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Cation distribution, cycling, and removal from mineral soil in Douglas-fir and red alder forests

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Abstract. Overstory species influence the distribution and dynamics of nutrients in forest ecosystems. Ecosystem-level estimates of Ca, Mg, and K pools and cycles in 50-year old Douglas-fir and red alder stands were used to determine the effect of overstory composition on net cation removal from the mineral soil, i.e. cation export from the soil in excess of additions. Net cation removal from Douglas-fir soil was 8 kg Ca ha^{-1} yr^{-1}, 1 kg Mg ha^{-1} yr^{-1}, and 0.3 kg K ha^{-1} yr^{-1}. Annual cation export from soil by uptake and accumulation in live woody tissue and O horizon was of similar magnitude to leaching in soil solution. Atmospheric deposition partially off-set export by adding cations equivalent to 28–88% of cation export. Net cation removal from red alder soil was 58 kg Ca ha^{-1} yr^{-1}, 9 kg Mg ha^{-1} yr^{-1}, and 11 kg K ha^{-1} yr^{-1}. Annual cation accumulation in live woody tissue and O horizon was three times greater than in Douglas-fir, while cation leaching in soil solution was five to eight times greater. The lack of excessive depletion of exchangeable cations in the red alder soil suggests that mineral weathering, rather than exchangeable cations, was the source of most of the removed cations. Nitric acid generated during nitrification in red alder soil led to high rates of weathering and NO_3-driven cation leaching.

Introduction

Trees influence the distribution of cations within ecosystems by cation uptake from soil and subsequent accumulation in living tissue or in decomposing detritus following tissue death. Different species can have large effects on cation distribution (Alban 1982), because of differences in inherent growth and nutritional characteristics. Species also affect leaching of cations through the soil (Van Miegroet & Cole 1984, 1985). The cumulative result of these influences can be different mineral soil properties under different overstory species, despite similar initial soil conditions (Alban 1982; Ovington 1958).

Net cation removal from mineral soil occurs when soil leaching plus cation accumulation in vegetation and O horizons exceed atmospheric inputs. Accumulation in organic matter was the dominant cause of a reduction in exchangeable Ca^{2+} in the mineral soil over an 11-year period in four southeastern USA hardwood forests; in contrast, leaching was the major cause of reduction in exchangeable Mg^{2+} in three of the four forests (Johnson & Todd 1990). Uptake and accumulation in organic matter was the dominant pathway of Ca and K removal from the mineral soil in four northern USA hardwood and conifer stands, whereas both accumulation in organic matter and leaching contributed substantially to Mg removal (Alban 1982). Establishing rates and pathways of cation removal from the mineral soil is important because of the potential effect of cation loss on long-term forest productivity (Federer et al. 1989; Johnson et al. 1988).

Red alder (*Alnus rubra* Bong.) and Douglas-fir (*Pseudotsunga menziesii* (Mirb.) Franco) can occupy similar sites in western Washington and Oregon, USA. Due to differences in life cycles, deciduous vs. coniferous foliage, and soil processes affected by N enrichment associated with the N_2-fixing alder, Douglas-fir and red alder have the potential to differ sharply in cation cycling and distribution patterns. In comparing a 34-year old red alder stand on glacial till with a 36-year old Douglas-fir stand on glacial outwash, Cole et al. (1978) found tree uptake and litterfall transfer of Ca and K were much more rapid in the red alder stand. Turner et al. (1976) found lower mass of Ca and K in the red alder than Douglas-fir trees. In the comparison of slightly older stands on glacial till, however, Van Miegroet et al. (1990) found higher mass of Ca and K in the vegetation of a red alder than a Douglas-fir stand. Much higher cation leaching occurred in red alder soil due to nitrification and the resulting NO_3-induced cation movement (Van Miegroet & Cole 1984, 1985).

Our objectives in this study were (1) to determine the relative rates of net Ca, Mg, and K removal from the mineral soil in Douglas-fir and red alder ecosystems, and (2) to determine the contributions of accumulation in organic matter and soil leaching to net cation removal. The ecosystems under study consisted of forest vegetation, organic soil horizon, and mineral soil to a depth of 40 cm in the stands previously studied by Van Miegroet & Cole (1984, 1985, 1988) and Van Miegroet et al. (1990). We present a comprehensive comparison of cation distribution and cycling in those stands.

Study site

The study was conducted at the Thompson Research Center in the Cedar River Watershed, located 56 km SE of Seattle, Washington, USA, in the western foothills of the Cascade Mountains at an elevation of 220 m. Long-term mean annual precipitation is 130 cm, with most falling as rain between October and March. Average temperature is 3 °C in January and 17 °C in July.

As summarized by Cole et al. (1968) and Turner et al. (1976), the original forest was harvested between 1910 and 1920. After a series of wildfires, part of the area was replanted with Douglas-fir in 1931, and the remaining area was invaded by red alder in subsequent years, resulting in adjacent stands of nearly pure Douglas-fir and red alder. We refer to these as 50-year old stands, although red alder establishment lagged the Douglas-fir planting by several years (Turner et al. 1976). In this study, a 20 × 20 m plot was established in 1979 in each of the Douglas-fir and red alder stands. The two plots were approximately 200 m apart. Stands were on the Alderwood series soil, previously classified as a Dystric Entic Durocrept but recently reclassified as an Aquic Haplorthod. The Alderwood series is a gravelly, sandy loam developed in ablation till overlying compacted basal till at a depth of about 1 m. Comparison of soil from the two plots indicates similar mineralogy (April & Newton 1992). On a mass basis, the sand-size particles (0.063 to 2 mm) contain approximately 35% quartz, 10% K feldspar, and 30% plagioclase (Na:Ca molar ratio of approximately 3:2). Vermiculite dominates the clay-size particles (<2 μm), with kaolinite, chlorite, and mica also present. We have no information about the composition of the silt fraction.

Methods

Vegetation and soil

Live trees were numbered and diameters measured when plots were established in 1979. Tree status (alive or dead) was assessed and tree diameters were remeasured at 1 to 2-year intervals through 1988. Woody tissue biomass for live trees was estimated from the 1985 diameter measurements and regression equations (Dice 1970; Gholz et al. 1979). Four types of woody tissue were quantified: branches, bole bark, bole wood, and woody roots.

Woody tissue growth was determined for each live tree as the change in woody tissue biomass that occurred between successive measurements. Woody tissue mortality was defined as the transfer at tree death of live woody tissue to a detrital pool of coarse woody debris; this latter pool was not quantified but was considered to include dead standing trees, fallen logs, and large woody pieces (> 6 cm in diameter) lying on the surface of the O horizon. Net woody tissue increment was the difference between woody tissue growth and woody tissue mortality. Average rates of woody tissue growth, woody tissue mortality, and net woody tissue increment were determined for the 1979 to 1988 period.

Total foliar mass in red alder was determined as 1.12 times foliar litter, based on the data of Turner et al. (1976). Current foliage — that produced during the most recent year — was equivalent to total foliage for this deciduous species. Total foliar mass in Douglas-fir was determined as 5.88 times foliar litter, based on the studies of Marshall & Waring (1986) and Heilman & Gessel (1963a, b). Current foliage mass was assumed equivalent to annual foliar litter. Non-woody ('fine') root mass and production were not quantified.

