 1975)			
	Total annual input		1335.72 g		Total annual input		1373.54 g	
	Total annual input		1.74 g/m^2		Total annual input		1.79 g/m^2	

* Cones, twigs, bark, wood.

Miscellaneous inputs consisted of all other litter particulates (>800 μm) not easily grouped into the previous categories. The composition was primarily mosses and lichens (mainly *Lobaria* sp.) from the canopy. In season, floral parts, seeds, and insect frass contributed to the miscellaneous category. Nitrogen concentrations were uniformly higher in miscellaneous than in other litter categories (Table 3). Decomposition rate of miscellaneous debris was not determined but was presumably rapid, relative to other litter inputs, due to higher nitrogen concentration. Miscellaneous inputs were 6% of litterfall nitrogen (Table 2), with a mean annual input of 0.08 g/m^2. Microparticulate inputs (MICRO PN [<800 μm]) were not estimated by us but were determined by G. C. Carroll and L. H. Pike of the University of Oregon. Their results are reported in Sollins et al. (1980). Estimates, made from the particulate component of throughfall, were between 50 and 150 $kg \cdot ha^{-1} \cdot yr^{-1}$. We used an intermediate value of 100 $kg \cdot ha^{-1} \cdot yr^{-1}$ dry mass to calculate nitrogen input. Nitrogen concentration, from a composite of 100 of their samples, was 1.75 ± 0.21 (SE) percent of dry mass. This translates to 0.18 $g \cdot m^{-2} \cdot yr^{-1}$, 13% of litterfall nitrogen. A final source of litterfall nitrogen was coarse wood debris (CWD). Sollins et al. (1980) estimate input from logs at 1.1 $kg \cdot ha^{-1} \cdot yr^{-1}$ or 0.11 g/m^2. We used this estimate in our study.

Monthly comparison of inputs between years indicates some variation due in part to differences in collection dates and storm patterns. Seasonally, input amounts of all litter are similar, and on an annual basis are almost identical. Grier and Logan (1977), who estimated litterfall for 2 yr on the terrestrial component of Watershed 10, also found that yearly totals (including green litter) differed from the yearly average by <1%. Thus litterfall provided a remarkably uniform input of biologically fixed carbon and nutrients between years, but with strong seasonal trends.

Lateral nitrogen input

Conifer needles, the primary source of litterfall nitrogen, were the second largest lateral input. Nitrogen from coniferous needles constituted 17% (20% 1973–1974; 15% 1974–1975) of lateral movement (Table 4). Lateral movement of needles had seasonal trends similar to those of litterfall, but was more uniform throughout the year. As with litterfall, lateral needle inputs were highest during autumn. Fall, winter, and spring nitrogen concentrations were similar to those of litterfall, whereas summer concentrations were higher (Table 3). The summer increase may result from partial decomposition on the forest floor, with associated increase in nitrogen concentration. Mean annual nitrogen input by lateral movement of needle litter was 0.31 g/m^2.

Lateral movement of leaf litter added almost as much nitrogen to the stream as lateral needle input and almost twice as much as leaf litterfall. Most lateral leaf input was big-leaf maple and occurred during autumn. Unlike leaf litterfall, significant but decreasing inputs occurred December–May as leaves continued to slide downhill. For example, only 34% of total nitrogen input by leaf litter occurred during November for lateral movement, compared to 68% for litterfall. Nitrogen

concentrations from composite samples of lateral movement during autumn were similar to those of litterfall, 0.63% and 0.60% N, respectively (Table 3). Winter concentrations of nitrogen in lateral movement were slightly higher than those in litterfall, but summer concentrations were slightly lower. Leaf litter was 16% of lateral-movement nitrogen and amounted to 0.29 $g \cdot m^{-2} \cdot yr^{-1}$ (Table 4). As with litterfall, miscellaneous organic particulates had the highest nitrogen concentration of any lateral input (1.05%). Nitrogen contribution to the stream was 0.33 $g \cdot m^{-2} \cdot yr^{-1}$, four times the contribution of miscellaneous litterfall. Miscellaneous particulate nitrogen was 19% of lateral movement input and lacked seasonal trends.

The major lateral nitrogen input was CTBW. Various types of wood debris contributed 0.85 $g \cdot m^{-2} \cdot yr^{-1}$, 48% of total lateral movement (Table 4). Seasonal composite samples ranged between 0.29 and 0.39% total nitrogen concentration (Table 3). Concentrations were lowest during late autumn and highest during summer. CTBW was the most variable debris category, due to the heavier mass of individual pieces, and random input. With the exception of CTBW, lateral movement was only 75% as great in year 2 as in year 1. The reason for the apparent annual difference is unknown, and examination of monthly input (Table 4) indicates no special trends. Total annual nitrogen input was nearly identical due to a large input of wood debris in May 1974. Overall, the data indicate that surface erosion provided a steady contribution of organic debris. This more uniform input scheme mitigated the strong seasonal input of leaf litterfall and helped insure a constant source of organic debris for biotic processing.

Dissolved nitrogen input

Throughfall

Dissolved inputs consisted of subsurface flow and throughfall. Throughfall was a potential source of biologically labile nitrogen. Only 5–30% of precipitation reached the stream by direct interception. The remainder was nutrient enriched by dripping through the canopy, which provided 20–32 m^2 of leachable foliar surfaces per square metre of forest floor (Grier and Logan 1977, Waring et al. 1978*a*). This estimate of foliar surface did not include a high density of nitrogen-fixing lichens that inhabited the overstory. Abee and Lavender (1972) estimated mean annual throughfall nitrogen inputs at 0.34 $g \cdot m^{-2} \cdot yr^{-1}$ in a study of six old-growth stands. Highest nitrogen input in throughfall was at 0.40 $g \cdot m^{-2} \cdot yr^{-1}$. Using data from C. C. Grier (*personal communication*) for collections along the stream, throughfall input was 0.40 $g \cdot m^{-2} \cdot yr^{-1}$ during 1974 and 0.35 $g \cdot m^{-2} \cdot yr^{-1}$ during 1973. L. E. Glenn et al. (*personal communication*) estimated throughfall at Watershed 10 to be 0.27 $g \cdot m^{-2} \cdot yr^{-1}$ during 1973 and 0.21 $g \cdot m^{-2} \cdot yr^{-1}$ during 1974 from a set of six sample collectors placed along the stream. The reason for input differences is not known, but may have been related to sample preservation, the number of samplers, or their distribution. Kimmins (1973) indicated that the number of collectors required for adequate estimation of throughfall is larger than the number used in the individual studies cited. All throughfall N input estimates varied within a range of 0.20–0.40 $g \cdot m^{-2} \cdot yr^{-1}$, depending on year and sampler location, with most values at the higher end of that range. An estimate of 0.30 $g \cdot m^{-2} \cdot yr^{-1}$ represents a reasonable estimate of annual throughfall nitrogen input. This estimate is slightly lower than the 0.34 $g \cdot m^{-2} \cdot yr^{-1}$ canopy solution, including stemflow, which was used by Sollins et al. (1980), for their terrestrial nitrogen budget at Watershed 10.

Subsurface inputs

Seep inputs varied seasonally both in volume and nutrient concentration. Differences in seep chemistry were attributed to drainage area and soil depth. Based on seep chemistry, annual dissolved organic nitrogen input from subsurface flow was estimated at 8.49 kg, or 10.56 g/m^2 of channel. Annual nitrate input was an additional 0.38 kg or 0.50 g/m^2 (Table 5). Thus only 5% of dissolved inputs were inorganic, with 95% organic nitrogen. Our calculation of dissolved-nitrogen input may be an underestimate for two reasons. First, seep inputs were estimated by a series of grab samples rather than by continuous monitoring. Because DON concentration varies with streamflow (highest in rising flows, lowest in falling; Fredriksen 1972, Kennedy and Malcolm 1978) grab sampling can miss some initial periods of high nitrogen concentration. Second, nitrate was not present in detectable quantities during many periods of high discharge when even trace quantities would extrapolate to significant input.

Special geological features of many seeps caused nitrogen input to differ from that expected by area alone. For instance, Left Fork (LF) drained 32.5% of the watershed, but contributed 46% of subsurface nitrogen (Fig. 2, Table 5). This was an area of deep soils and permanent discharge. Tipping Bucket (TB), which drained 24% of the watershed area, contributed only 16% of dissolved nitrogen. This area had deep soils and also a subterranean lava dike that slowed runoff and allowed additional time for nitrogen uptake and sorption. Right Seep (RS), draining only 6.8% of watershed area, also contributed 16% of dissolved nitrogen. RS was an area of very shallow soils and rapid runoff. Total nitrogen concentrations at RS during early autumn storms were equivalent to those at LF, but were 2–2.5 times higher during late autumn and early winter. Concentrations at RS were approximately four times higher than TB during equivalent periods. As expected, overall input was related to discharge. Periods when absence of flow resulted in combining of seeps represented only 1% of total subsurface input (Table 5).

TABLE 5. Dissolved-nitrogen input 5 March 1974–18 March 1975 as subsurface runoff estimated at five seeps from Watershed 10, H. J. Andrews Experimental Forest. (···) indicates absence of flow during sample interval.

