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THE INTERNAL ELEMENT CYCLES OF AN OLD-GROWTH DOUGLAS-FIR ECOSYSTEM IN WESTERN OREGON¹

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Abstract. Information on primary production, decomposition, hydrology, and element cycling was integrated in annual budgets of accumulation and flux among components of a mature Douglas-fir forest ecosystem. Annual N input in precipitation and dust was 2.0 kg/ha, and an estimated 2.8 kg/ha were fixed by cyanophycophilous lichens in the canopy. Annual N loss to groundwater was 1.5 kg/ha. N appeared to be accumulating in the ecosystem. An annual decrease of ≈ 2.8 kg/ha in vegetation was offset by estimated increases of 5.0 kg/ha in fallen logs, and 2.8 kg/ha in soil organic matter. Microparticulate litterfall provided a large input of N to the forest floor ($3.3 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$).

Annual input of metallic cations in precipitation was only 545 eq/ha, whereas weathering input (net release of cations to solution from primary and secondary minerals) was estimated by difference at ≈ 9000 eq/ha. Total annual loss to groundwater was 9400 eq/ha and, because of little cation accumulation, loss almost exactly balanced input. Net transfers of P were small. Total annual input was 0.5 kg/ha, total loss was 0.7 kg/ha, and net accumulation was -0.2 kg/ha. Input of elements in precipitation and dryfall was small compared with that in the eastern United States.

Water chemistry profiles showed that the biologically important elements N, P, and K increased in concentration as water passed through the canopy and litter layer but decreased as water passed through the rooted part of the mineral soil. In contrast, Na increased by a factor of 20 as water passed through the rooted soil. Concentrations of all elements except Mg were lower in the stream water than in solution at 2.0-m depth in the subsoil.

At our site, unlike some eastern forests, Kjeldahl N (organic N plus NH_4^+) accounted for most of the measured N in solution. Nitrate levels were low, averaging $\leq 20 \mu\text{g/L}$ NO_3^- -N at all points in the profile. Titratable alkalinity dominated anion chemistry in the mineral soil, but in the upper parts of the water chemistry profile (precipitation, throughfall, and litter leachate) Cl^- and SO_4^{2-} together accounted for 30-40% of the negative charge.

Total return to the forest floor in litterfall was greater than that reported for other Douglas-fir stands mainly because of plentiful microparticulate forms and coarse woody debris. Leaf fall accounted for less than half of the total litterfall input of N to the forest floor. Element accumulations in coarse woody debris almost cancelled the negative net annual increments in the living vegetation compartments.

Overall cycling patterns show that only the biologically limiting element, N, was tightly conserved. For other elements, losses nearly equaled or even exceeded inputs. Redistribution from old to new foliage was also more important for N, P, and K than for Ca, Mg, and Na. Solution transport processes were important for all elements and dominated the cycling patterns of biologically less important elements such as Ca and Na. Vegetation absorbed metallic cations mainly from the mineral soil. However, much N and P were absorbed by roots penetrating up to or into the litter layer.

Fluxes of hydrogen ions (H^+) resulting from water flow were negligible ($\leq 10^2 \text{ eq} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) compared with H^+ release during carbonic acid dissociation and H^+ removal accompanying cation release in weathering (both $\approx 10^4 \text{ eq} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$). Uptake of metallic cations by vegetation and release during decomposition exceeded uptake and release of sulfur and phosphorus anions, resulting in a net H^+ flux of $\approx 3 \times 10^3 \text{ eq} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. An increase in acidity of the rainfall to pH 4.0 would increase H^+ input only $\approx 3 \times 10^2 \text{ eq} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$.

Key words: acidity; cations; fixation; leaching; litterfall; nitrogen; phosphorus; precipitation; streamflow; throughfall; uptake; weathering.

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INTRODUCTION

The usefulness of studying element input and loss from small watersheds is now well accepted. The practical limits of such input-output studies may have been approached in a study by Vitousek (1977) of element loss from some 57 watersheds. Vitousek was able to

explain the loss patterns as resulting from interactions among four processes: input in precipitation, accumulation in organic matter, input from weathering, and concentration of dissolved forms due to transpiration. He suggested that losses of limiting elements are high during and immediately after a disturbance, when return exceeds uptake, and again as the system approaches steady state and accumulation ceases. His study illustrates the extent to which input-output studies can be used to deduce the relative importance of internal cycling mechanisms. Verification requires quantitative study of the internal pathways.

Many internal pathways, such as litterfall and throughfall, have been studied over long periods in various forest types; but others, such as consumption by insects, root death, and N fixation have been studied only infrequently. Under the auspices of large ecosystem analysis projects, budgets of flux and accumulation were constructed that account for most transfer of a given element through the ecosystem. Among the earliest of these were the N, P, and cation budgets for a 40-yr-old Douglas-fir stand (Cole et al. 1967) and for temperate European forests (Duvigneaud and Denaeyer-De Smet 1970, Nihlgård 1972). Nitrogen budgets were later prepared by Henderson and Harris (1975) and Mitchell et al. (1975) for hardwood forests of the southeastern United States. More recently budgets for N, Ca, K, and several other elements have been published for a New England hardwood forest (Bormann et al. 1977, Likens et al. 1977, Whittaker et al. 1979). Some important processes, most notably solution transport through litter and soil, were not considered, but the papers are a major step forward. A similar budget that includes solution transport processes has been prepared for a 120–150 yr *Pinus silvestris* stand in Sweden (Bringmark 1977, Staaf and Berg 1977). The budgets show clearly that a comparison of element input with loss in drainage waters provides a good index of a system's leakiness with respect to that element, an attribute which may change markedly with disturbance. Accumulation and total uptake by vegetation are other ecosystem variables which allow us to compare natural and disturbed systems.

Still lacking is a means of integrating information about the system as a whole. Ideally, information on all processes, hydrologic, production, decomposition, and element cycling, should be combined into a single index of system behavior. All these processes interact. For example, metallic cation cycles can be affected by N dynamics if nitrification causes release of H^+ which displaces sorbed cations from exchange sites. These interactions must be considered systematically, particularly when building simulation models of element cycles (Terry and McCants 1968, Johnson et al. 1969, Dutt et al. 1972, McColl 1973, Ulrich et al. 1973, Sollins et al. 1974, Smith 1976).

We suggest that most, if not all, of these interactions involve the H^+ ion. In this paper, we show how this

component, usually considered a complicating nuisance, provides a common denominator in terms of which ecosystem processes can be interpreted.

To examine this hypothesis, we have assembled data from Watershed 10 (WS-10) on the H. J. Andrews Experimental Forest (HJA) in the Oregon Cascade Mountains, the site of intensive studies by the United States Forest Service and the Coniferous Forest Biome (United States/International Biome Program) during 1971–1975. The data are for the most part adequate for constructing the various metallic cation, P, and N budgets. Data on S and Cl were not gathered until much later in the study. We used some information on these elements from other sites to construct our H^+ budget. This should not cause a problem because we are emphasizing the approach, the conceptual model for the H^+ budget, rather than the specific data for the study site. Moreover, the data for the metallic cation, P, and N budgets are essentially complete and span years of widely differing rainfall and temperature.

STUDY SITE

WS-10 is a 10.24-ha watershed located on the western boundary of the H. J. Andrews Experimental Forest in the western-central Cascade Mountains of Oregon. The HJA is located near the town of Blue River and forms part of the McKenzie River drainage. WS-10 was clear-cut during May–June 1975; all data, except that for Cl and S, refer to the period before clear-cutting.

Elevations on WS-10 range from 430 m at the stream gauging station to ≈ 670 m at the southeastern ridge-line. The main stream slope averages $\approx 25^\circ$; steeper side slopes range from 25° to 50° . Annual precipitation, mostly rainfall between October and May, averaged 240 cm for May 1972–1976 (Waring et al. 1978). Winter snow accumulations of up to 30 cm are common but seldom persist more than 2 wk. Mean air temperature was 7.9°C over the 1972–1976 period; daily averages ranged from -20°C to $+39^\circ\text{C}$.

WS-10 is in an area underlain by andesitic tuffs and breccias (Harr 1977, James 1977). Soils, formed either in residual parent material or in colluvium originating from these deposits, are classified as typic dystrochrepts (Soil Survey Staff 1960). They consist of a weakly developed A1 horizon 20 cm thick overlying a weakly developed B1-B2-B3 sequence 50–80 cm thick. Soil textures range from gravelly, silty clay loam to very gravelly clay loam. Clay content averaged $25.3 \pm 3.1\%$ in the top 100 cm (R. Brown, *personal communication*).

Before clear-cutting during the summer of 1975, the forest floor (O_1 plus O_2 horizons) on WS-10 averaged ≈ 50 Mg (metric ton)/ha dry mass excluding logs, and was classified duff-mull according to the system of Hoover and Lunt (1952). Fallen logs were conspicuous on the WS-10 landscape; they occupied $\approx 20\%$ of land

TABLE 1. Water volume and solute concentrations along the profile at WS-10; SE in parentheses.

Variable	Precipitation	Throughfall	Litter solution	Soil and subsoil solution				
				30 cm	100 cm	200 cm	Seeps	Weir*
Number of locations sampled	1	54	2	4	4	4	7	1
Water volume† (Mg·ha ⁻¹ ·yr ⁻¹)	23 700	20 050	19 800	...	15 450	15 450
NO ₃ ⁻ -N (μg/L)‡	12 (5)	1 (0.05)	1 (<0.01)	20 (10)	13 (8)	16 (5)	2 (0)	19 (2)
Kjeldahl N (mg/L)	0.047 (0.030)	0.17 (0.01)	0.237 (0.001)	0.194 (0.021)	0.098 (0.027)	0.078 (0.019)	0.067 (0.020)	0.035 (0.003)
Na (mg/L)	0.24 (0.04)	0.32 (0.01)	0.36 (0.02)	6.72 (0.36)	3.42 (0.98)	4.44 (1.98)	2.09 (0.44)	1.96 (0.12)
K (mg/L)	0.040 (0.022)	0.69 (0.06)	1.29 (0.21)	0.952 (0.294)	0.613 (0.215)	0.535 (0.164)	0.299 (0.005)	0.339 (0.024)
Mg (mg/L)	0.050 (0.031)	0.14 (0.01)	0.28 (0.02)	0.437 (0.192)	0.555 (0.236)	0.642 (0.266)	0.901 (0.134)	0.834 (0.057)
Ca (mg/L)	0.15 (0.04)	0.36 (0.03)	1.16 (0.02)	7.45 (3.65)	7.97 (3.95)	6.50 (3.03)	3.19 (0.50)	3.20 (0.23)
H (μg/L)	6.3	5.2 (2.1)§	1.5 (0.5)	0.14 (0.05)	0.42 (0.19)	0.32 (0.15)	...	0.20 (0.06)
Alkalinity (mg/L)	0.40 (0.02)	0.66 (0.04)§	1.1 (0.10)	9.75 (3.10)	8.96 (4.07)	4.42 (3.13)	3.78 (0.66)	4.17 (0.17)
Total P (mg/L)	0.006 (0.002)	0.059 (0.006)	0.092 (0.025)	0.068 (0.003)	0.045 (0.007)	0.056 (0.015)	0.084 (0.009)	0.054 (0.003)
SO ₄ ²⁻ -S (mg/L)¶	0.16 (0.04)¶	0.30 (0.04)	0.89 (0.11)	...	8.28 (6.19)	1.73 (0.90)
Cl (mg/L)¶	1.55 (0.13)#	1.83 (0.17)	2.87 (0.81)	1.42 (0.13)	3.69 (2.05)	1.46 (0.21)

* Data from proportional sampler at weir (Fredriksen 1975) during May 1972–1975. H data based on grab samples taken at 3-wk intervals during May 1973–1975.

† All volumes based on hydrologic model of WS-10 (Sollins et al. 1979) for period May 1972–1975.

‡ May include small amounts of NO₂.

§ Based on five collectors at two locations on WS-10 during October 1972–May 1975.

¶ Unless otherwise noted, data based on a range of 4 to 35 samples collected during December 1976–November 1977 from forested area near base of WS-10. Values are unweighted means and standard errors are based on all samples.

¶ Datum is volume-weighted average for October 1971–1972 only.

Based on 10 samples from the clear-cut area during December 1976–November 1977.

surface (R. Fogel and M. Ogawa, *personal observation*) and averaged 190 Mg/ha (Grier and Logan 1977). Highly decomposed logs lacking structural integrity were included in the forest floor total rather than in this estimate of log mass (C. Grier, *personal observation*).