Foliage, branch, bole wood, and bole bark samples were taken from ten trees in each stand in late May 1985. Woody root samples were taken from five trees in each stand in September 1988. Samples were analyzed for Ca, Mg, and K by lithium sulfate/sulfuric acid digestion (Parkinson & Allen 1975) followed by atomic absorption of the digest. Cation pools were estimated by multiplying average concentrations by estimated tree-component masses for each entire plot.

Understory was collected in July 1986 from four 1 × 1 m subplots per plot. In the Douglas-fir stand, understory consisted mainly of salal (*Gaultheria shallon* Pursh.), Oregon grape (*Berberis nervosa* (Pursh.) Nutt.), and bracken fern (*Pteridium aquilinum* Kuhn var. *pubescens* Underw.). In the red alder stand, understory was predominantly sword fern (*Polystichum munitum* (Kaulf.) Presl.) and bracken fern intermixed with some Oregon grape.

Organic (O) horizon was collected from a 0.5 × 0.5 m area within each understory subplot and separated into (i) wood and (ii) litter plus humus. Wood included all woody material within the O horizon plus woody material < 6 cm in diameter on the surface. Wood > 6 cm in diameter on the surface was not quantified. Samples were dried (70 °C), weighed, and analyzed for Ca, Mg, and K by the method of Parkinson & Allen (1975). Cation pools were calculated separately for each subplot.

Mineral soil was sampled by depth (0—7, 7—15, 15—30, 30—45 cm) in June 1985 (four soil pits in red alder plot, five in Douglas-fir). Soil was air dried and sieved. The < 2 mm fraction was analyzed for exchangeable cations by extraction with unbuffered 1 *M* NH_4Cl, total cations by HF digestion (Lindberg et al. 1989), and organic C by Leco combustion. Cation exchange capacity was determined by saturating soil with unbuffered 1 *M* NH_4Cl, rinsing with ethyl alcohol, extracting with 1 *M* KCl, and analyzing the extract for NH_4^+ (Lindberg et al. 1989). Bulk density and gravel (>2 mm) content of mineral soil were determined by depth in areas adjacent to the plots (two measurements per stand in 1980 plus eight measurements per stand in 1984).

Dry atmospheric deposition

Atmospheric deposition samplers were located on a tower extending 2 m above the canopy of the Douglas-fir stand. Collection methods are described in detail by Lindberg et al. (1989). Aerosol concentrations were determined by drawing air at a known rate through 2-μm Teflon filters, extracting the filters with deionized water, and analyzing extracts for cations by atomic absorption. Filters were changed at 3 to 21-day intervals from September 1986 through August 1988. Calculated concentration was multiplied by deposition velocity to determine deposition on an areal basis. Deposition velocity was estimated with a model using canopy surface area and meteorological measurements as inputs (S.E. Lindberg, Oak Ridge National Laboratory, personal communication); for red alder it was 0.093 cm sec^{-1} during the growing season (April through October) and 0.003 cm sec^{-1} during the dormant season, while for Douglas-fir it was 0.14 cm sec^{-1} throughout the year. Coarse-particle deposition onto inert surfaces (glass Petri dishes) was measured from May through August 1987 and multiplied by a scaling factor of 2.8 to estimate deposition to the canopies; this scaling factor was determined from leaf area index and the relationship between scaling factor and leaf area index presented by Lindberg et al. (1988).

Solution fluxes

Solutions were collected continuously and sampled monthly from September 1986 through August 1988 except during dry summer months when insufficient sample volumes were available for analysis. Collection volumes were recorded at time of sampling. Wet deposition was collected with a wet/dry collector (Aerochem Metrics, Miami, FL) adjacent to the dry deposition collectors. Throughfall (4 replicates per plot) was collected in plastic bottles fitted with 16-cm diameter funnels covered with 1-mm mesh nylon cloth. Stemflow (4 replicates per plot) was delivered to plastic drums by rubber stemflow collars attached to trees with silicone sealant.

Ceramic (18-cm diameter) or sintered-glass (6-cm diameter) tension (−10 kPa) lysimeters collected soil solution beneath the O horizon, in the A horizon (10 cm soil depth) and in the B horizon (40 cm soil depth; 3 to 5 replicate lysimeters per horizon per plot). Red alder lysimeters had been in place and used continuously since 1979 and Douglas-fir lysimeters since March 1986. We made no attempt to prevent degassing of CO_2 from soil solutions.

Unfiltered solutions were analyzed for pH by glass electrode and for HCO_3^- by titration to pH 5.0. Solutions were filtered through glass-fiber filters (Whatman GF/A) and filtrates were analyzed for Ca, Mg, and K by atomic absorption following addition of La and Cs. Soil solutions were also analyzed for SO_4^{2-}, Cl^-, NO_3^-, and orthophosphate by ion chromatography; and Al by inductively coupled plasma spectrometry.

Cation fluxes on an areal basis were calculated for the different solutions by different approaches. For precipitation and throughfall, cation flux equaled cation concentration times collection volume divided by cross-sectional area of collector. For stemflow, cation flux equaled cation concentration times collection volume per tree times tree density.

For soil solutions, cation flux equaled average volume-weighted concentrations for replicate lysimeters times soil water flux at the depth of the lysimeter. The latter was estimated as throughfall plus stemflow minus water extracted by vegetation for transpiration from above the lysimeter depth. Extracted water as a function of soil depth was estimated by an approach similar to that of Friedland & Johnson (1985), which incorporates the concept that greatest water extraction occurs close to the soil surface where root density is highest. In this approach,

$$y = K \ln(x) \qquad [1]$$

where y is the cumulative extracted water (expressed as % of precipitation) to a depth x (cm). The constant K is equal to total transpiration from throughout the entire soil profile divided by ln (total soil profile depth).

Total transpiration was calculated as the sum of overstory transpiration plus understory transpiration. Overstory transpiration (43.4% of precipitation for Douglas-fir and 28.5% for red alder) was estimated from results of the PROSPER model (Vose & Swank 1992). Understory transpiration was assigned values of 2% of precipitation for Douglas-fir and 10% for red alder, with the difference between these values due to higher understory mass and its greater exposure to sunlight in the deciduous red alder stand. Total soil depth was taken as O-horizon depth (3 cm for Douglas-fir and 6 cm for red alder) plus 100 cm mineral soil, because there is a horizon of very low permeability at this depth. The resulting K values for Eq. [1] were 9.80 for Douglas-fir and 8.35 for red alder.

Litterfall

Litterfall was collected continuously in 0.5 × 0.5 m frames with 1-mm nylon mesh bottoms (4 per plot) from September 1985 through August 1988. Litter was removed monthly, oven dried (70 °C), sorted into foliage and other components, weighed, composited over 6-month periods, and analyzed for Ca, Mg, and K by the method of Parkinson & Allen (1975). Cation flux on an areal basis was determined for each individual collector.

Data evaluation

For measurements where there were replicate samples, samplers or subplots within each plot, the red alder and Douglas-fir plots were compared with t-tests. Such comparisons were performed for throughfall and litterfall fluxes, understory and O-horizon pools, soil characteristics, and soil solution concentrations. Because of lack of replication of plots, these comparisons only tested for differences between plots, but did not indicate if differences were due to overstory species (red alder vs. Douglas-fir). Factors other than overstory species that might contribute to differences between plots include differences in soil properties at time of stand establishment and hydrologic variability.

