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Aluminum, Fe, Ca, Mg, K, Mn, Cu, Zn and P in above- and belowground biomass. I. *Abies amabilis* and *Tsuga mertensiana*

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Abstract. In a mature mixed subalpine stand of *Tsuga mertensiana* and *Abies amabilis*, significantly higher Al levels were found in foliage, branch and root tissues of *T. mertensiana*. *Tsuga mertensiana* had significant increases in Al, Ca and Mn levels with increasing foliage age. In current foliage, *T. mertensiana* had lower levels of Ca, similar levels of Mg and P, and higher levels of Mn than *A. amabilis*. Both tree species had Cu and Fe present at higher levels in branch than foliage tissues. Fine roots had the highest concentrations of Al, Fe and Cu but the lowest Ca and Mn concentrations of all tissues analyzed. In the roots of both species, phloem tissues always had significantly higher Al levels than xylem. Fine roots (< 1 and 1–2 mm) of *T. mertensiana* had higher Al levels than were found in *A. amabilis*. Roots greater than 2 mm in diameter exhibited no significant differences in Al levels in phloem or xylem tissue between *A. amabilis* and *T. mertensiana*. The two species show a clear difference in their ability to accumulate specific elements from the soil.

Introduction

Prior research has shown that some tree species (i.e. eastern and western hemlock) may accumulate aluminum in their tissues (Messenger 1975; Ryan et al. 1986a, b). Whether species accumulate Al in relatively high concentrations in their tissues has interesting ecological and pedological implications on an ecosystem level. For example, Messenger et al. (1978) suggested that plant successional patterns could be modified if Al cycling plants increase soluble Al in the environments where other species are not tolerant of Al.

Differences between plant species in the accumulation of Al, Fe and required nutrients should result in some species having greater modifying influence on the rate of soil forming processes. This would be especially significant in ecosystems where Al plays a prominent role in the soil forming process of podzolization and Al accumulating plants are present.

The purpose of this study was to determine if significant differences in elemental accumulation exists between *Tsuga mertensiana* and *Abies amabilis*. Comparison of these two specifies is ideal since both are present on the same site characterized by naturally high levels of Al due to podzolization. It is of interest to know how Al and other elements are biocirculated by different tree species in natural ecosystems to understand what effect acid precipitation induced mobilization of Al (Cronan & Schofield 1979) may have on forests.

Materials and methods

Site description

The research was conducted in a mature *Abies amabilis* stand located at the Findley Lake research area in the City of Seattle's Cedar River Watershed ~ 80 km southeast of Seattle, Washington. The stand is located at an elevation of 1150 m. Annual precipitation is 230 cm with only 10% falling during the summer (Vogt et al. 1981). Winter snow accumulations are commonly over 3 m deep, however, the soils remain unfrozen beneath the snow packs (Vogt et al. 1981). Mean annual air temperature is 5.5 C, with a January average of −3.2 C and July average of 14.4 C (US Weather Bureau, Stampede Pass Station).

The site is dominated by *Abies amabilis* (Dougl.) Forbes with *Tsuga mertensiana* (Bong.) Carr. as one of the associated species. Based on total aboveground biomass, *A. amabilis* accounted for approximately 80% and *T. mertensiana* most of the remaining 20% of total aboveground biomass. The mean age of both tree species was 185 years at the time of the study. This stand was established following fires which occurred approximately 185 years ago (Grier et al. 1981).

Soils of the study area are typical spodosols, derived from 6–10 cm of Mount St. Helens W and Y volcanic ash overlying andesitic glacial till (Ugolini et al. 1977). The mean forest floor depth is 7.0 cm (Vogt et al. 1982). Underlying the forest floor is a well-developed E horizon and beneath this is a well-developed Bhs horizon (Vogt et al. 1981, 1982). Soil texture ranges from a sandy loam in the E horizon to gravelly clay loam in the Bhs horizon.

