

Nutrient Budgets of Appalachian and Cascade Region Watersheds: A Comparison

G. S. HENDERSON

W. T. SWANK

J. B. WAIDE

C. C. GRIER

ABSTRACT. Precipitation inputs and streamflow outputs of nitrogen, calcium, potassium, magnesium, and sodium were compared for two deciduous forest watersheds and a coniferous forest watershed. While nitrogen inputs varied by nearly tenfold among the watersheds, ammonium and nitrate discharge in streamflow was uniformly small resulting in net accumulation within all three ecosystems. In contrast, cation discharge was more variable among the watersheds than cation input and was strongly related to the bedrock of each watershed. The internal distribution and cycling of nitrogen, potassium, and calcium within each of the three watershed ecosystems were also compared. There were interpretable differences between nutrient cycling patterns in the coniferous and deciduous forests. Overall, however, all three ecosystems were effectively retaining and recycling these nutrients. *FOREST SCI.* 24:385-397.

ADDITIONAL KEY WORDS. Nutrient cycling, nitrogen, potassium, calcium, ecosystem analysis.

IN RECENT YEARS, experimental watersheds have increasingly become the focus for ecosystem research on nutrient cycling. Intensive studies have been undertaken to quantify nutrient cycles, and to investigate factors controlling nutrient distribution and movement. While much basic understanding of landscape nutrient cycling processes can be gained from single watershed studies, the degree of generalization and variability of process rates can be examined by comparing results from experimental watersheds with differing characteristics. This paper summarizes results from three catchments located in diverse geographic regions within the United States, and provides a comparison of nutrient inputs and outputs, internal distribu-

The authors are, respectively, Research Ecologist, Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tenn.; Principal Plant Ecologist, Coweeta Hydrologic Laboratory, Southeastern Forest Experiment Station, USDA Forest Service, Franklin, N.C.; Assistant Professor, Department of Zoology, Clemson University, Clemson, S.C.; and Research Associate, College of Forest Resources, University of Washington, Seattle, Wash. The research was supported in part by the Energy Research and Development Administration; in part by the USDA Forest Service; in part by the Eastern Deciduous Forest Biome, US/IBP, funded by the National Science Foundation under interagency agreement AG-199, 40-193-69; and in part by the Coniferous Forest Biome funded by the National Science Foundation under grant DEB 74-20744-A02. Publication No. 1135, Environmental Sciences Division, Oak Ridge National Laboratory (operated by Union Carbide Corporation under contract W-7405-eng-26 with the U. S. Department of Energy). Contribution 309 from the EDFB, US/IBP. Contribution 300 from the CFB, US/IBP. Manuscript received 26 September 1977.

tion and cycling, and factors controlling nutrient movement. In these regions, relatively undisturbed forest ecosystems were examined, since they represent a baseline for evaluating man's impact on the landscape.

WATERSHED DESCRIPTIONS

The three experimental watersheds from which data were obtained for this comparison are Watershed 10 at the H. J. Andrews Experimental Forest, Watershed 18 at the Ceweeta Hydrologic Laboratory, and Walker Branch Watershed at Oak Ridge National Laboratory. A brief description of each catchment follows. Additional information on each site can be found in Grier and others (1974), Johnson and Swank (1973) and Henderson and Harris (1975) for Andrews, Ceweeta, and Walker Branch, respectively.

The H. J. Andrews Experimental Forest is located on the western slopes of the Cascade Mountain Range about 70 km east of Eugene, Oregon. Watershed 10 is 10.2 ha in area and rises from an elevation of 430 to 670 m with slopes that average 45 percent but frequently exceed 100 percent. Underlying bedrock is andesitic. Soils are classed as typic dystrochrepts, and are derived from volcanic tuff and breccia. Dominant vegetation on upper slopes and ridgeline positions is 60-80 m tall, 450-year-old Douglas-fir (*Pseudotsuga menziesii*). Western hemlock (*Tsuga heterophylla*) co-dominates middle and lower slope positions with Douglas-fir. Basal area averages 76 m²/ha on the watershed. Climate is characterized by cool summers and winters. Average annual precipitation on watershed 10 is 233 cm, with only 25 percent falling as rain between April and October. Thus, large soil moisture deficits are common during summer months. Snow may accumulate on the watershed, but seldom persists longer than 2 weeks. Stream discharge is quite variable due to seasonal precipitation patterns, and is highest during winter and spring and lowest during summer and fall.

