

Aluminum, Fe, Ca, Mg, K, Mn, Cu, Zn and P in above- and belowground biomass. II. Pools and circulation in a subalpine *Abies amabilis* stand

K.A. VOGT¹, R. DAHLGREN, F. UGOLINI, D. ZABOWSKI,
E.E. MOORE & R. ZASOSKI²

College of Forest Resources AR-10, University of Washington, Seattle, Washington 98195, USA; (¹present address: School of Forestry & Environmental Studies, Yale University, New Haven, CT 06511, USA); (²present address: Land, Air, Water Department, University of California, Davis, CA 95616, USA)

Key words: aluminum trace elements, *Abies amabilis*, above- and belowground cycling

Abstract. Elemental concentrations of above- and belowground tissues were determined in an *Abies amabilis* stand in the Cascade Mountains, Washington, USA. These data were used to calculate the pools and circulation of trace elements and micronutrients on a stand level. For all elements except Al, a greater proportion (from 62 to 87%) was distributed in above- rather than belowground tissues. This contrasted sharply with the biocirculation of elements where 97% of the Al and Fe, 88% of the Cu and 67–84% of the Ca, P, and Mg of total detrital cycling was from the belowground components. Aboveground tissues, however, contributed 69% of the Zn, 65% of the K and 68% of the Mn found in annual detritus production. The proportion of total element pool circulated annually was the highest for Al (82%) and Fe (32%) followed by 13% and less for the remaining elements. Copper, Fe and Al were accumulated in root tissues, while Mn and Zn accumulated in foliage.

We hypothesize that roots are an effective mechanism for avoiding Al toxicity in these subalpine ecosystems. The large root biomasses of these stands allow for high Al levels to be taken up and immobilized in roots; this is observed in the significantly higher Al accumulations in below- than aboveground tissues. The high root turnover in these stands is hypothesized to be a result of root senescence occurring in response to high Al accumulation. Furthermore, Al inputs into detritus production occur by soil horizon so that roots with high Al concentrations located in the Bh_s horizon turnover and are retained within that horizon. These roots also decompose very slowly (99% decay = 456 years) due to the high Al and low Ca, Mn and Mg present in these tissues and therefore have very little impact on short-term elemental cycling.

Introduction

One of the concerns related to acid deposition is that soils will be acidified and that this could cause both the release of toxic trace elements (i.e. Al) into

soil solution, and increased nutrient leaching losses (Khanna & Ulrich 1984). Soil acidification could result in decreased availability of nutrients required by plants because of reduced availability or because of Al toxicity to roots. Research has shown increased mobility of aluminum in response to acid rain and tephra deposition in forest ecosystems (Cronan & Schofield 1979; Johnson et al. 1981; Dahlgren 1984).

To assess the impact of increased amounts of soluble Al on forest growth, it is important to study Al tolerances of forest species and determine what concentrations of Al constitute toxic levels under natural conditions. Considerable data are available on aluminum levels in plants and on the physiology of metal toxicity, but most of these studies have been conducted on non-woody species (Foy et al. 1978; Kabata-Pendias & Pendias 1984). Only selective aspects of Al distribution and circulation, and Al effects on other nutrients, have been studied in woody plants (Quesnel & Lavkulich 1981; Abrahamsen 1983; Ulrich & Pankrath 1983; Amaury de Medeiros & Haridasan 1985; Turner et al. 1985). Detailed biological budgets containing above- and belowground data are not available on an ecosystem level in forests.

The purpose of this research was to investigate the importance of the biological component (in particular roots) in facilitating the cycling of aluminum and other elements within a forested ecosystem. A mature subalpine *Abies amabilis* stand, relatively unaffected by acid rain, was selected for this study. Because the podzolization process dominates in this soil, Al and Fe are mobile and are present at high levels (Ugolini et al. 1977a, b). This site was considered ideal for examining the effect of Al on uptake and distribution of other elements without the confounding effects created by acid precipitation.

If naturally high Al levels are present in the soil, we hypothesize that it could be advantageous for the plants to invest a large portion of net primary productivity in belowground components because roots can play a critical part in enabling trees to avoid trace elements toxicity. Roots sequester trace elements in their tissues (see Foy et al. 1978; Kabata-Pendias & Pendias 1984) and thus may play a role in reducing the amount transported to aboveground tissues.

The large root biomass of these subalpine stands (Vogt et al. 1986) may function as a positive adaptation for trees growing on soils where soluble Al and Fe occur naturally, since a large root biomass increases the potential for sequestering trace elements. Once trace elements accumulated at toxic levels in these tissues, root senescence would be an effective mechanism for removing them from the biological component. The hypothesis suggests that, in terms of a carbon budget, it is more economical for a plant to senesce roots than foliage when trace element accumulation has occurred. Moreover, plants can respond to metal accumulation on a microsite level by senescing

roots at localized areas. Foliage, retained for a longer time than roots in these evergreen coniferous forests, has a more systematic pattern of senescence occurring with needle age. Therefore, foliage is not able to respond in as opportunistic a manner as roots to trace element accumulation in the soil.

Materials and methods

Site description

The site is dominated by *Abies amabilis* (Dougl.) Forbes with *Tsuga mertensiana* (Bong.) Carr. and *Tsuga heterophylla* (Raf.) Sarg. as associated species. This stand is typical of the *Abies amabilis* zone forests described by Franklin & Dyrness (1973). This mature stand was established following fires (~185 years ago) (Grier et al. 1981). Site soil and environmental data are presented in Vogt et al. (1987).