A seral, site class III (Dilworth 1974) Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] forest covered WS-10. Dominants ranged in age from 350 to 550 yr. The understory was western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], Douglas-fir, and other conifers, and broad-leaved species. The WS-10 environment ranged from hot and dry near ridgetops and on south-facing slopes to cool and moist near the stream (Dyrness et al. 1974, Zobel et al. 1976, Hawk 1979). Biomass of aboveground vegetation averaged 720 Mg/ha; net primary production (aboveground) was 8.0 Mg·ha⁻¹·yr⁻¹ (Grier and Logan 1977).

METHODS AND DATA SOURCES

Analytical methods

In water samples, nitrate (plus nitrite) was determined by diazotization after cadmium reduction (Rand 1976), alkalinity by titration to pH 4.5, and pH with a glass electrode. The micro-Kjeldahl method was used to determine organic N plus ammonium (Jackson 1958). Sulfate and chloride were measured on an Autoanalyzer using Technicon methods 226-72W and 99-70W. Total S was not measured. After digestion with persulfate and sulfuric acid, total P was determined by the molybdate-blue method with ascorbic acid as the reducing agent (Rand 1976). Cations were determined by standard methods of absorption spectroscopy. All water samples were passed through glass-fiber filters before analysis.

Tissue samples were first digested with nitric and perchloric acid and then analyzed in essentially the same way as water samples. Exchangeable cations were extracted from soil samples with 1 N ammonium acetate at pH 7. Extractable P was determined by the method of Bray and Kurtz (1945).

Solution sampling

Precipitation was collected in a clear-cut area near WS-10 from May 1971 to May 1975 (Fredriksen 1975). Values in Table 1 are volume-weighted means for the latter 3 yr.

Throughfall was collected from November 1973 to May 1975 with 54 collectors (317.3 cm²) distributed at regular intervals over the watershed. Values in Table 1 are volume-weighted means for that period. Throughfall included both drip from the canopy and precipitation (including snowfall) that passed directly through to the forest floor. Throughfall collectors were covered with nylon screens of the same mesh (0.1 mm) used for litterfall traps. We assumed that leaching of elements from material trapped on the throughfall screens was compensated for by leaching from litter trapped on the litterfall screens. Because throughfall samples were filtered before analysis, throughfall values do not include microparticulate matter, which was measured separately. (See the section *Litterfall and root death*.)

Stemflow volume averaged only 1.8% of incident precipitation on WS-10 from November 1973 to December 1974; element concentrations in stemflow were two to four times those in throughfall (C. Grier, *personal observation*). If concentrations were four times those in throughfall, separate accounting for stemflow and throughfall would increase the value for element

input to the forest floor only 5.4%, an error negligible in the overall budgets. To simplify calculations, therefore, we did not treat stemflow separately.

Litter leachate was sampled with Alundum tension plate lysimeters (Cole 1958) installed parallel to the slope immediately beneath the litter. A suction of 10 kPa was maintained at the litter-lysimeter boundary with a hanging water column. Ten plate lysimeters were installed, five on the portion of WS-10 to be clear-cut and five at a control location not scheduled for cutting on the north-facing slope above the base of WS-10.

Soil and subsoil solution was sampled with porous ceramic cups (Parizek and Lane 1970) placed at 0.3-, 1.0-, and 2.0-m depth in the soil profile. The ceramic cups and plates prevented entry of particles ≤ 0.004 and 0.015 mm in diameter, respectively, so that illuvial transfers could not be estimated directly. The depths were chosen to correspond with the bottom of the A horizon, the bottom of the rooting zone, and a point well below the rooting zone. "Soil solution" will refer here only to solutions from the intensively rooted portion of the mineral soil because extensive sampling on WS-10 by Santantonio et al. (1977) showed that few roots were present below 100 cm. Solution extracted from the partially weathered bedrock (saprolite) below 100 cm will be referred to as "subsoil solution." Because many roots and mycorrhizal hyphae penetrate upward into the litter layer, "rooting zone" will refer to both the litter and rooted portion of the mineral soil. Solution flux at 1.0-m depth was assumed to represent export from the rooting zone.

Twenty-seven cups (three locations, three depths, three replications) were placed along a transect perpendicular to the stream across the south-facing slope of the watershed, and nine cups were placed at the control location above the base of WS-10. Cups were installed by augering holes, sealing the bottom with bentonite slurry, backfilling with quartz sand, and sealing the top with bentonite to prevent water from percolating down the installation shaft (Parizek and Lane 1970). Cups were emptied and evacuated to their bubble pressure (-80 kPa) three times weekly. Vacuum decreased to at most -50 kPa between evacuations, depending on the sample volume that accumulated.

Cups were installed first at the control site and holes were backfilled with reagent-grade 200-mesh ($<75 \mu\text{m}$) SiO_2 . Reagent-grade sand proved prohibitively expensive, so the cups installed at the three slope positions on the portion of the watershed scheduled for cutting were backfilled with 80-mesh ($<180 \mu\text{m}$) acid-washed beach sand. The two sand types gave different results for some elements as discussed further later.

Cup and plate collection vessels were emptied at 3-wk intervals, plates beginning in October 1972 and cups beginning in March 1973. Sampling was suspended in May 1975 when the watershed was clear-cut.

Data from the period after cutting began will be published elsewhere.

To summarize plate and cup data, we first established a single value for each location over a given collection interval and at a given depth. During dry periods, samples from replicate plates or cups at each location and depth were composited to obtain sufficient volume for analysis; in such cases, the laboratory results provided the single value directly. During wetter periods, a sample from each replicate was analyzed separately, and the values were averaged using the measured volumes as weighting factors.

Next, we used a hydrologic simulation model of WS-10 (Sollins et al. 1979) to obtain a single estimate of water flux for the entire watershed at each depth and each 3-wk interval. To estimate flux of each substance during the 3-wk interval, we multiplied water flux by concentration.

The hydrologic model calculated water flux only at 100-cm depth. Water flux over the 3-wk intervals was assumed to be the same at 200 cm as at 100 cm because little rooting occurred below 100 cm at WS-10 (Santantonio et al. 1977). Because three-quarters of the fine roots were in the top 30 cm of the soil in a nearby Douglas-fir stand (Santantonio 1979), we calculated water flux at 30 cm assuming that three-quarters of the transpirational water loss at WS-10 occurred in the top 30 cm of soil.

We used simulated rather than measured water volumes because we were confident that the hydrology model correctly estimated water flux over 3-wk intervals. The measured volumes may have been subject to systematic errors (Cochran et al. 1970) and may not accurately have reflected the water flux. A major problem appears to be that large amounts of water move downward through macropore channels, rather than through the bulk soil in saturated or unsaturated flow (Beasley 1976, De Vries and Chow 1978). Because the lysimeters occupied but a small fraction of the land area, it is likely that the channelized flow was not sampled adequately and that the measured volumes were systematically low. Although the hydrologic model did not consider channelized flow explicitly, it was adjusted to predict streamflow correctly over the 3-wk intervals. Hence the volumes based on it should be more reliable than the measured volumes.

Because channelized flow was not sampled adequately, an additional error may have occurred. Element concentrations would be expected to be low in rapid-flowing water of short residence in the soil, hence all of our concentration data may be overestimates. However, given the complex soil structure and topography at WS-10, there may be no way to correct concentration data for this effect.

Fluxes at each location and depth were summed over the study period and divided by total simulated water volume (Fig. 1) for the study period to produce a weighted mean for each location and depth. Values

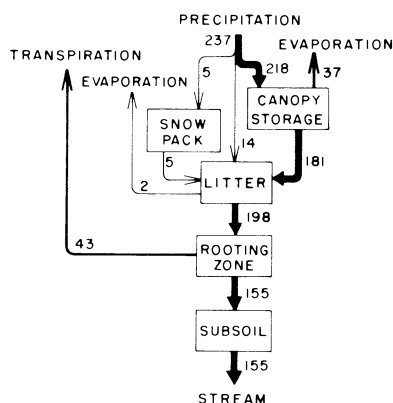


FIG. 1. Hydrologic budget for Watershed 10 based on data of Rothacher et al. (1967) and Harr (1977) and on computer simulations (Sollins et al. 1979). Values are centimeters per year. Thickness of arrow is proportional to flux.

for the plates in Table 1 are means of the two locations. The cup data required a more complex procedure because results seemed to be affected by the type of sand used to backfill holes. Cation values differed most, the higher values coming from the cups installed with coarse sand. Comparing values for cups at 2.0-m depth with those for seeps (discussed later), we found that seep (spring) values were consistently intermediate between values for coarse sand and fine sand cups. We decided that cups installed with the two sand types were sampling water of different residence time in the soil but that both "types" of water entered the groundwater and contributed to streamflow in roughly equal proportions. Consequently we chose to give equal weight to data from cups of each sand type. We first averaged the weighted means from the three locations along the slope transect (coarse sand). The resulting arithmetic mean was then averaged with the weighted mean for the control site (fine sand) to produce the values shown in Table 1.

We also sampled water from seven seeps (springs) along the stream at WS-10 every 3 wks in conjunction with the soil solution sampling and at more frequent intervals during major storms. The values reported in Table 1 are unweighted means and tend to emphasize periods of high flow because sampling was more frequent during storms and because many of the seeps were intermittent and could not be sampled during dry periods. Values for seeps are therefore not strictly comparable to others in Table 1 and are included only to illustrate in general the water chemistry profiles on the watershed.

Standard errors of estimate reported in Table 1 were calculated two different ways depending on position in the profile. Precipitation and stream chemistry were measured at only one point on the watershed; the weighted means in Table 1 are means over time alone, not over space, and the standard errors of estimate are based on all 3-wk interval data summed without

weighting. Throughfall was measured at 54 locations on the watershed. Averages were calculated for the entire preclear-cut period at each location using measured volumes as weighting factors; then the location means were themselves averaged and a standard error calculated. Consequently, these standard errors reflect only variability in space, not variability in time. Litter solution data were treated identically although only two locations were sampled. For the seep concentrations, unweighted means were calculated first for each location and then these were averaged and standard errors calculated. Standard errors of estimate reported for the cup data (Table 1) were calculated by summing over all locations regardless of installation procedure. They therefore reflect two sources of variability in the data and are larger than those for the plate and throughfall data.

Particulate input and export

Input of N and P in dust in a clear-cut near WS-10 averaged $0.61 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for October 1970 to October 1973 and $0.14 \text{ kg P} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for October 1971 to October 1973 (Fredriksen 1975). Export of fine suspended particles across the weir at WS-10 averaged $0.61 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ and $0.05 \text{ kg P} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Fredriksen 1975). Particulate input and export of cations was not measured. Ideally, element export in all particle size classes (not just suspended particles) should have been considered, but this was beyond our resources.

Element accumulation in vegetation

Requirements for growth of stems, branches, roots, and new foliage were calculated from measured concentrations of each element in each plant component for each major species on the watershed. The trees were selected by species and diameter class in the same proportion in which they occurred at WS-10 (Gholz et al. 1979). Branches from each tree were selected randomly from the top, middle, and bottom of the canopy. All new foliage, old foliage, and twigs (current elongation) were removed and combined into single composite samples which were subsampled for element analysis. At the same time, samples were taken of stem wood, stem bark, branch wood plus bark, and large roots ($>5 \text{ mm}$). Concentrations in Table 2 are means by component of all trees sampled ($\pm 1 \text{ SE}$). The standard error of estimate for the dry mass values in Table 2 was computed by summing across the five community types described by Grier and Logan (1977).

Fine roots at WS-10 were sampled extensively by Santantonio et al. (1977) but were not analyzed for Mg. We obtained new subsamples from their cores, which we analyzed as described. Our values for N, P, K, Ca, and Na were almost identical to theirs although analytical procedures were for the most part quite different. To analyze variability, we grouped cores from three parts of the watershed: dry, moderate, and

TABLE 2. Mean element concentrations (percent of the element on a dry mass basis) in vegetation. Values based primarily on data collected during late October from the H. J. Andrews Experimental Forest near WS-10; SE in parentheses.

Substance	Current year foliage	Old foliage	Boles, branches, twigs	Large roots (>5 mm diameter)	Fine roots* (≤5 mm diameter)	Epi-phytes†
Dry mass (Mg/ha)‡	3.1	10.8	704.5 (87.9)	141.3 (17.1)	11.3 (1.8)	—
N	1.07 (0.09)	1.03 (0.05)	0.056 (0.001)	0.090 (0.007)	0.62 (0.05)	1.73
Na	0.013 (0.001)	0.011 (0.001)	0.0048 (<0.001)	0.003 (0.001)	0.002 (0.001)	—
K	0.84 (0.04)	0.50 (0.03)	0.022 (0.001)	0.030 (0.002)	0.17 (0.03)	0.57
Ca	0.39 (0.03)	0.82 (0.08)	0.091 (0.003)	0.148 (0.010)	0.69 (0.09)	0.17
Mg	0.11 (0.01)	0.11 (0.01)	0.012 (<0.001)	0.031 (0.001)	0.12 (0.01)	0.030
P	0.22 (0.02)	0.24 (0.01)	0.008 (<0.001)	0.008 (<0.001)	0.10 (0.02)	0.24

* Based on soil cores from WS-10 at HJA (Santantonio et al. 1977).