The Ceweeta Hydrologic Laboratory is situated in southwestern North Carolina within the Blue Ridge Province of the southern Appalachians. Watershed 18 is 12.5 ha in area and has an elevation range from 721 to 1006 m; slopes average 52 percent and range from 40 to 70 percent. Soils on the watershed are classed as typic hapludults and are formed in the residuum from bedrock which is composed of granodiorite, mica gneiss, and mica schist. Watershed vegetation has a basal area of approximately 25 m²/ha, and is an uneven-aged stand of mixed hardwoods, of which 70 percent is composed of oak (*Quercus* spp.), hickory (*Carya* spp.), and red maple (*Acer rubrum*). The climate is characterized by moderately cool summers and mild winters. Average annual precipitation for watershed 18 is 181 cm (< 5 percent snow), and is distributed rather uniformly throughout the year. Stream discharge is also relatively uniform throughout the year, with highest flows occurring in February or March and lowest flows in September and October.

Walker Branch Watershed is located in eastern Tennessee within the Ridge and Valley province of the southern Appalachians. The watershed is composed of two subcatchments with a total area of 97.5 ha. Elevation ranges from 265 to 360 m, and slopes range from 5 to 60 percent and average 30 percent. Soils on the watershed are classed as typic paleudults and are derived from dolomite bedrock. An uneven-aged stand of mixed hardwoods with a basal area of 21 m²/ha occupies the watershed and is dominated by oaks (*Quercus* spp.) and hickories (*Carya* spp.), with lesser amounts of pine (*Pinus virginiana* and *P. echinata*) and yellow-poplar (*Liriodendron tulipifera*). Climate is similar to that at Ceweeta with moderately cool summers and mild winters. Precipitation averages 151 cm annually (< 5 percent snow) with maximum monthly precipitation generally occurring during winter months and slightly lower amounts during late summer and early autumn. Stream-

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MATERIALS AND METHODS

Andrews Watershed 10.—Annual nutrient budgets were prepared from measurements of quantity and chemistry of input and outflow water. Methods used are reported by Fredriksen (1972). Bulk precipitation samplers were placed on an 18 m tower in a clearcut opening and were emptied approximately every 3 weeks. Streamflow is measured with a H-flume. Stream samples were composited proportional to streamflow and also collected at 3-week intervals. Cation concentrations were determined by atomic absorption, ammonium by distillation and detection colorimetrically by Nesslerization, and nitrate by reduction to nitrite and reaction with sulphanilamide.

Methods used to estimate nutrient distribution in ecosystem components and transfers between components have been reported by Grier and others (1974), Grier (1977), and Grier and Logan (1977). In general, the procedures were similar to those used at Coweeta and Walker Branch.

Coweeta Watershed 18.—Details of methods used to derive nutrient budgets for Coweeta watersheds have been given elsewhere (Johnson and Swank 1973). Bulk precipitation chemistry is measured weekly at 12 sites over the Coweeta basin, and includes nutrients received as particulate fallout and in solution. Concentrations for all gages are averaged (Swank and Douglass 1975), and nutrient input to a watershed is obtained by multiplying concentrations by the areal precipitation received by Watershed 18 as determined from an isohyetal weighting system (Swift, L. W., Jr. 1968). Comparison of methods for estimating areal precipitation totals for a mountain watershed. Paper available from the files of Coweeta Hydrologic Laboratory, Franklin, North Carolina). Stream discharge is measured continuously with a 90° sharp-crested V-notch blade, and samples for stream chemistry are collected weekly above the gaging site. Outputs are calculated from discharge-concentration measurements. Analytical methods used at Coweeta are similar to those for Walker Branch, and are detailed by Swank and Henderson (1976).