Stand level sampling

Procedures for collecting foliage, foliage bearing branches, stemwood and stembark samples for chemical analyses are described in Vogt et al. (1987). Since stand level data on aboveground biomass components were not available separately for *A. amabilis* and *T. mertensiana* (Grier et al. 1981), only *A. amabilis* element data for foliage, foliage bearing branches, stemwood and stembark were used.

Litterfall samples for chemical analyses were collected monthly (August 1984 to September 1985, during the snow-free period) from 15 litterfall collectors (0.5 m × 0.5 m) in a 0.1 ha plot. Samples were sorted into overstory foliage, overstory twigs (< 1 cm) and a miscellaneous category which consisted of *A. amabilis* cone scales, *T. mertensiana* cones, frass, *Allectoria* spp. thalli and understory foliage and twigs. Litterfall samples were analyzed for elemental composition separately for each category and each collection time.

In August 1984, ten soil cores were obtained for collection of root tissues for chemical analysis. The root coring tool was the same as previously used to obtain root biomass and production by soil horizons for the same site (Vogt et al. 1981, 1982). Root cores were separated by root diameter (< 1, 1–2, 2–5 mm) and into live and dead categories for each generic soil horizon (forest floor, E and Bhs). Distinguishing live from dead roots was based on visual criteria supplemented by microscopic analysis of roots. For fine roots without secondary thickening, visual criteria had been developed from examination of stained root sections obtained with a freezing microtome (Vogt & Persson 1987). Roots were stained with Toluidine Blue to examine

the condition of cortical cells and with Iodine to stain for starch granules (only present in live tissues). Visually, live fine roots were more resilient, firm, had strong cohesion between cortical cells and stele, and were light colored in contrast to dead roots. Roots with secondary thickening were easily separated into live and dead categories by examination of the visual appearance of the inner root bark. Teasing apart the bark would show a light pink color for live roots and dark purple color for dead roots (Vogt & Persson 1987).

Subsamples of live and dead root tissue obtained from cores were ashed to determine soil contamination. Ash content of live roots (< 2 mm, $n = 5$) varied from $3.54 \pm 0.31\%$ for the forest floor, to $5.74 \pm 0.87\%$ for the E horizon and $8.50 \pm 1.13\%$ for the Bhs horizon. Dead root ash contents varied from $5.78 \pm 0.53\%$ in the forest floor to $13.48 \pm 1.59\%$ in the E horizon and $15.78 \pm 0.61\%$ in the Bhs horizon. The ash content of roots in the forest floor (organic horizons) was used to correct the E and Bhs horizon root element data for mineral soil contamination. Of all the elements analyzed, only root Al and Fe concentrations were increased by mineral soil contamination; adhering soil adding from 1–24 ppm Al and 1–44 ppm Fe to root material (the highest level of contamination occurred in the Bhs horizon).

Forest floor material for chemical analyses was obtained from 10 randomly chosen locations in the plot using a 15 cm diameter coring device. Roots greater than 1 mm in diameter were removed from the forest floor prior to analysis. The Oe and Oa horizons of the forest floor were not separated for analysis. The entire organic sample was dried at 70 C, ground to pass a 40 mesh screen in a Wiley mill and digested. Subsamples of forest floor material were ashed (ash content = $2.3 \pm 0.5\%$).

Element distribution and circulation calculation

Living biomass and organic matter distribution data previously obtained as part of other studies on the same plot were used to convert element data to a stand level. Stand level data on stemwood, stembark, branch, foliage, coarse root (> 5 mm in diameter) and forest floor biomass were available in Grier et al. (1981), Keyes (1982) & Meier (1981). Litterfall data by component averaged over a three year period were obtained from Vogt et al. (1983), and fine root biomass and turnover data for each horizon from Vogt et al. (1981). These data on component mass were multiplied by their respective element concentrations to obtain stand level element data.

Foliage weight distribution by age class within each canopy position and total foliage weight by canopy position were used to compartmentalize the proportions of total foliage weight within each category. Element pools in foliage were obtained by multiplying the foliar element concentration of each age and canopy position by its respective weighted foliar biomass.

Statistics

Statistical analysis of data was conducted using the Statistical Package for the Social Sciences (SPSS) software (Nie et al. 1975; Hull & Nie 1981). Group means were statistically compared using one-way analyses of variance and Scheffe's test since sample numbers were not equal.

Results

Stand level root data

Element concentrations in live and dead roots of this *A. amabilis* stand by diameter class and horizon are presented in Table 1. Element data for live and dead roots in relation to horizon and root diameter segregated into three groups:

- those that did not vary significantly between live and dead roots (Al and Fe)
- those that were present in significantly lower concentrations in dead roots than live in the E and Bhs horizons but exhibited no differences in the forest floor (Ca and Zn)
- those that had significantly lower concentrations in dead roots in all horizons (Mg, K, P, Cu and Mn)

Five distinct patterns of element change existed when comparing live roots of similar diameters in the various horizons (Table 1). Calcium, Mn and Zn decreased significantly as the soil depth increased in < 1 and 1–2 mm root diameters while no differences in concentrations occurred in the 2–5 mm diameter roots. Aluminum and Fe concentrations increased significantly with soil depth in the < 1 and 1–2 mm diameter root classes, while the 2–5 mm root diameter class had no significant difference in concentrations between the forest floor and E horizon but Al and Fe increased significantly in Bhs horizon samples. No significant differences by horizon or by root diameter class occurred for K while a significant decrease in Mg concentrations occurred only in the < 1 mm root diameter class by horizon. No significant differences in P concentrations were measured within each root diameter class in the forest floor and E horizon; however, all root diameter classes had significantly higher P concentrations in the Bhs horizon.