Other cation pools and fluxes had variability associated with them that we did not quantify. Therefore, statistical comparisons between the Douglas-fir and red alder plots were not possible for those estimates. However, based on parameters for which we did have variability estimates (Table 1), we considered differences to be real when the red alder and Douglas-fir values differed by more than a factor of two.

Table 1. Ratios of red alder to Douglas-fir mean values required to attain a difference at $P < 0.05$, based on 4 replicates per plot, for cation masses and fluxes.

	Ca	Mg	K
Cation masses			
Understory	1.84	1.77	1.82
Total O-horizon	2.15	2.13	2.07
Cation fluxes			
Throughfall	1.45	1.34	2.22
Overstory foliar litter	1.10	1.15	1.30
Overstory nonfoliar litter	1.70	1.93	2.20

Results and discussion

Cation distribution

Patterns of cation distribution on an areal basis varied among Ca, Mg, and K and between the red alder and Douglas-fir stands (Table 2). In the Douglas-fir stand, Ca was fairly evenly distributed among the overstory components, while Mg and K contents were lower in the overstory bark. In contrast, the understory stored lower amounts of Ca but similar amounts of Mg and K as individual overstory components. The O-horizon contained cations equivalent to 70% of the Ca, 100% of the Mg, but only 23% of the K contained in the total vegetation.

In the red alder stand, foliage and understory contained small amounts of Ca compared with the other vegetation components. Bole wood contained the largest amount of Mg, while bole wood, branches, and understory were of similar importance in storing K. The O horizon contained more Ca and Mg than the total vegetation, but only 25% of the K.

In the Douglas-fir stand, exchangeable cations in the mineral soil to a depth of 45 cm were equivalent to 154, 128, and 103% of Ca, Mg, and K contents associated with the vegetation plus O horizon. In contrast, these values were only 54, 37, and 22%, respectively, in the red alder stand. The cause of this difference in relative distribution was due largely to the much higher cation contents in the red alder vegetation and O horizon rather than to lower exchangeable cation pools in the red alder soil.

Foliar mass and cation contents in the red alder stand were quite similar to those measured by Turner et al. (1976) in the same stand 13 years previously; this is consistent with canopy closure in red alder stands occurring early in stand development. Mass of woody tissue in live trees was greater in this study, but nutrients in woody tissue did not parallel the increased biomass due to very different tissue concentrations measured in the two studies. Calcium and K concentrations were much greater while Mg concentration was less in the present study. Changes during tree maturation may have contributed to these differences in concentrations, but differences in analytical methods must also be considered. The cation concentration for wood-plus-bark and branches from the present study are within the ranges of concentrations for other deciduous stands (based on data in Johnson & Lindberg 1992), while branch K and all wood-plus-bark cations from Turner et al. (1976) lie outside those ranges. Both understory biomass and O-horizon mass were higher in the present study, continuing a trend of accumulation with stand age previously observed by Turner et al. (1976).

Differences both in component biomasses and in cation concentrations

Table 2. Component mass and cation contents of adjacent stands of 50-year-old Douglas-fir and red alder.

Component	Stand[1]	Mass	Ca	Mg	K
		Mg ha^{-1}		(kg ha^{-1})	
Total vegetation	DF	319	317	29	160
	RA	278	681	80	506
Overstory foliage	DF	6.2	38	7	38
	RA	3.5	23	6	43
Overstory woody tissue					
Branch	DF	22.9	86	8	39
	RA	29.4	96	11	91
Bole wood	DF	216	48	6	17
	RA	174	143	31	160
Bole bark	DF	26.3	52	2	6
	RA	19.4	261	9	29
Woody roots	DF	44.5	68	5	31
	RA	45.8	134	12	74
Understory	DF	3.1	25	6	29
		(1.0)[2]	(16)	(2.6)	(10)
	RA	6.0	24	11	109
		(2.1)	(8)	(2.4)	(34)
	P[3]	0.05	NS	0.05	0.01
O Horizon					
Total	DF	36.7	227	30	36
		(24.4)	(77)	(13)	(18)
	RA	98.5	831	97	120
		(36.1)	(423)	(46)	(26)
	P	0.05	0.01	0.01	0.01
Litter and humus	DF	23.5	182	23	28
		(6.1)	(17)	(5)	(5)
	RA	79.6	666	86	112
		(12.4)	(240)	(30)	(20)
	P	0.001	0.001	0.001	0.001
Wood[4]	DF	13.2	45	8	9
		(18.4)	(66)	(12)	(14)
	RA	18.9	165	11	8
		(23.8)	(253)	(16)	(8)
	P	NS	NS	NS	NS

Table 2 (continued)

Component	Stand[1]	Mass Mg ha^{-1}	Ca	Mg (kg ha^{-1})	K
Mineral soil to 45 cm					
Total	DF	2000	33000	21000	17000
	RA	1800	28000	19000	14000
Exchangeable	DF		839	75	203
	RA		817	66	137

[1] DF, Douglas-fir; RA, red adler.

[2] Standard deviation.

[3] Probability that Douglas-fir and red alder values are the same; based on t-tests of nontransformed or log-transformed data; $n = 4$. Only understory and O horizon components were tested. Other components were estimates for entire plots and could not be statistically tested. NS, not significant, $P < 0.1$.

[4] Includes wood on surface <6 cm in diameter plus all wood within O horizon.

contributed to the differences in cation contents between Douglas-fir and red alder ecosystems. Foliar Mg and K contents in the two stands were similar, because higher foliar mass in the Douglas-fir was offset by higher cation concentrations in red alder foliage. In contrast, Ca concentrations were similar in Douglas-fir and red alder foliage, and lower Ca content of red alder foliage was primarily due to lower foliar biomass.

In the other vegetation components, the red alder stand generally had much greater cation storage, except for Ca in the understory. The higher cation contents in woody overstory components (branches, bole wood, bole bark, and roots) of the red alder stand were due to higher concentrations, rather than differences in biomass. In contrast, higher cation contents in the red alder O horizon were due mainly to higher O horizon mass. The higher O horizon mass may be a consequence of both greater litterfall (discussed below) as well as slower decomposition rate. Although red alder foliar litter decomposes more quickly than Douglas-fir needle litter during the first year (Edmonds 1980), thereafter it has a slower decomposition rate, leading to lower cumulative loss than Douglas-fir after four years (P.S. Homann unpublished data).

Soil properties

Estimates of masses of exchangeable and total cation pools in the upper 45-cm of mineral soil were generally too close to distinguish between the two stands (Table 2). However, there were distinct differences within the soil profiles. Exchangeable Ca was lower at the soil surface and higher at depth under red alder (Table 3). Although this trend was not highly statistically significant, two other comparative studies in these stands have yielded similar results, despite different sampling times and methodology (Fig. 1); therefore, the differences in Ca appear to be real. Mechanisms that could have produced this pattern include cation displacement and NO_3-induced leaching of cations from the surface of the red alder soil (Van Miegroet & Cole 1984, 1985).

