

WATERSHED BASE-CATION CYCLE DYNAMICS MODELED OVER FOREST REGROWTH IN A CENTRAL APPALACHIAN ECOSYSTEM

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Abstract. Watershed ecosystem analysis has been used to study aspects of nutrient cycles in many regions of the US. Here we quantify watershed input-output budgets and intrasystem cycling of the base cations Ca, K and Mg in a montane Virginia ecosystem. The intrasystem fluxes of uptake, return, canopy leaching and mineralization were simulated over the period of forest aggradation. A forest-dynamics model, based on previous models, was created to model biotically-driven fluxes at this site; biomass nutrient concentrations were parameterized with a field study.

A two-year watershed mass-balance study was then conducted to estimate geologic fluxes for comparison with modeled biotic fluxes. Results show the major biotic fluxes to be much greater, highlighting the importance of considering biomass dynamics in ecosystem nutrient-cycling studies. Mineralization from forest-floor biomass compartments proved to be an increasingly important avenue for internal recycling during aggradation. Accumulation of base cations in biomass also corresponded to a production of H^+ in soil at three times the H^+ levels in atmospheric deposition at this location. Such high levels of base removal in soils could exceed weathering rates and may result in a depletion of bases from the soil exchange complex.

Key words: biogeochemistry, watershed, watershed analysis, model, budget, input-output, base cations, dynamics, weathering, forest floor, nutrient cycles, soil, acidification, depletion, ecosystem.

1. Introduction

Synergism among the effects of forest regeneration, acid deposition and land-use history creates complex controls on nutrient and acid-base states of forest soils (Gilliam and Richter, 1991; Hornbeck and Swank, 1992). Changes in base status of the soil and nutrient capital at a site will depend not only on soil loss of dissolved ions, but also on rates of mineral weathering and on the magnitude of nutrient transfers within the ecosystem (Morrison *et al.*, 1992). Hydrogeochemical watershed studies sometimes adopt simplistic approaches to the role of vegetation in storing and cycling nutrients. Yet annual rates of base-cation cycling by vegetation may far outweigh the geochemical inputs and outputs of a watershed, depending on the particular system (Henderson *et al.*, 1978).

Watershed ecosystem analyses (Hornbeck and Swank, 1992) quantifying cycles of the base cations Ca, K and Mg have been conducted in several regions of North America, including New England, the Great Lakes, the Pacific Northwest and the Southeast. In the present study we quantify inputs, outputs and intrasystem cycles

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for a watershed in northern Virginia, in the Central Appalachian region. We develop and apply a new computer model of forest dynamics (based on previous models) to estimate biotically-driven nutrient fluxes during forest aggradation. Shaver Hollow Watershed (SHW) typifies an important type of landscape in the region in that its pedologically old soils were not recently glaciated and that it receives significant levels of acid deposition (Cosby *et al.*, 1989).

Our objectives were as follows: (1) To quantify the levels of base cations present in SHW-vegetation pools and cycled through biotically-driven fluxes; (2) to model dynamics in these fluxes and pools during forest aggradation; (3) to compare biotic intrasystem fluxes to present-day geologic input-output fluxes; and (4) to quantify the rate of input of H^+ equivalents to the soil due to the current buildup of base cations in biomass.

1.1. BACKGROUND

Forest soil acidification can have deleterious effects on forest regrowth (Mann *et al.*, 1988; Johnson *et al.*, 1988; Pitelka and Raynal, 1989; Joslin *et al.*, 1992). Soil base-cation availability also exerts a strong control on acid-neutralizing capacity (ANC) in streams (Cosby *et al.*, 1989). In previously cropped or timbered landscapes, harvest may have removed significant levels of base cations (Hornbeck, 1990). Regenerating vegetation removes still more base cations from soil, while producing carbonic acid through root respiration and organic acids in biomass (Sollins *et al.*, 1980). In eastern North America and parts of Europe these acidifying processes are exacerbated by acid deposition.

Both organic and pollution-derived acids can leach base cations from soil horizons (Richter *et al.*, 1983; Rampazzo and Blum, 1992; Mollitor and Raynal, 1982). In a Shenandoah watershed, correlations have been noted between bicarbonate (HCO_3^-) levels and base-cation levels in stream water (Castelle and Galloway, 1990), suggesting additional leaching by carbonic acid.

To the extent that vegetation takes up nutrient cation equivalents in excess of anion equivalents, the result is a reverse flux of hydrogen ions into soil (Sollins *et al.*, 1980, Nilsson *et al.*, 1982). The form of N taken up (cation or anion) plays a role in determining net cation uptake. However, a hydrogen ion budget for the Hubbard Brook Experimental Forest showed that atmospheric deposition dominated as the source of H^+ , closely followed by biomass aggradation, with both N transformations and carbonic-plus-organic-acid sources being a factor of 10 lower as a H^+ source (Driscoll and Likens, 1982).

A general approach remains unavailable for determining whether weathering can supply base cations at the rate needed to offset vegetative uptake and acid leaching. Where weathering did not supply cations at the needed rate, the soil cation-exchange complex would be depleted of bases.

As noted above, forest vegetation may play a significant or even dominant role in base-cation cycles over a given landscape. Computer models of nutrient cycles

coupled to forest dynamics have been used to simulate the processes controlling nutrient cycles over the time scale of forest aggradation and longer (Weinstein, 1982; Aber *et al.*, 1982; Pastor and Post, 1985). Such models provide an approach to quantify the levels of and dynamics in biotically-driven base-cation cycles.

1.2. SITE DESCRIPTION

Shaver Hollow Watershed (SHW) lies in central Shenandoah National Park in the Blue Ridge mountains of northern Virginia (38.62 N, 78.0 W). Altitude ranges from 503 to 1036 m, slopes from zero to 90%, with a watershed average of 47% (Harrison, 1987), with numerous rock outcrops. Three well-defined ridges bound the 223-ha western-slope watershed. A stream gauge and sampling point sit at 500 m elevation, just below the lower watershed boundary.

Climate in the area is temperate continental (Cosby *et al.*, 1989). Average annual rainfall (1951–1980) at Luray, at lower altitude and to the northwest, and at Big Meadows, at higher altitude and to the south, respectively, are 99.6 and 128.1 cm. Mean annual temperatures (1951–1980) at these two locations are 11.8° and 8.4°C, respectively (VA State Climatology Office).