Methods for estimating nutrients in ecosystem compartments and transfers between compartments have previously been reported by other investigators. Primary production and associated nutrient data were determined by Day (1974) and McGinty (1976); litter production and nutrient content by Cromack and Monk (1975); canopy leaching of nutrients by Best and Monk (1975) and Best (1976); forest floor and soil nutrients by Yount (1975), Cromack and Monk (1975), and Best (1976). Additional results were obtained from earlier syntheses of nutrient cycling data by Waide and Swank (unpublished data) and Mitchell and others (1975).

Walker Branch Watershed.—Atmospheric inputs are collected at five precipitation gaging sites on the watershed; separate samples of rain scavenged (wetfall) and dry particulate (dryfall) inputs were collected weekly for cation analysis from September 1, 1970, through August 31, 1974. Ammonium and nitrate inputs were measured only in the wetfall fraction from September 1, 1972, through August 31, 1974. Cation concentrations were determined by atomic absorption spectroscopy, while ammonium and nitrate concentrations were determined with a Technicon Auto-Analyzer. A more detailed description of sample preparation and analysis is presented in Swank and Henderson (1976). Concentrations of cations and ammonium and nitrate in streamwater were similarly determined from weekly flow-proportional samples collected from each subcatchment. Precipitation and stream

TABLE 1. Annual water and cation budgets for three forested watersheds.

Item	H. J. Andrews ^a	Coweeta ^b	Walker Branch ^c
Precipitation (cm)	233	208	158
Streamflow (cm)	153	125	94
Difference ($P - S$) (cm)	80	83	64
Ca, Mg, K, Na input (kg/ha)	8.0	12.2	23.4
Ca, Mg, K, Na output (kg/ha)	96.0	28.1	235.9
Net difference (kg/ha)	-88.0	-15.9	-212.5

^a Two-year average (10/1/69-9/30/71).

^b Seven-year average (6/1/69-5/31/76).

^c Four-year average (9/1/70-8/31/74).

discharge data used to transform concentrations to area loading or discharge values (kg/ha) were collected at 5-minute intervals at each gaging site. Streamflow is continuously gaged with a 120 sharp-crested V-notch blade (Henderson and others 1977b).

Methods for estimating amounts of nutrients in various ecosystem components and annual transfers between components are detailed by Henderson and Harris (1975). Briefly, vegetation biomass was determined from regression equations applied to tree diameter measurements from 298 0.08 ha plots. Nitrogen and cation concentrations were determined for bole, branch, twig, and leaf components of 40 trees of 15 different species. Incorporation of nutrients in woody growth increment was calculated by applying appropriate concentration values to estimates of net production determined from remeasurement of the 298 vegetation plots.

Nutrients in organic soil horizons and annual nutrient transfers due to canopy leaching were quantified on 24 of the permanent vegetation plots (Henderson and others 1977a). Litterfall returns were determined on 80 of the permanent plots (Grizzard and others 1976). Total and exchangeable (1 N ammonium acetate, pH 7) soil analyses were acquired for ten soil profiles representing the two dominant soil series on the watershed (Peters and others 1970).

RESULTS AND DISCUSSION

Hydrology and Nutrient Budgets.—For the time span of nutrient data reported in this study, annual precipitation (P) averaged 233, 208, and 158 cm for Andrews, Coweeta, and Walker Branch, respectively (Table 1). Corresponding streamflow (S) amounted to 153, 125, and 94 cm, while differences between precipitation and streamflow were 80, 83, and 64 cm (Table 1). Hydrologic components approximated long-term recorded averages for Andrews. Precipitation and streamflow were 20 percent above the 30-year average for Coweeta (Johnson and Swank 1973), but the net difference ($P - S$) was nearly identical to the long-term mean. Values for Walker Branch were 13 percent higher than the 29-year average. Thus, hydrologic contributions to net differences shown in Table 1 are representative of long-term averages, while quantitative cation inputs and outputs are slightly high for Coweeta and Walker Branch.