Discharge interval	Seep					
	Left fork	Tipping bucket	Right fork	Right seep	Opposite seep	"Combined"*
			Dissolved-nitrogen input (g)			
5–27 Mar	177.23	119.89	53.80	74.16	40.12	
28 Mar–19 Apr	107.45	95.41	69.57	158.79	117.06	
20 Apr–9 May	6.47	2.76	···	···	···	8.55
10–23 May	110.64	36.77	19.60	···	···	12.93
24 May–17 Jun	60.00	34.27	62.94	···	···	41.56
18 Jun–11 Jul	79.15	43.37	···	···	···	32.89
12–31 Jul	22.30	6.78	···	···	···	49.86
1–19 Aug	15.42	1.89	2.01	···	···	1.33
20 Aug–9 Sep	182.04	0.12	3.73	···	···	2.46
10–30 Sep	123.79	4.72	2.45			1.61
1–11 Oct	21.84	0.18	0.40	4.30	0.46	
12–25 Oct	21.84	0.18	0.40	4.30	0.46	
26 Oct–13 Nov	56.83	13.86	33.49	18.74	···	13.32
14 Nov–2 Dec	999.85	145.58	161.45	110.26	···	64.20
3–24 Dec	939.41	492.22	441.11	493.53	194.57	
24 Dec–15 Jan						
16 Jan–3 Feb	707.85	299.91	150.42	468.99	97.20	
4–26 Feb						
27 Feb–18 Mar	62.85	14.45	···	···	···	83.15
NO_3N	62.96	170.65	100.04	14.32	36.17	
Seep total	3757.92	1483.01	1101.41	1347.39	486.04	311.86
Total dissolved nitrogen			8487.43			

* When seeps ceased flowing, their proportional contribution was determined using the dissolved-nitrogen concentrations from seep RF, which was still flowing. (See Methods: Hydrological-meteorological inputs).

To assess the significance of dissolved nitrogen flux seasonally we emphasized discharge patterns and major particulate input events rather than calendar seasons. So defined, the four seasons of our study were approximately: Autumn (1 October–2 December), Winter (3 December–19 April), Spring (20 April–17 June), Summer (18 June–30 September). The autumn season, 1 October–2 December, was the most active period of dissolved nitrogen retention. DON input was 1.73 kg and output 0.82 kg, indicating a net retention of almost 0.9 kg DON by various physical, chemical, and biological mechanisms. Biological retention was facilitated by high particulate organic loading. In litterfall ≈32% of needle litter nitrogen and 87% of leaf litter nitrogen fell during these 2 mo. Autumn also coincided with the beginning life cycle of many invertebrates. Anderson and Cummins (1979) note that the life cycle of many shredder invertebrates is "keyed to the autumnal pulse of leaf fall with major growth during late autumn and winter." Potential biotic interactions were further facilitated by low discharge (<3% annual discharge), which maximized water contact with biologically active surfaces. This combination of factors presumably promoted microbial uptake on litter substrates, resulting in nitrogen retention with subsequent passage to higher trophic levels.

A second period of high nitrogen retention was summer, 18 June–30 September (66%). In summer, subsurface nitrogen input was estimated at 0.58 kg and output 0.19 kg. Only 6% of annual DON input and <2% of discharge occurred during summer. As a result, although summer was a period of intense nitrogen flux, it was nearly insignificant to the annual nitrogen budget.

The winter storm season, 2 December–19 April, was characterized by high streamflow and low nitrogen concentration in stream water. This 4½ mo season had 89% of annual discharge. Some 69% of DON input (5.55 kg) and 78% (5.00 kg) of DON output occurred during winter. Despite high winter flows, net retention of DON (0.55 kg) was observed. This is less than half the 1.30 kg retained during the summer–autumn period, when <5% of discharge and 27% of DON was input to the stream.

Spring, 20 April–17 June, was a 2-mo period of rapidly declining discharge. About 6% of annual discharge occurred during spring. DON input and output nearly balanced, 0.39 kg vs. 0.43 kg, respectively. Leaf litter input was especially low in spring and followed the period of maximum surface scouring of epilithic and organic surfaces.

Annual net DON retention by the stream ecosystem was a high but realistic approximation of potential removal by litter decomposition pathways. Annual DON retention was ≈1.70 kg; litter inputs of all types averaged 2.32 kg. Our leaf pack studies indicate an ≈50%

TABLE 6. Nitrogen introduced seasonally by fixation (as measured by acetylene reduction) for four wood substrates. Data collected from incubated substrates at Watershed 2, H. J. Andrews Experimental Forest, and extrapolated to known standing crop.

Substrate type	Seasonal acetylene reduction rates ($nmol \cdot g^{-1} \cdot d^{-1}$)		Nitrogen fixed ($g \cdot m^{-2} \cdot yr^{-1}$)
	1 Apr–31 Oct	1 Nov–31 Mar	
Twigs	1129	21	0.09
Bark	269	6	0.17
Chips	993	4	0.10
Wood (3–10 cm diameter)	160	8	0.34

concentration gain in nitrogen following leaching and up to 100% nitrogen concentration increase in other litter inputs (Table 3). While much of the apparent gain resulted from carbon mineralization, a 50% gain by litter detritus would require 1.15 kg of nitrogen. Furthermore, the large amount of residual wood debris and fine organic particulates provided additional uptake sites. Therefore, the observed retention of dissolved nitrogen represents a reasonable nitrogen demand for carbon mineralization.

Aquatic biological input

Maximum nitrogen fixation (as measured by acetylene reduction) occurred during late summer (Table 6). Little or no activity was observed from late autumn through spring. Rates of nitrogen fixation on various wood types were extrapolated to the composition of the CTBW pool for wood debris <10 cm in diameter, and for seasons when fixation was observed. Nitrogen fixation was not attributed to large branches and bole wood, due to absence of reliable estimates. More recently, N-fixation has been detected in large boles in the H. J. Andrews Experimental Forest, but confined to discrete sites of activity that are difficult to extrapolate to an areal basis (Silvester et al. 1982). Rates of fixation were low on fine wood debris and required 24-h incubations, which may overestimate fixation (Silvester et al. 1982). Despite low rates, standing crop of CTBW was high, so the potential contribution of nitrogen fixation to the budget was significant. The greatest contribution to the particulate nitrogen pool from nitrogen fixation was associated with branch wood debris (BWD) at 0.34 g/m^2. Branch wood was 3–10 cm diameter. Contributions to the particulate nitrogen pool for small wood substrates were 0.09 g/m^2 for twigs, 0.17 g/m^2 for bark, and 0.10 g/m^2 for small wood chips. Total nitrogen fixation on various wood substrates was estimated at 0.70 $g \cdot m^{-2} \cdot yr^{-1}$, higher than the 0.008 g/m^2 estimated by Meyer et al. (1981) from terrestrial wood studies by Roskoski (1977).

Nitrogen fixation on moss was estimated in June 1975 and June and August 1976. Fixation was assumed to occur primarily during the warm months as observed for wood. Acetylene reduction per unit dry mass averaged 8769 $nmol \cdot g^{-1} \cdot d^{-1}$. Areal conversion of nitrogen amounted to 0.06 $g \cdot m^{-2} \cdot yr^{-1}$. Examination of moss plants did not reveal the presence of algal symbionts; therefore, fixation was presumably accomplished by bacterial association. Bacterial association between a moss and a nitrogen-fixing *Azotobacter* sp. has been reported by Snyder and Wullstein (1973).

Fixation of nitrogen on leaf material collected from the stream produced negative results. However, Howarth and Fisher (1976) have reported low rates of nitrogen fixation on leaf litter in experimental streams. Further evidence of fixation during the initial stages of decomposition of mangrove leaves (Gotto and Taylor 1976) and in cypress litter (Dierberg and Brezonik 1981) indicates fixation can occur at significant rates at that time in the decomposition process.

Particulate nitrogen pool

Because the stream's morphology was extensively controlled by debris dams, these wooden structures represented a large nitrogen pool. The standing crop of coarse wood debris (CWD) >10 cm diameter, amounted to 12 kg/m^2 particulate organic matter. Analysis of heartwood blocks disclosed a total-nitrogen concentration of 0.04%. This estimate is low compared to P. C. MacMillan and J. E. Means (*personal communication*) who estimated nitrogen content of 0.10% in fallen logs in a midaltitude Douglas-fir stand on the H. J. Andrews Experimental Forest. Even using the lower estimate (assuming N accretion after tree fall), the minimum standing crop of nitrogen in the stream from coarse wood debris was 3.8 g/m^2. As the biological role of this long-term pool is virtually unknown, the amount of nitrogen from large bole wood which enters the food chain was not determined. The most likely biological role of coarse wood debris in small streams is formation of FPOM by physical scouring and surface microbial activity. Maximum processing rate of coarse wood debris is 2–5% per year, based on disappearance rates of heartwood blocks (Triska and Cromack 1980) and is far slower for the larger pieces. A secondary role for wood debris is habitat for a wide variety of tunneling and surface-inhabitating invertebrates (Anderson et al. 1978).

Compared to CWD and BWD, CTBW has a much faster turnover rate. Gilson respirometry (Gilson 1963) conducted monthly at ambient stream temperature showed ≈18% annual decomposition for fine twigs. Fine twigs, bark, and wood chip substrates exhibited mineralization of 14–23% loss of mass within the 1st yr of stream incubation. Nitrogen concentration of composite standing crop samples ranged between 0.25 and 0.31% nitrogen by micro-Kjeldahl analysis. Highest nitrogen concentration was observed during summer (0.31%) when microbial activity measured by both respirometry and plate counts was highest. Nitrogen

TABLE 7. Standing crop of nitrogen associated with various particulate organic materials from the stream channel of Watershed 10. Each monthly estimate is the result of 10 core samples (15.25 cm diameter), 5 each from riffles and pools.