SHW had been settled and partially logged before national park designation in 1936. At that time there was evidence of farming and a lack of merchantable timber. The bottomlands had been cut in 1924, but trees up to 25 cm in diameter were present in 1936 (Harrison, 1987). The dominant species in the area had been *Castanea dentata* prior to the Chestnut blight of 1904 to ca. 1934 (Harrison and Shugart, 1990; Shugart and West, 1977). The six predominant species in SHW in 1986, together with the percentage of aboveground biomass composed by each were as follows: *Quercus prinus*, 36%, *Q. rubra*, 30%, *Tilia americana*, 5.5%, *Betula lenta*, 4.4%, *Q. velutina*, 4.0%, and *Tsuga canadensis*, 3.7% (Harrison and Shugart, 1990). The mix in this second-growth forest is typical of forests in the western, southern and eastern parts of the North American temperate deciduous biome (Whittaker, 1975).

SHW lies on Pedlar Formation bedrock, which comprises primarily granulites made up of quartz, potassium feldspar, plagioclase feldspar and pyroxene. Basaltic intrusions occur in SHW in apparent bands scattered throughout the watershed (Evans, 1988). Blue Ridge soils are sometimes classified with those of the Northeastern US (Ciolkosz *et al.*, 1989), and sometimes with those of the Southeastern US, being out of the range of recent glaciation (Cosby *et al.*, 1989).

SHW soils occur chiefly as well-drained, very rocky Hapludults, pedologically old, strongly acid and high in sand content (Heidel, 1988; Currie, 1992). These residual mineral soils forming from bedrock cover most of the watershed. Primary-material rocks and clasts down to mineral-grain size are present (Heidel, 1988).

Soils found on the ridge are cobbly clay loams with a depth to bedrock of 100 to 157 cm. Cambic B horizons are found from 37 to 100 cm depth. Side slope soils are very gravelly or sandy loams or clay loams, with a depth of 100 to 138 cm to

bedrock (Heidel, 1988). In the lower reaches of the watershed, soils are forming from colluvium. Textures are sandy loam, clay loam, cobbly clay, gravelly or cobbly colluvium. Depth to bedrock is greater than 153 cm. The sola, 76 to 153 cm thick, may contain multiple textural B horizons, buried in some cases (Heidel, 1988.)

Table 1 shows primary and secondary mineralogy in SHW. Clay mineralogy was determined by x-ray diffraction (Virginia Polytechnic Institute) for five B horizon samples taken from three soil pits excavated in 1987. Primary mineralogy was determined with a petrographic microscope for ten bedrock thin sections (Evans, 1988). Percent base saturation (%BS) of soil horizons was determined as NH_4OAc -extractable Ca^{2+} , K^+ and Mg^{2+} divided by NH_4OAc -extractable Ca^{2+} , K^+ , Mg^{2+} and H^+ . Base cations were extracted at pH 7.0, and H^+ was extracted (potential exchangeable acidity determined) at pH 8.2 (Virginia Polytechnic Institute). The %BS levels were found to be maximal in the B horizons: 4% on the ridge, 11% on the side slope, and 17% in the colluvium.

1.3. MINERAL SOURCES OF BASE CATIONS IN SHW

Potassium has only one major primary mineral source and one major secondary mineral source in SHW: potassium feldspar and muscovite, respectively. Muscovite mica probably weathers too slowly to impact nutrient budgets, however (Velbel, 1988). Illite, a 2:1 clay high in potassium, often found in residual soils deriving from granites (Yatsu, 1988), is notably absent from SHW.

Calcium, in contrast, is released by the weathering of four major primary minerals in SHW: plagioclase, pyroxene, epidote and actinolite. The most significant releases of Ca^{2+} appear to occur during the initial weathering of primary minerals to 2:1 clays. Magnesium has as its only major source in SHW the primary mineral actinolite. This mineral occurs only in the basaltic intrusions in SHW bedrock. Throughout the watershed, Mg^{2+} may be released as montmorillonite clay weathers further to kaolinite.

2. Methods

Our conceptual model of biotic fluxes and the interplay between biotic and geologic base-cation cycling fluxes is shown in Figure 1 (Henderson *et al.*, 1978; Sollins *et al.*, 1980; Johnson and Van Hook, 1989). Nutrient levels in biomass were assessed by using allometrics (Harris *et al.*, 1973a; Vitousek *et al.* 1988) to estimate biomass by tissue type and taking representative tissue samples (Binkley, 1986; Landsberg, 1986; D. W. Johnson *et al.* 1988). Net nutrient uptake flux was computed from growth requirements and tissue nutrient concentrations. Referencing a recent SHW forest inventory (Harrison and Shugart, 1990), we chose two sets of plots for field sampling. Set A consisted of 11 plots chosen at random within each of 5 site-factor (slope, elevation, aspect) plot clusters. Set B consisted of 5 of these 11, chosen at random, one from each plot cluster.

TABLE I
Primary and Clay Mineralogy in SHW^a

Bedrock: Mineral	Granulites % Composition	Basalt % Composition
Primary		
Quartz	30	
Potassium Feldspar	25	
Plagioclase Feldspar	25	25
Pyroxene	15	
Magnetite/Ilmenite	5	
Magnetite		10
Epidote		35
Actinolite		25
Sphene		5
Apatite	2	
Zircon	<1	
Garnet	<1	
Hornblende	<1	
Biotite	<1	
Soils:		
	Edneytown, Thurmont (Side slopes)	Porters (Ridge)
Mineral	% Composition	% Composition
Clays		
Kaolinite	46.8	16
Chloritized Vermiculite	26.0	45
Vermiculite	1.5	5
Montmorillonite	6.3	10
Mica	7.5	5
Chlorite	1.5	5
Quartz	3.3	3
Gibbsite	2.5	6
Feldspars	0.5	0
Interstratified		
Mica/Vermiculite	3.5	5

Reference: ^a Evans, 1988.

Sample collection

Foliar, branch and root samples were taken in August, 1990 from the 11 plots of Set A. At each plot six trees were sampled, three *Q. prinus* and three *Q. rubra*. By climbing trees with rope climbing gear, we made a nondestructive effort to sample leaves and branches comprehensively. From each tree three branch and three foliar samples were taken. Branch samples ranged in diameter from 0.3 to 4 cm. Three root samples (2 mm to 3.5 cm diameter) were taken from each tree at 6 to 15 cm.