† Data for *Lobaria oregana* at WS-10 (Pike 1978).

‡ From Grier and Logan (1977).

moist. Values in Table 2 are averages across the three habitats weighted in proportion to habitat area. Standard errors were calculated without weighting factors.

Net annual accumulation of each element, calculated by multiplying organic matter accumulation in each compartment (Fig. 2) by the appropriate concentrations, is shown circled in Fig. 3. Fine roots and foliage were assumed to be in steady state (see Grier and Logan 1977).

Litterfall and root death

Five components of litterfall were considered separately (Table 3): needles, broadleaves, fine woody litter (twigs, bark, branches, cones), coarse woody litter, and microparticulate matter (mainly frass, pollen, and lichen fragments).

Litterfall other than coarse wood and microparticulate matter was collected by Grier and Logan (1977) with 54 traps (0.26 m²) placed at regular intervals on the watershed. They divided the watershed into five habitat types and allocated traps to each type in proportion to its area. Litter traps were lined with nylon fabric (≈0.1-mm mesh) and emptied every 4 wk. Material was sorted into six categories: needles, broad leaves, fine wood, reproductive parts, live foliage, and other material (epiphytes, frass, and unidentifiable fragments). Composite samples consisting of all material from each category and habitat type were analyzed for elements. Dry mass and element amounts were summed for each category and habitat type over the study period. Dividing element amounts by dry masses gave weighted mean concentrations for each habitat type which we averaged to give the values in Table 3. Standard errors in Table 3 represent variation among habitat types, not variation over time. Dry mass of leaf fall was measured for two consecutive years (Grier and Logan 1977). Yearly totals (including green foliage) differed from the 2-yr average by <1%.

Input of coarse wood (material >15 cm diameter) was estimated from a 2-yr record of live stem mortality on WS-10 (Grier and Logan 1977). To calculate element transfers, we multiplied their value for organic

matter transfer by measured concentrations in the live branch-plus-bole category (Table 3). Standing dead material was included in the fallen log compartment in order to simplify presentation of the budgets.

Epiphytic litterfall was not separated, but Grier and Logan (1977) estimated that it accounted for ≈10% of the material in their "other" category. Based on population estimates at WS-10 (Pike 1978), the cyanophyllous lichen *Lobaria oregana* (Tuck.) Müll. Arg. should have accounted for most of the 10%.

Microparticulate litterfall (microlitterfall) was measured at WS-10 in a detailed study by G. Carroll and L. Pike (University of Oregon, *personal communication*). They estimated that small particles in throughfall amounted to 50–150 kg·ha⁻¹·yr⁻¹. We used an intermediate value of 140 kg·ha⁻¹·yr⁻¹ for total microlitterfall beneath the WS-10 canopy. We lumped approximately 100 of their microlitterfall samples to provide nine samples for total N analysis and three samples for analysis of other elements (Table 3).

Much material is leached initially from the cyano-

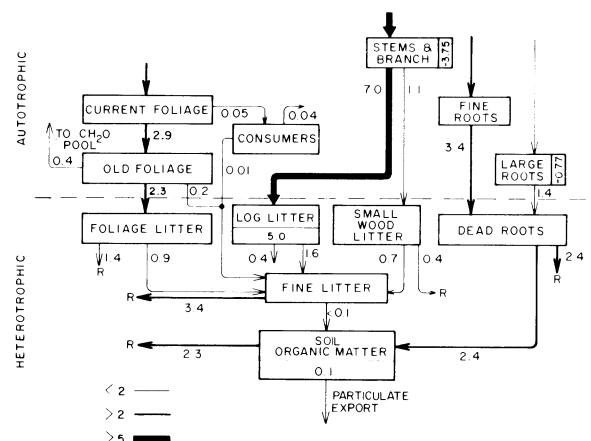


FIG. 2. Organic matter budget for WS-10 (after Grier and Logan 1977). R indicates respiration. Values in small rectangles are annual accumulation. All values are Mg dry mass·ha⁻¹·yr⁻¹. Thickness of arrow is proportional to flux.

TABLE 3. Element concentrations (percent of the element on a dry mass basis) in litterfall. Unless otherwise noted, data are from Watershed 10 for June 1973–1975; SE (among habitat types) in parentheses.

Substance	Needle*	Broad leaf	Average woody†	Other‡	Micro-particulate§
Dry mass ($\text{Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$)	1.86 (0.26)	0.48 (0.05)	1.12 (0.08)	0.41 (0.05)	0.14
N	0.46 (0.02)	0.46 (0.04)	0.34 (0.02)	0.69 (0.07)	1.75 (0.21)
Na	0.01 (0.002)	0.009 (0.002)	<0.005	0.008 (0.002)	0.21 (0.03)
K	0.22 (0.01)	0.30 (0.02)	0.11 (0.01)	0.11 (0.01)	0.10 (0.02)
Ca	1.16 (0.03)	1.39 (0.20)	0.50 (0.02)	0.39 (0.03)	0.28 (0.03)
Mg	0.081 (0.005)	0.20 (0.02)	0.034 (0.003)	0.049 (0.007)	0.42 (0.11)
P	0.16 (0.02)	0.088 (0.023)	0.045 (0.017)	0.077 (0.005)	0.19 (0.04)

* Includes green foliage.

† Weighted average of concentrations in cones, bark, twigs, and small branches.

‡ Mainly frass, bark fragments, bryophytes, and lichens.

§ Data for microparticulate matter in dryfall and throughfall beneath the canopy of WS-10 (G. Carroll and L. Pike, *personal communication*).

phycophilous lichens, such as *Lobaria* (Cooper and Carroll 1978, Pike 1978), and immobilized by canopy bacteria (Bernstein and Carroll 1977) which then form a major component of microlitterfall. This can be true for any element, and we must recognize that any material in microlitterfall may derive from epiphytes or from rooted plant tissues (e.g., foliage, bark, and twigs), either of which may have obtained it in turn from the atmosphere or the rooting zone. For all elements but N this phenomenon creates no problem because all input in precipitation, and (to the extent it was measured) in dryfall, already appears in the throughfall transfer. Any additional material in the throughfall must at some point have been transported from the rooting zone to the canopy. Lacking data, we assumed that half of the cations and P in microlitterfall was of epiphytic origin and half of foliar origin. We added the epiphytic component to the value for epiphyte material collected in litter traps to give the values for total epiphyte fall (Fig. 3). Alternative assumptions are discussed later.

The N cycle is more complicated. The N in microlitterfall or throughfall may have been transported to the canopy from the rooting zone, or it may be atmospheric N fixed in the canopy. To calculate N fixation in the canopy, we assumed that half was fixed, half transported from the rooting zone. Effects of alternate assumptions are discussed later.

We assumed that 30% of the fine roots died annually and that large roots (>5 mm diameter) died only when whole trees died (cf. Grier and Logan 1977). Element concentrations in large roots were determined from samples taken either on or near WS-10 (Table 2).

Forest floor components

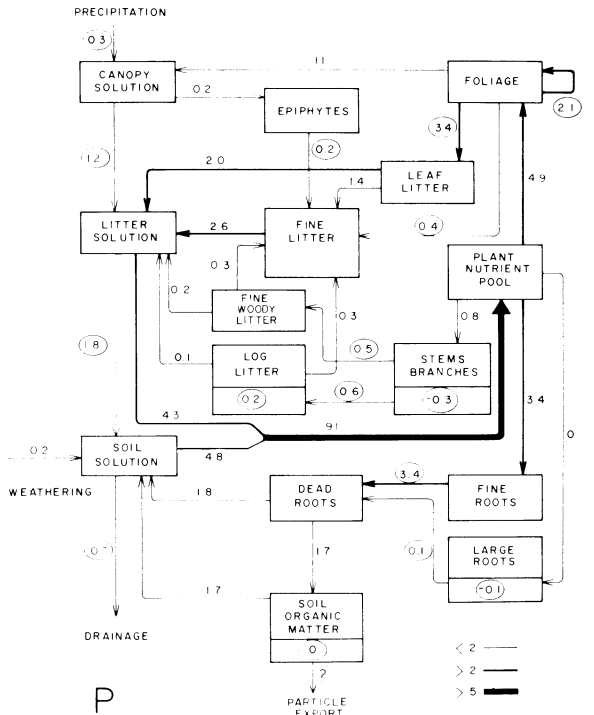
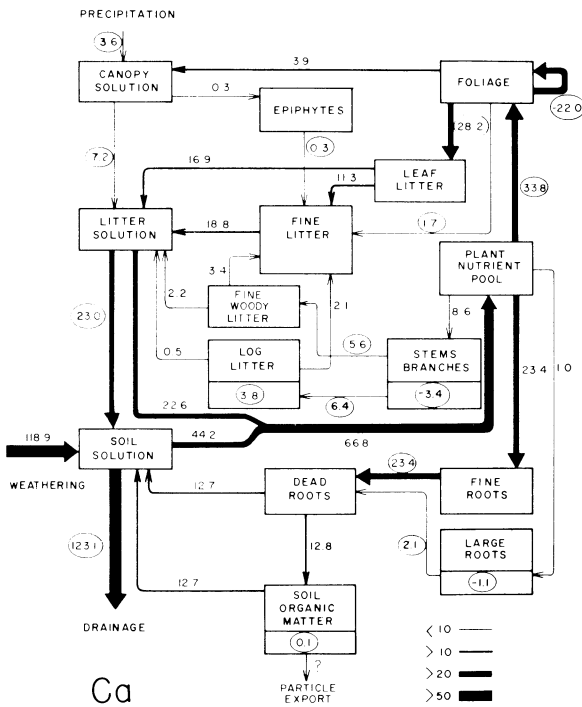
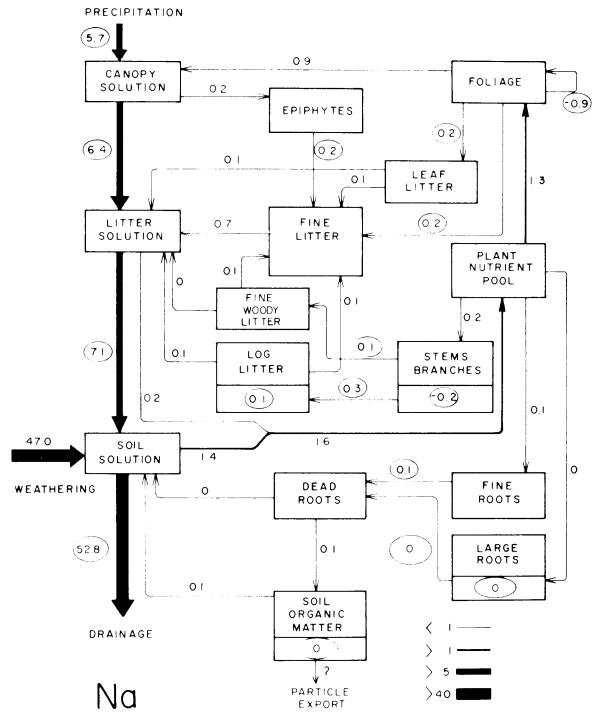
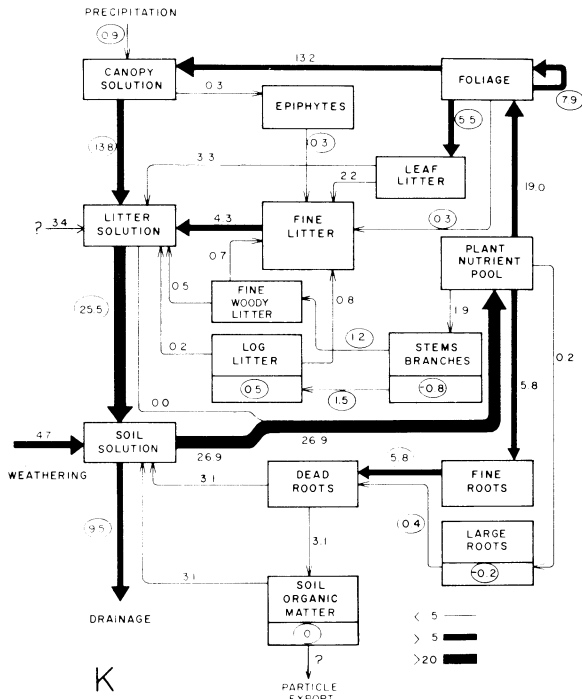
Element content of the forest floor other than logs (Table 4) is based on analysis of 52 circular samples (30 cm diameter) taken at regular intervals on WS-10. Total forest floor dry mass (excluding logs) was 51.2 Mg/ha (Grier and Logan 1977), which we apportioned into foliage litter (28%), fine woody litter (38%), and

fine litter (34%; fragments of unidentifiable origin) based on a detailed sort of 1-m² samples from a nearby old-growth stand (M. Ogawa and R. Fogel, *personal observation*). Concentrations in fallen logs (defined as woody debris >15-cm diameter) are means of samples from 61 logs from a midelevation stand of old-growth Douglas-fir at HJA (P. MacMillan, J. Means, and K. Cromack, Jr., *personal observation*).