Total cation balances (Ca, Mg, K, and Na) for the three watersheds are also given in Table 1, while inputs and outputs of these four ions are shown separately in Figure 1. Cation inputs at Walker Branch are about double the inputs at Coweeta, and about triple the values for Andrews. This ranking of cation inputs is exactly opposite that of precipitation amounts and illustrates the large differences between sites in average annual cation concentrations in precipitation. At all sites

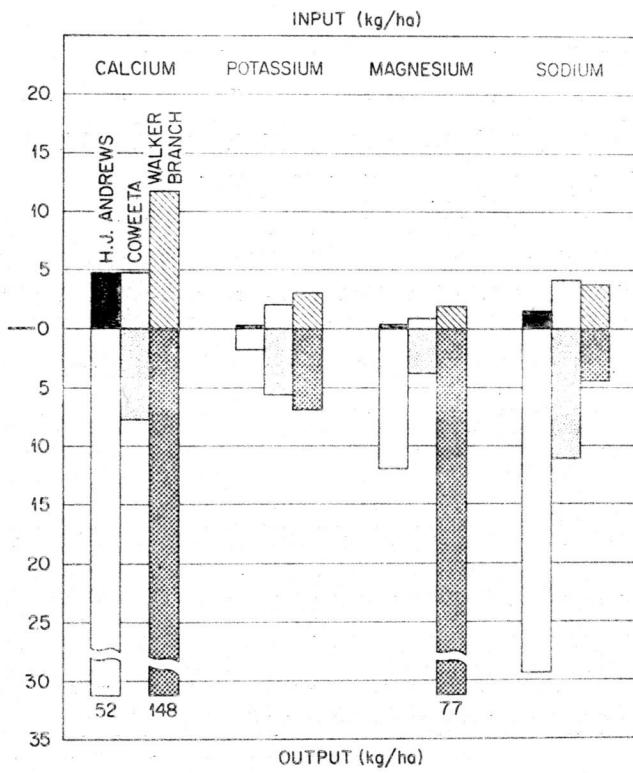


FIGURE 1. Annual atmospheric deposition (input) and streamflow loss (output) of calcium, magnesium, potassium, and sodium for three forested watersheds.

the input of calcium is greater than other elements, and sodium inputs rank second in amount. Previous comparisons of inputs at Coweeta and Walker Branch have shown that dry fallout (gravitational settling) from the atmosphere contributes a significant portion of total inputs, and that greater inputs at Walker Branch are likely due to local industrial sources (Swank and Henderson 1976). Low inputs at Andrews probably reflect the site's remoteness from industrial sources.

Transport of cations from the three watersheds in streamflow is very different. All three sites are losing more cations than they are gaining through atmospheric inputs (Table 1), but at Walker Branch cation discharge is 2.5 times greater than at Andrews, and over 8-fold greater than at Coweeta. Cation discharge from these undisturbed watersheds primarily reflects geology, in terms of both relative enrichment for individual cations and total amounts of loss. At Walker Branch, 95 percent of the total cation discharge is Ca and Mg, and the ratio of Ca:Mg in streamflow is about 2:1 (Fig. 1). The streamflow loss of these nutrients is a direct result of the weathering of the dolomitic bedrock underlying Walker Branch that also has a 2:1 Ca:Mg ratio. Similarly, losses of Ca and Na at Andrews reflect andesitic bedrock, which has abundant Ca- and Na-rich feldspars. Moreover, the amount of loss is a function of the relative solubilities of the various bedrock types. Dolomite is much more easily weathered (dissolved) than the other two bedrock types, and andesite more so than the granitic-metamorphic type at Coweeta. The latter is apparently especially resistant to chemical weathering, and streamflow losses at Coweeta are quantitatively similar to atmospheric inputs. However, the relative strengths with which cations adhere to the soil exchange complex (generally Ca >