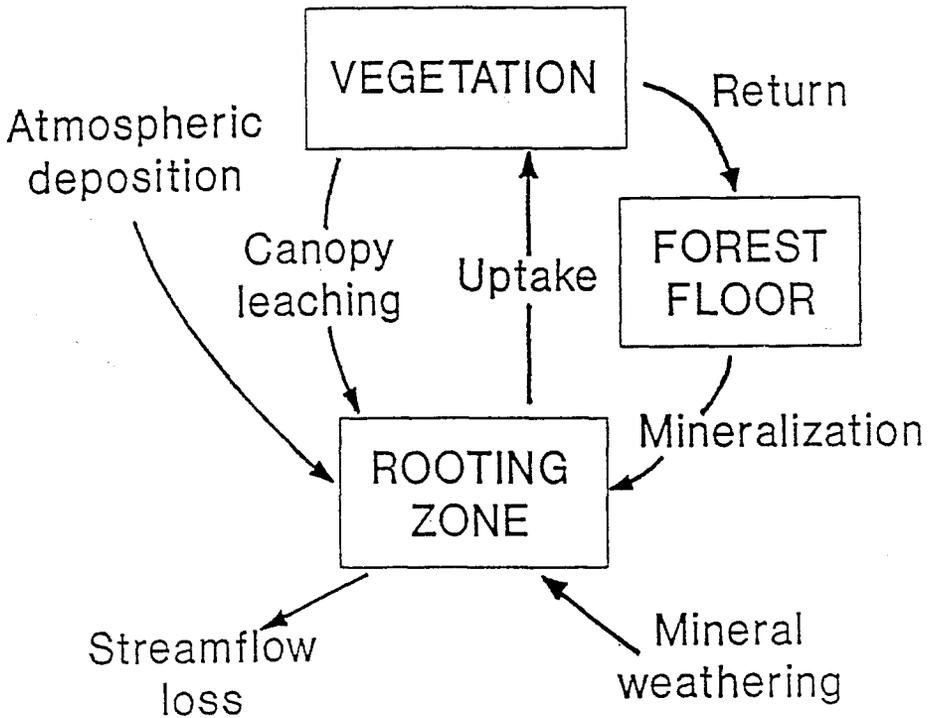


Figure 1. Conceptual model of base cation cycles in FORSWAS.

depth. Fine roots and hairs were preserved. Workers placed samples in airtight plastic freezer bags. For bole samples, ten tree cores were taken in June 1991, one from a *Q. prinus* tree and one from a *Q. rubra* tree from each of the 5 plots of Set B. All samples were handled with plastic gloves in the field and laboratory. Sample bags were stored in a refrigerator at 8°C for up to three weeks.

Litter traps were placed on the 5 plots of Set B. At each plot, four litterfall traps were set out in random locations on 25 October 1990 and litter collected after 15 to 18 days. Freshly-fallen *Q. prinus* and *Q. rubra* leaves were selected for chemical analysis. Throughfall samples were collected in SHW on the ridge from May 10 to October 18, 1988 (Galloway, unpublished data).

Laboratory analysis

Root samples were rinsed under running deionized (DI) water for approximately 30 seconds (Likens and Bormann, 1970), and scrubbed to remove embedded dirt. (Unfortunately, this step removed approximately half of the fine root hairs). Care was taken, in preparing the bole tissue samples, to preserve the correct relative amounts of bark, sapwood and hardwood.

Samples were oven-dried and stored at 25°C for up to ten months. After grinding in a Wiley Mill, subsamples of 0.5 or 1.0 g (depending on tissue type) were then

weighed out into dried, tared ceramic crucibles, dried a second time and removed to a dessicator before dry weight determination. Samples were ashed at 500°C for 16 hours. The digestion technique we used derives from that described by Likens and Bormann (1970). Ash was transferred to teflon beakers with 5 N HNO₃, which was then boiled off on a hotplate at 180° to 200°C. In a second digestion, 6 N HCl was pipetted into each beaker and similarly boiled off. More 6 N HCl was then added to the residue to facilitate transfer. Samples were vacuum-filtered through Whatman #42 filter paper that had been previously washed with 10 mL 6 N HCl and rinsed well with DI water. Filtrate was then diluted 10x and stored in high-density polyethelene bottles. Cation analyses were conducted by atomic absorption spectrophotometry.

2.1. FOREST DYNAMICS MODEL

The conceptual model of watershed base-cation cycles (Figure 1) was developed into a nutrient-cycling model coupled to a simulation of forest dynamics. In the family of gap-replacement models deriving from JABOWA and FORET (Botkin *et al.*, 1972; Shugart, 1984; Shugart and West, 1977), individual trees grow according to logistic curves based on species parameters. Ecological interactions between individual trees are simulated in order to produce community dynamics. For each year of simulation, for each tree a potential diameter-at-breast-height (DBH) increase is calculated from the tree age and a logistic curve for the species. The stem-diameter growth equation used in FORSWAS follows:

$$\frac{d}{dt}(D) = \frac{GD(1 - DH/D_{\max}H_{\max})}{2H + (b + cE + dS)} \quad (1)$$

where D is DBH, H is tree height, D_{\max} and H_{\max} are maximum diameter and height for the species, E is elevation, S is slope, and G , b , c , d are species growth coefficients (Harrison and Shugart, 1990). Growth in each year, for each tree is then reduced under limiting factors: shading, moisture availability, growing season degree-days, and nitrogen availability (Pastor and Post, 1986).

In constructing FORSWAS, site-specific forest growth parameterizations derived from an extensive forest survey and used to model SHW forest dynamics in OVALIS (Harrison and Shugart, 1990), were incorporated into the more general LINKAGES model (Pastor and Post, 1985). This created a hybrid model with the process-based moisture and decomposition routines in LINKAGES but the site-specific growth characteristics of the SHW forest.

In FORSWAS simulations, biomass and nutrient-flux averages over 80 simulated 0.1-ha plots were calculated. Here we consider the aggradation phase, in which biomass grew until a peak was reached after 120 to 140 simulated years (175 to 210 years forest age).

2.2. FLUX CALCULATIONS AND MODEL PARAMETERIZATION

2.2.1. Requirement Fluxes

We define *requirement* fluxes as the sum total of cations incorporated into bole, branch, and root growth, plus the full quantity of foliage and annual roots produced each year. Total root biomass for each tree was calculated as 25.6% of the tree above-ground biomass (Harris *et al.* 1973b; Rolfe *et al.* 1978). Biomass produced in each component was then multiplied by component-specific nutrient levels.

2.2.2. Return Fluxes

Foliar litter, annual root litter, fallen branches, and dead major roots and boles comprise the *return* fluxes. Tissue concentrations of base cations were the same as those for living tissue for all components but foliage.