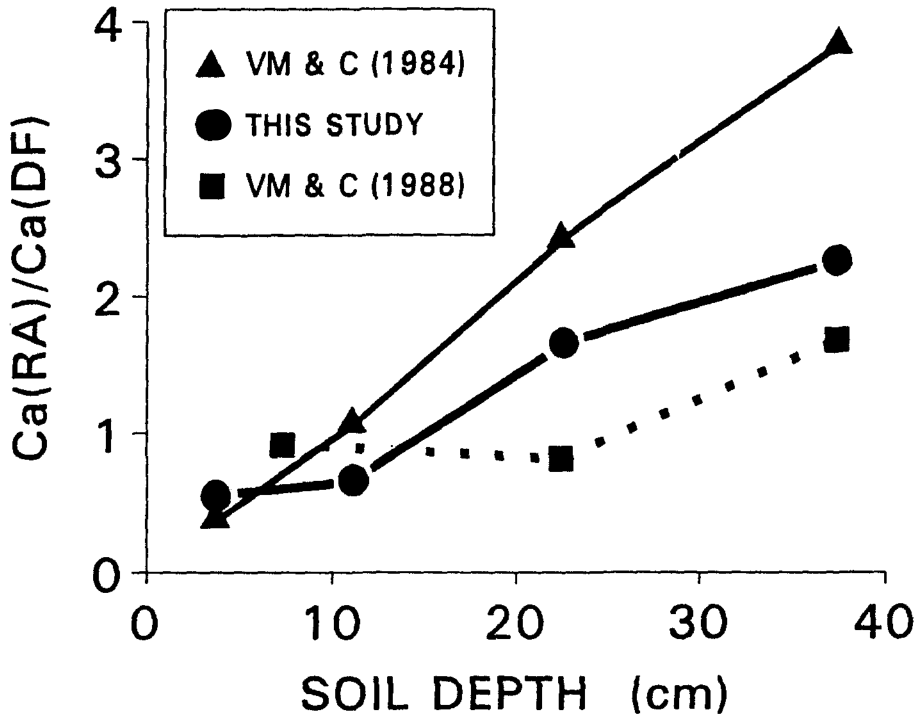

Fig. 1. Ratio of exchangeable Ca concentration in red alder (RA) soil to exchangeable Ca concentration in Douglas-fir (DF) soil as related to soil depth; based on data from this study and Van Miegroet & Cole (1984, 1988).

Table 3. Soil properties for adjacent stands of 50-year-old Douglas-fir and red alder.

Horizon & Depth (cm)	Stand[1]	pH (H_2O)	pH ($CaCl_2$)	Organic C (mmol kg^{-1})	CEC[2]	Exchangeable Ca	Exchangeable Mg	Exchangeable K	Total Ca	Total Mg	Total K
					(mmol$_c$ kg^{-1})						
A 0–7	DF	5.0	4.3	6670	164	55	7.7	4.9	780	690	190
		(0.2)[3]	(0.3)	(1330)	(10)	(24)	(2.8)	(1.5)	(65)	(50)	(17)
	RA	4.3	3.8	8800	191	30	4.1	3.9	740	750	190
		(0.4)	(0.2)	(2920)	(32)	(16)	(2.3)	(1.3)	(185)	(240)	(35)
	P[4]	0.01	0.05	NS	NS	0.1	0.1	NS	NS	NS	NS
A 7–15	DF	5.6	4.7	3820	112	24	3.4	3.0	790	760	210
		(0.2)	(0.2)	(1120)	(19)	(12)	(1.5)	(0.7)	(68)	(102)	(24)
	RA	4.8	4.3	5230	148	15	1.9	2.4	750	860	190
		(0.3)	(0.2)	(1400)	(20)	(3)	(0.6)	(0.8)	(56)	(74)	(25)
	P	0.01	0.05	NS	0.05	NS	0.1	NS	NS	0.1	NS
B 15–30	DF	5.5	4.8	2740	93	12	2.0	2.1	810	810	210
		(0.3)	(0.3)	(1010)	(20)	(6)	(0.8)	(0.4)	(51)	(63)	(25)
	RA	5.2	4.5	4310	113	20	2.4	1.5	820	890	210
		(0.3)	(0.3)	(480)	(7)	(7)	(1.7)	(0.7)	(129)	(84)	(16)
	P	NS	NS	0.05	0.1	0.1	NS	NS	NS	0.1	NS

Table 3 (continued)

Horizon & Depth (cm)	Stand[1]	pH (H$_2$O)	pH (CaCl$_2$)	Organic C (mmol kg^{-1})	CEC[2]	Exchangeable Ca	Exchangeable Mg	Exchangeable K	Total Ca	Total Mg	Total K
					(mmol$_c$ kg^{-1})						
B 30—45	DF	5.5	4.8	2350	101	12	1.9	1.6	910	1010	250
		(0.1)	(0.1)	(1030)	(16)	(13)	(1.8)	(0.5)	(63)	(66)	(17)
	RA	5.5	4.7	3620	109	27	3.8	1.4	720	860	210
		(0.3)	(0.1)	(550)	(10)	(15)	(2.6)	(0.7)	(67)	(71)	(15)
	P	NS	NS	0.1	NS	NS	NS	NS	0.01	0.01	0.01

[1] DF, Douglas-fir; RA, red alder.

[2] Cation exchange capacity by saturation with 1 *M* NH$_4$Cl.

[3] Standard deviation.

[4] Probability that Douglas-fir and red alder values are the same; based on t-tests of nontransformed or log-transformed data; $n = 4$ or 5. NS, not significant, $P < 0.1$.

Cation cycling

Cations were added to the ecosystems by both wet and dry deposition (Table 4). Dry deposition made up approximately one-third of total cation deposition, which is within the range reported for a variety of temperate forests (Ragsdale et al. 1992). Coarse particles were responsible for 90% or more of the dry deposition; this is consistent with observations at other temperate forests (Ragsdale et al. 1992). The coarse particles are considered to be inputs to the forests rather than material that has been released from the forest canopies and redeposited to them. This interpretation is supported by observations of Lindberg & Lovett (1985), which indicated coarse particles deposited in a chestnut oak forest were fly ash and soil dust. Furthermore, the coarse particles deposited in the Douglas-fir and red alder stands contained large amounts of Na (Ragsdale et al. 1992), suggesting marine sources.

Table 4. Cation fluxes in adjacent stands of 50-year-old Douglas-fir and red alder.

Flux	Stand[1]	Solution	Mass	Ca	Mg	K
		(cm yr^{-1})	- - - - - - - - (kg ha^{-1} yr^{-1}) - - - - - - - -			
Dry aerosol deposition	DF, RA		ND[2]	< 0.1	< 0.02	< 0.1
Dry coarse particles	DF, RA		ND	0.9	0.21	0.9
Wet deposition	DF, RA	114		2.1	0.68	1.3
Throughfall	DF	95		2.9	0.99	7.0
		(9)[3]		(0.8)	(0.25)	(3.7)
	RA	109		4.3	1.56	16.1
		(11)		(0.7)	(0.12)	(7.5)
	P[4]	0.1		0.05	0.01	0.05
Stemflow	DF	1.3		0.3	0.06	0.6
	RA	0.7		0.05	0.01	0.5
Canopy leaching[5]	DF		ND	0.2	0.16	5.4
	RA		ND	1.3	0.68	14.4
Resorption[6]	DF		ND	−4.6	0.1	−1.5
	RA		ND	−13.6	0.7	15.2
Overstory foliar litter	DF		1050	10.9	0.92	2.6
			(82)	(0.7)	(0.09)	(0.5)
	RA		3120	34.2	4.67	13.4
			(190)	(1.5)	(0.28)	(1.5)
	P		0.001	0.001	0.001	0.001