Litterfall, forest floor

Element concentrations in different litterfall components and the forest floor are presented in Table 2. Lower Al and Fe and higher Zn and Mn concentra-

Table 1. Element concentrations for roots by soil horizon, root diameter and root status in an *Abies amabilis* stand (mean \pm one standard deviation).

Horizon	Root diameter (mm)	Root status	n	Al ppm	Cu	Mn
Forest floor	< 1	Live	5	1,390aA* (340)	8.5aA (0.8)	170aA (40)
		Dead**	5	1,340a (160)	4.5b (0.3)	60b (10)
	1-2	Live	5	760aA (120)	5.2aA (0.4)	240aA (80)
		Dead	3	1,310b (160)	3.1b (0.4)	50b (10)
	> 2-5	Live	5	500aA (110)	3.0aA (0.6)	210aA (80)
		Dead	2	460a (250)	2.8a (0.0)	40b (20)
E Horizon	< 1	Live	4	3,960aB (410)	7.0aB (0.4)	70aB (20)
		Dead	5	3,500a (240)	3.0b (0.2)	10b (0)
	1-2	Live	5	2,200aB (410)	4.2aB (0.4)	110aB (30)
		Dead	4	2,500a (600)	1.8b (0.4)	10b (0)
	> 2-5	Live	4	1,080aA (210)	2.8aA (0.2)	180aA (80)
		Dead	5	1,250a (550)	1.5a (0.6)	30b (40)
	< 1	Live	1	9,300 —	6.7 —	30 —
		Dead	5	9,840 (1,410)	—	20 (0)
Bhs horizon	1-2	Live	4	5,560aC (870)	5.0aAB (0.4)	60aB (10)
		Dead	4	8,390b (1,080)	3.1b (0.2)	10b (0)
	> 2-5	Live	5	3,630aB (1,760)	3.2aA (0.4)	100aA (70)
		Dead	5	8,530a (4,490)	2.0b (0.3)	10b (0)

Table 1. Cont.

Zn	Ca	Fe ppm	K	Mg	P
79.6aA	2,150aA	1,040aA	1,720aA	660aA	1,020aA
(10.9)	(360)	(120)	(620)	(110)	(140)
66.0a	2,210a	980a	470b	370b	440b
(7.3)	(320)	(80)	(110)	(50)	(50)
42.8aA	2,180aA	550aA	880aA	420aA	620aA
(6.2)	(280)	(100)	(70)	(50)	(30)
43.2a	2,160a	660a	320b	310b	290b
(6.9)	(170)	(50)	(40)	(30)	(40)
26.4aA	2,400aA	320aA	1,430aA	740aA	480aA
(7.7)	(700)	(40)	(530)	(160)	(100)
25.5a	2,200a	160b	240b	200b	180b
(3.7)	(420)	(70)	(30)	(40)	(30)
57.6aB	1,400aB	2,140aB	1,430aA	430aA	1,040aA
(12.0)	(210)	(240)	(420)	(100)	(60)
35.2b	910b	1,780a	310b	150b	360b
(4.8)	(150)	(100)	(50)	(20)	(30)
34.5aB	1,630aB	910aB	1,100aA	490aA	690aA
(3.4)	(140)	(150)	(180)	(60)	(40)
20.7b	640b	820a	180b	100b	230b
(6.6)	(140)	(190)	(20)	(20)	(50)
23.9A	2,100aA	410aA	810aA	600aA	620aA
(2.8)	(490)	(130)	(270)	(210)	(260)
14.3b	750b	390a	280b	150b	190b
(5.0)	(260)	(70)	(170)	(70)	(100)
31.3	760	3,420a	1,840	420	1,270
20.7	450	3,980a	740	250	740
(1.6)	(40)	(640)	(190)	(40)	(80)
27.3aB	1,320aC	1,940aC	860aA	480aA	880ab
(1.4)	(150)	(180)	(150)	(80)	(90)
13.3b	390b	2,180a	360b	170b	460b
(1.8)	(50)	(460)	(60)	(20)	(10)
23.6aA	1,940aA	910aB	1,140aA	770aA	1,120aB
(6.7)	(280)	(360)	(220)	(230)	(300)
11.3b	370b	1,190a	190b	80b	310b
(1.8)	(30)	(490)	(50)	(10)	(30)

*Numbers followed by the same lower case letter (a) are not significantly different when comparing live and dead roots within each root diameter class by horizon (Scheffes, $p < 0.05$). Numbers followed by the same upper case letter (A) are not significantly different when comparing live roots by horizon for each specific root diameter (Scheffes, $p < 0.05$).