To calculate rates of organic matter accumulation in the foliage litter and fine woody litter, we first calculated steady state levels of these compartments using the relation $X = L/k$ (Jenny et al. 1949), where X is the steady state pool size, L is measured annual litterfall of that type (Table 3), and k is the decay rate constant (per year). Rate constants for decay of foliage and fine woody litter were measured near WS-10 by Fogel and Cromack (1977). We used the measured rate constants and litterfall rates to calculate steady state values for these pools which we then compared with measured values for WS-10. Pool sizes so estimated were within measurement error of those predicted with the steady-state relation, which confirms our hypothesis that these compartments were indeed in steady state.

To estimate annual organic matter accumulation in fallen logs, we used a decay constant of 0.009/yr, intermediate between 0.012/yr reported for a coastal hemlock-spruce forest (Grier 1978) and 0.006/yr for a midaltitude Douglas-fir stand (P. MacMillan, J. Means, and K. Cromack, Jr., *personal observation*). This gave a dry matter transfer rate from the log compartment of $\approx 2.0 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. Subtracting this from the current input of $7.0 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ gave a dry matter accumulation rate of $5.0 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, which we multiplied by measured concentrations in fallen logs (Table 4).

Though the fallen log compartment was increasing in mass, we felt that this was a comparatively recent phenomenon and that log decay would not yet be providing input to the fine litter compartment. Consequently, because foliage and fine woody litter were in



steady state. we assumed that fine litter would be also. We had no data available on the dynamics or size of the dead root compartment but assumed it to be in steady state with respect to dry mass and the elements of interest.

Soil organic matter

Soil organic matter in this paper means organic matter other than roots in the mineral soil rooting zone to a depth of 100 cm. This zone was sampled at eight

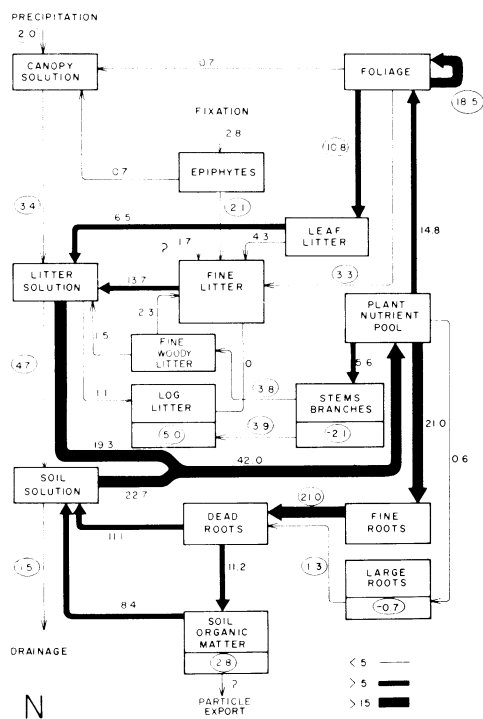


FIG. 3. Element budgets for WS-10. Values are kilograms per hectare per year. Circled values were calculated independently; others were calculated by difference from other fluxes (see text). Values in small rectangles are annual accumulation. Standing amounts are not shown. Thickness of arrow is proportional to flux.

locations on WS-10 by Grier and Logan (1977) and at seven additional locations by R. L. Fredriksen (*personal observation*). In both studies, samples were sieved through 2-mm mesh screens and all recognizable roots removed. After correcting for stone content, Grier and Logan's value for the 1-m profile was 1.13%, Fredriksen's $1.52 \pm 0.17\%$. We used the mean

of 1.33% for our budget calculations. Total (Kjeldahl) N was also determined by Fredriksen; mean for the seven pits was 0.053%. As part of a separate study of seasonal variation, D. G. Moore and F. M. McCorison (*personal observation*) collected 568 soil cores at 3-wk intervals (May 1973–1975) near two of the lysimeter sites on WS-10. We analyzed the cores for exchangeable cations and extractable P, and corrected the results for stone content (Table 4).

In order to include information on element accumulation in soil in element cycle budgets, we must define the system carefully in both space and time. Simply setting the system boundary at the bottom of the rooting zone or at the saprolite-bedrock contact is insufficient because some of the material in the regolith (soil plus saprolite) derives directly from the bedrock without having ever entered solution. Such "inactive" material has had no opportunity to cycle through the vegetation, at least not since the present bedrock was formed. Because this material has not participated in the element cycles, we wanted to exclude it from the budgets reported here, even though it may be accumulating in the regolith or exported from a watershed in particulate form. Primary minerals such as quartz and feldspar clearly fall into this category, as do many secondary minerals, including most clays. However, cations sorbed on clay surfaces may have been in solution and consequently may have cycled through the vegetation.

To construct annual budgets, we assumed that all N was "active" in the sense that it had accumulated as a result of cycling processes, though much may not have been immediately available to vegetation. We assumed that extractable P constituted the "active" pool of that element. We included only exchangeable cations in the pool, though this clearly underestimated the pool size. For example, cations in the lattice structure of clays may have been in solution when the clays were formed but certainly were not extracted with our

TABLE 4. Element concentrations (percent of the element on a dry mass basis) in detrital components and bedrock. Data are from WS-10 unless otherwise noted; SE in parentheses.

Substance	Fallen logs*	Fallen foliage and fine woody litter	Soil organic matter† (0–100 cm depth)	Bedrock‡
Dry mass (Mg/ha)§	215 (103)¶	51.2 (5.4)	133	...
N	0.10 (0.01)	0.50 (0.02)	2.8 (0.2)	...
Na	0.0024 (0.0003)	0.014 (0.001)	0.0017 (0.00004)	2.68
K	0.011 (0.001)	0.11 (0.005)	0.025 (0.0005)	1.36
Ca	0.076 (0.010)	0.87 (0.04)	0.077 (0.002)	1.96
Mg	0.0076 (0.0009)	0.26 (0.02)	0.020 (0.0007)	1.42
P	0.0031 (0.0005)	0.098 (0.004)	0.0057 (0.0002)	0.053

* Data for a midaltitude Douglas-fir stand at HJA (P. McMillan and J. Means, *personal communication*). Weighted mean of their decay classes 2–4. Wood only; bark not included.

† Cations and P are extractable forms only. Element concentration expressed as percent of organic matter (see text).

‡ Weighted mean of three locations at WS-10 (James 1977).

§ Data from Grier and Logan (1977) except for soil organic matter.

¶ Includes standing dead wood (24.6 Mg/ha).

procedure (ammonium acetate at pH 7). Kinetic extraction procedures have been proposed that might better define this "active" pool (Thompson et al. 1977, Talibudeen et al. 1978).

We next considered the rate at which these "active" forms might be expected to accumulate in the soil at WS-10. In most areas, erosional processes, some operating continuously over long periods of time, others at infrequent, irregular intervals, dominate the balance between input and loss to the "active" soil compartments and create a spatial mosaic so complex as to be indecipherable. A site more complex than WS-10, with its deep ridgetop soils, midslope rock outcrops, and intrusive dikes, would have been hard to find. Nonetheless, we did want to establish a value for the accumulation rate in order to carry through the process of budget construction, and illustrate some of the problems that must be addressed.

In contrast to WS-10, an unusual quirk of topography at Mt. Shasta, California creates an ideal situation in which to study soil development and organic matter accumulation. At Mt. Shasta, ≈ 250 km to the south of WS-10, large masses of loosely consolidated, volcanoclastic tuff and breccia have sloughed off into a gully at irregular intervals and have flowed onto the surrounding alluvial plain. These mudflows (lahars) have followed similar paths, each flowing either onto or alongside its predecessors. Dickson and Crocker (1953, 1954) studied soils developed along an elevational contour across five flows that are at or near the present soil surface. The sites are all of gentle slope, and erosion is minimal. Climate and parent material are virtually identical across the sequence, and soils are quite uniform within each flow. Sites differ only in vegetation and, of course, age. Because of similar parent material, soils of the oldest flow (1200+ yr) are mineralogically similar to those at a geomorphologically stable site near WS-10 (G. Spycher, Oregon State University, *personal communication*).

The 205-yr and 566-yr-old flows appeared at first to offer the best basis for extrapolation to WS-10 because the vegetation on these flows most closely resembled the 350- to 550-yr-old stand at our watershed. The accumulation rate based on these flows was ≈ 0.2 Mg·ha⁻¹·yr⁻¹. If this were to hold true at WS-10, the 130 Mg/ha present there now would have required <1000 yr to accumulate. This is unreasonable in the sense that there is no evidence of recent glaciation in the vicinity of WS-10 (Swanson and James 1975) and therefore soils should have had much longer than 1000 yr in which to develop. However, such a high accumulation rate may be very reasonable in the sense that erosional processes, nearly absent at the gently sloping Mt. Shasta mudflows, are important at WS-10 and undoubtedly cause rapid removal of soil organic matter, perhaps almost as fast as it is formed. F. Swanson (United States Forest Service, *personal communication*) has estimated that episodic and continuous ero-

sion processes account for export of ≈ 70 kg·ha⁻¹·yr⁻¹ of organic matter, but he acknowledged that his estimate could be in error by at least a factor of two. It is equally likely that respiration rates are greater at WS-10 because of warmer temperatures, particularly in the winter. Unfortunately there does not seem to be a good method for measuring directly the accumulation rate at WS-10. The value of 0.2 Mg·ha⁻¹·yr⁻¹ is therefore probably best thought of as an upper bound on a value for gently sloping terrain in the Cascade Range.

We are presently analyzing the export data for WS-10 systematically and studying rates of root turnover and decomposition, which may enable us to estimate the soil organic matter (SOM) accumulation rate by difference. We are also engaged in an intensive study of the Mt. Shasta flows in order to document better the accumulation rate there and to obtain a better basis for extrapolation to WS-10. In the meantime, we chose to use a value of 0.1 Mg·ha⁻¹·yr⁻¹ for WS-10 to try to take into account more rapid respiration there, but we want to emphasize that most of this organic matter does not actually accumulate but is exported from the watershed in particulate form (Fig. 3). We would like to have included particulate export in the budget but this was not practical. Swanson's estimate was not strictly relevant because it referred to export across the weir, whereas the system boundary in our budget analysis was at the bottom of the rooting zone. Furthermore, particulate forms can enter the stream channel by a variety of processes and can include fresh foliage and litter, as well as soil material. These components originate from different compartments in our model, and separate treatment of the fluxes was vastly beyond the scope of this project.

Although we now had established a rate of organic matter accumulation, the next problem was that organic matter does not account for all of the "active" material in the soil. Specifically, large amounts of cations can be adsorbed on mineral surfaces in readily exchangeable forms. Consequently we must first establish how fast the amounts of cations on mineral exchange sites are accumulating and then partition the exchangeable cations between those on mineral and those on organic exchange sites. The first question was disposed of by assuming that soils at WS-10 were old enough so that amounts of mineral surface exchange sites were not increasing. However, if erosion is as rapid at WS-10 as we suspect, this assumption may be invalid. We next apportioned cation exchange capacity (CEC) between organic matter and minerals using measured values for clay, silt, and organic matter content at three locations at WS-10 (R. Brown, *personal communication*) and a CEC of 150 meq/100 g for organic matter and 35 meq/100 g for clay plus silt (Pratt 1961, Helling et al. 1964). From these data we calculated that 4–23% of the CEC in the top 100 cm of the soil was attributable to organic matter. The mean was

10% which seemed reasonable given the large clay content and relatively low organic content of the soil at WS-10. We multiplied our values for exchangeable cations by 0.10 and then divided the corrected cation values, and our measured concentrations of Kjeldahl N and extractable P, by organic matter concentrations to give element concentrations in the SOM alone (Table 4). We then multiplied these by the assumed rate of SOM accumulation ($0.1 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) to get the values shown in Fig. 3.

ELEMENT BUDGETS

The analysis we have described provided the circled numbers in the budget diagrams (Fig. 3). The remaining transfers were calculated by difference, on the principle that input less accumulation equals loss.

Metallic cation and P budgets

Procedures were identical for P, K, Ca, Mg, and Na. The N budget required a different procedure.