	Needle	Leaf	CTBW*	Miscellaneous	Large FPOM (0.25 mm)	Medium FPOM (0.075 mm)
	Nitrogen standing crop, $\bar{x} \pm$ SE (g/m^2)					
1973						
Mar	0.31 ± 0.19	0.14 ± 0.08	1.63 ± 0.72	0.34 ± 0.19	0.35 ± 0.16	0.58 ± 0.15
Jun	0.19 ± 0.07	0.06 ± 0.05	2.40 ± 0.80	0.41 ± 0.07	0.30 ± 0.07	0.60 ± 0.19
Jul	0.33 ± 0.15	0.03 ± 0.02	0.61 ± 0.20	0.30 ± 0.10	0.62 ± 0.16	1.59 ± 0.30
Aug	0.24 ± 0.06	0.03 ± 0.02	1.76 ± 0.98	0.92 ± 0.40	0.66 ± 0.18	1.07 ± 0.17
Sep	0.26 ± 0.06	0.04 ± 0.02	1.11 ± 0.41	0.67 ± 0.17	0.31 ± 0.06	0.43 ± 0.07
Oct	0.51 ± 0.19	0.09 ± 0.03	1.58 ± 0.60	0.81 ± 0.21	0.33 ± 0.08	0.55 ± 0.12
Nov	0.59 ± 0.13	0.09 ± 0.03	3.70 ± 1.11	2.44 ± 0.59	0.90 ± 0.31	0.64 ± 0.23
Dec	0.34 ± 0.16	0.16 ± 0.09	3.55 ± 1.06	0.48 ± 0.18	0.88 ± 0.31	0.89 ± 0.26
1974						
Jan	0.15 ± 0.08	0.05 ± 0.02	2.94 ± 1.44	0.73 ± 0.29	0.82 ± 0.30	0.95 ± 0.29
Feb	0.08 ± 0.03	0.05 ± 0.02	3.22 ± 1.35	0.32 ± 0.10	0.61 ± 0.15	0.58 ± 0.12
Mar	0.09 ± 0.02	0.09 ± 0.04	2.84 ± 0.87	0.32 ± 0.12	0.59 ± 0.29	0.78 ± 0.45
Apr	0.17 ± 0.06	0.18 ± 0.08	0.84 ± 0.31	1.15 ± 0.40	0.62 ± 0.18	0.74 ± 0.20
Mean annual	0.27	0.08	2.18	0.74	0.58	0.78

* Cones, twigs, bark, wood.

concentration dropped to 0.29% during fall and winter and to 0.24% by spring (Table 3). The small differences in nitrogen concentration probably reflect changes in our sample composition rather than biological activity, since samples were composites of a wide variety of wood types. In controlled litterbag studies, nitrogen concentration does increase during decomposition of fine wood debris (Triska and Cromack 1980). The nitrogen pool in CTBW samples averaged 2.18 g/m^2 (Table 7).

Standing crop of both coniferous and deciduous leaf litter constituted a source of biologically available nitrogen. Mean standing crop of nitrogen was 0.27 g/m^2 for needles and 0.08 g/m^2 for deciduous leaves (Table 7). Proportionally, the nitrogen pool in leaf litter was 77% in needles and 23% in deciduous leaves. This is comparable to input composition of 68% and 32%, respectively, but with some suggestion that needle litter is more effectively transported. As with inputs, concentrations of nitrogen in standing crop varied seasonally. Needle litter N concentrations were lowest June–November, the time of major needle input (Table 3). Nitrogen concentrations were higher winter through spring, as observed in previous decomposition studies of needle litter (Triska et al. 1975). The highest nitrogen concentration occurred during spring, the time of needle litter consumption by invertebrates (Sedell et al. 1975), and may represent an important nitrogen pool for shredding invertebrates during final instars. The needle litter component of the nitrogen pool was largest in October and November, the months of maximum needle input (Table 7). However, coniferous needles were present throughout the year.

Big-leaf maple and vine maple leaves were the most readily available source of nitrogen for leaching and consumption by higher trophic levels. Mean estimate of nitrogen in leaf standing crop was low (0.08 g/m^2), despite large inputs during November. Leaves were readily incorporated into small debris dams not sampled by coring the stream bottom. Debris dam measurements were conducted during summer, after leaf decomposition; hence mean standing crop underestimated this contribution. Estimates of nitrogen concentration from summer and fall composite samples had the highest nitrogen concentration of any litter debris.

LFPOM and MFPOM of unidentifiable origin constituted a major component of the stream's nitrogen pool (totalling 1.36 g/m^2). LFPOM was especially prominent during late autumn and early winter (November–January) (Table 7). This size-class possibly originated from physical, microbial, and invertebrate processing of deciduous litter that entered during October and November. MFPOM was prominent at the same time, particularly during December and January. A second period of accumulation occurred during low discharge (July and August). MFPOM deposition during midsummer may have resulted from microbial activity on wood, or chemical flocculation. SFPOM, measured quarterly, is not included on Table 7, but it was the largest component of the FPOM nitrogen pool, at 3.41 g/m^2.

The mean nitrogen concentration of FPOM (Table 3) is based on few samples due to the difficulty of obtaining FPOM free of fine sediment. Nitrogen estimates from FPOM were obtained from export samples, which contained the least inorganic sediment. Nitrogen concentrations were corrected for ash and extrapolated to the core estimates of standing crop. The FPOM nitrogen pool at 4.77 g/m^2 was the stream's largest pool of particulate organic nitrogen.

Two minor nitrogen pools were moss and inverte-

brate consumers. Moss, where present, had an ash-free dry mass (AFDM) standing crop of 40 g/m². Mean moss AFDM standing crop amounted to 8 g/m² for the entire stream bottom, ≈2.5 times the 3.1 g/m² reported by Fisher and Likens (1973). Nitrogen concentration of moss averaged 0.92% for nine samples analyzed, or 0.07 g/m².

Annual moss primary production was not determined and few literature estimates are available. Fisher and Likens (1973) estimated gross primary production of moss at 2.14 g/m² annually at Bear Brook, New Hampshire. Net primary production could not be determined because moss and its surface microbial flora had a respiration rate that exceeded gross primary production. As moss grows slowly, most gross primary production is probably expended as respiration. Tamm (1953) found that nutrient uptake (N, P, K) by the forest moss *Hylocomium splendens* occurred simultaneously with growth, and that the nitrogen content did not decrease in older segments. Assuming the above is true for aquatic mosses, annual increments of growth would occur primarily by direct uptake from stream water. The lifespan of mosses varies by species (Binkley and Graham 1981), and observation of particulate organic export indicated that winter scour removes substantial biomass annually (included in miscellaneous export). Assuming 40% of standing mass represents that year's net production, and that uptake equals the nutrient content, the annual amount of nitrogen captured for elaboration of moss tissue would be only 22.58 g/channel (0.03 g/m²) over the entire study reach. The amount of nitrogen flux within the moss community for tissue maintenance is unknown.

Invertebrates were partitioned on the basis of functional groups (Cummins 1973, 1974, 1975). Invertebrate data from core samples indicated shredder plus collector functional groups averaged 70% of total invertebrate biomass. Grazers constituted <1% of invertebrate biomass, which reflected the terrestrial nature of the fixed carbon inputs and shading by the canopy. Measurement of ammonia production conducted by Grafius (1977) on *Lepidostoma quercina*, a common shredder invertebrate, was used to compute invertebrate ammonia production. Ammonia-N released under laboratory conditions (15°C) averaged 3.7 mg·g dry mass·d^{-1}. Shredder invertebrates, including *Lepidostoma* sp., constituted most invertebrate biomass in the stream.

Invertebrate biomass was lowest in January due to the small size of early instars and high waterflow that confined invertebrates to protected areas. Maximum mean biomass (dry mass), determined from core samples, was 1.45 g/m² during August, a period of low flow. The annual mean of insect biomass was 0.194 g/m² of wetted channel. As a nitrogen pool, mean invertebrate biomass amounted to 0.02 g/m² channel. Potential production of ammonia was estimated monthly, assuming a wetted area of 300 m² during December–May at base flow and 150 m² during June–November at base flow. Annual ammonia-nitrogen contributions to the nitrogen pool by invertebrates was estimated at 0.20 kg for the entire stream, or 0.26 g/m² channel. Emergence of 470 mg/m² dry mass (Grafius 1974) constituted an additional 0.06 g/m² of wetted area annually, or 0.02 g/m² of stream channel, an insignificant part of the stream's nitrogen budget.

TABLE 8. Nitrogen loss from Watershed 10, 1 October 1973–30 September 1974 resulting from export of particulate organic matter.

CPOM		FPOM	
Substrate	N loss (g/m²)	Size	N loss (g/m²)
First quarter (1 Oct–31 Dec)			
Needle	0.11	Large and medium	0.15
Leaf	0.02	Small	0.70
CTBW	0.19		
Misc.	0.15		
Second quarter (1 Jan–31 Mar)			
Needle	0.04	Large and medium	0.13
Leaf	0.01	Small	0.65
CTBW	0.27		
Misc.	0.08		
Third and fourth quarter			
Combined	0.003	Large and medium	0.005
		Small	0.025

Nitrogen export

Major nitrogen loss from the stream occurred during winter periods of high discharge. Some 95% of the dissolved organic nitrogen left the stream between October and April. Annual dissolved organic nitrogen losses amounted to 6.42 kg for the watershed or 8.38 g/m² of stream bottom (Table 9). Nitrate loss was estimated at 0.33 kg for the watershed, or 0.43 g/m² of stream channel. This estimate is based on grab samples at the base of the stream, collected simultaneously with seep samples. Our grab sample estimates were comparable to the continuous sampler estimate of 6.07 kg DON (R. Fredriksen, *personal communication*) or 7.92 g/m².

Because particulate organic matter was effectively captured and decomposed within the stream, processing of particulate organic inputs was high and output was dependent on total runoff. Most particulate organic output (Table 8) occurred during the first quarter (October–December). In this period, the first major storms flush the stream of debris accumulated during low summer discharge. Virtually all measurable particulate output occurred between October and March.