**Dead root data adjusted for carbon loss at senescence.

Table 2. Element concentrations of litterfall components and forest floor in an *Abies amabilis* stand (mean \pm standard deviation).

	n	Al	Cu	Mn	Zn	Ca ppm	Fe	K	Mg	P
<i>Litterfall</i>										
Foliage	13	635 (151)	1.7 (0.9)	1,412 (312)	386 (238)	4,495 (544)	64 (11)	1,457 (603)	704 (134)	702 (195)
Twigs	14	237 (93)	4.1 (1.7)	349 (80)	138 (99)	2,305 (621)	119 (81)	444 (239)	229 (91)	253 (68)
Frass	8	554 (93)	8.7 (6.7)	1,049 (376)	2,421 (3,126)	4,064 (686)	172 (61)	1,690 (1,115)	492 (136)	550 (130)
Misc.	14	473 (164)	5.6 (0.9)	419 (65)	1,392 (815)	2,393 (648)	439 (223)	1,193 (307)	403 (78)	506 (102)
<i>Forest floor</i>										
	10	1,704 (305)	6.3 (0.9)	64 (35)	25 (6)	1,643 (501)	1,283 (336)	824 (254)	407 (56)	553 (109)

tions occurred in the aboveground litterfall components than in the forest floor and roots (Table 1 and 2).

Stand level element budgets

Above- and belowground biomass distribution for the mature *A. amabilis* stand are presented in Table 3. Seventy-six percent of the total living biomass was aboveground. Except for Al (40%), more than 60% of the Cu, Mn, Zn, Ca, Fe, K, Mg and P contents were in aboveground living tissues.

Stand level element transfers

Ninety percent of the total detrital production occurred in the belowground for the *A. amabilis* stand (Table 4). Nearly all detrital Al and Fe cycling (97%) was contributed by the belowground components. Calcium, Cu, Mg and P had greater proportions (67–84%) of detrital cycling being contributed by the belowground. Aboveground detrital production contributed more to Mn (68%), Zn (69%) and K (65%) cycling than did the belowground.

In the belowground, the greatest contribution of Al and Fe to total detrital input occurred in the Bhs horizon (Table 4). No pattern of Cu, K or P inputs through detrital root production were apparent by soil horizon. Manganese, Zn, Ca and Mg input through root turnover decreased with increasing horizon depth.

Of the total standing pools, 4% of the biomass, 82% of the Al, 32% of the Fe, 13% of the Zn, 9% of the Cu, 5% of the P, 4% of the Ca, 4% of the Mg, 3% of the Mn and 3% of the K contents were circulated annually as part of detritus production (Tables 3, 4).

Table 3. Tree living biomass, organic matter distribution and elemental contents for an *Abies amabilis* stand.

	Biomass	Al	Cu	Mn	Zn	Ca	Fe	K	Mg	P
<i>Aboveground tree</i>										
Foliage	21,650	3.4	0.031	10.9	0.558	81	1.6	70	12.6	13.3
Branches	67,800	13.8	0.285	30.6	2.217	219	11.6	219	40.7	50.2
Stemwood	294,000	3.5	0.028	29.2	7.703	137	29.8	224	20.6	13.7
Stembark	62,200	8.6	0.137	23.7	1.580	232	3.0	108	15.9	22.9
Above ground total	445,650	29.3	0.481	94.4	12.058	669	46.0	621	98.8	100.1
<i>Belowground tree</i>										
<i>Fine roots</i>										
Forest floor < 1 mm diam.	4,580	6.4	0.039	0.8	0.366	9.8	4.8	7.9	3.0	4.7
Forest floor 1–2 mm diam.	2,810	2.1	0.015	0.7	0.121	6.1	1.5	2.5	1.2	1.7
Forest floor > 2–5 mm diam.	810	0.8	0.002	0.2	0.021	1.9	0.3	1.2	0.9	0.4
E. horizon < 1 mm diam.	1,670	6.6	0.012	0.1	0.097	2.3	3.6	2.4	0.7	1.7
E horizon 1–2 mm diam.	2,500	5.5	0.011	0.3	0.085	4.1	2.3	2.8	1.2	1.7
E. horizon > 2–5 mm diam.	1,480	1.6	0.004	0.3	0.035	3.1	0.6	1.2	0.9	0.9
Bhs horizon < 1 mm diam.	570	5.3	0.004	0.02	0.018	0.4	1.9	1.0	0.2	0.7
Bhs horizon 1–2 mm diam.	1,460	8.1	0.007	0.09	0.039	1.9	2.8	1.3	0.7	1.3
Bhs horizon > 2–5 mm diam.	550	2.0	0.002	0.06	0.013	1.1	0.5	0.6	0.4	0.6
Course roots (> 5 mm diam.)	124,980	6.1	0.190	34.3	1.004	152.4	4.1	185	37.4	47.0
Belowground total	141,310	44.5	0.286	36.9	1.799	183	22.4	206	46.6	60.7
<i>Detritus</i>										
Forest floor	149,500	255	0.942	9.5	3.663	246	192	123	61	83
<i>Soil organic matter</i>										
E horizon	40,000	620					980			
— organically bound		330					160			
— inorganic		290					820			
Bhs horizon	190,800	18,330					12,790			
— organically bound		12,000					5,030			
— inorganic		6,330					7,760			

Table 4. Detritus production and elemental transfers for an *Abies amabilis* stand.