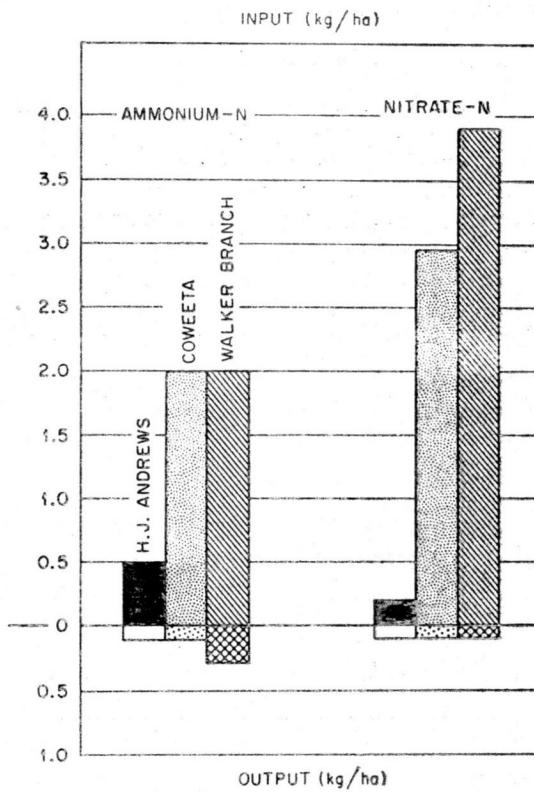


FIGURE 2. Annual atmospheric deposition (input) and streamflow loss (output) of ammonium-N and nitrate-N for three forested watersheds.

Mg > K > Na) also influence the degree of retention within a watershed and, therefore, the composition of streamwater.

In contrast to input-output patterns for cations (outputs > inputs), nitrogen is accumulating in all three watershed ecosystems (Fig. 2). Inputs of ammonium- and nitrate-N are greater at Walker Branch and Coweeta than at Andrews, the same pattern observed for cations. At Walker Branch and Coweeta nitrate inputs are greater than ammonium inputs, whereas at Andrews the reverse is true. The remoteness of Andrews from industrial and agricultural activity may partially explain the low deposition of nitrate. Outputs of ammonium and nitrate in streamflow are extremely low at all sites. While the majority of streamwater nitrogen loss from undisturbed forested watersheds occurs in organic form (Fredricksen 1972, Henderson and Harris 1975), it is more than offset by organic nitrogen inputs in precipitation and further contributes to the net accumulation pattern shown in Figure 2 for inorganic nitrogen forms.

However, it must be emphasized that these comparisons are appropriate only for nitrogen gains and losses through hydrologic processes. Inputs and outputs of nitrogen also occur in gaseous form, as nitrogen fixation and denitrification, respectively. These components of total gains and losses may predominate in undisturbed forested watersheds (Todd and others 1975). Thus, any conclusion regarding net nitrogen accumulation must remain qualified until gaseous transfers have been quantified at all sites.

TABLE 2. Biomass distribution in vegetation and forest floor for three watershed ecosystems.

Biomass location	H. J. Andrews	Coweeta	Walker Branch
-----kg/ha-----			
Vegetation			
Above-ground	718,000	139,000	122,000
Below-ground	153,000	51,000	34,000
Forest floor			
Wood (> 2.5 cm)	190,000	12,600	3,900
O Horizon	51,200	11,200	25,600

Nutrient Distribution Within Ecosystems.—Distributions of biomass, nitrogen, potassium, and calcium among vegetation, forest floor (organic soil horizons), and mineral soil horizons for the three watersheds are presented in Tables 2, 3, 4, and 5, respectively. Only N, K, and Ca will be discussed further, since data for Mg and Na are insufficient for comparison. The bulk of all three nutrients was found in the mineral soil at all sites. Nitrogen and potassium occur primarily in nonexchangeable organic and inorganic form, whereas a larger portion of calcium is associated with the soil exchange complex. More exchangeable potassium and calcium were found in the soil at Andrews for two reasons: cation exchange capacity at Andrews (25 meq/100 g) is three times greater than at either Coweeta or Walker Branch (5–8 meq/100 g), and the portion of the exchange complex retaining basic cations (base saturation) is also greater at Andrews. Soils at Andrews are developmentally younger than those at the other two sites, and consequently fewer bases have been leached from the soil profile. Smaller differences exist between Coweeta and Walker Branch in amounts of exchangeable nitrogen, potassium, and calcium although all three elements are higher in Coweeta soils than in soils at Walker Branch.

Dry weight of litter on the forest floor (organic soil horizons) at Andrews is between eight and ten times greater than that at either Coweeta or Walker Branch (Table 2). This difference accounts for the greater accumulations of nutrients in

TABLE 3. Nitrogen distribution and cycling in three watershed ecosystems.