2.2.3. Uptake Fluxes

Uptake of base cations is calculated from two other fluxes according to equation (2). Potential translocation of nutrients back to twigs from senescing foliage is shown in equation (2) though it was not addressed directly in FORSWAS, as it was outside of the scope of the present study.

$$\text{Uptake} = \text{Requirement} + \text{Canopy Leaching} - \text{Translocation.} \quad (2)$$

2.2.4. Mineralization

In estimating the base cations released *via* decomposition of organic matter in the forest floor, we incorporated a new model of base-cation release to the decomposition model in LINKAGES. Our mineralization model comprises three parts: leaching from fresh litter, short-term decomposition and long-term (humus) decay. As in LINKAGES, litter is separated into types (foliage, fine roots, and wood by size class), tracked in annual cohorts with litter-specific decay rates, and transferred to a long-term pool when it reaches its critical-C:N ratio (Aber *et al.*, 1982; Pastor and Post, 1986).

Based on leaching data (Gosz *et al.*, 1973, 1975; Blair, 1988), FORSWAS allows 25% of the K, 20% of the Mg, and none of the Ca present in leaf litter to be leached in the first year in an initial pulse unrelated to decomposition. In the second part of the mineralization model, base cations are released from each cohort based on its type, its weight loss and a nutrient-specific multiplier. In non-woody litter (including non-woody root litter), Ca is lost at a rate equal to weight loss, Mg is released at a 10% greater rate, and K at a 25% greater rate than weight loss. This model was constructed through a comparison of base-cation concentrations among forest-floor horizons at various locations (Cromack and Monk, 1975; Yount, 1975; Gosz *et al.*, 1976). From woody litter (including woody roots), the model mineralizes base cations more slowly than weight is lost, effectively concentrating the nutrients in well-decayed wood (Harmon *et al.*, 1986).

The well-decayed wood and humus pools are modeled as maintaining a constant concentration of each base cation (Weinstein, 1982). Cations are thus released at the same slow rate that mass is lost from these compartments. When litter in a given cohort passes to a long-term pool, its base cation contents are adjusted to the steady-state concentrations in that pool. In an important bookkeeping step, the surplus or deficit of base cations generated by passing litter to a long-term pool is subtracted from or added to the total mineralization flux for that year.

2.2.5. *Atmospheric Input and Canopy Leaching*

Annual precipitation varied stochastically in FORSWAS (mean and variance data from the Virginia State Climatology Office). Throughfall hydrology was calculated from precipitation amount using a SHW site-specific regression (Gilliam and Sigmon, 1987). Stemflow hydrology was estimated as 3% of the throughfall amount (Eaton *et al.*, 1973).

National Atmospheric Deposition Program (NADP) averages (1981–1990) from the Big Meadows site provided precipitation chemistry. We divided the year in two – growing season and dormant season – for the purpose of modeling throughfall (TF) chemistry. For dormant-season TF base-cation concentrations we multiplied SHW growing-season TF data (Galloway, unpublished data) by seasonal factors reported by Henderson *et al.* (1977). We estimated stemflow chemistry by multiplying TF chemistry by throughfall-to-stemflow chemistry ratios reported by Gilliam and Sigmon (1987) for SHW.

In order to distinguish between base cations dry-deposited onto the canopy surfaces and those leached from the canopy, we used cation-specific factors as given by Mayer and Ulrich (1972), which are representative of results in the literature (Parker, 1983). We thus estimated that 65.0% of Ca, 74.3% of K, and 53.9% of Mg appearing in throughfall (relative to wet deposition) were leached from the canopy.

2.2.6. *Weathering and Exchange Input*

We refer to the net geologic input of base cations from soils and bedrock as ‘Weathering and Exchange Release’ since we have no means in this study for distinguishing between mineral-weathering release of base cations and release from the soil exchange complex. In order to estimate these inputs in SHW we calculated a two-year mass balance similar to those of Velbel (1985) and Sollins *et al.* (1980):

$$\begin{aligned} &\text{Weathering and Exchange Release} + \text{Deposition} \\ &= \text{Discharge} + \text{Biomass Accretion.} \end{aligned} \tag{3}$$

‘Biomass Accretion’ is defined as the absolute change in base cations stored in living and dead biomass per unit watershed area per year. In the forest dynamics model, accretion varied substantially from year to year. The accretion values we

report here were calculated as averages over periods chosen to represent 10 to 20-year trends, as calculated in equation (4):

$$\bar{A}_{ann(i)}(\text{Ca}) = \frac{1}{n} \left[\sum_j (Cbio_j[\text{Ca}]_j)_{\text{year}(i+\frac{n}{2})} - \sum_j (Cbio_j[\text{Ca}]_j)_{\text{year}(i-\frac{n}{2})} \right] \quad (4)$$

where $A_{ann(i)}$ (Ca) represents the annual average Ca accretion flux for the period (n) of years centered about year i , $Cbio_j$ is the biomass in compartment j in kg ha^{-1} (compartments include living boles, foliage, branches and roots; all litter cohorts, which include wood and roots; and humus and well-decayed wood), and $[\text{Ca}]_j$ is the Ca concentration in compartment j .

Equation (3) requires the assumption that there is no significant change in base-cation storage in hydrologic storage pools. We have made the working assumption that any such storage is in steady-state over an annual period. In support of this assumption, the hydrologic cycle estimation method of Thornthwaite and Mather (1957) applied to SHW monthly rainfall in 1988 through 1990 (Galloway, unpublished data) showed that the watershed soils should have been fully recharged in the month of May in each year 1988, 1989, and 1990. The input-output balance calculation covers the two-year period from June 1, 1988 to May 31, 1990.

For deposition input fluxes, NADP precipitation chemistry (June 1988 to May 1990 average) from the Big Meadows site was multiplied by SHW precipitation levels over this period (Galloway, unpublished data). Export of base cations from SHW in dissolved form *via* North Fork Dry Run (NFDR) was calculated from weekly stream chemistry and continuous discharge data (K. Eshleman, unpublished data). Overland hydrologic flow was considered to be negligible (Johnson and Swank, 1973). As is usually done in watershed ecosystem analysis, the dissolved load was considered to characterize the net result of watershed leaching processes. Losses in the particulate load were also considered to be much smaller than those in the dissolved load (Likens *et al.*, 1967; Johnson and Swank, 1973).

3. Results and Discussion

3.1. FOREST DYNAMICS AND VEGETATION BASE-CATION LEVELS

Combining site-specific parameterizations with a general process-based model proved to be fruitful but did involve some subtlety in assuring consistency in the hybrid model. For example, LINKAGES' tree height-diameter relationship was replaced with that in SHW; litter calculations were amended to be consistent with allometry used in calculating biomass of various tissues, and so forth.