Element cycling processes in the canopy were considered first. We assumed that element return in epiphyte fall to the forest floor was balanced by uptake from the canopy solution. We added uptake by epiphytes to element outflow in throughfall and subtracted input in intercepted precipitation to give net input to the canopy solution from leaching of foliage. Next, we calculated element transfers to the foliage compartment from the plant element pool as the sum of leaching, microparticulate loss, and leaf fall. The four transfers from the plant element pool (Fig. 3) were summed to give the total required uptake from litter and soil solution. Redistribution from old to new foliage was computed by first calculating requirements for current foliage production and then subtracting transfers out of foliage in leaf fall, microlitterfall, and leaching.

Having established that the foliage litter and fine woody litter compartments were in steady state with respect to organic matter and assuming this for the dead roots, we reasoned that these compartments would also be in steady state with respect to each element. Overall transfer out was set equal to input. Element transfer from logs to fine litter and litter solution was calculated as input less accumulation.

We apportioned transfer from each detrital compartment (Fig. 3) between the processes of fragmentation and net mobilization (net release into solution). The apportionment varied with the substrate; percentage loss due to fragmentation was assumed to be lowest from the more finely textured substrates. Fragmentation was assumed to account for 40% of total loss from foliage litter, 60% from fine woody litter, 80% from log litter, 0% from fine litter and soil organic matter, and 50% from dead roots.

These percentages vary considerably among elements and could have been treated in more detail; for example, K is mobilized more readily from all of these substrates than is Ca (Grier 1978, Lousier and Parkin-

son 1978, Sollins et al., *in press*). Probably these ratios are overestimates for the covalently bonded elements such as N and S and underestimates for the mobile cations such as K and Na. However, these ratios are not overly important for constructing annual budgets. If the only significant loss from the litter results from uptake and transport out of the solution compartment, any material not accumulating in the litter must enter solution eventually. The ratio of fragmentation to mobilization affects only the route taken by this material, not its ultimate destination. However, to model short-term dynamics, the two processes, fragmentation and mobilization, must be quantified and predicted (Hunt 1977, Aber and Melillo 1980). Decomposition studies in progress should provide better estimates of ratios of mobilization to fragmentation through simultaneous measurements of mass and element loss from logs and litter.

It is important to note that these transfers from detrital to solution compartments are net transfers, representing the difference between "mineralization" and immobilization. The term "net mineralization" has been used frequently by soil scientists and microbial ecologists. We prefer the term "net mobilization." Geochemists find it hard to understand the term "mineralization" when no minerals are involved, and the term seems particularly inappropriate at WS-10 where, judging by the amount of organic N in solution, much of the material is released as soluble organic compounds.

Elements may be transferred in particles from litter to soil to subsoil as a result of water flow (illuviation), movement of organisms (bioturbation) and "root throw." Illuvial transport of particles is important in coarse-textured, sandy spodosols (Ugolini et al. 1977) but would probably not be as important in the more clayey soils at WS-10. Likewise, because earthworms are not abundant at WS-10, bioturbation should not be important.

In eastern forests, root throw is an important process by which soil is mixed and litter is incorporated into the mineral soil (Denny and Goodlett 1956, Stone 1975). It should be even more important under conifers which, because of their broad, shallow root systems, frequently tip rather than snap. If the coarse root system of a typical old-growth tree covers 10 m^2 , and if one such tree per hectare tipped over every 10 yr, the entire soil mantle would turn over to the rooting depth (1 m at WS-10) every 10 000 yr. However, none of these mixing processes appeared to be very important at WS-10 on an annual basis. Consequently, in the element cycle budgets reported here, we ignored particulate transfers and accounted for transfer downward of dissolved forms only.

On the assumption that fine litter was in steady state, we computed net release from fine litter to litter solution by difference. We next summed all flows into the litter solution compartment and compared the re-

sult with loss measured by the plate lysimeters. For most elements, the difference was positive and large (70% of input for P, 50% for Ca, and 20% for Mg); that is, loss from litter solution was less than total input to it. The difference was ascribed to uptake from the litter solution by the vegetation. (Note that transfers from litter components to the litter solution are net transfers; uptake by microflora has been subtracted.)

The difference was very small for Na and negative for K, both highly mobile elements. Measured solution transport of K out of the litter exceeded known input by 15%, and we set uptake from the litter by vegetation to zero and assumed that the excess outflow was balanced by an unknown input into the litter solution. The discrepancy may be a result of overestimation of the concentration values, as we have discussed. The discrepancy was small in view of the fact that concentrations of all cations varied over an order of magnitude during a year, and that weighted averages varied from year to year by $\approx 20\%$ of their long-term means.

To complete the budgets, we assumed the dead root compartment to be in steady state and calculated transfer to soil organic matter by difference. Loss from soil organic matter was assumed to be entirely from leaching. Only the weathering transfer remained (net release to solution from primary and secondary minerals in the rooting zone only), which we calculated as balancing other inputs to and outputs from the soil solution.

Nitrogen budget

The N budget (Fig. 3) is unique. Nitrogen alone is fixed by canopy epiphytes in large amounts (Pike 1978). Weathering of soil minerals, although an important input of metallic cations, provides no significant N input, and the reverse flow, net transfer from solution to solid phase minerals, does not appear to be important.

To construct the N budget, we first compared the amount entering the canopy solution (intercepted precipitation) with the amount exiting in throughfall. Because of leaching from the canopy, the amount exiting was consistently slightly greater. By the same reasoning we used in partitioning microlitterfall, we assumed that half of the leaching was from lichens and half from foliage. We then calculated fixation by epiphytes ($2.8 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) by adding together epiphyte fall and leaching from epiphytes to the canopy solution. Procedures for completing N transfers in and out of foliage, other vegetation compartments, and all detrital compartments except fine litter were the same as for other elements. For the N budget, in contrast to budgets of the other elements, we could assume that weathering did not result in N input to the soil solution, and we could calculate uptake by vegetation from that compartment by difference ($22.7 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$). Subtraction of this from the total uptake requirement

of $42.0 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ gave $19.3 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ uptake from the litter solution. We then calculated N transfer from decomposing fine litter to litter solution by difference. This left a $1.7 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ N deficit in the fine litter, which we balanced with a corresponding input to the fine litter from an unknown source (Fig. 3). (The choice of fine litter as the recipient compartment was arbitrary; any of the litter compartments could have been used.) This deficit is a consequence mainly of the large value for N accumulation in fallen boles. Most of the dry mass accumulation appeared to be occurring in the least decayed classes of logs. For example, if we multiplied the annual dry mass accumulation by N concentrations in fresh logs, the N accumulation in fallen boles would be reduced by $2.8 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ and the N deficit in the fine litter would disappear.

DISCUSSION

In computing transfers and constructing budgets for N, P, and four major cations, we made a series of assumptions. The assumptions are reasonable and constitute our best attempt to estimate transfers and accumulations that we were unable to measure. Their justification presented, what concerns us here is their effect. (The last assumption does not influence the discussion but was made simply to aid in preparing the budgets.)

- 1 No elements were taken up by vegetation from below 100 cm in the mineral soil.
- 2 Organic matter in dead root and fine litter compartments was in steady state.
- 3 Thirty percent of the fine roots ($\leq 5 \text{ mm}$) died back annually.
- 4 Large roots died only when entire trees died.
- 5 Half of the microlitterfall was of epiphytic origin, half of foliar origin.
- 6 Ten percent of the exchange capacity of the soil was attributable to organic matter, 90% to clays and other minerals.
- 7 Amounts of cations on mineral exchange sites did not increase from year to year.
- 8 Soil organic matter was accumulating at a rate of $0.1 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$.
- 9 Mixing of litter and mineral soil was negligible on an annual basis.
- 10 Half of the N leached from the canopy was of epiphytic origin, half of foliar origin.
- 11 There is no net N transfer between the soil mineral phase and the soil solution.
- 12 The ratio of net mobilization to fragmentation was the same for each element in a given substrate.

Solution transport processes

Concentrations in precipitation on WS-10 were low (0.023 meq/L) compared with those at most other sites. Moodie (1964) reported that in Washington total cation concentrations (Na, K, Ca, and Mg) were 0.142

meq/L during 1963, but many of his collection stations were in urban areas. Johnson (1975) found 0.095 meq/L total cations in rainfall at the Thompson Research Center in western Washington during 1973; the value included Mn^{++} , which we did not measure. The Thompson Research Center is ≈ 50 km downwind from an industrial area (Tacoma and Seattle) where higher concentrations would be expected. About 40 km northeast of Seattle, out of the zone of urban influence, Dethier (1979) found an average concentration of 0.017 meq/L. His values for Ca and Mg were about half of our values and his value for K nearly double. Even in the heavily industrialized northeast United States, metallic cation concentrations in precipitation averaged only 0.019 meq/L (Likens et al. 1977). However, H^+ and sulfate concentrations there were considerably higher and bicarbonate concentrations much lower than at WS-10.

Our weighted average concentration of total N (nitrate plus Kjeldahl N) in throughfall was 0.17 mg/L, almost identical to that reported by Tarrant et al. (1968) for a young hemlock-spruce stand at the Oregon coast. At a 37-yr-old Douglas-fir stand at the Thompson Research Center, N transfers in throughfall and stemflow totaled $1.7 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Cole et al. 1967), half the WS-10 value. Cole's values for K and Ca (12.3 and $4.6 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) were similar to ours (13.8 and $7.2 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$). Mg and Na were not reported. Johnson (1975) presented more recent throughfall data for the same stand; total cation concentration was 0.10 meq/L, slightly higher than that for WS-10 (0.06 meq/L).

At WS-10, annual transfers in litter leachate were 4.7, 1.8, 25.5, 23.0, 5.5, and $7.1 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for N, P, K, Ca, Mg, and Na (Fig. 3). At the Thompson site during 1964–1965, corresponding values for N, P, K, and Ca were 4.8, 0.95, 10.5, and $17.4 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, generally lower except for N. Grier and Cole (1972) remeasured litter leachate on the Thompson site in 1970–1971 and reported values for K, Ca, Mg, and Na of 26.0, 38.7, 11.0, and $21.9 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. K and Ca transfers more than doubled between measurements, perhaps from increased input to the forest floor in throughfall and litterfall. Cation transfer (K, Ca, Mg, Na) in litter leachate at the Thompson site in 1970–1971 was $4470 \text{ eq} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$; the WS-10 value was $2570 \text{ eq} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. Cations in leachate at two adjacent Douglas-fir plots at the Thompson site averaged 0.43 and 0.19 meq/L (Johnson 1975); the WS-10 value was 0.13 meq/L. At the Coweeta Experimental Forest in North Carolina, average weighted cation concentration (K, Ca, Mg, Na) in litter leachate was 0.39 meq/L on a white pine watershed and 0.31 meq/L on a hardwood watershed (Best and Monk 1975), both greater than the WS-10 value of 0.13 meq/L.

WS-10 values for solution transport of N, P, K, and Ca from (surface) soil to subsoil were 1.5, 0.7, 9.5, and $123.1 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Fig. 3). Values for the Thomp-

son site were much lower: 0.6, 0.02, 1.0, and $4.5 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Cole et al. 1967). Johnson (1975) reported cation concentrations totaling 0.25 meq/L, confirming these low values. The average total concentration was 0.61 meq/L at WS-10. Differences probably result from more rapid weathering of metallic cations (particularly Na and Ca) from volcanoclastic parent material at WS-10 (Table 4) than from granitic and acid-metamorphic parent material at the Thompson site.

Average cation concentrations in subsoil solution at WS-10 totaled 0.59 meq/L, higher than the 0.24 meq/L at the Thompson site (Johnson 1975). Total N transfer from subsoil to groundwater at WS-10 ($1.2 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) was also somewhat higher than the loss of $\approx 0.6 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ to groundwater at the 37-yr-old Thompson stand (Cole et al. 1967).

Concentrations at the WS-10 weir were compared with published values for other sites by Fredriksen (1975) and Henderson et al. (1978). Since then, Feller (1977) and Feller and Kimmins (1979) have reported export from a watershed in British Columbia forested by young hemlock and Douglas-fir. N (nitrate + ammonium only), K, and Ca were exported at rates of 0.6, 1.4, and $19.8 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. Exports from WS-10 were 0.8 (total N), 5.4, and $49.6 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. The hemlock stands were located on glacial till and outwash overlying acid igneous bedrock, where cation export would be much lower. The lack of organic N data from the British Columbia site precludes comparison of total N export.

These comparisons are only valid to the extent that weighted averages and fluxes were calculated the same way in all element cycle studies. Our results depend on assumption 1, and all the assumptions made in constructing and validating our hydrologic model. We also tried calculating simple arithmetic averages of the 3-wk interval solution data and weighted averages based on measured as well as simulated volumes. The three means often differed by as much as 30%.