	Production	Al	Cu	Mn	Zn	Ca	Fe	K	Mg	P
<i>Aboveground tree</i>										
Litterfall total	2,180	1.2	0.008	1.9	1.25	7.3	0.5	2.5	1.0	1.2
— Foliage	1,030	0.7	0.002	1.5	0.40	4.7	0.1	1.5	0.7	1.2
— Twigs	600	0.2	0.003	0.2	0.08	1.3	0.1	0.3	0.1	0.2
— Misc.	550	0.3	0.003	0.2	0.77	1.3	0.3	0.7	1.2	0.3
Throughfall	—	0.3	—	0.4*	—	2.5	0.2	11.6	1.0	0.1*
Aboveground total	2,180	1.5	0.008	2.3	1.25	9.8	0.7	14.1	2.0	1.3
<i>Belowground tree</i>										
<i>Fine roots</i>										
Forest floor < 1 mm diam.	3,320	4.5	0.015	0.2	0.22	7.3	3.3	1.6	1.2	1.5
Forest floor 1–2 mm diam.	2,030	2.7	0.006	0.1	0.09	4.4	1.3	0.6	0.6	0.6
Forest floor > 2–5 mm diam.	1,780	0.8	0.005	0.1	0.05	3.9	0.3	0.4	0.4	0.3
E horizon < 1 mm diam.	1,720	6.0	0.005	0.02	0.06	1.6	3.1	0.5	0.3	0.6
E horizon 1–2 mm diam.	2,580	6.5	0.005	0.03	0.05	1.7	2.1	0.5	0.3	0.6
E horizon > 2–5 mm diam.	1,290	1.6	0.002	0.10	0.02	1.0	0.5	0.4	0.2	0.3
Bhs horizon < 1 mm diam.	1,030	10.1	0.007	0.02	0.02	0.5	4.1	0.8	0.3	0.8
Bhs horizon 1–2 mm diam.	2,650	22.2	0.008	0.03	0.03	1.0	5.8	0.9	0.3	1.2
Bhs horizon > 2–5 mm diam.	480	4.1	0.001	0.00	0.01	0.2	0.6	0.1	0.04	0.2
<i>Coarse roots</i> > 5 mm diam.	3,200	0.1	0.003	0.5	0.02	2.3	0.1	1.7	0.4	0.6
Belowground total	20,080	58.6	0.057	1.10	0.57	23.9	21.2	7.5	4.0	6.7
<i>Belowground</i>										
Below + aboveground (%)										
Detritus		97	88	32	31	71	97	35	67	84
Forest floor		9.2	0.034	2.3	1.59	23.0	5.4	5.1	3.2	3.6

*Estimated using ratio of litterfall to throughfall from Turner & Singer (1976).

Table 5. Element/Al ratios for roots, forest floor and litterfall in an *Abies amabilis* stand.

Type	Root diameter (mm)	Horizon	Element/Al ratios				
			Ca/Al	Fe/Al	Mg/Al	Mn/Al	P/Al
Live roots	< 1	Forest floor	1.55	0.75	0.47	0.12	0.74
		E	0.35	0.54	0.11	0.02	0.26
		Bhs	0.08	0.37	0.05	0.004	0.14
	1–2	Forest floor	2.86	0.72	0.55	0.31	0.81
		E	0.74	0.42	0.22	0.05	0.31
		Bhs	0.24	0.35	0.09	0.01	0.16
	> 2–5	Forest floor	4.80	0.65	1.48	0.42	0.96
		E	1.94	0.38	0.55	0.17	0.57
		Bhs	0.53	0.25	0.21	0.03	0.31
Forest floor			0.96	0.75	0.24	0.04	0.32
Litterfall foliage			7.08	0.10	1.11	2.22	1.11
Litterfall twigs			9.73	0.50	0.97	1.47	1.07

Element/Al ratios

The Ca, Mg, Mn or P to Al concentration ratios increased from the < 1 to the 1–2 mm and 2–5 mm root diameter classes by horizon (Table 5). In each specific root diameter class, these ratios decreased from the forest floor to the Bhs horizon. The Fe/Al ratios of roots decreased with soil depth but the Fe/Al ratio did not vary with increasing root diameters within each horizon.

Except for the Fe/Al ratio, roots always had higher Ca, Mg, Mn or P to Al ratios than the forest floor (Table 5). Litterfall foliage and twig Ca/Al and Mn/Al ratios were always higher than in any of the root categories or the forest floor.

Discussion

The varying contribution of above- and belowground biomass to nutrient distribution and circulation is apparent from examination of element budgets for a subalpine *A. amabilis* stand. A greater proportion of the essential elements (Cu, Fe, Mn, Mg, Zn, P, Ca, K) were distributed in above- rather than belowground living biomass. Only Al, a non-essential element, was distributed in greater quantities in the below- than aboveground living biomass. Despite this aboveground accumulation of elements, the belowground components contributed more to the total detrital cycling for Fe (97% of total), Cu (88%), P (84%), Ca (71%) and Mg (67%). Zinc, K and Mn were exceptions with 31%, 35% and 32% respectively being derived

from belowground detritus. The disparity between standing pools of nutrients and their relative contribution to nutrient circulation within the ecosystem is related to two factors. First, root turnover exceeds annual foliage turnover in this ecosystem (Vogt et al. 1982) and secondly, selective element accumulation occurs in root material (i.e. Al, Fe, Cu) and in foliage (i.e. Mn, Zn). Although the greater distribution of macronutrients in above- versus belowground biomass has been commonly reported in the literature (see Van den Driessche 1984), results of this study cannot be compared with other element studies since belowground detrital production element contributions to total element cycling traditionally have not been examined.