Item	H. J. Andrews	Coweeta	Walker Branch
-----kg/ha-----			
Amount in:			
Vegetation	560	995	470
Forest floor ^a	740	140	310
Mineral soil: ^b			
Exchangeable	5	117	75
Total	4500	6800	4700
Annual transfers as:			
Litterfall	21	33	39
Canopy leaching	4	4	3
Woody increment	-2	13	15
Uptake	23	50	57

^a 01 and 02 horizons (organic).

^b A and B horizons to a 60 cm depth.

TABLE 4. Potassium distribution and cycling within three watershed ecosystems.

Item	H. J. Andrews	Coweeta	Walker Branch
kg/ha			
Amount in:			
Vegetation	360	400	340
Forest floor ^a	90	20	20
Mineral soil: ^b			
Exchangeable	860	510	170
Total	*	124,000	38,000
Annual transfers as:			
Litterfall	9	18	19
Canopy leaching	15	31	19
Woody increment	-1	13	8
Uptake	23	62	46

^a 01 and 02 horizons (organic).^b A and B horizons to a 60 cm depth (exchangeable).

* Data not available.

the forest floor at Andrews. Accumulation of nitrogen and calcium in the forest floor at Walker Branch is 2-3 times greater than at Coweeta. Concentrations of nutrients in organic soil horizons (forest floor) at Andrews and Coweeta are lower than at Walker Branch. These lower concentrations result because about 80 percent and 55 percent of the litter mass at Andrews and Coweeta, respectively, is decaying wood compared to 15 percent at Walker Branch (Table 2) and wood has lower nutrient concentrations than leaf and twig litter.

Although vegetation biomass at Andrews is about five times greater than the other two sites, amounts of potassium and calcium incorporated in vegetation at the three sites are similar. Nitrogen in vegetation at Coweeta is about twice that at Andrews and Walker Branch. Thus, the concentrations of Ca and K follow the pattern Walker Branch = Coweeta > Andrews, whereas for N the order is Coweeta > Walker Branch > Andrews.

Annual Nutrient Transfers.—The magnitude of four annual transfers (litterfall, canopy leaching, incorporation in woody increment, and uptake) for nitrogen, potassium, and calcium are also shown in Tables 3, 4, and 5, respectively. Litterfall has generally been regarded as the most important mechanism in cycling most nutrients from vegetation to soil (Rodin and Bazilevich 1965, Duvigneaud and DeSmet 1970). However, Henderson and Harris (1975) concluded that root mortality can be a more important cycling mechanism than litterfall at Walker Branch based on a detailed examination of *Liriodendron tulipifera*. Comparative root mortality data are not yet available for all sites, and therefore this transfer was not included.

Litterfall amounts to 4300, 4300, and 4200 kg/ha annually at Andrews, Coweeta, and Walker Branch, respectively. Amounts of nitrogen, potassium, and calcium returned in litterfall are slightly greater at Walker Branch than at Coweeta. Nitrogen and potassium cycled by litterfall in the coniferous forest at Andrews is less than at the other two sites while calcium return is similar. These patterns are probably due to differences in internal redistribution and leaching of nutrients between coniferous and hardwood ecosystems. Whereas hardwoods lose their leaves each autumn, Douglas-fir retains needles for up to 8 years, and western hemlock retains

TABLE 5. *Calcium distribution and cycling within three watershed ecosystems.*

Item	H. J. Andrews	Coweeta	Walker Branch
----- kg/ha -----			
Amount in:			
Vegetation	750	830	980
Forest floor ^a	570	130	430
Mineral soil: ^b			
Exchangeable	4450	940	710
Total	*	2500	3800
Annual transfers as:			
Litterfall	41	44	55
Canopy leaching	8	8	14
Woody increment	-4	23	31
Uptake	45	75	100

^a 01 and 02 horizons (organic).^b A and B horizons to a 60 cm depth (exchangeable).