We considered two types of model validation. First, we ensured that the hybrid model simulated what we intended to simulate; and second, we compared predictions against field data from other locations. In checking the forest dynamics we

ensured that FORSWAS produced the same type of dynamics that OVALIS had. Oaks dominated the biomass, with *Q. prinus* overtaking *Q. rubra* after 75 years. The third most dominant species through the simulation, *T. americana*, is the third in OVALIS and the third in SHW. Peak above-ground biomass reached approximately 200 Mt/ha, in agreement with OVALIS (Harrison and Shugart, 1990). The model of forest succession in SHW was to some extent hypothetical, of course; there were only two descriptions of SHW vegetation to compare model outputs with: a qualitative description of the blighted, partially logged forest in this early century and a precise snapshot of the vegetation in 1986 (Harrison, 1987). Our model also treats forest dynamics in the absence of allochthonous disturbance.

For comparisons of predictions with data, we present standing-crop base cation levels. These are not input data but result from central calculations in the base-cation-cycling model. FORSWAS was parameterized with the results of our field study of nutrient levels by tissue type (Table II). Standing-crop calculations (Table III) serve as a check on model calculations because they are obtained by multiplying forest growth in each component by nutrient concentrations and summing across all components and over the watershed. Total base cation contents expressed as biomass concentrations are comparable between FORSWAS results and actual forests over a range of ages. The Walker Branch, Tennessee site was aged 30–80 years and lies atop soils derived from dolomite, a parent material high in Ca and Mg content; the Virelles-site forest was aged 115–160 years and stands upon calcareous brown soil. Both forests contain significant *Quercus*-spp. vegetation. The last column in Table III contains averages over all 14 IBP temperate deciduous forests (Cole and Rapp, 1981).

3.2. REQUIREMENT AND RETURN FLUXES

During simulated forest aggradation, requirement and return fluxes were high and unequal (Figures 2, 3 and 4). Later, as the forest neared peak biomass (120 to 140 simulation years), requirement fluxes diminished but remained substantially higher than return fluxes. We see three potential explanations for the gap. First, reproductive parts in litterfall, not included in this study, return significant levels of base cations to the forest floor. The sum of acorns, flowers and debris in a hardwood stand at Coweeta was found to comprise 13% of the annual litterfall, with Ca, K and Mg levels of 7, 24 and 5% (respectively) that of total litterfall (Cromack and Monk, 1974).

Second, our study found significantly lower K and Mg levels in leaf litter compared with late summer foliage (Table II). These differences were too large to be compensated for by the canopy leaching fluxes in our model. The differences in K levels in Table II, for example, suggest a loss of K from senescing leaves of $32 \text{ kg ha}^{-1} \text{ yr}^{-1}$, which is much higher than the $7.9 \text{ to } 8.3 \text{ kg ha}^{-1} \text{ yr}^{-1}$ estimated in the FORSWAS canopy leaching model. Since oaks often hold their leaves long after senescence, the foliage we collected may have undergone significant leaching

TABLE II
Base-cation contents in various components of living biomass in SHW

Tissue Component	Cation	SHW ^a [ppt] ^c	IBP ^b Temperate Deciduous [ppt]
Foliage	Ca	10.6 ±2.8 (63)	9.3 ±3.7
	K	11.1 ±1.9 (63)	9.8 ±2.3
	Mg	1.95±0.58 (63)	1.9 ±1.0
Branches	Ca	7.96±1.90 (63)	6.4 ±4.8
	K	2.46±0.73 (63)	1.8 ±0.9
	Mg	0.613±0.15 (63)	0.53±0.48
Roots	Ca	8.23±2.50 (63)	4.5 ±3.2
	K	2.83±1.06 (63)	2.4 ±1.3
	Mg	0.986±0.33 (63)	0.44±0.19
Boles	Ca	3.61±0.21 (4)	2.9 ±1.5
	K	0.999±0.20 (4)	1.6 ±1.9
	Mg	0.0778±0.0083 (4)	0.24±0.08
Fresh leaf litter	Ca	10.2 ±1.4 (10)	
	K ^d	3.84±0.77 (10)	
	Mg	1.11±0.21 (10)	

^a Number of samples, after combining for analysis (in bole and litter samples), shown in parentheses.

^b Averages from 14 Temperate Deciduous forests studied in the International Biological Programme (Cole and Rapp, 1981) shown for comparison.

^c Parts per thousand.

^d Significantly different ($p = 0.05$) from green foliage for K only.

before abscission. The fact that requirement-return flux differences decreased in the order K, Mg, Ca is consistent with such a mechanism (Gosz *et al.*, 1975). However, these differences would also be consistent with translocation of nutrients before abscission (Johnson and Henderson, 1989).

Johnson and Henderson reported levels of translocation of 19 and 10 kg K ha⁻¹ yr⁻¹ for *Quercus prinus* and *Quercus-Carya* forest types, respectively, At Walker Branch Watershed. This could account for approximately half of the difference we calculated between requirement and return fluxes near peak forest biomass in SHW.

Morrison and others (1992) made precisely the measurements we did, sampling late summer foliage *versus* foliar litterfall, in an *Acer saccharum* forest in Ontario, Canada. They reported the differences (39.9 kg K ha⁻¹ yr⁻¹, less for Mg and still less for Ca) to be entirely due to translocation. We have chosen not to attribute the

TABLE III
Comparisons among vegetation base cation pools and concentrations

	FORSWAS year 140 ^b	Walker Branch site 1 ^c	Virelles, Belgium ^c	IBP Temperate Deciduous ^c
biomass [Mt/ha]	199	122	327	152 ± 58
Ca [kg/ha]	1061	856	1444	557 ± 273
Ca, %	0.53	0.70	0.44	0.37
K [kg/ha]	347	220	510	224 ± 100
K, %	0.17	0.18	0.16	0.15
Mg [kg/ha]	61	67	120	57 ± 26
Mg, %	0.031	0.055	0.037	0.038

^a Above ground living vegetation (roots not included).

^b Forest age 195 to 210 years; first peak biomass at the end of steady aggradation.

^c Cole and Rapp, 1981.

differences solely to translocation, however, because of the known importance of foliar leaching of base cations by throughfall (Eaton *et al.*, 1973; Parker, 1983) and the inability of our sampling scheme to distinguish between the effects.

3.3. BIOTIC VERSUS GEOLOGIC FLUXES DURING AGGRADATION

The major biotically-driven fluxes through the 140-year aggradation period, modeled by FORSWAS, are summarized in Table IV with results from other studies shown for comparison.