Since root turnover is the largest contributor to detrital production, the two elements accumulating in high concentrations in roots (Al, Fe) had a greater proportion of element pools in standing biomass circulated annually to detritus. Annual circulation of 82% and 32% of the total element pool in standing biomass was measured for Al and Fe respectively. A much smaller proportion of element pools in standing biomass was circulated annually for the remaining elements. Except for Cu (which was present in very low concentrations in the ecosystem), the remaining elements did not accumulate in root tissues. Manganese and Zn were present in higher concentrations in foliage than in roots, but since foliage contributed less to detrital production than roots, Mn and Zn had low circulation rates in this ecosystem. Accumulation of Cu, Zn and Fe in root tissues have been reported for conifer seedlings (Nelson & Selby 1974; Van den Driessche 1978; West 1979). However the subalpine *A. amabilis* stand of this study accumulated more Cu, Fe and Al but not Zn in root tissue than in foliage. Accumulation should also be related to soil levels of these elements and would likely vary from ecosystem to ecosystem.

The magnitude of Al and Fe accumulation in roots follows the concurrent increases in soil inorganic Al and Fe levels with increasing soil depth. In this subalpine stand, inorganic Al was $290 \text{ kg} \cdot \text{ha}^{-1}$ in the E horizon and increased to $6330 \text{ kg} \cdot \text{ha}^{-1}$ in the Bhs horizon while inorganic Fe was $8230 \text{ kg} \cdot \text{ha}^{-1}$ in the E horizon and increased to $7760 \text{ kg} \cdot \text{ha}^{-1}$ in the Bhs horizon (Dahlgren 1984). In the Bhs horizon, higher Al and Fe levels in roots result in root turnover in this horizon contributing 63% of the Al and 50% of the Fe of belowground detrital cycle. This occurs despite the fact that only 25% of the entire profile root turnover (< 5 mm in diameter) occurs in this horizon. This shows that roots can modify the circulation rate of elements in specific soil horizons when element accumulation occurs. Copper is also accumulated by roots but root Cu concentrations do not vary by soil depth resulting in no pattern of Cu input via roots.

High concentrations of Al and Fe in roots may affect the input of other elements by horizon. The increasing inputs of Al and Fe into detrital pools

with soil depth is in contrast to decreased inputs of Mn, Zn, Ca, and Mg. This results in root turnover in the Bhs horizon contributing 25% annually to belowground detrital production but only 8.3% of the Mn, 11.2% of the Zn, 7.9% of the Ca and 17.6% of the Mg.

Numerous studies have shown that there is an interaction between Al and nutrients such as P, Ca, K and Mg. As Al levels increase in soil solution, cation uptake by plants is reduced (Kabata-Pendias & Pendias 1984). This is usually measured as lower levels of Ca and Mg in plant tissues growing in the presence of high levels of inorganic Al. Similarly, acid rain studies have shown that increasing soil acidity results in greater quantities of extractable Al and greater amounts of Ca and Mg leaching from the soil (Cronan & Schofield 1979; Cronan 1980; Abrahamsen 1983).

Comparison of element/Al ratios for live roots by diameter class and by horizon show similar patterns of decreasing ratios of Ca, Mg, Mn and P to Al with increasing soil depth. Higher Ca/Al ratios were measured for roots in the forest floor (1.55–4.80) than the mineral soil (0.08–1.94). This would be expected: complexing of Al in the forest floor decreases the amount of mineral aluminum ions present and therefore root uptake of aluminum. Comparison of different root diameters in the same horizon showed the < 1 mm root diameter class with the lowest Ca/Al ratio. If most of the Al uptake occurs in the very fine roots, then higher Al concentrations would be expected in these roots since Al is suggested to precipitate with P or nucleic acids in the cell wall (Foy et al. 1978).

The Ca/Al ratios of < 1 mm roots in the E and Bhs horizons was less than 1 which, according to Ulrich (1983), is toxic for roots and soil. Ulrich (1983) considered a Ca/Al molar ratio of < 0.2 to be critical for roots. This suggests fine roots in the Bhs horizon of this study (Ca/Al ratio = 0.08) were exposed to toxic Al levels. These low Ca/Al ratios for very fine roots in the Bhs horizon may result in inefficient element uptake by the roots and may be the reason that high root occupancy of this horizon never occurs. High Al and Fe levels in the Bhs may restrict fine root growth to the E horizon and forest floor in these subalpine forests. The remaining root diameters have Ca/Al ratios in which root growth is potentially not inhibited by Al toxicity.

The accumulation of Al in roots results in aboveground Ca/Al, Mg/Al, Mn/Al and P/Al ratios much higher than those found in root tissues. Apparently elements are taken up by the plant in sufficient levels so that element deficiencies do not occur for aboveground tissues.