Methods for numerical analysis of water chemistry data have not been discussed in previous papers, but we suspect that the problems are not unique to our project. More research is necessary before solution fluxes can be calculated and their uncertainty estimated. Until then it seems advisable to regard flux calculations as tentative and to look carefully at element concentrations and ratios in addition to fluxes.

Water chemistry profiles

Element concentrations changed as water passed downward through the forest. Water chemistry profiles (Table 1) help separate the influences of precipitation, biological process, and weathering. On WS-10, total cation concentrations increased only slightly as water passed through the canopy, but rose dramatically between the base of the litter layer and the 30-cm depth in the mineral soil, presumably as a result

of weathering. Concentrations then decreased gradually as the water passed through the subsoil and stream to the weir. K and Mg, both less important components of the parent material at WS-10 (Table 4), increased little through the profile (Table 1). Indeed, K decreased between the litter layer and 30-cm depth ($P < .01$), presumably because of uptake by rooted plants. On the other hand, Na and Ca, more important constituents of the parent material, increased markedly (both with $P < .01$), presumably because amounts of these elements released during weathering exceeded requirements of the vegetation.

Uptake by nonmycorrhizal microflora is not responsible for the decrease in K concentration between litter and soil. We included these microflora in our budget analysis in the detrital compartment that provides their substrate. From the annual budgets we can see that the net flow is from detrital into solution compartments. Over shorter periods, of course, this net flow may reverse. This conclusion is, however, strongly affected by assumption 2, specifically that the dry mass of dead roots is in steady state, and to a lesser extent by assumptions 3, 4, 6, 7, and 8. For example, if we found that cations were accumulating in the dead root compartment, then our estimate of weathering input would increase. The net flow from dead roots to soil solution might reverse as microflora associated with dead roots took up cations from solution.

Nitrogen behaved differently, typifying an element profile regulated almost totally by biological phenomena. Unlike metallic cations, N in precipitation accounted for a substantial fraction (30%) of the input to the system, and large increases also occurred as water passed through the canopy and litter. Total N concentration decreased between the litter and 100-cm depth in the soil and between 100-cm depth and the weir (both with $P < .01$). Biological uptake may explain the decrease between litter and 150-cm depth. The decrease between 100 cm and the weir is probably due to absorption on mineral surfaces (Greenland 1971), but deep roots may have taken up some N.

Levels of NO_3^- -N at WS-10 were always low; concentrations in 91% of the soil solution samples were < 0.05 mg/L. Organic N and ammonium accounted for most of the N in solution. By contrast, NO_3^- -N at Hubbard Brook averaged 1.43 mg/L in precipitation, 1.9–3.4 mg/L in throughfall, and 1.93 mg/L in stream water. Organic forms accounted for 23% of the N in throughfall and an unreported but presumably small fraction of the N in stream water (Eaton et al. 1973, Likens et al. 1977). Some of the difference is no doubt due to the greater atmospheric input of NO_3^- at Hubbard Brook, but some may also be due to differences in the structure and functioning of the two ecosystems.

The P profile was similar to N and cation profiles, except that P decreased only slightly between 30 cm and the weir. The solution P:N ratio increased from 0.10 in precipitation and 0.40 in litter leachate to 0.48

and 1.7 at 30 cm and 200 cm, respectively, in the soil, and 1.1 at the weir, where losses of dissolved P slightly exceeded losses of dissolved N. The large ratios support the hypothesis that N rather than P was limiting at WS-10, a phenomenon noted in other Douglas-fir forests of the Pacific Northwest (Gessel and Walker 1956).

These patterns are similar to those observed by Feller (1977), Feller and Kimmins (1979), and Johnson (1975) and agree with general patterns suggested by Vitousek and Reiners (1975, 1976) and Vitousek (1977) for relative roles of precipitation chemistry, biological processes, and weathering in controlling stream water chemistry.

Canopy N fixation

Our estimated N fixation rate was substantial, $2.8 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, about equal to the measured input in precipitation and dryfall. Denison et al. (1976) reported a nitrogen fixation rate for *Lobaria oregana*, the most abundant N-fixing lichen on WS-10, of $8 \text{ mg N} \cdot \text{kg}^{-1} \cdot \text{hr}^{-1}$ under nearly optimum conditions. Given a standing crop of N-fixing lichens of $\approx 900 \text{ kg dry mass/ha}$ (Pike 1978), this rate would extrapolate to $\approx 68 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. Because of the lack of summer rainfall and the low winter temperatures, Denison et al. (1976) suggested that the annual total might be much less. Our estimate of $2.8 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ based on litterfall and throughfall data may be somewhat low because of assumptions 5 and 10. For example, if we assume instead that all N in microlitterfall and throughfall was fixed by epiphytes, fixation increases to $3.5 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. Pike (1978) reported a growth rate for *Lobaria* of 0.34/yr, a standing crop of 900 kg/ha, and N concentration of 1.73%. Multiplying these three gives an annual N requirement of 5.3 kg N/ha , presumably an upper bound on the actual rate of N fixation because at least part of the requirement could be met by uptake of N leached from foliage. The value is, however, very low compared to rates of 30–300 $\text{kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ reported for *Alnus* and *Ceanothus* stands in the Pacific Northwest (Tarrant and Miller 1963, Youngberg and Wollum 1976, Cromack et al. 1979, Tripp et al. 1979).

Litterfall and fallen logs

Element input in litterfall on WS-10 was large. Falling microlitterfall and epiphytes accounted for 20% of the N input to the forest floor but only $\approx 5\%$ of the dry matter input. Concentrations in coarse woody debris (> 15 cm diameter) were low, but total amounts were important (16% of the total N in litterfall). These components were not measured in most other studies. Total return of N in litterfall and throughfall in younger Douglas-fir stands (22–95 yr) was similar to that observed on WS-10, although partitioning among litterfall components was substantially different. Return on young stands ranged from 18 to $27 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Ges-

sel and Turner 1976). Our value was $27.3 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. The corresponding values for P were 2.5–4.8 and 6.3; for K, 5.2–9.7 and 22.6 kg/ha .

The large amount of wood debris in the stand raises questions about the role of this material in element cycles. According to Grier (1978), and MacMillan and J. Means (*personal communication*), amounts of at least some elements in fallen logs in the Pacific Northwest increase little as decay proceeds. However, their values did not include elements in hemlocks growing on the logs and roots growing into them, although both presumably derive much of their nutrients from the logs.

Our values for element input to the log compartment are also likely to be underestimates. We can expect that, because logs occupied $\approx 20\%$ of the surface area on WS-10 (R. Fogel and M. Ogawa, *personal observation*), as much as 20% of the throughfall and litterfall input to the forest floor may have been intercepted by and stored in logs. Also, N fixation by free-living bacteria in logs has been reported (Cornaby and Waide 1973, Roskoski 1977, Larsen et al. 1978), though not yet in the Pacific Northwest. Results of Roskoski (1977) and Larsen et al. (1978) agree closely, whereas those of Cornaby and Waide (1973) were about five times greater. Rates based on the two more recent studies ranged from 8 to $90 \text{ mg N} \cdot \text{Mg dry mass}^{-1} \cdot \text{day}^{-1}$, which when multiplied by the log biomass at WS-10 gives an N fixation input of $0.6\text{--}6.3 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ compared with a potential N input to logs through throughfall of 0.7 kg/ha , and from leaf litterfall and microlitterfall of 3.0 kg/ha . The loss rate from logs certainly was also underestimated, because much foliage from hemlock seedlings and shrub species growing on logs falls onto the adjacent forest floor rather than back on the logs. Both roots and fungal rhizomorphs frequently extend between logs and underlying litter, which suggests the likelihood of transfers in both directions.

Our estimate of element accumulation in logs was based on comparatively short-term mortality data and weighted average concentrations of all decay classes. In fact, mortality is an episodic phenomenon, and these concentrations change substantially during decay (Grier 1978). We have undertaken a large-scale sampling and experimental program at HJA which should resolve these uncertainties.

Forest floor turnover and nutrient content

Values for element transfers between detrital and solution compartments are based on our conclusions about detrital accumulation. We were relatively confident of results for foliage and fine woody litter and fallen logs. However, data on fine litter and dead roots were insufficient to establish that these were in steady state (assumption 2). If organic matter was accumulating in these compartments, our estimates of cation and P weathering would have to be increased. In one

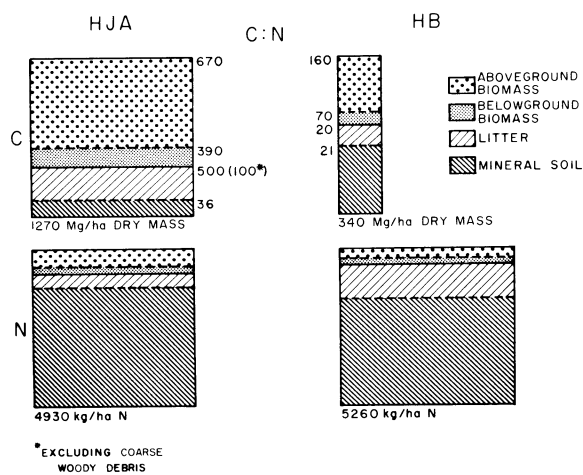


FIG. 4. Carbon and nitrogen content, and C:N ratio (center) of vegetation, litter, and soil at WS-10, H. J. Andrews Experimental Forest (HJA) and WS-6, Hubbard Brook Experimental Forest (HB).

of the few studies of forest floor accumulation, Covington (*in press*) found that steady state was reached in northern hardwood stands after only 60–70 yr. Even though northwestern coniferous forests continue to accumulate biomass far longer than do northern hardwood forests, it seems likely that the fine litter compartment was at steady state at WS-10.

Forest floors in the northeastern United States typically contain several times as much N as do forest floors under Douglas-fir in the Pacific Northwest (Stone 1973). For example, forest floor N content during late summer at Hubbard Brook averaged 2.6% on WS-6 (Covington, *in press*) and 2.5% on WS-3 and WS-1 (Dominski 1971), or $\approx 1260 \text{ kg N/ha}$ (Likens et al. 1977). N content in our stand, excluding wood $> 15 \text{ cm}$ in diameter, was 0.5% (Table 4), or $\approx 260 \text{ kg N/ha}$ (Fig. 4). In both stands, N concentrations were greater in the forest floor than in litterfall because N is largely conserved during decomposition, whereas C is released as CO_2 to the atmosphere. In general, N concentrations are lower in forest floors under coniferous stands than under broad-leaved stands, although coniferous forest floors in the northeastern United States tend to have higher concentrations than those elsewhere (Stone 1973, Vitousek et al. 1979).

N concentrations have traditionally been expressed as a C:N ratio, assuming a carbon content of 50%. C:N of the forest floor at Hubbard Brook WS-6 is ≈ 20 (Dominski 1971, Gosz et al. 1976), whereas at WS-10, forest floor C:N (excluding logs) averaged ≈ 100 (Fig. 4). N is only released into solution during decomposition when C:N falls below a range of 20–30 (Jensen 1929). The forest floor at WS-10 was well above this range whereas that at Hubbard Brook was within the range. The C:N of the vegetation also differs substantially at Hubbard Brook and HJA. In fact, the total

amount of N in the two systems is about the same (although it is distributed differently); it is the much larger amount of C at WS-10 that leads to the difference in C:N (Fig. 4).

The difference in C:N ratio between Hubbard Brook and HJA may explain in part the greater nitrate loss from both disturbed and undisturbed watersheds at Hubbard Brook. Mean annual nitrate concentrations in stream water from undisturbed forests ranged from 0.7 to 3.3 mg/L at Hubbard Brook (Likens et al. 1970) but from 0.013 to 0.04 mg/L at HJA (Fredriksen et al. 1975). Differences were even more striking for clear-cut sites: 38–53 mg/L at Hubbard Brook and 0.09–0.9 mg/L at HJA.

More NH_4^+ -N should be released at Hubbard Brook where the C:N is ≈ 20 than at HJA where it was ≈ 100 . Greater NH_4^+ release favors nitrification because nitrifying bacteria grow slowly and compete effectively with heterotrophic bacteria for ammonium only in substrates in which ammonium is abundant (Jansson 1958, Jones and Richards 1978, Vitousek et al. 1979). An alternative way of stating this is that ammonium-oxidizing bacteria can compete effectively with carbon-oxidizing bacteria only in substrates in which readily metabolized C is limiting. In this sense, the Hubbard Brook ecosystem can be considered C limited with respect to N dynamics, which is reflected not only in the higher nitrate concentrations but also in the relative lack of dissolved organics in the outflow water. At WS-10, where C is abundant relative to N, nitrate concentrations are low and organic N dominates in the outflow water.