Geologic watershed input-output fluxes were not modeled throughout aggradation, only current fluxes were quantified in a two-year mass-balance study, with the contemporary rate of forest growth used to estimate requirement fluxes in equation (3). Though two years is too short a time period over which to characterize annual geologic fluxes with a high degree of confidence, our budget (Table V and Figure 5) shows them to be substantially lower than modeled annual biotically-driven fluxes (Figures 2, 3 and 4) in SHW. This is a common result in forested-watershed studies (Johnson and Swank, 1973; Weinstein, 1982). Annual stream discharge amounted to approximately 8%, 4% and 25% (Ca, K and Mg respectively) of the annual biotic uptake.

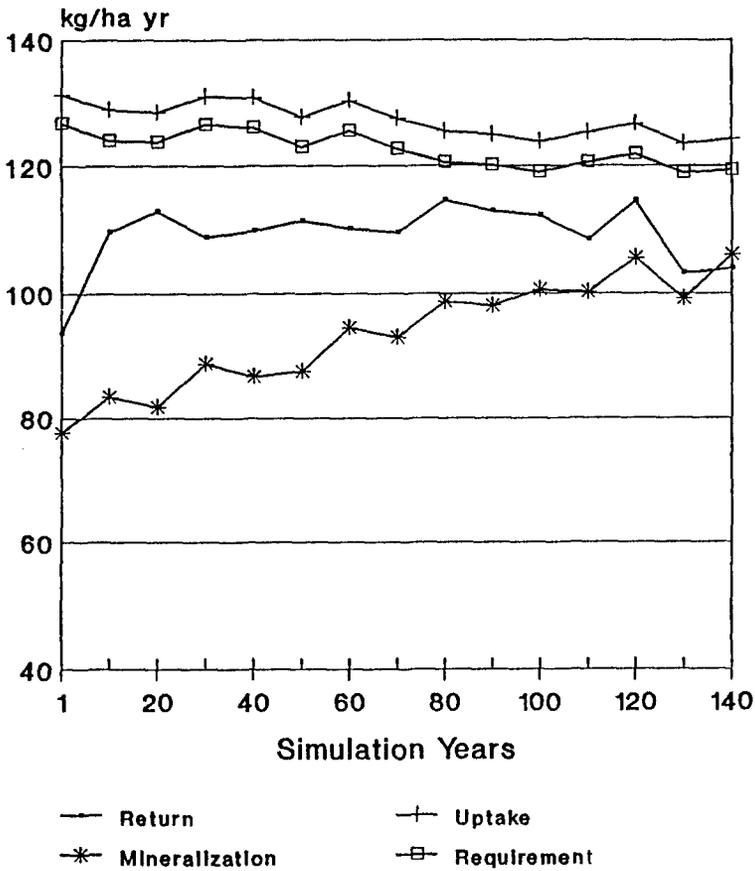


Figure 2. FORSWAS biotic calcium fluxes at SHW. (Year 1 = 1987, forest age 55–70 years.)

Decade-to-decade differences in FORSWAS biotic base-cation cycles (in Figures 2, 3 and 4), resulting from forest dynamics, were at times significant in magnitude compared with watershed input-output fluxes. In particular, the model showed return fluxes to become erratic as the forest matured. Temporal variability in biotic cycles may help account for high interannual variability in stream discharge (Table V), which could not be accounted for by variability in deposition inputs.

The most dramatic change in fluxes over the time scale of aggradation was the steady increase in mineralization. This was a direct result of the steady growth in litter, humus and well-decayed wood biomass. Since the release of base cations from litter was tied to net forest floor decomposition in the model, and since net decomposition increased with forest floor biomass increase, naturally the base-cation mineralization fluxes increased with time. Decomposition thus provided an increasingly important avenue for intrasystem recycling as the forest matured.

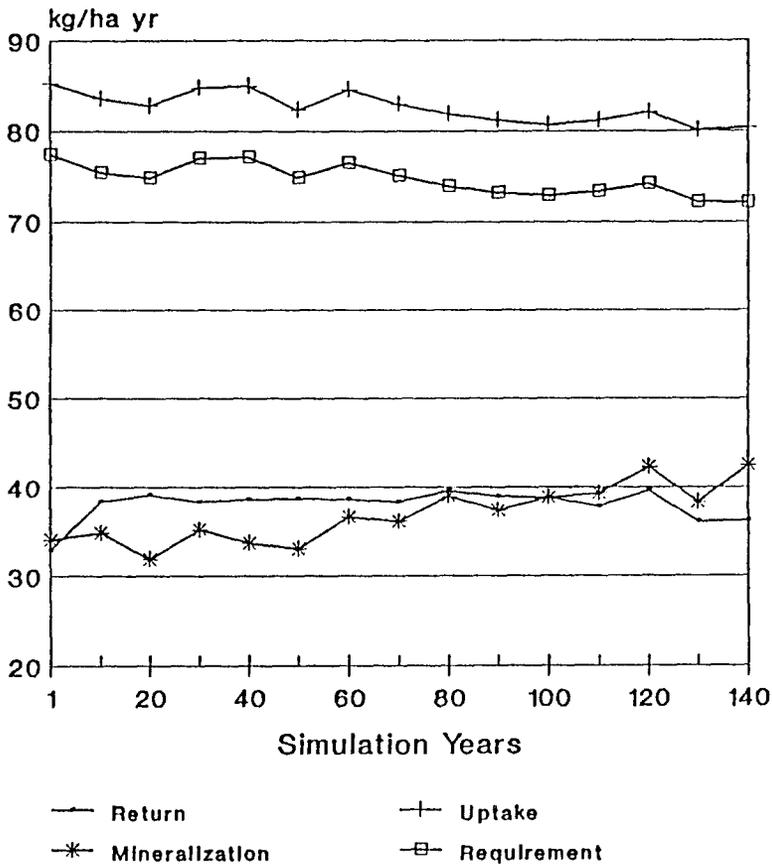


Figure 3. FORSWAS biotic potassium fluxes at SHW. (Year 1 = 1987, forest age 55–70 years.)

Before aggradation was complete, mineralization reached levels high enough to supply the bulk of modelled base-cation growth requirements.

Increases in forest-floor litter and soil organic matter mass also provided a mechanism of system base-cation retention. Base cations thus stored exemplified time delays in intrasystem cycling (Nilsson *et al.*, 1982). When forest products are removed, however, as has happened in the past century in SHW, intrasystem fluxes are diminished as nutrient capital is lost from the ecosystem. FORSWAS shows that the forest in SHW is replenishing biomass base-cation pools during biomass aggradation. The watershed analysis presented here shows that the source of base cations for these growing pools is the forest soil.