* Data not available.

foliage for 3 to 6 years. Calcium is not readily redistributed within plants (Kramer and Kozlowski 1960), and therefore the similar amount returned in litterfall at Andrews reflects the similar leaf mass return at the three sites. Nitrogen, on the other hand, is more readily translocated from old to new plant growth (Kramer and Kozlowski 1960). Thus, the 3-to-8-year persistence of needles facilitates internal redistribution of nitrogen from older foliage to sites of new growth in coniferous ecosystems. The additional time of exposure to precipitation apparently does not result in significantly greater leaching of nitrogen from the foliage as evidenced by the low (4 kg/ha) nitrogen content in throughfall (Table 3). The much lower return of potassium in litterfall at Andrews is due to continual leaching of conifer foliage during the years it persists on trees prior to litterfall, as well as to translocation to new growth. Internal redistribution of N prior to litterfall is also important in the two hardwood forests (Henderson and Harris 1975; Mitchell and others 1975; Waide and Swank, unpublished data).

Canopy leaching, or the return of nutrients in throughfall, is next in importance to litterfall as a cycling mechanism for N and Ca. For K, however, it is often more important than litterfall because of the susceptibility of this nutrient to leaching from senescing foliage. The small amount of canopy leaching of nitrogen at all sites (3-4 kg/ha) indicates that significant amounts of this nutrient are being redistributed internally. Comparing deciduous sites, the reasons for greater foliar leaching of potassium at Coweeta and calcium at Walker Branch are not presently understood, but correspond to relatively greater foliar contents at these sites.

Differences between sites in amounts of N, K, and Ca incorporated into annual woody increments are due both to differences in their concentrations in wood and to relative growth rates. Net production of wood is similar at the eastern sites, ranging from 3300 kg/ha/yr at Walker Branch to 3700 kg/ha/yr at Coweeta. In contrast, annual woody increment is negative, -4300 kg/ha, at Andrews because of high mortality in the old-growth stand. In addition, hardwood vegetation has three to five times greater N, K, and Ca concentrations in wood than conifers. Coweeta and Walker Branch have similar elemental incorporation in woody production.

Uptake was calculated as the sum of litterfall, canopy leaching, and incorporation in wood. Thus, it accounts for the amount of a nutrient annually cycled through

TABLE 6. *Losses of nitrogen, potassium, and calcium from three watershed ecosystems in relation to the amounts of these nutrients in vegetation, on the soil exchange complex, and the quantity annually cycling within the indicated ecosystems. Value presented represents what percentage the total loss in stream discharge (also shown in kg/ha/yr) is of the indicated compartment size or transfer.*

Nutrient and watershed loss as—	H. J. Andrews	Coweeta	Walker Branch
Nitrogen^a			
kg/ha	0.1	0.1	0.4
Percent of vegetation	<1	<1	<1
Percent of exchangeable	2	<1	<1
Percent of amount cycling ^b	<1	<1	<1
Potassium			
kg/ha	1.7	5.6	6.8
Percent of vegetation	<1	1	2
Percent of exchangeable	<1	1	4
Percent of amount cycling ^b	7	9	15
Calcium			
kg/ha	52.0	7.7	147.5
Percent of vegetation	7	1	15
Percent of exchangeable	1	1	21
Percent of amount cycling ^b	116	10	148

^a Ammonium and nitrate.

^b Equals uptake in Tables 3-5.

the vegetation and returned to the soil via an external route as well as that stored by the vegetation in woody tissue. Uptake of N, K, and Ca in the two hardwood ecosystems is greater than that at the Andrews. Comparing the three sites, differences in uptake tend to parallel variations in elemental incorporation in annual wood increment. Annual uptake of N, K, and Ca by the coniferous forest at Andrews is only 35 to 60 percent of that for the hardwood sites. This difference is partly due to lower nutrient requirements for old-growth conifer forests when mortality exceeds growth and results in negative net biomass accumulation. The low uptake value for the coniferous ecosystem may also indicate a greater importance of internal recycling, especially for N and K.

Comparisons of Nutrient Losses with Compartment Sizes and Annual Transfers.—Characterization of internal nutrient cycles for experimental watersheds allows us to consider nutrient losses in streamflow in relation to nutrient contents within and transfers among various ecosystem components. In comparing Andrews, Ceweeta, and Walker Branch, losses of N, K, and Ca have been considered in this context (Table 6).