We are hypothesizing that the roots become an effective filtering mechanism for avoiding trace element toxicity for the rest of the plant. We are suggesting that it may be a more cost effective mechanism for trees growing on sites with high availabilities of trace elements in the soil to concentrate

them in root tissues that turnover rapidly rather than increase the turnover rate of photosynthetic tissues. Trees on these sites have already optimized photosynthetic efficiency by retaining foliage for 20 years and replacing only 6% of the foliage annually. This is contrasted by the fine roots where almost 100% of root tissue is replaced annually (Vogt et al. 1982).

Results of this study show the importance of the biological components (especially those belowground) in Al and Fe circulation within this ecosystem. High annual circulation rates of Al and Fe occur as part of detritus production. It would be important to know how readily available during decomposition are the Al and Fe complexed in root tissues. Estimates of Al and Fe mean residence time (MRT) in the forest floor (calculated using root input as outlined by Vogt et al. 1983), were calculated to be 27.7 years and 35.6 years respectively in the forest floor. Copper had the same mean residence time (27.7 years) as Al in the forest floor; both elements also accumulated in root tissues. Al and Fe mean residence are not much different from those for Mg (19.1 years), P (23.1 years) and K (24.1 years). Interestingly, Zn and Mn had short mean residence times in the forest floor: Zn = 2.3 years and Mn = 4.1 years. It appears that Mn and Zn, which are not present in quantities to meet annual root growth requirements, are also circulated quite rapidly in the forest floor.

It appears that Al and Fe are turning over slowly in the forest floor. However, mean residence time for organically bound Al and Fe in the soil horizons (calculated in a similar manner to the forest floor), was 21 years for Al and 24 years for Fe in the E horizon. This contrasts the Bh horizon where a MRT of 456 years for Al and 782 years for Fe was estimated. The MRT of Al in the BHS horizon is not too different from the 330–465 years calculated by Tamm & Holman (1967) and the 180–610 years reported by Guillet (1972) and Guillet & Robin (1972) using ^{14}C dating for humus in the Bh horizon of podzols. The estimates obtained during this study suggest that Al and Fe are being transferred faster through the E horizon than the forest floor.

In addition, Al and Fe accumulating in the Bhs horizon are relatively unavailable in organically bound complexes. The high amount of Al in roots, in potentially toxic levels, and the decreased content of other elements (Ca, Mn, Mg) required by decomposers should reduce microbial degradation of root material in deeper soil horizons. Trace elements have been shown to affect the decomposition rate of plant material when complexed with organic material (Martin et al. 1966; Ruling & Tyler 1973). Even though a greater proportion of total belowground Al and Fe input occurs in the Bhs horizon, the decomposition rate of roots added to detrital production in this horizon is so slow that these contributions are probably insignificant to total ecosystem level cycling. The significant sites of Al and Fe additions into nutrient pathways occurred in the E horizon followed by the forest floor.

Acknowledgements

We would like to acknowledge Daniel J. Vogt for extremely useful data discussion and his aid in data manipulation. This research was supported by National Science Foundation grant No. BSR8407710.

We would like to thank John Aber and anonymous reviewers for useful input in improving the quality of this paper.

References

- Abrahamsen, G. (1983) Sulphur pollution: Ca, Mg and Al in soil and soil water and possible effects on forest trees. In: B. Ulrich & J. Pankrath (Eds) *Effects of Accumulation of Air Pollutants in Forest Ecosystems* (pp. 207–218) D. Reidel Publishing Co. Dordrecht, Holland
- Amaury de Medeiros, R. & M. Haridasan (1985) Seasonal variation in the foliar concentrations of nutrients in some aluminum accumulating and non-accumulating species of the cerrado region of central Brazil. *Plant Soil* 88: 433–436
- Cronan, C.S. & C.L. Schofield (1979) Aluminum leaching response to acid precipitation: Effects on high elevation watersheds in the northeast. *Science* 204: 304–306
- Cronan, C.S. (1980) Controls on leaching from coniferous forest floor microcosms. *Plant and Soil* 56: 301–322
- Dahlgren, R.A. (1984) Impact of tephra perturbation on a forest soil in the *Abies amabilis* zone. Masters Thesis. University of Washington, Seattle, Washington
- Foy, C.D., R.L. Chaney & M.C. White (1978) The physiology of metal toxicity in plants. *Annual Review Plant Physiology* 29: 511–566
- Franklin, J.F. & C.T. Dyrness (1973) Natural vegetation of Oregon and Washington. United States Forest Service General Technical Report PNW-8
- Grier, C.C., K.A. Vogt, M.R. Keyes & R.L. Edmonds (1981) Biomass distribution and above- and belowground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Canadian Journal of Forest Research* 11: 155–167
- Guillet, B. (1972) Detention des sols par le ^{14}C naturel. II. Application à la détermination et à la signification des âges d'horizons Bh et Bs de podzols vosgiens. *Bulletin Ecole Nationale Supérieure Agronomique Nancy* 14: 123–131
- Guillet, B. & A.M. Robin (1972) Interprétation de datations par le C d'horizons Bhy de deux podzols humo-ferrugineux, l'un formé sous callune, l'autre sous chênaie-hêtraie. *Comptes Rendus Académie des Sciences, Paris*. 274D: 2859–2861
- Hull, C.H. & N.H. Nie (1981) SPSS Update 7–9. McGraw-Hill, New York
- Johnson, N.M., C.T. Driscoll, J.S. Eaton, G.E. Likens & W.H. McDowell (1981) "Acid rain", dissolved aluminum and chemical weathering at the Hubbard Brook Experimental Forest. New Hampshire. *Geochimica et Cosmochimica Acta* 45: 1421–1437
- Kabata-Pendias, A. & K. Pendias (1984) *Trace Elements in Soils and Plants*. CRC Press, Inc., Boca Raton, Florida
- Keyes, M.R. (1982) Ecosystem development in *Abies amabilis* stands of the Washington Cascades: root growth and its role in net primary production. Unpublished Dissertation. University of Washington, Seattle, Washington
- Khanna, P.H. & B. Ulrich (1984) Soil characteristics influencing nutrient supply in forest soils. In: G.D. Bowen & E.K.S. Nambiar (Eds) *Nutrition of Plantation Forests* (pp. 79–117) Academic Press, London
- Martin, J.P., J.O. Ervin & R.A. Shepherd (1966) Decomposition of the Fe, Al, Zn and Cu salts