Output of nitrogen as needle litter amounted to 0.15 g/m², or 115 g/yr. Output as intact needles was only 16% of input. Deciduous leaves were incorporated even more readily into debris dams, so only minor amounts

TABLE 9. Export of dissolved organic nitrogen (DON) based on water samples collected at the base of Watershed 10, 5 March 1974–18 March 1975. (···) indicate no DON export samples were taken 25 December 1974–15 January 1975 or 4–26 February 1975. DON concentration 16 January–3 February was used to compute DON export for the total interval.

Discharge interval	Mean discharge (L/s)	DON export (g)
5–27 Mar 1974	13.66	181.77
28 Mar–19 Apr	5.94	702.61
20 Apr–9 May	1.73	11.37
10–23 May	4.47	162.12
24 May–17 Jun	1.61	252.27
18 Jun–11 Jul	0.74	130.06
12–31 Jul	0.35	32.18
1–19 Aug	0.22	1.41
20 Aug–9 Sep	0.14	13.91
10–30 Sep	0.09	11.35
1–11 Oct	0.03	1.70
12–25 Oct	0.03	1.70
26 Oct–13 Nov	0.37	131.15
14 Nov–2 Dec	2.47	684.11
3–24 Dec	11.97	2890.00
25 Dec–15 Jan 1975	17.60	···
16 Jan–3 Feb	8.03	1161.61
4–26 Feb	12.02	···
27 Feb–18 Mar	8.61	59.56
Total		6428.88

were exported as recognizable leaf fragments. Particulate nitrogen loss as leaf litter amounted to only 0.03 $g \cdot m^{-2} \cdot yr^{-1}$ or 7% of annual deciduous leaf input. The amount of nitrogen lost as CTBW varied, depending on discharge. In 1974–1975, with discharge of 173 cm, 0.46 $g \cdot m^{-2} \cdot yr^{-1}$ was lost as woody debris, ≈33% of the annual input. This is the estimate used in the budget. In 1973, a very dry year (80 cm discharge), virtually no wood was exported.

Nitrogen not exported as intact litter was either mineralized, leached, or converted to FPOM. FPOM nitrogen output in the large and medium size-classes alone amounted to 0.28 g/m^2 channel, a larger nitrogen loss than needle and leaf material combined. Estimates of small FPOM nitrogen output were not undertaken at Watershed 10 prior to clearcutting. This fraction constituted >80% of transport in Devil's Club Creek, another first-order stream of similar gradient in the H. J. Andrews Experimental Forest (Naiman and Sedell 1979). Assuming the nitrogen concentration of 1.44% nitrogen and equal susceptibility to export as Devil's Club Creek, estimated nitrogen loss was 1.38 $g \cdot m^{-2} \cdot yr^{-1}$. Total nitrogen export was 11.36 $g \cdot m^{-2} \cdot yr^{-1}$.

DISCUSSION

Early carbon budgets made by stream ecologists (Teal 1957, Minckley 1963, Minshall 1967, Tilly 1968) emphasized the role of fixed carbon from allochthonous sources as the biological energy base of small forested streams. They concluded that carbon fixed within the terrestrial system dominated that fixed within the aquatic system to provide the stream's energy base. Until the work by Fisher and Likens (1973), dissolved organic carbon was not considered a significant input to the carbon budget of streams, and no previous studies considered inorganic carbon as a component of the carbon budget. As a result, carbon budgets have been valuable in understanding the energetics of streams, but are not nutrient budgets for carbon.

Early budgets for nutrients other than carbon often took the opposite approach. These nutrient budgets for watersheds have followed the logic developed by Bormann and Likens (1967): basically, that loss of dissolved nutrients from the terrestrial component of a watershed can be measured at its base. Emphasis was placed on geological outputs, primarily dissolved inorganic nutrients (Bormann et al. 1968, Likens et al. 1970), while particulate and dissolved organic nitrogen and potential fixation and transformation of nitrogen between the soil system and the base of the watershed were deemphasized.

More recently Woodall (1975), in a study of small mountain streams, indicated salamanders and crayfish were major agents of nutrient flux in the detritus pool and may constitute an important nutrient sink. Hynes et al. (1974) also speculated on the role of leaves in both releasing nutrients and serving as a nitrogen sink. Meyer and Likens (1979) and Meyer et al. (1981) report significant input of phosphorous and nitrogen from allochthonous organic debris to Bear Brook, New Hampshire. Thus the flux of allochthonous debris and associated physical, chemical, and biologic processes can constitute or modify significant components of stream nutrient budgets.

Biological input-output

In this study, terrestrial biological inputs (litterfall, lateral movement, and throughfall) contributed ≈20% of the annual nitrogen budget, and once within the stream represented a biologically available source of particulate nitrogen, especially leaf litter inputs. Virtually all species of leaf litter entering the stream had the potential for microbial mineralization within 1 yr (Sedell et al. 1974, 1975, Triska et al. 1975, Triska and Sedell 1976). Although mineralization of litter-associated nitrogen could be accomplished entirely by microbial decomposition, enzymatic reduction of size class (Suberkropp 1980), physical fragmentation, and invertebrate consumption can restrict direct microbial mineralization to <25% of leaf litter inputs (Cummins and Klug 1979).

The proportion of leaf litter nitrogen subjected to physical or chemical transformation in the particulate nitrogen pool depends upon the stream's retention capacity. In this study, bed roughness (generated largely by organic debris dams) captured ≈87% of nitrogen

associated with intact leaf litter. This effective retention by the stream's morphology allowed nitrogen associated with litter to enter biological pathways despite the exporting influence of unidirectional flow.

Once litter entered the water, processing occurred by both physical and biological vectors, including leaching, microbial mineralization, and reduction in size class. Four days of leaching at 5°C in three springs of the Washington Cascades resulted in a loss of 42%, 62%, and 50% of the nitrogen capital for vine maple, Douglas-fir, and big-leaf maple litter, respectively (Triska and Sedell 1976). These species provide the overwhelming predominance of leaf litter inputs to the stream at Watershed 10, and represent a potential contribution of 0.16 kg DON from deciduous leaf litter, and 0.48 kg DON from coniferous leaf litter.

Despite nitrogen loss by leaching, a seasonal increase in nitrogen concentration was typically observed on all litter substrates (Table 3). Nitrogen concentration of various litter substrates was lowest at abscission and increased as decomposition proceeded. Nitrogen in needle litter even had an absolute gain from the low concentration which resulted from leaching (Triska and Buckley 1978). Maximum absolute nitrogen content typically occurred at 30–40% loss of mass for leaf packs of Douglas-fir needle litter.

Post-leaching replenishment of nitrogen presumably occurred by uptake of dissolved nitrogen as stream water passed over microbially colonized surfaces. While most DON was undoubtedly refractory, significant uptake, biological utilization, and subsequent output in a different form has been reported (Cummins et al. 1972, Wetzel and Manny 1972). The composition of DON (labile vs. refractory) for the estimated 0.83 g/m^2 leachate and 10.56 g/m^2 subsurface input is unknown; however, only 8.38 g/m^2 was exported. Inorganic nitrogen uptake is also active on microbially colonized litter surfaces (Hynes and Kaushik 1969, Howarth and Fisher 1976). However, low seepwater concentrations minimized its potential impact in this study.

Increase in nitrogen concentration does not guarantee biological availability. Complexation with refractory carbon, particularly lignin and phenolics, results in residues characterized by: (1) an increase in nitrogen content particularly associated with lignin, (2) decrease in particle size, and (3) resistance to decomposition. Such residues have been reported in lotic environments by Suberkropp and Klug (1976), Suberkropp et al. (1976), and Odum et al. (1979). After 33 d of stream incubation at Watershed 10 the percent of litter nitrogen associated with the lignin fraction increased from 13 to 40% in alder, 17 to 67% in Douglas-fir, 9 to 26% in vine maple, and 24 to 74% in big-leaf maple. Nitrogen complexation has been observed to inhibit consumer assimilation despite lowering of C/N ratio (Ward and Cummins 1979), although Martin et al. (1980) report that some invertebrate species may have evolved a digestive strategy of high gut pH to utilize nitrogen-lignin complexes.

Petersen and Cummins (1974) estimate invertebrate processing of 15–20% of leaf litter inputs to a third-order stream in Michigan. Such litter consumption by invertebrates results in both passage of nutrient to higher trophic levels and fragmentation of egested materials. At Watershed 10, low invertebrate biomass in the stream indicates a smaller role for invertebrates. Consumption rates for Douglas-fir litter reported by Grafius (1977) varied from 0.10 mg·mg^{-1}·d^{-1} (*Lepidostoma quercina*) to 0.84 mg·mg^{-1}·d^{-1} (*L. unicolor*) depending on invertebrate instar, temperature, food density, and litter conditioning time. Assuming a consumption rate of 0.3 mg·mg^{-1}·d^{-1}, litter nitrogen turnover would be 0.13 g/m^2 of wetted area. Based on a 300 m^2 wetted area, invertebrate turnover was only ≈4% of leaf litter nitrogen. Since only 18% of needle litter nitrogen and 5% of leaf litter nitrogen was exported in the form of intact litter, physical fragmentation and microbial processing were presumably more important proportionally at our site than in more productive higher order streams.