Table VI compares the potential mineral-soil-acidification effect of base-cation accretion in SHW with the maximum potential effect of acid deposition, by comparing H^+ charge equivalents entering soils from the two processes. The aggradation effect is estimated to be greater by a factor of three. Ultimately, weathering of

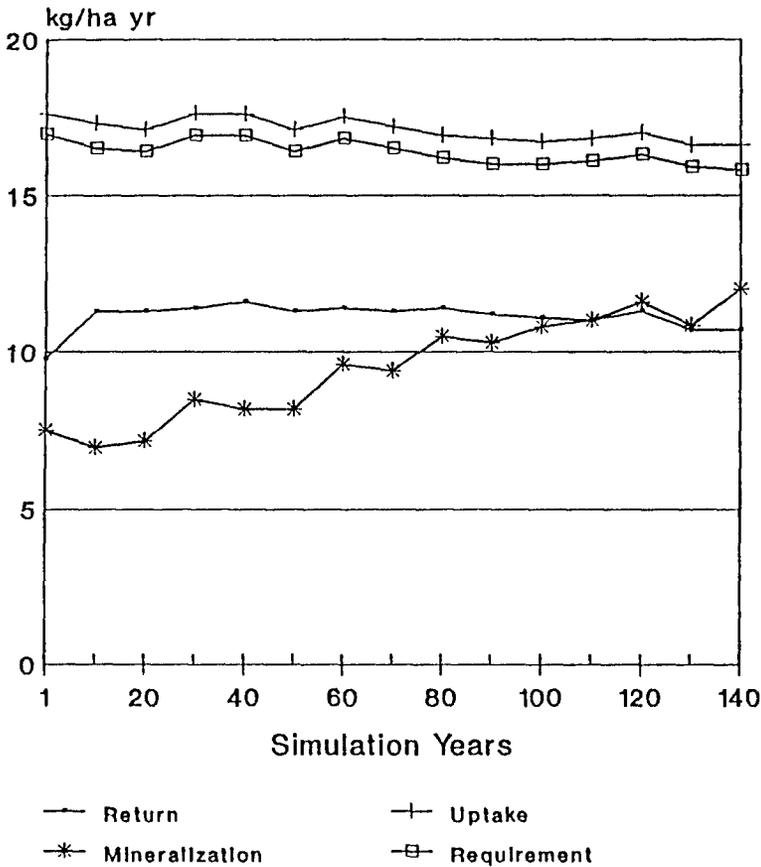


Figure 4. FORSWAS biotic magnesium fluxes at SHW. (Year 1 = 1987; forest age 55–70 years.)

parent rock consumes some H^+ and provides the primary source of base cations to the system. Whether the past removals and the current sequestering of base-cation nutrients in biomass has impacted soil %BS or stream ANC depends largely on the rates of base-cation release by primary and secondary mineral weathering.

Miller (1991) studied acid neutralization in column-leaching experiments on soils similar to those in SHW. She observed that 95% of base-cation release could be attributed to exchange and only 5% to weathering. The total base-cation release observed was insufficient to satisfy vegetation accretion in SHW. Taken together, unless roots stimulate increased weathering these facts suggest that (a) vegetation can take up base cations not leached into solution by soil water, and (b) that the soil-exchange complex in SHW is being depleted of bases.

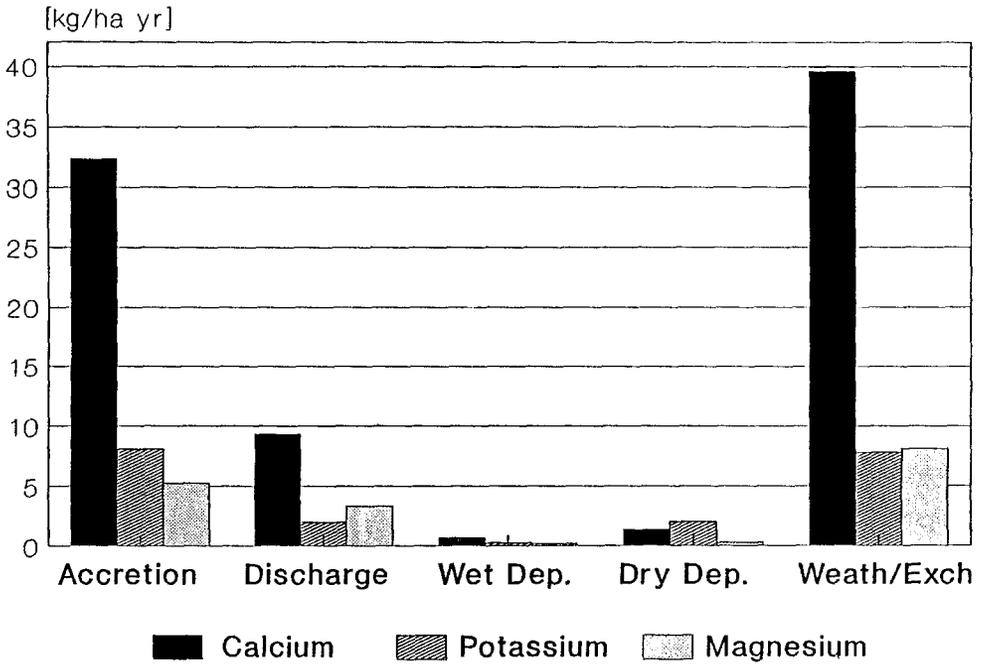


Figure 5a. Two-year watershed input-output budget at SHW for base cation fluxes [kg/ha yr].