Table 4 (continued)

Flux	Stand[1]	Solution (cm yr^{-1})	Mass	Ca	Mg	K
			- - - - - - - - (kg ha^{-1} yr^{-1}) - - - - - - - -			
Overstory nonfoliar litter	DF		730	4.5	0.58	1.6
			(250)	(1.8)	(0.33)	(1.1)
	RA		1360	10.8	1.62	5.2
			(190)	(1.8)	(0.29)	(1.2)
	P		0.01	0.01	0.01	0.01
Woody tissue growth	DF		6800	5.1	0.44	1.9
	RA		6850	15.6	1.55	8.3
Woody tissue mortality	DF		4220	3.6	0.32	1.3
	RA		3840	11.2	1.02	6.2
Net woody tissue increment[7]	DF		2580	1.5	0.12	0.6
	RA		3010	4.4	0.53	2.1
Overstory uptake[8]	DF		ND	20.7	2.10	11.5
	RA		ND	61.9	8.52	41.3
O-Horizon solution	DF	84		33.2	7.0	8.1
	RA	93		47.0	11.8	41.5
A-Horizon solution	DF	67		13.6	2.8	7.8
	RA	84		34.4	8.8	10.6
B-Horizon solution	DF	54		4.9	1.4	1.2
	RA	74		39.9	7.8	8.7

[1] DF, Douglas-fir; RA, red alder.

[2] ND, not determined.

[3] Standard deviation.

[4] Probability that Douglas-fir and red alder values are the same; based on t-tests of nontransformed or log-transformed data; $n = 4$. Only throughfall and overstory litter fluxes were tested. Other fluxes were estimates for entire plots and could not be statistically tested.

[5] Canopy Leaching = Throughfall + Stemflow − Dry Deposition − Wet Deposition.

[6] Resorption = Current Foliage − Foliar Litter − Canopy Leaching.

[7] Net Woody Tissue Increment = Woody Tissue Growth − Woody Tissue Mortality.

[8] Overstory Uptake = Canopy Leaching + Foliar Litter + Nonfoliar Litter + Woody Tissue Growth.

In the Douglas-fir stand, throughfall plus stemflow fluxes of Ca and Mg were similar to total deposition, indicating low amounts of canopy leaching (Table 4). In the red alder stand, some canopy leaching of Ca and Mg was indicated. The much greater flux of K in throughfall plus stemflow than in total deposition in both stands was a result of high canopy leaching (Table 4). This greater importance of canopy leaching of K in comparison to Ca and Mg has previously been observed in a variety of forests (Cole & Rapp 1980; Parker 1983). In the assessment of changes in solution composition as wet deposition passes through forest canopies, Parker (1983) attributed 35—95% of the increase in Ca, 5—70% of the increase in Mg, and 90—100% of the increase in K to canopy leaching, with the remainder due to wash-off of dry deposition. The high proportion of K attributed to canopy leaching was observed in both stands of this study, where analogous values were 18% for Ca, 22% for Mg, and 86% for K in the Douglas-fir stand and 58, 76, and 94 in the red alder.

Litterfall exceeded solution fluxes in delivering Ca to the O horizons in both stands. Throughfall plus stemflow was the dominant transport mechanism for K in the Douglas-fir stand, while litterfall and throughfall plus stemflow were of similar importance in the red alder. The proportion of cations that are transported from the canopy in litter versus solution fluxes varies considerably among forests. Based on data summarized by Parker (1983), litterfall accounted for 40—95% (median 75%) of the total Ca, 25—85% (median 65%) of the total Mg, and 5 to 80% (median 40%) of the total K delivered to the O horizon. This trend of Ca > Mg > K was observed in both stands of this study, where analogous values were 83% for Ca, 59% for Mg, and 36% for K in the Douglas-fir stand and 92%, 80%, and 53% in the red alder.

Of the Ca and Mg taken up by the overstory in each stand, approximately half was returned to the O horizon in foliar litter, one-quarter in nonfoliar litter, and one-quarter incorporated into woody tissue growth. In contrast, of the K taken up, half went to foliar leaching in the Douglas-fir and one third in the red alder, with the remainder divided among foliar litter, nonfoliar litter, and woody tissue growth. In both stands, cation incorporation into woody tissue growth was largely offset by woody tissue mortality, yielding a net woody tissue increment only one-third of woody tissue growth.

The rates of nearly all cycling processes were greater in the red alder than Douglas-fir stand. The canopy processes were affected by the deciduous vs. coniferous nature of the trees. Although the red alder had lower foliar mass than the Douglas-fir (Table 2), the entire red alder mass underwent annual senescence and conversion to litter compared with only one-sixth of the Douglas-fir foliage. Higher Mg and K fluxes in red alder litter were due to both higher litter mass and higher concentrations, while higher Ca flux was due primarily to higher litter mass. These results are consistent with a previous comparison of a variety of forests which indicated deciduous litter had both higher mass and higher cation concentrations (Cole & Rapp 1980). The greater foliar leaching of the alder yielded a higher cation flux in throughfall plus stemflow, particularly for K and to a lesser extent for Mg and Ca. Red alder also had high resorption of K prior to leaf senescence, and high accumulation (negative resorption) of Ca between end of leaf expansion and leaf senescence. Woody tissue growth and woody tissue mortality were similar for red alder and Douglas-fir. Therefore, higher cation fluxes associated with these processes in the red alder were due to higher cation concentrations of the woody tissue.

Cation fluxes in soil

Calcium, Mg, and K transfers in soil solutions within the Douglas-fir profile were highest immediately beneath the O horizon and decreased with depth (Table 4). This decrease with depth was due both to lower water fluxes at greater depth and to lower cation concentrations. Calcium had the highest flux of the three cations, which was consistent with the relative dominance of this cation on the exchange complex (Table 3). Magnesium transfer was 20 to 35% of Ca, while K transfer was more variable. Cation fluxes were consistently greater in the red alder than the Douglas-fir soil profile (Table 4), due largely to higher cation concentrations (Table 5). Cations other than Ca, Mg, and K were also important in the soil solutions (Table 5). Sodium, Al, and H^+ contributed up to half the cationic charge in the solutions.

Table 5. Cation concentrations[1] in soil solutions from adjacent Douglas-fir and red alder stands, September 1986 through August 1988.

Horizon	Stand[2]	H^+	Ca^{2+}	Mg^{2+}	K^+	Na^+	NH_4^+	Al^3
		- - - - - - - -	- - - - - - - -	(μmol$_c$ L^{-1})	- - - - - - - -	- - - - - - - -	- - - - - - - -	(μmol L^{-1})
O	DF	4	198	68	25	43	1.4	49
		(1)[4]	(69)	(23)	(3)	(6)	(0.2)	(22)
	RA	52	253	104	115	50	9.6	92
		(22)	(73)	(21)	(47)	(14)	(10.0)	(63)
	P[5]	0.001	NS	0.05	0.001	NS	0.05	NS
A	DF	3	102	34	30	44	0.7	20
		(1)	(51)	(13)	(17)	(6)	(0.6)	(17)
	RA	30	205	86	32	54	1.3	112
		(4)	(53)	(24)	(18)	(11)	(0.9)	(44)
	P	0.001	0.05	0.05	NS	NS	NS	0.01

Table 5 (continued)

Horizon	Stand[2]	H^+	Ca^{2+}	Mg^{2+}	K^+	Na^+	NH_4^+	Al[3]
		(μmol$_c$ L^{-1})						(μmol L^{-1})
B	DF	1	45	22	6	50	0.4	< 1
		(1)	(9)	(5)	(2)	(6)	(0.2)	(< 1)
	RA	7	269	86	30	54	0.5	6
		(1)	(42)	(6)	(8)	(6)	(0.2)	(3)
	P	0.001	0.001	0.001	0.001	NS	NS	0.001

[1] Each value is the arithmetic mean of volume-weighted concentrations from 3 to 5 lysimeters.