A potentially important loss of nitrogen not determined in this study was microbial denitrification. Hill (1979, 1981) reported denitrification was a major nitrogen sink in Duffin Creek, Ontario, and recent investigations indicate 80–90% of nitrate removed from Duffin Creek sediments is via denitrification (A. R. Hill 1983 and *personal communication*). Kaushik and Robinson (1976), Sain et al. (1977), and Chatarpaul et al. (1979, 1980) also report significant denitrification in laboratory experiments using fine stream sediments. Background NO_3-N in the above studies generally exceeded 1000 μg/L. Swank and Caskey (1982) report denitrification in a second-order mountain stream following disturbance by road building and clearcutting in stream reaches impacted by high sediment loading. Background NO_3-N concentrations in these upland areas were raised to 160–200 μg/L from a predisturbance concentration of ≈20 μg/L. Denitrification was not estimated in our study since most measurements were made prior to general acceptance of the acetylene inhibition technique. Although denitrification is of potentially great importance in streams dominated by fine sediments and high nitrate loads, some subsequent estimates indicate it may be less important in highly oxygenated, gravel-bottom streams with low nitrate concentration. Meyer et al. (1981) indicated denitrification was probably insignificant at Bear Brook, New Hampshire, based on low levels of activity observed in denitrifier cultures and microcosm studies by Sloane (1979). Triska and Oremland (1981) and J. H. Duff (*personal communication*) report significant denitrification associated with algal mats from high-nitrate waters (>800 μg/L) but insignificant denitrification in mats (J. H. Duff, *personal communication*) or sediments (R. S. Oremland, *personal communica-*

tion) from a pristine stream environment (20–40 μg/L). Ventullo and Rowe (1982) also report denitrification associated with epilithic communities in streams; however, exogenous addition of nitrate was required to induce N_2O production. Hill (1981), who compared five streams characterized by high nitrogen depletion during transport, reported that high nitrate concentration appeared to be the main factor accounting for high nitrate loss. Nitrate was nearly undetectable in input seepage water (<10 μg/L) at our site and constituted <5% of nitrogen output. Channel disturbance was also minimal. As a result the role of denitrification is unknown, but probably not a significant component of the stream's nitrogen budget.

Ammonia is produced as the major nitrogen waste of both microbial mineralization and consumer metabolism. Ammonia concentrations in stream water were low on both an instantaneous and annual basis, mostly below the limits of detection. Total annual production of ammonia nitrogen by stream invertebrates (0.26 $g \cdot m^{-2} \cdot yr^{-1}$) and microbial metabolism was probably followed by rapid sorption or uptake on detrital surfaces. Within the stream network lies some potential for nitrification, as nitrate concentration does increase in a downstream direction (Gregory1980).

Hydrological-meteorological input-output

Although our goal was to examine in detail the role of allochthonous organic particulates as a nitrogen source, 77% of nitrogen export was in the form of dissolved nitrogen. The dissolved nitrogen fraction consisted of DON (95%), nitrate (5%), and insignificant amounts of nitrite and ammonia. This dissolved nitrogen composition contrasts with Bear Brook, New Hampshire, where 87% of nitrogen transport was nitrate and ammonia, and only 13% was DON (Meyer et al. 1981). The major difference between sites was the absence of nitrate in our stream. Two potential sources of nitrate at Bear Brook include higher nitrate input in precipitation (nitrate concentration doubled between 1955–1979, Bormann and Likens 1979), and nitrification on the watershed. Vitousek et al. (1982) estimated nitrogen mineralization by a trenching experiment at 17 sites in four states. They reported the highest potential nitrate production in a New Hampshire northern hardwood site, while net nitrate production lagged by months at a poor site Douglas-fir forest in Washington. Meyer et al. (1981) also reported nitrification activity on selected stream substrates from experiments at Bear Brook by Sloane (1979). Vitousek et al. (1982) suggest at least nine processes are potentially responsible for delaying solution losses of nitrate. In the absence of a controlled study, the mechanism for low nitrate input-output at Watershed 10 is unknown.

Element limitation

Low dissolved nitrogen and high dissolved phosphorus (relative to nitrogen) concentrations in stream water (Table 1) support the conclusion that nitrogen limited biological production in the stream at Watershed 10. Elwood et al. (1981) define a nutrient as limiting if an increase in supply of that nutrient affects the parameter in question. A parameter whose value is limited by a given nutrient may also respond to a simultaneously limiting nutrient or to changes in other rate-controlling factors. Using this definition, light was the rate-controlling factor to epilithic algal autotrophs, and nitrogen the limiting nutrient. Gregory (1980), who experimentally added both light and nutrients to the stream at Watershed 10, found no enhancement of primary production or chlorophyll *a* by nitrate addition alone. Standing crop of chlorophyll *a* was 5 times greater when light was added alone, and 20 times greater when both light and nitrate were added. In more open-canopy sections of larger streams in the same forest, Gregory (1980) found significant diel fluctuations in nitrate concentration, whereas orthophosphorus concentration had no diel pattern at any site. Factors controlling primary production by bryophytes are unknown. Mosses are adapted to low light conditions and had nitrogen fixation associated with epiphytic bacteria. Assuming some fraction of nitrogen fixed by epiphytic bacteria is eventually available, bryophytes are presumably less nitrogen limited than epilithic algae.

Another index of nutrient limitation is determination of element ratios. The atomic element ratio of algal-zooplankton tissue composition calculated by Redfield et al. (1963) is 106 C:16 N:1 P, and that of cultured algal tissue is as high as 30 N:1 P (Rhee 1978). The atomic N:P (total dissolved nitrogen : total dissolved phosphorus) at our site was only 0.74:1 and DIN : ortho P was even lower at 0.32:1. This compares with a N:P ratio of 440:1 for fluvial inputs and 291:1 for subsurface inputs at Bear Brook, New Hampshire (Meyer et al. 1981). Our stream water N:P is also lower than the dissolved inorganic nitrogen : soluble reactive phosphorus atomic ratio of ≈30:1 at Walker Branch, Tennessee (Elwood et al. 1981). Both of the above locations were considered phosphorus limited. The low N:P ratios from stream water indicate biotic production is far more likely to be nitrogen limited at our site than streams in the eastern United States.

Low N:P ratio was also reflected in litter inputs, and in litter tissue undergoing decomposition in the stream at Watershed 10. Litter inputs had atomic N:P (Kjeldahl nitrogen : organic phosphorus) ratios of 7:1 for coniferous litter, 7.5:1 for deciduous litter (big-leaf maple), and 26:1 for twig litter. Greater leaching of phosphorus than nitrogen, however, raised N:P to 18:1 for coniferous litter and to 19:1 in deciduous leaf litter (big-leaf maple) as a result of immersion. Low level PO_4-P enrichment experiments (60 μg/L) by Elwood et al. (1981) resulted in N:P ratio of ≈19 after 32 d in red oak leaf packs. They found that mass loss, P content, N content, and respiration were not significantly different than litter exposed to even higher

phosphorus enrichment (450 μg/L). Since mean ortho-P concentration in stream water at our site was 42 μg/L, it is not likely that phosphorus was limiting decomposition processes. High atomic C:N ratios in decomposing litter substrates ($\bar{x}$ = 131:1 coniferous litter, 104:1 deciduous litter) instead indicate demand for nitrogen for carbon mineralization from the watershed's nitrogen-dilute waters (DON, 27 μg/L; NO_3-N, 6 μg/L). Previous studies on nitrate addition in controlled experimental channels at 5°C, however, failed to stimulate decomposition (Triska and Sedell 1976). Perhaps as in the case of light for the autotrophic community, some additional factor such as low temperature masked the effect of nitrate addition on litter decomposition in the above study. Based on theoretical element composition nitrogen would be assumed limiting to both autotrophic production and litter decomposition in the stream at Watershed 10.

Nitrogen associated with inorganic particulates

Nitrogen input-output associated with inorganic particulates was not specifically included in our study; however, the significance of erosional processes is currently being examined by F. J. Swanson (*personal communication*). Available data include a mean annual estimate of suspended sediment from Watershed 10 of 90 $kg \cdot ha^{-1} \cdot yr^{-1}$ between 1969–1973 (Fredriksen 1975, Swanson et al. 1982*a*). Suspended sediment export was estimated with a discharge proportional water sampler, which weighted sediment load identically to dissolved constituents. The above estimates include the total suspended component of water samples, and therefore include nitrogen we measured as FPOM. Assuming most sediment export occurs during fall and winter, and in years of greatest discharge, then 0.53% nitrogen concentration ($\bar{x}$ nitrogen concentration fall-winter 1972, Fredriksen 1975) would result in a nitrogen loss of 6.25 $g \cdot m^{-2} \cdot yr^{-1}$, 3.8 times that listed as FPOM. The largest inorganic particulate input to the stream was surface erosion (the inorganic component of lateral movement). Swanson et al. (1982*a*) estimated surface erosion of inorganic particulates at 480 kg/yr to the stream channel at Watershed 10. Assuming a nitrogen content similar to suspended sediment, nitrogen input associated with inorganic particles would be 3.32 $g \cdot m^{-2} \cdot yr^{-1}$. Atmospheric dust input was an additional 0.06 $g \cdot m^{-2} \cdot yr^{-1}$ (Sollins et al. 1980). Using these preliminary figures, surface erosion plus atmospheric input at 3.38 $g \cdot m^{-2} \cdot yr^{-1}$ is less than export of 4.63 $g \cdot m^{-2} \cdot yr^{-1}$ (suspended sediment − FPOM). If large mass movements such as soil creep, or episodic inputs such as root throw or debris torrents are included, however, significant retention of nitrogen associated with the particulate inorganic load is predicted within the channel (Swanson et al. 1982*a*). Since nitrogen is not a component of most minerals, associated nitrogen presumably represents sorption or flocculation of organic nitrogen with fine soil particles, especially clay fractions, which probably participate minimally in nitrogen cycling.