We attribute the higher N content of the Hubbard Brook forest floor to greater N input in precipitation and greater N content of living vegetation. Foliar N concentrations in the six common species on WS-6 at Hubbard Brook were 1.26–2.78% (Likens and Bormann 1970), whereas weighted average values on WS-10 (Table 2) were 1.07% for current foliage and 1.03% for older foliage. N concentrations in woody tissues are also much greater at Hubbard Brook than at HJA. N content of all aboveground biomass at Hubbard Brook was 0.26% (Whittaker et al. 1974, Bormann et al. 1977), whereas aboveground biomass on WS-10 at HJA averaged only 0.07% (Table 3). The greater N concentrations in Hubbard Brook vegetation might be ascribed to greater N availability but, except for more input in precipitation (perhaps only a recent phenomenon), the argument is circular. A better explanation might involve differences in climate between the two sites (Waring and Franklin 1979) or anatomical differences between broad-leaved and coniferous species. For example, angiosperm trees dominating at Hubbard Brook contain more ray parenchyma (living tissue with high N content) in woody tissues than do gymnosperm trees dominating at HJA (Esau 1960, Cowling and Merrill 1966).

Soil organic matter (SOM)

Turnover times based on input to the SOM compartment are short at WS-10, indicating rapid recycling through the vegetation. With 30% annual mortality of fine roots (<5 mm diameter) (assumption 3), a smaller mortality rate for coarse roots, and no accumulation of identifiable dead roots (assumption 2), annual input to amorphous SOM was 11.2 kg N/ha, 2.4 Mg dry matter/ha, and 1.7 kg P/ha, corresponding to turnover times of ≈ 330 , 55, and 5 yr. Turnover times are dependent, however, on several assumptions. Input to the dead root and SOM compartments will have been overestimated if element concentrations in roots decrease before senescence, as they do in foliage. Also, if the dead root compartment has increased annually as old-growth trees died on WS-10 (see assumption 2), our estimate for transfer from dead roots to SOM would have to decrease. However, the input values may be low if fine roots turn over as rapidly in old-growth Douglas-fir stands (assumption 3) as they do in younger stands (Fogel and Hunt 1979, Santantonio 1980). This would result in even shorter turnover times for the SOM.

Assumptions 6–8 about SOM have profound impact on our element cycle budgets. Our treatment of the N cycle was such that an increase in the value for accumulation (or export) of N in SOM ($2.8 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) would have to be balanced by an increase in the value for the unknown input into the forest floor. Such an increase in the rate of cation accumulation would have to be balanced by an equal increase in the weathering rate. Clearly, long-term, gradual changes in stores of detritus (logs, litter, dead roots, and SOM) must be much better quantified before definitive element budgets can be calculated.

Element cycling patterns

Annual budgets allowed comparison of input and loss of elements from various processes in the portion of the ecosystem extending to the bottom of the rooting zone (Table 5). Loss of N from the rooting zone was $\approx 20\%$ of total N input to the forest. Over 99% of the input of P, K, Ca, Mg, and Na to the system was lost. Woodwell and Whittaker (1967) estimated that cation loss to groundwater ranged from 56% to 65% of input in a successional oak-pine forest that was accumulating biomass at a rapid rate relative to WS-10.

Nitrogen losses from the rooting zone at WS-10 were only slightly greater than those reported for a 37-yr-old Douglas-fir ecosystem (Cole et al. 1967). The similarity supports the hypothesis of Vitousek and Reiners (1975) that losses of limiting elements remain small as long as organic matter is accumulating. Though biomass of live vegetation was decreasing slowly in this old-growth forest (Grier and Logan 1977), this appeared to be more than offset by accumulation in detrital compartments. We calculated net

TABLE 5. Input, accumulation, and loss of elements at WS-10 (in Kilograms per hectare per year) for an average year during 1972–1975. Ratio of item to total input of element is in parentheses.

Process	N	P	K	Ca	Mg	Na
Precipitation	2.0 (0.31)	0.3 (0.6)	0.9 (0.10)	3.6 (0.03)	1.2 (0.14)	5.7 (0.11)
Nitrogen fixation	2.8 (0.43)
Weathering	0	0.2 (0.4)	4.7 (0.52)	118.9 (0.97)	7.2 (0.86)	47.0 (0.89)
Unknown input	1.7 (0.26)	0	3.4 (0.37)	0	0	0
Total input	6.5	0.5	9.0	122.5	8.4	52.7
Accumulation in vegetation	-2.8 (-0.43)	-0.4 (-0.8)	-1.0 (-0.11)	-4.5 (-0.04)	-0.6 (-0.07)	-0.2 (-0.004)
Accumulation in detritus	7.8 (1.20)	0.2 (0.4)	0.5 (0.06)	3.9 (0.03)	0.4 (0.05)	0.1 (0.002)
Total accumulation	5.0 (0.77)	0.0 (0.0)	-0.2 (-0.02)	-0.2 (-0.002)	0.1 (0.01)	-0.1 (-0.002)
Total loss (hydrologic transport out of rooting zone)	1.5 (0.23)	0.8 (1.6)	9.5 (1.05)	123.1 (1.00)	8.6 (1.02)	52.8 (1.00)

ecosystem production at $0.7 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ and net N accumulation at $5.0 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, though some of this may have been offset by erosional losses for which we did not account (see Swanson et al., *in press*).

At Hubbard Brook, data are not available for the soil and subsoil solution; loss was measured only across the weir at the base of the watershed. At WS-10, concentrations in the subsoil solution were much higher than those at the weir (Table 1). Consequently, comparisons with input give different results. Based on concentrations at the weir, export from WS-10 was only 40% of total Ca input and 8% of total N input. At Hubbard Brook, losses were 60% and 20% of input (Bormann et al. 1977, Likens et al. 1977).

Weathering constituted the major input for all elements except P and N. Atmospheric input of P exceeded weathering, but values for both were small. The N cycle was unique in that biological fixation accounted for at least 40% and perhaps as much as 70% of total input. At most other sites, input from weathering and fixation are not yet estimated. Because weathering rates must be estimated by difference, their accuracy depends on the accuracy with which accumulations, outputs, and other system inputs are measured (Clayton 1979). The uncertainty in results from both Hubbard Brook and HJA is difficult to estimate.

Indices of the cycling pattern of each element were obtained by dividing uptake by total input in fixation, precipitation, and weathering (Table 6). Large ratios for N, P, and K indicate a tightly closed cycle; fairly

small ratios for Ca, Mg, and Na indicate an open cycle. Dividing uptake by total output produces a similar pattern except that the ranking of N and P are reversed.

Our measurement of solution transport between litter and soil enabled us to calculate the relative importance of litter solution and soil solution as sites of nutrient uptake by the vegetation. Much N and P are absorbed from the litter solution, but metallic cations other than Ca are absorbed largely from the soil solution (Table 6). Input to litter solution expressed as a percentage of total input to soil and litter solutions shows the same ranking of element groups, which means that elements are absorbed by vegetation from the layer in which they are most readily available.

Vegetation can obtain nutrients needed for each year's production of foliage either from the soil and litter solutions or from old foliage (redistribution). Vegetation at WS-10 used both mechanisms (Table 6). Internal redistribution supplied 56% of the N, 31% of the P, and 30% of the K required for new foliage production. Redistribution of Ca, Mg, and Na was negative. Concentrations increased rather than decreased with foliar age. The major difference between these sets of elements would seem to be that soils are only rarely deficient in Ca, Mg, and Na, whereas deficiencies in N, P, and K are common.

Cole et al. (1977) discuss the importance of redistribution in a series of even-aged Douglas-fir stands (9–95 yr) in western Washington. The percent of total nutrient requirement met by redistribution was greater than at WS-10. It ranged from 43 to 47% for N, from

TABLE 6. Ratios of element transfers within an old-growth coniferous forest.

Ratio	N	P	K	Ca	Mg	Na
Uptake by vegetation/Total input	6.5	18.2	2.99	0.55	1.19	0.03
Uptake by vegetation/Total loss	28.0	13.0	2.83	0.54	1.16	0.03
Uptake from litter solution by vegetation/ Total uptake by vegetation	0.46	0.48	0	0.34	0.14	0.12
Redistribution to new foliage/Total requirement for new foliage production	0.56	0.31	0.30	-1.8	-0.38	-2.2

46 to 95% for P, and from 12 to 25% for K. In a north-eastern hardwood forest at Hubbard Brook, redistribution of N accounted for only 33% of the annual growth requirement (Bormann et al. 1977), perhaps because large amounts of N were readily available in the rooting zone.

The annual budgets show that solution transport and organic matter transport account for roughly comparable fluxes of N, P, and K (Fig. 3). Yet these elements are present in organic matter at concentrations some 10 000 times greater than in water, testimony to the ability of the vegetation to extract and conserve nutritionally important elements.

Although this difference in concentration has been noted often, for example by Epstein (1972), its corollary, that time scales are similarly disparate, has received little attention. Elemental quantities in solution compartments can change from essentially zero to near maximum in a few weeks of warm, rainless weather. The reverse process, flushing of accumulated elements out of solution, can occur during a few hours of intense rain. However, elements continue to accumulate in the vegetation for centuries and in the soil for millennia before steady state is reached.

The difference in time scale creates several problems when comparing transfers and when modeling element cycles. For example, how do we integrate episodic events, such as log-fall, into element budgets? Must we consider rapid fluctuations in concentrations of dissolved elements to predict annual uptake? Would longer term averages of solution concentrations be more useful in predicting annual uptake or plant growth? If we are to model the element cycles, we must seek ways to reconcile the differences in time scale between hydrologic and organic matter transport processes.

Patterns of acidity and alkalinity—the H⁺ budget

Attempts to discuss H⁺-creating and H⁺-absorbing processes in relation to element cycles and biochemical processes frequently bog down in details and contribute little to our understanding of an ecosystem. This is unfortunate. The H⁺ dynamics of a system, precisely because they are affected by so many phenomena, offer a unique opportunity to integrate information about many chemical and biological processes. Consideration of H⁺ dynamics has led to hypotheses about functioning of rooted plants (Raven and Smith 1976, Blevins et al. 1978) and of mycorrhizas and saprophytic fungi (Sollins et al., *in press*). We next show how a simplified H⁺ budget can be constructed for a portion of a system, the numbers of which constitute a synthesis of information about most processes, including water and organic matter fluxes and fluxes of the important nutrient elements.

Our interest in constructing an H⁺ budget developed after WS-10 had been clear-cut. We suspected that S

and Cl were often the dominant anions in solution and began measuring S and Cl in all solution samples (S had been measured in precipitation during 1971–1972 before the period of intensive study). Because we lacked the resources to gather an additional set of vegetation, litterfall, and litter samples, we constructed the H⁺ budget with values for S and Cl from other stands, choosing those species and sites at which N, P, and K concentrations were most similar to those at WS-10. We did not attempt to extrapolate concentrations of Mn, Fe, and Al from those measured at other sites. Mn alone accounted for 10% of cations (in equivalents per hectare) in the aboveground portion of a Washington subalpine fir-hemlock stand (Turner and Singer 1976). Mn and Fe accounted for 18–23% of cations in the forest floor of 120-yr-old Alaskan stands of aspen and birch (Van Cleve and Noonan 1971). In one of the few studies in which all three were measured, Al, Fe, and Mn together accounted for only 2–13% of foliar cations in wetland stands of *Larix laricina* (Tilton 1977). Ideally, we should measure all major elements simultaneously, but this is an expensive and elusive goal, and we believe our data suffice for construction of an illustrative H⁺ budget.

Concentrations of S and Cl were measured at the control site during a period of extended drought in 1976 and 1977 (Table 1). Concentrations of all elements were high compared with the previous 3 yr, therefore we adjusted S and Cl concentrations (Table 1) downward to make them comparable with data before clear-cutting. We calculated the ratio of average total cation concentration (in meq/L) during the pre-clear-cut period to average total cation concentration during the period when S and Cl were measured, and we multiplied average concentrations of S and Cl by this ratio. Ratios for S were 0.37 for throughfall, 0.42 for litter leachate, and 0.35 for soil solution at 100-cm depth.

The assumption that ratios of cations to S and Cl are unchanged by drought may be roughly correct since a large portion of these substances enter solution through congruent weathering processes. The assumption, in any case, seemed preferable to using concentrations from an abnormal period.