[2] DF, Douglas-fir; RA, red alder.

[3] For September 1987 through August 1988 only.

[4] Standard deviation.

[5] Probability that Douglas-fir and red alder values are the same; based on t-tests of nontransformed or log-transformed data; $n = 3$ to 5 lysimeters. NS, not significant, $P < 0.1$.

Based on the mobile-anion concept (Johnson & Cole 1980), the movement of cations through the soil is controlled by the presence of anions in soil solutions: HCO_3^- from CO_2 production, carbonic acid formation and dissociation; NO_3^- from nitrification or atmospheric deposition; Cl^- from atmospheric deposition; SO_4^{2-} from atmospheric deposition, mineralization or desorption; organic acids from litter leaching and organic matter decomposition. In the Douglas-fir O horizon, the large anion deficit and the concomitant large dissolved organic C concentration (Table 6) suggested that organic acids were the dominant anions, accounting for 78% of the total anionic charge. Organic acids continued to play a dominant role in the A horizon, but were negligible in the B-horizon solution. The anionic charge collectively contributed by Cl^-, SO_4^{2-} and HCO_3^- was fairly constant throughout the profile (110—120 μmol$_c$ L^{-1}), but the relative importance increased from 22% of total anionic charge in the O horizon to 93% in the B horizon as organic acids decreased with depth. Nitrate was negligible throughout the profile.

In contrast, NO_3^- comprised 52 to 87% of the total anionic charge in red alder soil solutions. Organic acids were also important in the O horizon, accounting for 35% of the total anionic charge, and decreased with depth. Chloride, SO_4^{2-}, and HCO_3^- collectively contributed < 15% to the total anionic charge. Bicarbonate was lower in the red alder than Douglas-fir soil profile due to the lower pH (higher H^+ concentration, Table 5) of the red alder solutions limiting the dissociation of H_2CO_3 to

Table 6. Anion and organic carbon concentrations[1] in soil solutions from adjacent Douglas-fir and red alder stands, September 1986 through August 1988.

Horizon	Stand[2]	NO_3^-	HCO_3^-	Cl^{-1}	SO_4^{2-}	Max. anion deficit[3]	Organic C[4]	Max. charge density[3]
		($\mu mol_c\ L^{-1}$)					($\mu mol\ L^{-1}$)	($\mu mol_c \mu mol^{-1} C$)
O	DF	1	33	50	24	384	2900	0.13
		(1)[5]	(13)	(9)	(6)	(156)		
	RA	404	2	83	20	271	4200	0.06
		(131)	(3)	(28)	(11)	(93)		
	P^6	0.001	0.01	0.05	NS	NS	NT	NT
A	DF	<1	31	55	35	135	1130	0.12
		(<1)	(11)	(17)	(8)	(108)		
	RA	556	0	42	12	59	700	0.08
		(179)	(0)	(14)	(3)	(14)		
	P	0.001	0.001	NS	0.01	NS	NT	NT

Table 6 (continued)

Horizon	Stand[2]	NO_3^-	HCO_3^-	Cl^{-1}	SO_4^{2-}	Max. anion deficit[3]	Organic C[4]	Max. charge density[3]
		- - - - - - - -	- - - - - - - -	($\mu mol_c\ L^{-1}$)	- - - - - - - -	- - - - - - - -	($\mu mol\ L^{-1}$)	($\mu mol_c \mu mol^{-1} C$)
B	DF	<1	30	37	52	9	<300	—
		(0)	(9)	(12)	(17)	(3)		
	RA	398	7	42	11	−2	<300	—
		(26)	(5)	(7)	(8)	(6)		
	P	0.001	0.01	NS	0.01	0.05	NT	NT

[1] Each value (except organic C and maximum charge density) is the arithmetic mean of volume-weighted concentrations from 3 to 5 lysimeters.

[2] DF, Douglas-fir; RA, red alder.

[3] For September 1987 through August 1988 only. Maximum anion deficit calculated as the sum of cation charge minus sum of anion charge. Orthophosphate contributed $<5\ \mu mol_c\ L^{-1}$ in all horizons and was not included in anion-deficit calculation. Al was assigned a charge of +3 for the calculation; because actual average Al charge may be less than +3, the anion-deficit is a maximum value. Therefore, charge density (anion deficit divided by organic C concentration) is also a maximum value.

[4] For September 1987 through August 1988 only. Based on multiplying organic N concentrations by organic-C: organic-N ratios determined for a subset of solutions. See Homann et al. (1990) for analytical procedures.

[5] Standard deviation.

[6] Probability that Douglas-fir and red alder values are the same; based on t-tests of nontransformed or log-transformed data; $n = 3$ to 5 lysimeters. NS, not significant, $P < 0.1$. NT, not tested.

H^+ and HCO_3^-; the lower pH was caused by nitrification (Van Miegroet & Cole 1984). Sulfate concentration was lower in the red alder A and B-horizon solutions compared with the Douglas-fir solutions.

This study substantiated two principal conclusions from previous assessments of control of cation movement through soils in the Douglas-fir and red alder systems (Van Miegroet & Cole 1984, 1985): (i) the dominance of NO_3^- as the driving force of cation leaching in the red alder stand, and (ii) the negligible transport of organic anions below the B horizon, indicating their lack of contribution to leaching of cations out of either the red alder or Douglas-fir ecosystem.

This study also included measurements that allowed revision of previous estimates concerning the importance of organic anions, SO_4^{2-}, and HCO_3^- to total anionic charge within the soil profile. First, Al was measured in this study. It contributed considerably to the total cation charge in the O and A-horizon solutions. The assignment of a charge of +3 to Al in determining solution charge balance, as we did (Table 6), indicates its maximum potential charge. Its actual average charge will be less than this, depending on the amount that is organically complexed, the charge of organically complexed Al, and the distribution among inorganic species, which is influenced by pH and solution composition. We did not fractionate Al into organically complexed and noncomplexed forms. Therefore, we cannot estimate its actual average charge.

Second, estimates of organic C paralleled the anion deficit, with both decreasing with soil depth in both stands. This suggests that organic anions are important to charge balance in the O and A horizons but not the B horizons. To the extent that the actual average charge of dissolved Al is less than +3, we have overestimated the organic anions and the charge densities of the organic C. The charge densities estimated in this study were similar to those calculated from the data of Dahlgren & Ugolini (1989); charge densities of soluble organics for their subalpine Spodosol were 0.06 $\mu mol_c\ \mu mol^{-1}$ C for O-horizon, 0.12 for E-horizon, and 0.10 for Bhs-horizon solutions. In determining the charge balances from which the charge densities were calculated, they assigned a charge of +3 to organically complexed Al, which made up 90% of total dissolved Al, and speciated the remaining Al among inorganic complexes based on thermodynamic data. Therefore, for that study the calculated average Al charge was close to +3. In a study of Adirondack Spodosols, Cronan & Aiken (1985) reported average charge densities of 0.05 to 0.06 $\mu mol_c\ \mu mol^{-1}$ C, but did not specify how much of the Al was organically complexed or the charge assigned to organically complexed Al for their charge balance calculations.