At all three sites, losses of nitrogen as ammonium and nitrate are an extremely small percentage (< 1 percent) of nitrogen amounts in vegetation or soil, or of amounts being cycled annually. All three ecosystems are effectively retaining this nutrient, which has no significant bedrock source. The primary mechanism of nitrogen retention appears to be one of keeping the amount of nitrogen in inorganic form at a minimum in order to reduce leaching losses. Disruption of processes responsible for conversion of inorganic nitrogen to organic forms can result in large increases in streamwater nitrogen losses (Likens and others 1970). In fact,

increased nitrogen discharge as nitrate appears to be symptomatic of various types and degrees of disturbance within forested ecosystems (Swank and Douglass 1975).

Potassium and calcium losses in streamflow generally constitute a greater percentage of nutrient pool sizes and annual transfers than does nitrogen. This is primarily due to the contribution of bedrock weathering processes to streamflow concentrations. For example, based on lysimeter collections below the rooting zone it is estimated that about 80 percent of the calcium discharge from Walker Branch is due to bedrock weathering. However, with the exception of calcium discharge at Andrews and Walker Branch largely due to bedrock weathering, streamflow losses of cations are generally less than 10 percent of amounts cycled annually. These ecosystems are functioning relatively efficiently with respect to the conservation of Ca and K although not as efficiently as they are for nitrogen. This difference is largely due to the fact that nitrogen has a gaseous cycle, and is more strongly regulated by biological processes, whereas geochemical processes are more important in calcium and potassium cycles. Stream chemistry does not reflect the internal cycling dynamics of cations as well as it does for nitrogen. However, it must be emphasized again that in the absence of quantitative estimates of gaseous nitrogen inputs and losses, values shown in Table 6 must remain tentative.

CONCLUSIONS

The validity and generality of single watershed studies can only be assessed from comparisons of results obtained in a variety of such studies. In this paper we have attempted to provide a summary comparison of watershed studies in three diverse regions of the United States. Analyses presented here suggest that deciduous forest ecosystems at Coweeta and Walker Branch are exhibiting similar nutrient cycling patterns, which differ in interpretable ways from nutrient cycles in coniferous forests at Andrews. Analyses also suggest that undisturbed forests at all three sites are effectively retaining and recycling nutrients, especially nitrogen, and thereby minimizing nutrient losses in streamwater.

Net budget data for selected ions provide integrated measures of ecosystem response, but they do not reveal the dynamics of nutrient cycles within a landscape. Quantification of nutrient cycles allows examination of the relative importance of various cycling mechanisms among ecosystems while input-output data provide a means of studying differences in total ecosystem behavior, both in undisturbed and perturbed states. In the present comparison, internal cycling data combined with input-output data were used to separate the influence of geologic and biologic processes on nutrient cycling. It was determined that biotic processes controlled the loss of nitrogen from these ecosystems whereas geology largely determined the loss of cations. However, differences among ecosystems in nutrient distribution and internal transfers were small relative to differences in nutrient output. There is a pronounced similarity in nutrient cycling processes among the diverse landscapes. Thus, although input-output data reveal interesting contrasts among ecosystems, they do not provide information on what factors regulate ecosystem nutrient cycles in the absence of supporting biological information. Such information is especially critical in predicting an ecosystem's response to disturbance. For example, net cation budgets for Coweeta and Walker Branch are quite different, and strongly reflect bedrock differences between the two sites. However, closer examination of nutrient pool sizes and annual transfers suggest that nutrient cycles are quite similar in the deciduous forests at the two sites and suggest that the two ecosystems would respond similarly to a common disturbance such as forest cutting.

Indeed, the ability to use information from such watershed studies as those discussed here to evaluate and present consequences of management and alteration of

the landscape is a major benefit of such studies. However, the ability to use such studies in an applied context demands a thorough analysis of the biogeochemical factors responsible for input-output behaviors of forested watersheds. Discussions in this paper provide an initial analysis of such factors for Appalachian and Cascade forested watersheds, but much remains to be learned in terms of the biogeochemistry of these experimental watersheds.

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