Individual tree samplings

In August 1984, ten individual trees (five. *A. amabilis* (Dougl.) Forbes and five *Tsuga mertensiana* (Bong.) Carr.) were sampled to obtain tissues for chemical analyses. Trees were selected to represent the range of diameter distributions present on the site; each tree sampled was greater than 25 m in height.

Foliage and branch samples were obtained from the mid-point of the upper, middle and lower one-third portions of each tree canopy. For each tree, all branches and foliage samples at each canopy position were separately processed and chemically analyzed. Foliage and associated foliage bearing branches were further separated into age classes: 20 separate age classes for *A. amabilis* (current, 1 through 19 years) and 5 separate age classes for *T. mertensiana* (current, 1 yr, 2 yr, 3 + years and yellow senescing foliage). (It was impossible to obtain 20 age classes for *T. mertensiana* since the foliage does not have a distinctive visual appearance after the second year). Foliage and foliage bearing branches were each composited by age for each branch. The percent of total foliage biomass within each age class was determined for each canopy position (n = 6). Subsamples from each composited sample were then used to determine ash contents, foliage weight per 100 needles, and for nutrient analyses by age and canopy position.

A battery-powered drill with a plug-cutter bit was used to obtain live and dead bark samples at breast height (1.4 m) from each tree bole. Sapwood and heartwood were sampled immediately adjacent to the site of bark sampling.

Individual tree root samples were obtained by excavating at the base of each tree, with sample collection occurring one meter away from the tree base in the forest floor and E horizons. Each root sample by diameter class was a composite obtained from three excavated lateral roots. Root samples were sorted into 5 diameter classes (< 1, 1–2, $>$ 2–5, $>$ 5–10 and > 10 mm); roots greater than one mm in diameter were separated into phloem and xylem tissue.

Element chemical analyses

Prior to conducting chemical analyses, three digestion solutions (lithium sulfate, nitric acid, nitric-perchloric acid) were compared to choose a digest that gave the best recovery for aluminum. Since the nitric acid digest gave a high percent recovery of Al from Standard Reference material No. 1575, it was chosen as the digest for all elements.

Chemical analyses were conducted on dried tissue samples (0.4 g) digested in 5 mls of concentrated nitric acid. Samples were heated at 150 C for a minimum of 3 h, after which the temperature was reduced to 100 C and

samples were taken to dryness. Subsequently samples were brought up to 50 ml volume with 1 N nitric acid. A Jarrel-Ash 955 Atomcomp ICP was used to analyze the solutions for Al, Cu, Mn, Zn, Ca, Fe, K, Mg, P, Cd, Co and Cr. None of the data for Cd, Co, and Cr are included in this paper since levels were either below one ppm or below detection limits.

Percent element recovery was determined from analysis of NBS Standard Reference material No. 1572 (Citrus leaves) for Mg, Mn and Zn and No. 1575 (Pine needles) for the remaining elements. Mean percent recovery and standard deviation (n = 15) was 76 ± 5% for Al, 104 ± 9% for Cu 80 ± 9% for Mn, 100 ± 9% for Zn, 91 ± 6% for Ca, 78 ± 7% for Fe, 90 ± 8% for K, 79 ± 9% for Mg, 90 ± 9% for P.

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 ($p < 0.01$ and $p < 0.05$) when sample numbers were not equal and Student-Newman-Keuls test ($p < 0.05$) when sample numbers were equal (Snedecor & Cochran 1967). A T-test was used to compare element concentrations between similar age foliage and foliage bearing branches within all age classes. Since no significant differences in individual element concentrations occurred consistently with canopy position when comparing similar age classes of foliage or branches, element data were pooled by age for each tree.

Results

Foliage and foliage bearing branches

Element concentrations in foliage and foliage bearing branches for *T. mertensiana* and *A. amabilis* are presented in Table 1. For *T. mertensiana*, Ca, Mn and Al concentrations increased significantly while K, P, Cu concentrations decreased significantly with increasing foliage age. Unlike foliage, *T. mertensiana* branches showed no change in Ca, Mn and Al concentration while Fe concentrations increased significantly with increasing age. Similar to foliage, K, P, and Cu concentrations decreased significantly in branches while Mg and Zn remained the same with increasing age.