The nitrogen budget

After all major inputs and outputs were considered, a nitrogen budget for the stream was constructed. Total nitrogen input was estimated at 15.25 $g \cdot m^{-2} \cdot yr^{-1}$ (Fig. 3). Hydrological inputs of nitrogen account for 11.06 $g \cdot m^{-2} \cdot yr^{-1}$ or 73% of the input total, 0.50 g/m^2 of which was dissolved inorganic nitrogen. Dissolved nitrogen on an instantaneous basis was never an important component of the standing crop, but DON was 69% of input nitrogen. Biological uptake and/or sorption to debris captured ≈25% of the DON load. DON utilization was greater than indicated by input-output because leaching and decomposition of particulate organic inputs were an additional source of DON. Throughfall amounted to 2% of nitrogen inputs (0.30 $g \cdot m^{-2} \cdot yr^{-1}$) from leaching in the canopy. Direct interception of precipitation was not a significant nitrogen input to the stream. Internal fixation of molecular nitrogen was ≈5% of the nitrogen budget, or 0.76 $g \cdot m^{-2} \cdot yr^{-1}$. Major terrestrial biological sources of nitrogen were CTBW and leaf litter.

Wood debris was stored annually. Stored wood formed debris dams which captured organic particulates, created habitat, and produced FPOM. Leaf and needle litter also contributed to the particulate organic nitrogen pool but intact leaf litter was only 3% of the standing crop. Particulate biological inputs, primarily litterfall and lateral movement, amounted to 3.13 $g \cdot m^{-2} \cdot yr^{-1}$, or 20% of the nitrogen input. Of these sources, leaf and needle litter, the most easily processed particulate organic inputs, contributed 1.41 g/m^2, only 0.18 g/m^2 (or 13%) of which was exported in a recognizable state. The remainder was either leached, converted to FPOM, or mineralized. Nitrogen in wood debris amounted to 1.13 g/m^2 input and 0.46 g/m^2 export; the remainder passed into storage, less that which was leached or fragmented to FPOM. FPOM, the major product of particulate organic processing, had a nitrogen input of 0.18 g/m^2 but amounted to 4.77 g/m^2 on the stream bottom. Total nitrogen output as dissolved components was 78%. This estimate is identical to the total solution losses reported by Bormann et al. (1969) for 1966 at 78% but lower than the 94% solution loss reported in 1965 from Hubbard Brook, New Hampshire, or 96% for Bear Brook, New Hampshire (Meyer et al. 1981). Total nitrogen input exceeded output by 34% in this study, compared to 8% reported by Meyer et al. (1981) at Bear Brook, New Hampshire. The difference is due to storage of nitrogen as refractory particulate organic matter and to the far higher input of dissolved inorganic nitrogen at Bear Brook. Both budgets indicated significant uptake by the stream ecosystem.

Independent estimation of input-output constituents indicated significant particulate organic storage. The particulate component of the nitrogen pool consisted

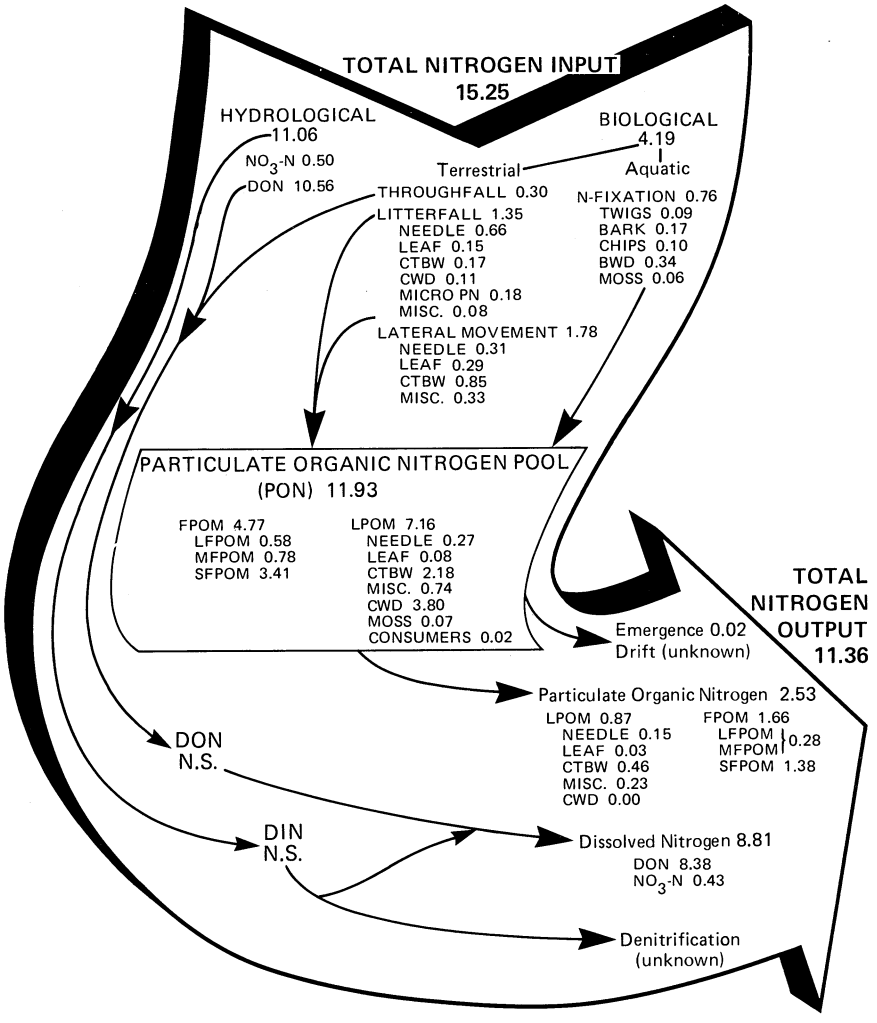

FIG. 3. Nitrogen budget for the stream at Watershed 10 (g/m^2), indicating the source and magnitude of annual nitrogen inputs, mean pool size, and annual exports. Acronyms are defined as follows: DON, dissolved organic nitrogen; DIN, dissolved inorganic nitrogen; CTBW, cones, twigs, bark, and wood (>1.0 mm and <15.0 cm); CWD, coarse wood debris (>15.0 cm diameter); BWD, wood blocks (to estimate N-fixation associated with wood debris); MICRO PN, nitrogen input associated with microparticulate litterfall (<800 μm diameter); LPOM, large particulate organic matter (>1.0 mm diameter); FPOM, fine particulate organic matter (<1.0 mm diameter). DON and DIN as an instantaneous pool are not significant (NS).

of three major components: (1) total wood (51%), 5.98 g/m^2, (2) leaf litter (3%), 0.35 g/m^2, and (3) FPOM (40%), 4.77 g/m^2. Particulate storage of wood debris (CTBW) was an annual event whose magnitude was determined by storm frequency and discharge pattern. In 1974–1975, nitrogen addition was estimated at 0.57 g/m^2 as CTBW, which was 4% of total nitrogen input. CTBW is readily incorporated into the nitrogen pool, has a long turnover time, and is resistant to export (Triska and Cromack 1980, Swanson et al. 1982*b*). Such refractory organic debris has been recognized as an essential stabilizing property of ecosystems (O'Neill et al. 1975, Reichle et al. 1975, Webster et al. 1975).

Nitrogen in coarse wood debris (CWD) was present at a minimum of 3.80 g/m^2, a pool equal to $\approx$25% of the nitrogen budget. Coarse wood is processed by both biologic and hydrologic means with a time frame in excess of 100 yr. Finer wood components (CTBW) constitute a nitrogen sink of some 2.18 g/m^2, $\approx$15% of the annual nitrogen budget, and are similarly processed in perhaps 10–20 yr. Due to slow processing times, wood accumulates on the stream bottom, forms habitat, and captures leaf litter (Triska and Cromack 1980, Swanson et al. 1982*b*).

Including the 5% of the nitrogen budget represented by fixation, 34% of the nitrogen input passed into storage during our study year (February 1974–1975). Thus the stream was not operating under annual steady-state

conditions as found by Fisher and Likens (1973) for organic carbon. Steady state, if it exists, operates on a time frame related to the decomposition rate of the most significant refractory input and to the cycle of storm events that purge the channel of stored debris. Both Meyer et al. (1981) and Triska et al. (1982) emphasized the importance of year-to-year variation in discharge in examining annual nutrient budgets. Furthermore, Swanson et al. (1982*a*) estimate that massive debris torrents at Watershed 10 (occurrence intervals ≈580 yr) result in export of organic particulate matter equal to almost 30% of the organic budget of all intervening years. Thus events with occurrence intervals of half a millennium help shape the export history of a watershed. Between these long intervals of accumulation and export the large reservoir of refractory detritus aids in the internalization of the nitrogen cycle despite the open nature of the lotic ecosystem.

Summary

Except for potential minor losses to the atmosphere, the stream at Watershed 10, whose channel area was <0.1 ha, transported or accumulated virtually all nitrogen losses of the 10.1-ha watershed. Although induced by physical vectors (gravity, wind, precipitation), almost all nitrogen inputs to the stream were derived from biotic processes in the forest. Major biotically derived inputs (litterfall, throughfall, lateral movement, DON in groundwater, and fixation) constituted >90% of nitrogen input to the stream. Inorganic nitrogen inputs, nitrate, nitrite, and ammonium in subsurface flow constituted <5% of input nitrogen. Of the 92% of organic nitrogen input excluding fixation, 76% was dissolved and 24% was particulate. Although nitrogen loss on a per hectare basis was small for the 10.1-ha watershed, all particulate and dissolved losses passed through or were accumulated in an environment encompassing <1% of the watershed area. This concentration permitted the establishment of a separate ecosystem whose processing efficiency and capacity for nutrient cycling are related to the stream's retention capacity and carbon quality of inputs within the reach.