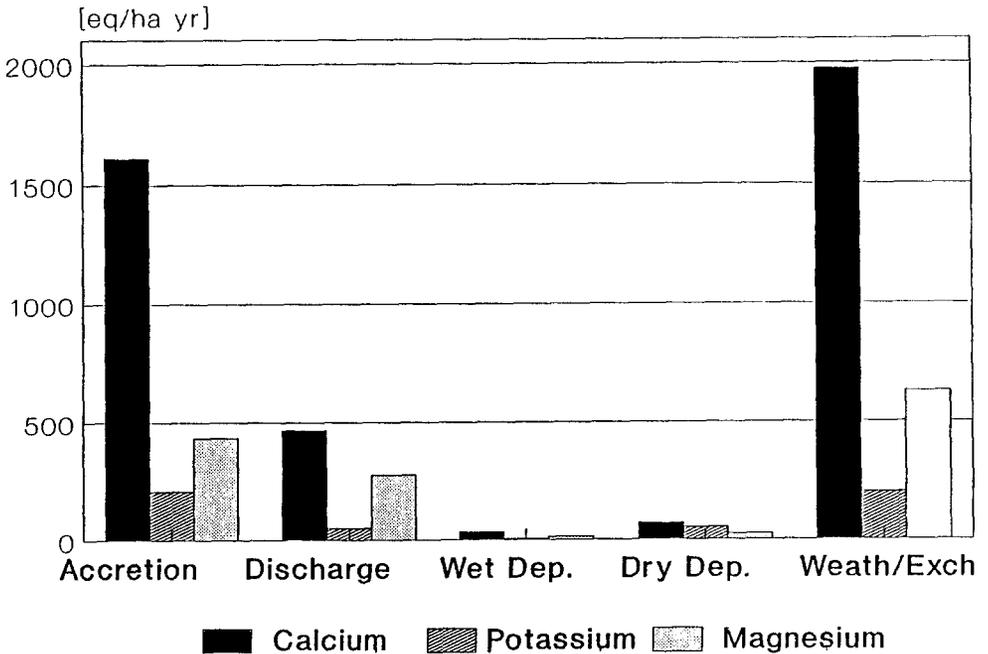


Figure 5b. Two-year watershed input-output budget at SHW for base cation fluxes [eq/ha yr].

TABLE IV
Major biotic base cation fluxes as found in various studies [kg/ha yr]

Flux	FORSWAS	IBP ¹	Hubbard Brook ²	HJ Andrews ⁴	FORNUT ⁴
Uptake					
Ca	118–130	84	67.0	66.8	105–188
K	47.6–51.7	48	68.7	26.9	50–87
Mg	12.7–13.8	13	10.4	--	14–20
Return ^a					
Ca	98.0–119	68	40.2	67.4	85–145
K	37.1–40.7	42	18.8	14.7	45–75
Mg	10.7–11.8	11	5.8	--	12–19
Mineralization					
Ca	63.3–102	--	43.7	63.8	105–175
K	21.0–39.3	--	24.3	17.9	53–94
Mg	4.0–11.0	--	6.8	--	15–24

References:

- ¹ Averages from 14 IBP temperate deciduous forest studies; Cole and Rapp, 1981.
² Whittaker *et al.*, 1979, Hubbard Brook, New Hampshire.
³ Sollins *et al.*, 1980, HJ Andrews Experimental forest, Oregon. (Note this is an old-growth *Pseudotsuga menziesii* [Douglas Fir] forest shown for comparison; all others are deciduous, and most are aggrading.)
⁴ Weinstein, 1982, Walker Branch Watershed, Tennessee.

Notes:

^a Litterfall returned to the forest floor from the vegetation annually (does not include canopy leaching). FORSWAS, FORNUT, and Andrews contain root litter; others do not.

4. Conclusions

The vegetation in SHW shows an apparent selection of K over Mg; vegetation accretion of K supersedes that of Mg, while watershed losses of Mg in stream discharge exceed losses of K. We may conclude only that Mg is relatively more important in providing ANC to the streams in SHW while K is more important as a plant nutrient in SHW.

Green foliar and foliar litterfall differ in K content in SHW, causing a difference in requirement *versus* return fluxes at the watershed scale (likewise for Mg and Ca, though the foliar differences were not statistically significant). The difference is partly due to canopy leaching and may also be partly due to translocation.

The rate of net accumulation of base cations by biomass (living and dead) should decline as the forest matures and mineralization increases. Forest-floor litter and humus in SHW should become an increasingly important avenue for the recycling of base-cation nutrients as aggradation proceeds.

TABLE V
Two-year input-output budget to base cations in SHW
[kg/ha yr]

	Ca	K	Mg
Accretion in Biomass ^a	32.3	8.12	5.27
Loss <i>via</i> stream discharge			
6/1/88–5/31/89	5.72	1.26	2.04
6/1/89–5/31/90	13	2.74	4.66
Annual average	9.36	2	3.35
Wet deposition input			
6/1/88–5/31/89	0.60	0.21	0.15
6/1/89–5/31/90	0.83	0.29	0.20
Annual average	0.71	0.25	0.17
Dry deposition input ^b	1.36	2.03	0.30
Weathering/exchange input ^c	39.6	7.84	8.14

^a Includes above ground biomass, roots, forest floor and soil organic matter accretion. Annual average over FOR-SWAS simulation years 1–25 (forest age equals FOR-SWAS year plus 55–70 years).

^b Annual average 1988–1989.

^c Inferred *via* mass balance.

This study has shown that in a watershed in Central Appalachia receiving high levels of acid deposition and containing low %BS in soils, an aggrading forest is sequestering and retaining base cations at levels significantly greater than watershed losses. Intrasystem cycles proceed at flux levels greater still. This study highlights the importance of considering forest dynamics in ecosystem nutrient-cycling studies, because temporal changes in biotically-driven fluxes can outweigh geologic fluxes.

Base-cation accretion in biomass in SHW (studied independently of N and S transformations and organic acid production) results in a flux of H⁺ equivalents to soil at three times the rate of atmospheric deposition during the years of steady forest regrowth.

Rates of weathering in the field are poorly understood, but our study taken together with the Miller (1991) study suggests that quantities of base cations are being removed from the soil exchange complex through acid leaching and forest uptake in SHW at rates greater than the rates of supply by weathering, depleting soil-exchangeable pools.

Acknowledgements

This work comprises part of the Shenandoah Watershed Study (SWAS), which began in 1979 to assess the impact of acid deposition on soil and stream systems in

TABLE VI
Charge equivalent flux comparisons [eq/ha yr]

	Ca ²⁺	K ⁺	Mg ²⁺	Total ^b
A. Weathering and exchange ^a , White Oak Run, VA (Miller, 1991)	--	--	--	560
B. Weathering and exchange, SHW (Table V)	1975	201	670	2800
C. Biomass accretion, present day (Table V)	1610	207	434	2300
D. Biomass accretion, FORSWAS year 25 ^c	1652	224	422	2300
E. Biomass accretion, FORSWAS year 125 ^c	425	60	111	600
F. H ⁺ input from atmospheric deposition ^d	--	--	--	690

^a Leached into solution during acid neutralization.

^b All totals rounded to two significant digits.

^c Forest age is FORSWAS simulation year plus 55–70 years.

^d Wet deposition from NADP data (1980–1990), with dry deposition of H⁺ estimated as an equivalent annual amount (see Galloway and Rodhe, 1991).

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