Third, SO_4^{2-} values were lower in this study because analyses were conducted by anion chromatography rather than by auto-analyzer methods (Van Miegroet & Cole 1984, 1985) where interference by dissolved organics apparently yielded overestimates of SO_4^{2-}. In the auto-analyzer procedure, dissolved organics produce background interference during the methylthymol-blue color reaction that cannot be properly compensated by methods of standard addition or by normal procedures of correcting values for light absorption by organics (Cronan 1979).

Fourth, HCO_3^- values were lower in this study because estimates were made by titration of solutions to pH 5 rather than pH 4.5 (Van Miegroet & Cole 1984, 1985). Theoretically, the correct pH endpoint of the titration depends on the sum of the dissolved CO_2 and HCO_3^- in the solution: the lower the dissolved CO_2 and HCO_3^-, the higher is the correct pH endpoint (Snoeyink & Jenkins 1980). Degassed soil solutions, as were analyzed in this study, have dissolved CO_2 equivalent to that in equilibrium with air containing less than 10 times natural atmospheric CO_2 levels (Zabowski & Sletten 1991). Solutions from the soils in our study were known to have HCO_3^- concentrations of < 100 μmol_c L^{-1} (Van Miegroet & Cole 1985). For solutions with these characteristics, principles of carbonate equilibria (Snoeyink & Jenkins 1980) indicate that pH 5 is an appropriate titration endpoint for determining HCO_3^-. Titrating to a lower pH results in an overestimate of HCO_3^- for these solutions.

Overall, these revisions in estimates of solution composition indicate greater importance of organic anions in the O and A-horizon solutions and lesser importance of SO_4^{2-} and HCO_3^- throughout the soil profile than had previously been recognized (Van Miegroet & Cole 1984, 1985). The interpretation of the importance of organic anions in the Douglas-fir stand contrasts not only with the previous studies in this stand (Van Miegroet & Cole 1984, 1985), but also with a nearby Douglas-fir stand on glacial outwash (Johnson et al. 1977). In the latter study, the presence of organics in O-horizon solutions was recognized, but the organics were not considered to be anionic in nature because the calculated anion deficit was near zero. However, the calculation of the anion deficit did not include Al as a cation, and HCO_3^- was estimated by titration to pH 4.5; these factors could have contributed to not observing an anion deficit. In contrast, at a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) site in Alaska and a Pacific silver fir (*Abies amabilis* (Doug.) Forbes) subalpine site in Washington state, USA, Johnson et al. (1977) did recognize an anion deficit in upper-horizon soil solutions and attributed it to organic anions, while HCO_3^- was more important deeper in the profile. Studies of pedogenesis at the latter site summarized by Ugolini & Sletten (1991), have substantiated this pattern. Aluminum has also been recognized as an important component of the upper-horizon soil solutions at that site (Dahlgren & Ugolini 1989).

Therefore, our observation of the importance of organic anions vs. HCO_3^- in the soil solutions from the Douglas-fir stand parallels the previous observations for forests in colder environments.

Cation removal from mineral soil

We estimated the current rates of cation removal from the mineral soil by using a mass-balance approach that considers the following fluxes: (i) net accumulation in live woody tissue, (ii) net accumulation in the O horizon, and (iii) solution flux from the B horizon. These removal processes are partially off-set by atmospheric deposition of cations to yield net cation removal rates from the mineral soil (Table 7).

Table 7. Net cation removal from mineral soil in Douglas-fir and red alder stands.

	Stand[1]	Ca	Mg	K
		------	($kg\ ha^{-1}\ yr^{-1}$)	------
Net live woody tissue increment[2]	DF	1.5	0.12	0.6
	RA	4.4	0.53	2.1
Net O-horizon increment[3]	DF	4.5	0.60	0.7
	RA	16.6	1.94	2.4
B-horizon solution flux[2]	DF	4.9	1.4	1.2
	RA	39.9	7.8	8.7
Atmospheric deposition[2]	DF, RA	3.0	0.9	2.2
Net cation removal from soil[4]	DF	7.9	1.2	0.3
	RA	57.9	9.4	11.0
% of Soil exchangeable yr^{-1}	DF	0.9	1.6	0.1
	RA	7.1	14.2	8.0
% of Soil total yr^{-1}	DF	0.024	0.006	0.002
	RA	0.207	0.049	0.079

[1] DF, Douglas-fir; RA, red alder.

[2] From Table 4; Atmospheric deposition = Dry coarse particles + wet deposition.

[3] Net O-horizon increment was calculated as total O-horizon content (from Table 2) divided by 50 years.

[4] Net cation removal from soil = Net live woody tissue increment + Net O-horizon increment + B-horizon solution flux − Atmospheric deposition.

Net cation removal, as well as each contributing removal process, was much greater for red alder than Douglas-fir (Table 7). In both the red alder and Douglas-fir stands, rates of Ca and Mg accumulation in live woody tissue were lower than accumulation in the O horizon, while rate of

K accumulation was similar (Table 7). In the Douglas-fir, B-horizon solution flux was of the same magnitude as accumulation in organic matter (live woody tissue plus O horizon). In the red alder, by contrast, solution flux was much greater than accumulation in organic matter. Atmospheric deposition was important in off-setting the cation removal in the Douglas-fir stand, where it was equivalent to 28% of Ca removal, 42% of Mg removal, and 88% of K removal. For red alder, atmospheric deposition was < 17% of cation removal.

Implicit in the estimates of net cation removal are several assumptions. First, we calculated O-horizon accumulation rate as current O-horizon content divided by stand age. This implicitly assumes minimal O horizon at stand initiation, which is reasonable because of the fires prior to stand establishment. It further assumes a constant accumulation rate during stand development. This is in general agreement with the assessment of O-horizon masses for a Douglas-fir chronosequence (Turner & Long 1975) and with the increase in O-horizon mass of the red alder stand over a 13-year period, as determined by comparison of our data with Turner et al. (1976). Second, we assume no net change in cations in coarse woody debris because of inadequate information to estimate current rates of change. However, an increase in coarse woody debris is expected during stand development (Harmon et al. 1987). Third, we assumed no cation uptake by deep roots, i.e. from below the 40-cm depth of the lowest lysimeters. We acknowledge some rooting and water uptake below this depth, but we have insufficient information to estimate cation uptake. The presence of O horizon at stand initiation and uptake by deep rooting would lower our estimate of current rate of cation removal from soil, while the expected accumulation of coarse woody debris would increase the estimate. Therefore, deviations from the assumptions tend to offset one another, and we accept the estimates in Table 7 as our best approximations to current net cation removal rates.