Although formation of the input-output budget provided only the most minimal glance at internal dynamics, certain potentials for internal nitrogen cycling were observed. Leaf litter, which may lose up to 50% of its initial nitrogen content to the dissolved nitrogen pool, regained lost nitrogen within 40 d by various processes. During biological mineralization, nitrogen was complexed to leaf lignin, a process similar to humification in terrestrial environments. Microbial mineralization, invertebrate consumption, and physical abrasion resulted in the formation of FPOM from wood and litter debris. FPOM generated in this manner was characterized by a nitrogen content of leaf litter and a total fiber content of wood. FPOM constituted a nitrogen sink equal to 32% of the annual nitrogen budget and constituted 66% of the particulate nitrogen export. Biologically preprocessed detritus was, therefore, a major nitrogen contribution to downstream biological communities.

The events described above occurred within a first-order stream of a major drainage. Nitrogen that escapes the first order, while classified as export, constitutes the upstream input to a second-order stream. At each successive stream order the distance between uptake and release of nitrogen, spiraling length (Webster et al. 1975, Webster and Patten 1979, Newbold et al. 1981, Elwood et al. 1983), may vary, and biotic community structure can be modified in response to upstream import (Vannote et al. 1980). Some imported DON becomes available for microbial utilization, and inorganic nitrogen becomes available for uptake by periphyton and riparian vegetation. Nitrogen tied to detrital tissue becomes available to shredding invertebrates and fine particulate organic matter to collector organisms. In addition to leaching and biological processing, nitrogen incorporated in particulate organic matter may be returned to the terrestrial landscape by deposition on flood plains. Physical abrasion in conjunction with biotic activity will result in an overall size reduction of output compared to input, even for wood debris. Through each link in the lotic network, biotic processes will present numerous opportunities for internal cycling before nitrogen lost from the terrestrial landscape finally reaches the river's estuary.

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Literature Cited

Abee, A., and D. Lavender. 1972. Nutrient cycling in throughfall and litterfall in 450-year-old Douglas-fir stands. Pages 133–143 *in* J. F. Franklin, L. J. Dempster, and R. H. Waring, editors. Research on coniferous forest ecosystems: a symposium. United States Forest Service Pacific Northwest Range and Experiment Station, Portland, Oregon, USA.

Anderson, N. H., and K. W. Cummins. 1979. Influences

of life histories on the diet of aquatic invertebrates. Journal of the Fisheries Research Board of Canada **36**:335–342.

Anderson, N. H., and E. J. Grafius. 1975. Utilization and processing of allochthonous material by stream Trichoptera. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen **19**:3022–3028.

Anderson, N. H., and J. R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annual Review of Entomology **24**:351–377.

Anderson, N. H., J. R. Sedell, L. M. Roberts, and F. J. Triska. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. American Midland Naturalist **100**:64–82.

Barlocher, F., and B. Kendrick. 1973. Fungi in the diet of *Gammarus pseudolimnaeus* (Amphipoda). Oikos **24**:195–200.

Barlocher, F., and B. Kendrick. 1981. The role of aquatic hyphomycetes in the trophic structure of streams. Pages 743–760 *in* G. C. Carroll and W. T. Wicklow, editors. The fungal community: its organization and role in the ecosystem. Marcel Decker, New York, New York, USA.

Bergersen, F. J. 1970. The quantitative relationship between nitrogen fixation and the acetylene reduction assay. Australian Journal of Biological Science **23**:1015–1025.

Binkley, D., and R. L. Graham. 1981. Biomass production and nutrient cycling of mosses in an old growth Douglas-fir forest. Ecology **62**:1387–1389.

Bormann, F. H., and G. E. Likens. 1967. Nutrient cycling. Science **155**:424–429.

Bormann, F. H., and G. E. Likens. 1970. The nutrient cycles of an ecosystem. Scientific American **223**:92–101.

Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, New York, USA.

Bormann, F. H., G. E. Likens, and J. S. Eaton. 1969. Biotic regulation of particulate and solution losses from a forest ecosystem. Bioscience **19**:600–610.

Bormann, F. H., G. E. Likens, D. W. Fisher, and R. S. Pierce. 1968. Nutrient loss accelerated by clear-cutting of a forest ecosystem. Science **159**:882–884.

Busch, D. E., and S. G. Fisher. 1981. Metabolism of a desert stream. Freshwater Biology **11**:301–307.

Chatarpaul, L., J. B. Robinson, and N. K. Kaushik. 1979. Role of tubificid worms on nitrogen transformations in stream sediment. Journal of the Fisheries Research Board of Canada **36**:673–678.

Chatarpaul, L., J. B. Robinson, and N. K. Kaushik. 1980. The effects of tubificid worms on denitrification and nitrification in stream sediment. Canadian Journal of Fisheries and Aquatic Sciences **37**:656–663.

Cummins, K. W. 1973. Trophic relations of aquatic insects. Annual Review of Entomology **18**:183–206.

———. 1974. Structure and function of stream ecosystems. Bioscience **24**:631–641.

———. 1975. Macroinvertebrates. Pages 170–198 *in* B. A. Whitton, editor. River ecology. University of California Press, Berkeley, California, USA.

Cummins, K. W., and M. L. Klug. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics **10**:147–172.

Cummins, K. W., M. L. Klug, R. G. Wetzel, R. C. Petersen, K. F. Suberkropp, B. A. Manny, J. C. Wuycheck, and F. O. Howard. 1972. Organic enrichment with leaf leachate in experimental lotic ecosystems. Bioscience **22**:719–722.

Cushing, C. E., and E. G. Wolf. 1982. Organic energy budget of Rattlesnake Springs, WA. American Midland Naturalist **107**:404–407.

Davis, S. F., and M. J. Winterbourn. 1977. Breakdown and colonization of *Nothofagus* leaves in a New Zealand stream. Oikos **28**:250–255.

Dierberg, F. E., and P. L. Brezonik. 1981. Nitrogen fixation (acetylene reduction) associated with decaying leaves of pond cypress (*Taxodium distichum* var. *nutans*) in a natural and sewage-enriched cypress dome. Applied and Environmental Microbiology **41**:1413–1418.

Elwood, J. W., J. D. Newbold, R. V. O'Neill, and W. Van Winkle. 1983. Resource spiraling: an operational paradigm for analyzing lotic ecosystems. Pages 3–27 *in* W. T. Fontaine III and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, Michigan, USA.

Elwood, J. W., J. D. Newbold, A. F. Trimble, and R. W. Stark. 1981. The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. Ecology **62**:146–158.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to ecosystem metabolism. Ecological Monographs **43**:421–439.

Fredriksen, R. L. 1972. Nutrient budget of a Douglas-fir forest on an experimental watershed in western Oregon. Pages 113–131 *in* J. F. Franklin, L. J. Dempster, and R. H. Waring, editors. Research on coniferous forest ecosystems: a symposium. United States Forest Service Pacific Northwest Range and Experiment Station, Portland, Oregon, USA.

———. 1975. Nitrogen, phosphorus, and particulate matter budgets of five coniferous forest ecosystems in the western Cascades Range, Oregon. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Froehlich, H. 1973. Natural and man caused slash in headwater streams. Loggers Handbook 18, Pacific Logging Congress, Portland, Oregon, USA.

Gilson, W. E. 1963. Differential respirometer of simplified and improved design. Science **141**:531–532.

Gotto, J. W., and B. F. Taylor. 1976. N_2 fixation associated with decaying leaves of the red mangrove *Rhizophora mangle*. Applied and Environmental Microbiology **31**:781–783.

Grafius, E. J. 1974. Conversion of allochthonous detritus by stream detritivores. Thesis. Oregon State University, Corvallis, Oregon, USA.

———. 1977. Bioenergetics and strategies of some Trichoptera in processing and utilizing allochthonous materials. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Gregory, S. V. 1980. Effects of light, nutrients and grazing on periphyton communities in streams. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Grier, C. C., and R. S. Logan. 1977. Old-growth *Pseudotsuga menziesii* of a western Oregon watershed: biomass distribution and production budgets. Ecological Monographs **44**:373–400.

Hill, A. R. 1979. Denitrification in the nitrogen budget of a river ecosystem. Nature **281**:291–292.

———. 1981. Nitrate-nitrogen flux and utilization in a stream ecosystem during low summer flows. Canadian Geographer **3**:225–239.

———. 1983. Nitrate-nitrogen mass balances for two Ontario rivers. Pages 457–477 *in* W. T. Fontaine III, and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, Michigan, USA.

Hodkinson, I. D. 1975. Dry weight loss and chemical changes in vascular plant litter of terrestrial origin occurring in a beaver pond ecosystem. Journal of Ecology **63**: 131–142.

Howarth, R. W., and S. G. Fisher. 1976. Carbon, nitrogen, and phosphorus dynamics during leaf decay in nutrient-enriched stream microecosystems. Freshwater Biology **6**: 1–8.

Hynes, H. B. N., and N. K. Kaushik. 1969. The relation-

ship between dissolved nutrient salts and protein production in submerged autumnal leaves. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen **17**:95–103.

Hynes, H. B. N., N. K. Kaushik, M. A. Lock, D. L. Lush, Z. S. J. Stockner, R. R. Wallace, and D. D. Williams. 1974. Benthos and allochthonous organic matter in streams. Journal of the Fisheries Research Board of Canada **31**:545–553.

Iversen, T. M. 1973. Decomposition of autumn-shed beech leaves in a springbrook and its significance for the fauna. Archiv für Hydrobiologie **72**:305–312.

Jackson, M. L. 1958. Soil chemical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Kaushik, N. K., and H. B. N. Hynes. 1968. Experimental study on the role of autumn shed leaves in aquatic environments. Journal of Ecology **52**:229–243.

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

Kaushik, N. K., and J. B. Robinson. 1976. Preliminary observations on nitrogen transport during summer in a small spring fed Ontario stream. Hydrobiologia **49**:59–63.

Kennedy, V. C., and R. L. Malcolm. 1978. Geochemistry of the Mattole River of Northern California. United States Geological Survey Open-File Report 78–205, Menlo Park, California, USA.