For *A. amabilis*, no significant changes in Ca, Fe, Mg, Cu, Mn, Zn and Al concentrations occurred with increasing foliage age (Table 1). Only P and K concentrations decreased significantly with increasing foliage age. Unlike foliage, *A. amabilis* branches showed significant increases in Al and Fe and significant decreases in Mg concentrations with increasing age. Similar to

foliage, K and P concentrations decreased significantly with increasing branch age.

Comparisons between foliage and branch element concentrations within the same age class and species showed significantly higher concentrations of Ca, K, Mg, P and Mn in foliage than in branches (Table 1). However, Cu and Fe accumulated in branches rather than foliage for both species. No differences in Zn or Al concentrations occurred between foliage and branches for *A. amabilis* but *T. mertensiana* had higher concentrations of Zn in branches and Al in foliage.

When comparing element concentrations of similar age foliage, only Mn and Al concentrations differed significantly between the two species (Table 1). Current, 1 and 2 year old *A. amabilis* branches had significantly higher Ca, K, Mg and P concentratons but lower Al concentrations than comparably aged *T. mertensiana* branches. If data from all ages and canopy positions are averaged and comparisons are made between the two species, *T. mertensiana* had significantly higher concentrations of all elements except for Ca in both foliage and branches.

Bole components

Except for Zn, significantly higher element concentrations were generally located in the bark than in woody tissues for both *T. mertensiana* and *A. amabilis* (Table 2). Comparison of similar tissue types showed no significant differences in Al concentrations between the two species (Table 2). When significant differences between similar tissue types occurred, *A. amabilis* always had lower concentrations of Ca, K, Mg, P, and Cu in the heartwood and P in the sapwood than *T. mertensiana*. However, dead bark concentrations of Fe, K, Cu and Zn were significantly higher in *A. amabilis* than *T. mertensiana*.

Root tissue

For both *T. mertensiana* and *A. amabilis*, phloem tissue always had higher concentrations of elements than xylem tissue across all root diameter classes (Table 3). In general for both tree species, once root diameters 2 mm or greater were reached, element concentrations did not change significantly in either phloem or xylem tissue with increasing root diameter. The highest Al, Cu, P and Fe concentrations occurred in roots < 2 mm in diameter for both *A. amabilis* and *T. mertensiana*.

Except for Al and Mg, similar root diameters and tissue types showed few significant differences in element levels between species. *Abies amabilis* had significantly higher Mg concentrations in the < 1 mm roots than *T. mertensiana*, while *T. mertensiana* had significantly higher Al concentrations in the < 1 mm and 1–2 mm phloem root tissues than *A. amabilis*.

Table 1. Element concentrations in foliage and foliage bearing branches by tissue age for *A. amabilis* and *T. mertensiana*.