Net cation removal rates for the Douglas-fir and red alder stands are compared with estimates for other forest and soil types in Table 8. The other studies were also mass-balance estimates, but differed from this study and among themselves with respect to specific approaches and assumptions, including input estimates by bulk precipitation vs. sum of wet and dry deposition, output estimates by leaching from plots vs. stream output from watersheds, and consideration vs. lack of consideration of changes in O-horizon mass. Net cation removal from Douglas-fir soil was generally the lowest of all the stands, while removal from red alder soil was generally the highest (Table 8). The high rates for the red alder were largely due to the NO_3-driven cation leaching (Tables 6 and 7), although uptake and accumulation in live woody tissue and O horizon also contributed.

Table 8. Net cation removal from mineral soil in forest ecosystems determined by plot or watershed mass-balance.

Forest type, soil order, Type of study, & reference	Ca	Mg	K
	-----	(kg ha^{-1} yr^{-1})	------
Douglas-fir, spodosol/inceptisol Plot, this study	8	1.2	0.3
Ponderosa pine/Douglas-fir, Entisol/Inceptisol, Watershed, Clayton (1988)	20	ND[1]	4.3
Red pine, entisol, Plot, Bockheim et al. (1983)	22	5.0	6.9
Northern hardwood, spodosol, Watershed, Whittaker et al. (1979)	22	3.5	6.9
Yellow poplar, ultisol, Plot, Johnson and Todd (1990)	22	9.2	9.0
Shortleaf pine, ultisol, Plot, Johnson and Todd (1990)	25	7.8	7.0
Chestnut oak, ultisol, Plot, Johnson and Todd (1990)	33	7.0	10.0
Oak/Hickory, ultisol, Plot, Johnson and Todd (1990)	40	2.9	5.8
Red alder, spodosol/inceptisol, Plot, this study	58	9.4	11.0
Douglas-fir, inceptisol, Plot, Sollins et al. (1980)	119	7.2	4.7

[1] ND, not determined.

Removal of cations from the mineral soil by accumulation in live woody tissue and by leaching has important implications for long-term forest productivity. For 14 forests throughout the USA, a single stand rotation culminating with whole tree harvesting was estimated to remove 1 to 60% of total soil Ca, 1 to 40% of total soil Mg, and < 1 to 7% of total soil K through the combination of removal of woody tissue from the site and leaching in excess of atmospheric deposition (Johnson et al. 1988; Federer et al. 1989). The variation in these percentages is due to a combination of differences in cation accumulation in wood, leaching rates, rotation length, and soil cation content. The high proportions of total soil cations removed at some forests indicate limitation of Ca or Mg may occur within several rotations at those sites. Similar calculations for this study indicate < 1% of the total soil cations would be removed from the Douglas-fir soil, but 8% of total soil Ca, 2% of total soil Mg, and 4% of total soil K would be removed from the red alder soil in a 50-year rotation. These values were based on removal of all aboveground overstory woody tissue at age 50 (Table 2) and current leaching and atmospheric deposition rates (Table 4) existing over the entire 50-year period. The values are in error to the extent that current leaching and atmospheric deposition rates do not reflect average rates over the entire rotation, but actual long-term rates are not known. Cation leaching can be influenced by harvesting, but the direction, magnitude, and duration of response vary from site to site (Mann et al. 1988). For red alder forests cation leaching decreases following harvest, coincident with a decline in nitrification (Mann et al. 1988; Van Miegroet et al. 1990). In contrast, harvesting Douglas-fir stands has resulted in slight increase in Ca leaching or decrease in K leaching (Mann et al. 1988). Long-term studies of both atmospheric deposition and leaching are required to determine better estimates over entire rotations.

Whether cation removal will affect future cation availability and forest productivity depends, in part, on the source of the removed cations. Cations may be removed from cation exchange sites and released during mineral weathering. A measurable reduction of exchangeable cations was observed in forested Ultisols in Tennessee over an 11-year period (Johnson et al. 1988). In contrast, Clayton (1988) argued that mineral weathering was sufficient to account for cations removed from forested Entisols in Idaho. In the latter case, weathering appeared to replenish exchangeable cations following their removal by short episodes of leaching or vegetation uptake.

We were unable to distinguish the source of cations removed from the Douglas-fir soil, because we did not have previously collected soil samples that would provide an adequate comparison with exchangeable cation pools measured in this study. Total cation removal from the Douglas-fir soil occurred at a rate equivalent to only <1 to 2% of the exchangeable cations per year (Table 7); if exchangeable cations were being depleted at this rate, several decades would be required before a change in exchangeable cation pools could be detected by repeated field sampling.

In contrast, the annual removal from the red alder soil was equivalent to 7 to 14% of the exchangeable cations (Table 7). If exchangeable cation pools were the sole source of the removed cations, exchangeable cations would be totally depleted in 7 to 14 years at current removal rates. Although we do not know cation removal rates over the entire stand history, it is likely that removal rates were high for much longer than 14 years, because NO_3-driven cation leaching can commence during the first decade following establishment of red alder (D.W. Cole, unpublished data). The lack of excessive depletion of exchangeable cations suggested that mineral weathering is the source of most cations removed from the red alder soil (Table 7). These high weathering rates in the red alder soil are consistent with the high rates of nitric acid produced during nitrification (Van Miegroet & Cole 1985), and the subsequent reaction of this acid with soil minerals, as proposed by Berthelin et al. (1985).

Conclusions

Adjacent 50-year old red alder and Douglas-fir stands that developed on the same soil type had very different patterns of cation distribution, cycling, and leaching. Because of lack of replication of plots, we cannot conclusively infer that all differences were due to overstory vegetation. Confounding factors might include differences in soil properties at time of stand establishment and hydrologic variability. However, many differences in cation dynamics are consistent with differences in organic matter and nitrogen dynamics that exist between these two species due to the symbiotic N_2-fixation and deciduous nature of the red alder in contrast to the coniferous Douglas-fir.

The red alder ecosystem had similar or lesser masses of Ca, Mg, and K in foliage, but greater amounts in woody tissue and O horizon than the Douglas-fir. Red alder cycled cations more quickly via throughfall, canopy leaching, litterfall, and uptake. Both differences in biomass and in cation concentrations contributed to differences in cation pools and fluxes. Cation leaching from the B horizon was much higher in the red alder stand, where the negative charge associated with high concentrations of NO_3^- was largely balanced by Ca^{2+}, Mg^{2+}, and K^+.

Cations were removed from the mineral soil by uptake and accumulation in live woody tissue; uptake, litterfall and subsequent accumulation in O horizon; and leaching from the soil in excess of wet and dry deposition inputs. The rate of net cation removal from mineral soil was an order of magnitude greater in the red alder than the Douglas-fir stand, but exchangeable cation pools were not depleted by this removal. From these observations, we inferred that mineral weathering provided most cations removed from the red alder mineral soil. The rate of cation removal from the red alder soil exceeded rates for many other forest soils; this was largely due to enhancement of weathering by the nitric acid produced during nitrification and the subsequent NO_3-driven cation leaching.

The alteration of soil properties by red alder, including the distribution of cations, other nutrients, and organic matter, has important implications for future site productivity. In comparative studies of nutrient dynamics and sapling growth in young red alder and Douglas-fir plantations established on sites previously occupied by mature red alder or Douglas-fir, we are investigating both the effect of previous site-occupancy by red alder on future productivity, as well as the nutritional mechanism of the effect (Cole et al. 1990). On-going monitoring of those sites will also provide more definitive assessments of the temporal patterns of cation accumulation in the O-horizon, cation redistribution in the mineral soil, and cation leaching during the early stages of red alder stand development.

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