Kimmins, J. P. 1973. Some statistical aspects of sampling throughfall precipitation in nutrient cycling studies in British Columbian coastal forests. Ecology **54**:1008–1019.

Likens, G. E., F. H. Bormann, N. M. Johnson, D. W. Fisher, and R. S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook Watershed Ecosystem. Ecological Monographs **40**:23–47.

Martin, M. M., J. S. Martin, J. J. Kukor, and R. W. Merritt. 1980. The digestion of protein and carbohydrate by the stream detritivore *Tipula abdominalis* (Diptera, Tipulidae). Oecologia (Berlin) **461**:360–364.

Meyer, J. L., and G. E. Likens. 1979. Transport and transformations of phosphorus in a forest stream ecosystem. Ecology **60**:1255–1269.

Meyer, J. L., G. E. Likens, and J. Sloane. 1981. Phosphorus, nitrogen, and organic carbon flux in a headwater stream. Archiv für Hydrobiologie **91**:28–44.

Minckley, R. L. 1963. The ecology of a spring, Doe Run, Meade County, Kentucky. Wildlife Monographs **11**.

Minshall, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland spring brook community. Ecology **48**:139–149.

———. 1978. Autotrophy in stream ecosystems. Bioscience **28**:767–771.

Naiman, R. J., and J. R. Sedell. 1979. Characterization of particulate organic matter transported by some Cascade Mountain streams. Journal of the Fisheries Research Board of Canada **36**:17–31.

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

Noonan, L., and E. Holcombe. 1975. Procedures for chemical analyses of plant and soil samples. Internal Report 160, International Biological Program Coniferous Forest Biome, Oregon State University, Corvallis, Oregon, USA.

Odum, W. E., P. W. Kirk, and J. C. Zieman. 1979. Nonprotein nitrogen compounds associated with particles of vascular plant detritus. Oikos **32**:363–367.

O'Neill, R. V., W. F. Harris, B. S. Asmus, and D. E. Reichle. 1975. A theoretical basis for ecosystem analysis with particular reference to element cycling. Pages 28–40 *in* F. G. Howell, J. B. Gentry, and M. H. Smith, editors. Mineral cycling in southeastern ecosystems. Environmental Research and Development Administration Symposium Series (CONF-740513), Washington, D.C., USA.

Petersen, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream ecosystem. Freshwater Biology **4**:343–368.

Rand, M. C. 1976. Standard methods for the examination of water and wastewater. 14th edition. American Public Health Association, Washington, D.C., USA.

Redfield, A. C., B. H. Ketchum, and F. A. Richards. 1963. The influence of organisms on the composition of seawater. Pages 26–77 *in* M. N. Hill, editor. The sea. Volume 2. Wiley-Interscience, New York, New York, USA.

Reichle, D. E., R. V. O'Neill, and W. F. Harris. 1975. Principles of energy and material exchange in ecosystems. Pages 27–43 *in* W. H. van Dobber and R. H. Lowe McConnell, editors. Unifying concepts in ecology. Dr. W. Junk, The Hague, The Netherlands.

Rhee, G-Yull. 1978. Effects of N/P ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. Limnology and Oceanography **23**:10–25.

Roskoski, J. P. 1977. Nitrogen fixation in northern hardwood forests. Dissertation. Yale University, New Haven, Connecticut, USA.

Sain, P., J. B. Robinson, W. N. Stammers, N. K. Kaushik, and H. R. Whitley. 1977. A laboratory study on the role of stream sediment in nitrogen loss from water. Journal of Environmental Quality **6**:274–278.

Sedell, J. R., F. J. Triska, J. D. Hall, N. H. Anderson, and J. H. Lyford. 1974. Sources and fates of organic inputs in coniferous forest streams. Pages 57–69 *in* R. H. Waring, editor. Integrated research in the coniferous forest biome. Proceedings, AIBS Symposium Coniferous Forest Ecosystem. Bulletin Number 5, Coniferous Forest Biome, University of Washington AR-10, Seattle, Washington, USA.

Sedell, J. R., F. J. Triska, and N. S. Triska. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen **19**: 1617–1627.

Silvester, W. B., P. Sollins, T. Verhoeven, and S. P. Cline. 1982. Nitrogen fixation and acetylene reduction in decaying conifer boles: effects of incubation time, aeration and moisture content. Canadian Journal of Forest Research **12**: 646–652.

Sloane, J. 1979. Nitrogen flux in small mountain streams in New Hampshire. Thesis. Cornell University, Ithaca, New York, USA.

Snyder, J. M., and L. H. Wullstein. 1973. Nitrogen fixation on granite outcrop pioneer ecosystems. Bryologist **76**:196–199.

Sollins, P., C. C. Grier, F. M. McCorrison, K. Cromack, Jr., R. Fogel, and R. L. Fredricksen. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecological Monographs **50**:261–285.

Suberkropp, K. F. 1980. The maceration of deciduous leaf litter by aquatic hyphomycetes. Canadian Journal of Botany **58**:1025–1031.

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

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

Swank, W. T., and W. H. Caskey. 1982. Nitrate depletion in a second-order mountain stream. Journal of Environmental Quality **11**:581–584.

Swanson, F. J., R. L. Fredriksen, and F. M. McCorrison. 1982*a*. Material transfer in a western Oregon forested wa-

tershed. Pages 233–266 *in* R. L. Edmonds, editor. Analysis of coniferous forest ecosystems in the western United States. Hutchinson Ross, Stroudsburg, Pennsylvania, USA.

Swanson, F. J., S. V. Gregory, J. R. Sedell, and A. G. Campbell. 1982*b*. Land-water interactions: the riparian zone. Pages 267–291 *in* R. L. Edmonds, editor. Analysis of coniferous forest ecosystems in the western United States. Hutchinson Ross, Stroudsburg, Pennsylvania, USA.

Tamm, C. O. 1953. Growth, yield and nutrition of a forest moss *Hylocomium splendens*. Middelanden Fran Statens Skogsforskningsinstitut **43**:1–140.

Teal, J. M. 1957. Community metabolism in a temperate cold spring. Ecological Monographs **27**:283–302.

Tilly, L. J. 1968. The structure and dynamics of Cone Spring. Ecological Monographs **38**:167–197.

Triska, F. J. 1970. Seasonal distribution of aquatic hyphomycetes in relation to the disappearance of leaf litter from a small woodland stream. Dissertation. University of Pittsburgh, Pittsburgh, Pennsylvania, USA.

Triska, F. J., and B. M. Buckley. 1978. Patterns of nitrogen uptake and loss in relation to litter disappearance and associated invertebrate biomass in six streams of the Pacific Northwest, USA. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen **20**: 324–332.

Triska, F. J., and K. Cromack. 1980. The role of wood debris in forests and streams. Pages 171–190 *in* R. H. Waring, editor. Forests: fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis, Oregon, USA.

Triska, F. J., and R. S. Oremland. 1981. Denitrification associated with periphyton communities. Applied and Environmental Microbiology **42**:745–748.

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

Triska, F. J., J. R. Sedell, and B. M. Buckley. 1975. The processing of conifer and hardwood leaves in two coniferous forest streams. II. Biochemical and nutrient changes. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen **19**:1628–1639.

Triska, F. J., J. R. Sedell, and S. V. Gregory. 1982. Coniferous forest streams. Pages 292–332 *in* R. L. Edmonds, editor. Analysis of coniferous forest ecosystems in the western United States. Hutchinson Ross, Stroudsburg, Pennsylvania, USA.

Van Soest, P. J. 1963. A rapid method for the determination of cellulose and lignin. Journal of the Association of Official Agricultural Chemists **16**:829–835.

———. 1965. Use of detergents in analysis of fibrous feeds. III. Study of the effect of heating and drying on yield of fiber and lignin in forages. Journal of the Association of Official Agricultural Chemists **48**:785–790.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130–137.

Ventullo, R. M., and J. J. Rowe. 1982. Denitrification potential of epilithic communities in a lotic environment. Current Microbiology **7**:29–33.

Vitousek, P. M., J. R. Gosz, C. C. Grier, J. M. Melillo, and W. A. Reiners. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecological Monographs **52**:155–177.

Ward, G. W., and K. W. Cummins. 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera:Chironomidae). Ecology **60**: 57–64.

Waring, R. H., W. H. Emmingham, H. L. Gholz, and C. C. Grier. 1978*a*. Variation in maximum leaf area of coniferous forests in Oregon and its ecological significance. Forest Science **24**:131–140.

Waring, R. H., H. R. Holbo, R. P. Bueb, and R. L. Fredriksen. 1978*b*. Documentation of meteorological data from the Coniferous Forest Biome primary station in Oregon. United States Forest Service General Technical Report **PNW-73**.

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

Webster, J. R., J. B. Waide, and B. C. Patten. 1975. Nutrient recycling and the stability of ecosystems. Pages 1–27 *in* F. G. Howell, J. B. Gentry, and M. H. Smith, editors. Mineral cycling in southeastern ecosystems. Energy Research and Development Symposium Series (CONF-740513), Washington, D.C., USA.

Wetzel, R. G., and B. A. Manny. 1972. Decomposition of dissolved carbon and nitrogen compounds from leaves in an experimental hardwater stream. Limnology and Oceanography **17**:927–931.

Whittaker, R. H., G. E. Likens, F. H. Bormann, J. S. Eaton, and T. G. Siccama. 1979. The Hubbard Brook Ecosystem Study: forest nutrient cycling and element behavior. Ecology **60**:203–220.

Woodall, W. 1975. Mineral pathways in small Appalachian streams. Pages 408–422 *in* F. G. Howell, J. B. Gentry, and M. H. Smith, editors. Mineral cycling in southeastern ecosystems. Energy Research and Development Administration Symposium Series (CONF-740513), Washington, D.C., USA.