We used S data of Beaton et al. (1964, 1965) for Douglas-fir from various sites in British Columbia for foliage. For other vegetation components, we used S data on *Picea abies* from southern Sweden (Nihlgård 1972). These values were close to those for *Picea rubens* at Hubbard Brook (Likens and Borman 1970). S content of organic matter in the mineral rooting zone was estimated assuming an N:S ratio of 7 typical of many soils (Russel 1973). We decided, from the very limited data on Cl concentrations in vegetation and detritus (Rodin and Bazilevich 1967) and on the basis of watershed input-output studies (Vitousek 1977), that biological uptake and return were sufficiently un-

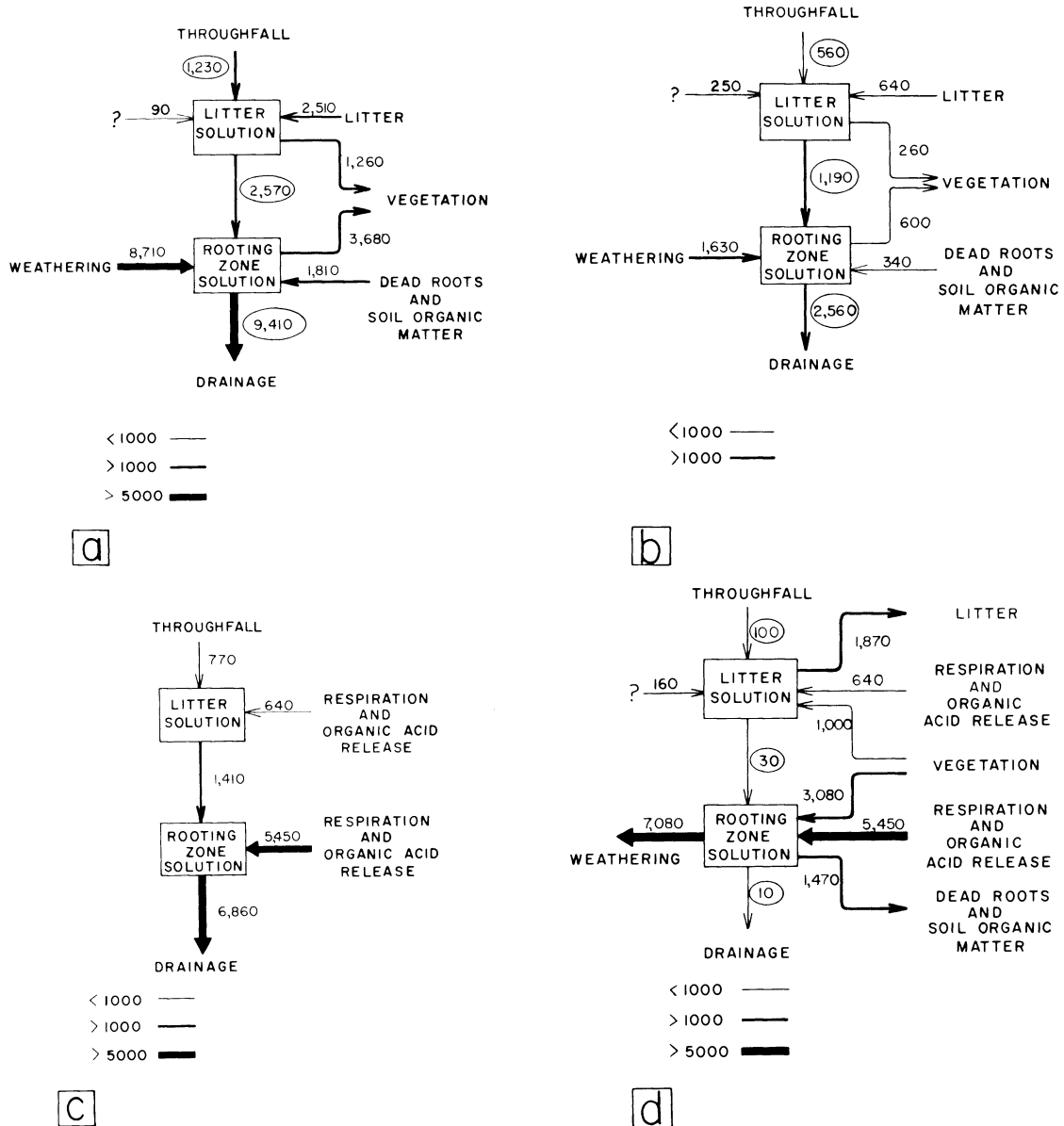


FIG. 5. Total ion budgets for litter and soil solutions only. All values are equivalents per hectare per year. Circled values were calculated independently; others were calculated by difference. Thickness of arrow is proportional to flux. (a) Metallic cations (Na, K, Mg, Ca), (b) "noncarbon" anions (S, P, Cl), (c) "carbon" anions (HCO₃⁻ and organic anions), (d) H⁺.

important in the cycling of Cl that they need not be considered in constructing the H⁺ budget. Procedures and other assumptions used to complete the S and Cl budgets were then the same as those for metallic cations and P.

The H⁺ budget can be most readily understood if first we construct budgets (Fig. 5a,b) for total cations (K, Na, Mg, and Ca) and total "noncarbon anions" (S, P, and Cl). Next, we compute the amount of H⁺ transferred as water flows in and out of the solution

compartments. On WS-10, these transfers were small (all ≤ 100 eq · ha⁻¹ · yr⁻¹), but in other forests they could be substantial. The difference, in mole equivalents, between total cations (metallic cations plus H⁺) and noncarbon anions consists of HCO₃⁻ and organic anions. Lacking an accepted term, we call this difference "carbon anions." On WS-10, "carbon anion" concentrations were consistently less than measured (titratable) alkalinity, probably indicating insufficient data on "noncarbon anions" and trivalent cations.

Both measured alkalinity and the "carbon anion" concentration increased as water passed through the litter and rooted portion of the mineral soil; the input at each stage was presumed to be from respiration and biological production of organic acids (Fig. 5c). Note that the "carbon anion" budget is calculated entirely by difference. In principle, a "carbon anion" budget could be constructed from measurements, but construction by difference suffices for completing the H^+ budget. Moreover, if the "carbon anion" budget is constructed by difference, then the H^+ budget must always balance, providing a convenient check on the calculations.

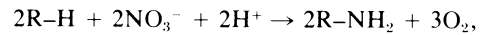
The next step added the effect of the "carbon anion" input on the H^+ budget. We assumed that in respiratory processes, substrate is oxidized to neutral end products such as water and CO_2 . The CO_2 combines with water and then partially dissociates, either inside the organisms (plants or decomposers) or outside. The net effect is the same: for every equivalent of HCO_3^- appearing in solution, one equivalent of H^+ must also have been created (shown in Fig. 5d as H^+ input to the solution compartments).

In the soil (though not in the litter layer), the H^+ created during dissociation of dissolved CO_2 is consumed mainly in weathering processes (cf. Cleaves et al. 1970, 1974). During the study period, weathering added $\approx 9000 \text{ eq} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ to solution at WS-10 which means an equivalent amount of H^+ must have been withdrawn from solution (Fig. 5d). The H^+ budget makes clear that weathering and respiration in the soil result in more or less balancing H^+ fluxes.

Nutrient uptake by the vegetation may also result in H^+ fluxes into or out of the solution compartments. Of the elements required for plant growth, more occur in solution as cations than as anions. In meeting nutritional requirements, plants would absorb more cations than anions, but, because electrical neutrality must be maintained, either nonessential cations must be excreted or nonessential anions must be absorbed. This phenomenon, unfortunately termed "excess" cation absorption, was first studied by Ulrich (1941), who showed that the plant either releases H^+ in exchange for the "excess" absorbed cations, or it absorbs HCO_3^- (or some other "carbon" anion) to balance the "excess" cation uptake. The result of either process is the same: when requirements for cations exceed requirements for anions, H^+ activity in the rooting solution increases in the absence of an effective buffering system (Dijkshoorn 1969, 1973, Kirkby 1969).

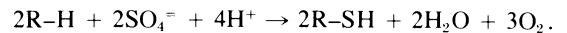
On WS-10, uptake of metallic cations from the soil solution exceeded uptake of noncarbon anions by $\approx 3000 \text{ eq} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. To prepare the H^+ budget, we assumed that plants released an equivalent amount of H^+ into the soil solution, smaller than H^+ fluxes resulting from respiration and weathering, but nonetheless significant.

Nitrogen absorption and assimilation have complex effects on the H^+ budget. If N is absorbed as NH_4^+ or an organic cation, the process is equivalent to absorption of any other cation. If not balanced by anion uptake, H^+ must be released. If the N is absorbed as NO_3^- , oxidation state changes as the N is reduced in the plant to the organic amino form. The stoichiometric equation for this is:



where R is an organic radical. The equation shows that for every mole of N so assimilated, one mole of H^+ is assimilated. The H^+ may be withdrawn from the external solution or supplied through the synthesis of organic acids from neutral carbohydrates. Raven and Smith (1976) have shown how this "pH-stat" mechanism operates in plants to maintain constant pH during NO_3^- assimilation. The extent to which the H^+ is supplied by uptake differs among plant species and is also affected by the ratio of NH_4^+ to NO_3^- in the external solution. Although much research is needed before the H^+ flux due to N uptake can be calculated, it is clear that the H^+ budget will be affected by the form in which N is taken up by the plants.

Sulfur and phosphorus dynamics also affect the H^+ budget for the system. The stoichiometry for S assimilation is:



The resulting H^+ flux is small on WS-10 ($< 1000 \text{ eq} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) because the amounts of S taken up are not large.

The effect of P cycling on H^+ dynamics is in some ways simpler. Because virtually all P in biological tissues occurs as phosphate groups, the oxidation state of P does not change during its assimilation. However, P may be present in solution as either $H_2PO_4^-$ or HPO_4^{2-} , depending on pH. At pH 7, the two species are present in equal concentration; above pH 7, the concentration of $H_2PO_4^-$ drops rapidly; below pH 7, the concentration of the other species drops at a similar rate (Brady 1974). Below pH 6, the concentration of HPO_4^{2-} is negligible. WS-10 litter solution pH averaged 5.8, whereas soil solution pH averaged 6.4 at 100-cm depth. Thus, the transfer of P in solution from litter to soil layer was accompanied by a small release of H^+ into solution, $\approx 15 \text{ eq} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, as the $H_2PO_4^-$ dissociated further. This is small compared with H^+ fluxes due to respiration, weathering, and differential ion uptake and release.

Decomposition processes can also be examined in terms of their effect on the H^+ budget. During decomposition, release of metallic cations greatly exceeds release of inorganic anions such as S and P, which is only reasonable because the cations were taken up in greater quantities when the organic matter was

formed. For the litter to remain electrically neutral, some $1900 \text{ eq} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ of H^+ must be withdrawn from solution (Fig. 5d).

Many other organic and inorganic reactions affect pH. For example, nitrification is essentially the reverse of nitrate assimilation and causes release of H^+ into solution (Likens et al. 1969, Reuss 1975). Rainfall acidity directly affects the H^+ load on the ecosystem, and may also indirectly affect pH through increases in sulfate inputs.

The H^+ budget integrates information on each process. Though the budget for WS-10 may be incomplete and the numbers accurate only within an order of magnitude, important patterns are clear. In both litter and soil, respiration results in a large flux of H^+ into solution. In the soil this is balanced by weathering; other processes are of minor importance, at least at WS-10. In the litter, however, the weathering sink does not exist, and the H^+ input is balanced by H^+ uptake during decomposition. As organic matter decomposes, metallic cation release into solution exceeds inorganic anion release, and H^+ is absorbed. The result is that the solution system is highly buffered in both the litter and soil. Concentrations of H^+ are kept small and constant. However, because buffering depends in part on biological phenomena, we might expect that disturbance of biological processes destroys some buffering power.

The overall effect of disturbance may be better interpreted by measuring effects on the system H^+ budget. For example, if we were to clear-cut our old-growth forest, killing most of the roots, we would decrease uptake by vegetation but increase the rate of element release into solution as fine roots and mycorrhizae begin decomposing. This will cause withdrawal of H^+ from solution, and therefore from exchange sites, and a corresponding increase in the tendency of the exchange sites to bind metallic cations and prevent their loss from the rooting zone in water flow. However, clear-cutting would also affect rates of CO_2 production and subsequent H^+ release through H_2CO_3 dissociation. Root respiration would decrease, but microbial respiration might increase because of higher temperatures and greater amounts of substrate. Effects of the bicarbonate equilibrium on H^+ status might thus cancel or enhance the effect of altered patterns of uptake and decomposition.

The interactions between biological, chemical, and hydrological processes are exceedingly complex but must be examined systematically if we are to predict effects of disturbance on stand growth and water quality. Variables such as net and gross ecosystem production, soil CO_2 production, streamflow, and evapotranspiration offer convenient indices for comparing carbon and water dynamics of natural and disturbed systems. Budgets for single elements or compounds provide opportunities for devising similar variables for individual cycles. But methods for summarizing infor-

mation on the interactions among all these processes, including carbon and water and the approximately 15 other important elements, have been lacking. We suggest that the H^+ budget provides precisely such a set of variables, a set sensitive to all the others, which can be used to compare ecosystems and to assess the effects of disturbance.

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