- or complexes of some microbial and plant polysaccharides in soil. Soil Science Society America Proceedings 30: 196–200
- Meier, C.E. (1981) The role of fine roots in N and P budgets in young and mature *Abies amabilis* ecosystems. Dissertation. University of Washington, Seattle, Washington
- Miller, H.G. (1984) Dynamics of nutrient cycling in plantation ecosystems. In: G.D. Bowen & E.K.S. Nambier (Eds) Nutrition of Plantation Forests (pp. 53–78) Academic Press, London
- Nelson, L.E. & R. Selby (1974) The effect of nitrogen source and iron levels on the growth and composition of Sitka spruce and Scots pine. Plant Soil 41: 573–588
- Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner & D.H. Bent (Eds) (1975). Statistical Package for the Social Sciences (SPSS). McGraw-Hill, New York
- Quesnel, H.J. & L.M. Lavkulich (1981) Comparison of the chemical properties of forest floors, decaying wood and fine roots in three ecosystems on Vancouver Island. Canadian Journal of Forest Research 11: 215–217
- Ruling, A. & G. Tyler (1973) Heavy metal pollution and decomposition of spruce needle litter. Oikos 24: 402–416
- Tamm, C.O. & H. Holmen (1967) Some remarks on soil organic matter turn-over in Swedish podzol profiles. Soils and Fertilizers 31 (1968), abstract 1576
- Turner, R.S., A.H. Johnson & D. Wang (1985) Biogeochemistry of aluminum in McDonalds Branch Watershed, New Jersey Pine Barrens. Journal of Environmental Quality 14: 314–323
- Ugolini, F.C. R. Minden, H. Dawson & J. Zachara (1977a) An example of soil processes in the *Abies amabilis* zone of central Cascades, Washington. Soil Science 124: 291–302
- Ugolini, F.C. H. Dawson & J. Zachara (1977b) Direct evidence of particle migration in the soil solution of a podzol. Science 198: 603–605
- Ulrich, B. (1983) Soil acidity and its relations to acid deposition. In: B. Ulrich and J. Pankrath (Eds) Effects of Accumulation of Air Pollutants in Forest Ecosystems (pp. 127–146) D. Reidel Publishing Co., Dordrecht, Holland
- Ulrich, B. & J. Pankrath (1983) Effects of Accumulation of Air Pollutants in Forest Ecosystems. D. Reidel Publishing Co., Dordrecht, Holland
- Van den Driessche, R. (1978) Response of Douglas-fir seedlings to nitrate and ammonium nitrogen sources at different levels of pH and iron supply. Plant Soil 49: 607–623
- Van den Driessche, R. (1984) Nutrient storage, retranslocation and relationship of stress to nutrition. In: G.D. Bowen & E.K.S. Nambiar (Eds) Nutrition of Plantation Forests (pp. 181–209) Academic Press, London
- Vogt, K.A., R.L. Edmonds & C.C. Grier (1981) Seasonal changes in biomass and vertical distribution of mycorrhizal and fibrous-textured conifer fine roots in 23- and 180-year-old subalpine *Abies amabilis* stands. Canadian Journal of Forest Research 11: 223–229
- Vogt, K.A., C.C. Grier, C.E. Meier & R.L. Edmonds (1982) Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. Ecology 63: 370–380
- Vogt, K.A., C.C. Grier, C.E. Meier & M.R. Keyes (1983) Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in western Washington, as affected by fine root input. Ecological Monographs 53: 139–157
- Vogt, K.A., C.C. Grier & D.J. Vogt (1986) Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. Advances in Ecological Research 15: 303–377
- Vogt, K.A. & H. Persson (1987) Root methods. In: J.P. Lassoie & T.M. Hinckley (Eds) Ecophysiology of Forest Trees. Vol. 1. Techniques and Methodologies. CRC Press, Boca Raton, Florida
- Vogt, K.A., R. Dahlgren, F. Ugolini, D. Zabowski, E.E. Moore & R. Zasoski (1987) Aluminum, Fe, Ca, Mg, K, Mn, Cu, Zn and P in above- and belowground biomass. I.

Concentrations in subalpine *Abies amabilis* and *Tsuga mertensiana*. Biogeochemistry (this issue)

West, P.W. (1979) Release to shoots of copper stored in roots of *Pinus radiata* D. Don. Annals of Botany 43: 237–240