Species	Tissue type	Tissue age (yrs)	n	Al	Cu	Mn
				ppm		
Tsuga mertensiana	Foliage	Current	10	500aAX+	3.9aAX	890aAX
		1	9	720abAX	2.4bAX	1,440abAX
		2	9	860abAX	1.9bcAX	1,690abAX
		3+	10	1,120bA	1.8bcA	1,940abA
		Yellow	9	1,110bA	0.8cA	2,090bA
		Total	47	860(440)X*	2.2(1.3)X	1,600(820)X
	Foliage bearing branches	Current	11	440aAX	7.0aBX	790aAX
		1	10	430aBX	5.8abBX	770aBX
		2	9	470aBX	4.9abBX	700aBX
		3+	11	660aA	4.4abB	800aB
		Yellow	9	710aA	3.5bB	860aB
		Total	50	540(340)X	5.2(2.6)X	780(200)X
Abies amabilis	Foliage	Current	10	110aAZ	3.7aAX	510aAZ
		1	9	130aAZ	1.6aAZ	620aAZ
		2	9	160aAZ	1.9aAX	720aAZ
		3–4	20	190–	1.7–	730–
				200aA	1.7aA	750aA
		5	10	210aA	1.9aA	690aA
		6–10	42	210–	1.3–	550–
				250aA	1.8aA	680aA
		11–13	20	220–	1.6–	550–
				260aA	1.8aA	750aA
		14–15	10	250–	2.0–	530–
				260aA	2.0aA	640aA
		16–17	7	210–	1.0–	540–
				220aA	1.5aA	600aA
		18	3	190aA	1.2aA	520aA
		19	3	260aA	1.9aA	540aA
		Total	143	200(70)Z	1.8(0.7)Z	640(280)Z
	Foliage bearing branches	Current	9	100aAZ	4.9aBZ	530aAZ
		1	8	130abAZ	5.0aBX	740aAX
		2	9	160abAZ	5.0aBX	700aAX
		3–4	19	180–	4.4–	530–
				190abA	4.6aB	600aA
		5	11	220abA	4.3aB	480aB
		6–10	45	200–	4.0–	350–
				240abA	4.5aB	450aB
		11–13	20	200–	3.6–	310–
				230abA	3.8aB	320aB
		14–15	11	200–	2.9–	330–
				200abB	3.7aB	330aB
		16–17	7	180–	2.7–	270–
				290abA	3.0aB	350aA
		18	3	360abA	3.4aA	310aA
		19	3	410bA	4.2aB	390aB
		Total	145	200(100)Z	4.2(1.2)Z	450(200)Z

+Numbers in each column followed by the same lower case letter (a) are not significantly different between tissue ages within each tissue type (Scheffes, $P < 0.05$) and within each species. Numbers in each column followed by upper case letter (A or B) are not significantly different between similar tissue ages compared between the two tissue types and within each species (Scheffes, $p < 0.05$).

Zn	Ca	Fe	K	Mg	P
ppm					
21.7aAX	2,230aAX	70aAX	8,580aAX	900aAX	1,800aAX
26.7aAX	3,150abAX	70aAX	5,780bAX	950aAX	1,310bAX
29.1aAX	3,410abcAX	70aAX	4,910bcAX	920aAX	1,250bAX
27.2aA	4,600bcA	130aA	4,260cA	1,020aA	1,370abA
26.1aA	5,120cA	80aA	2,110dA	1,110aA	1,060bA
22.2(9.1)X	3,690(1,570)X	80(60)X	5,180(2,300)X	980(170)X	1,370(380)X
27.5aAX	2,260aAX	50aAX	7,220aBX	720aBX	1,490aBX
31.5aBX	1,990aBX	70abAX	4,350bBX	540aBX	860bBX
28.0aAX	2,090aBX	70abAX	3,350bBX	530aBX	720bcBX
44.1aA	2,420aB	190aB	2,900bcB	660aB	670bcB
48.6aB	2,500aB	370cB	1,610cA	620aB	630cB
35.8(9.8)X	2,250(680)X	150(40)X	3,990(2,220)X	620(160)X	890(360)X
42.7aAX	3,040aAZ	60aAX	7,920aAX	910aAX	1,540aAX
22.5aAZ	2,940aAX	60aAX	5,250abAX	810aAX	1,060abAX
28.5aAX	3,630aAX	50aAX	4,610bAX	850aAX	1,010abaX
30.5–	4,420–	70–	4,070–	750–	880–
39.8aA	4,730aA	80aA	4,300bA	860aA	930abA
39.9aA	4,690aA	180aA	4,160bA	730aA	870abA
14.6–	4,380–	90–	3,230–	640–	720–
69.9aA	6,080aA	130aA	4,240bA	810aA	850abA
21.1–	5,820–	110–	3,130–	610–	720–
96.4aA	6,650aA	110aA	3,500bA	850aA	730bA
17.7–	6,150–	120–	3,280–	630–	720–
33.1aA	6,860aA	140aA	3,640bA	700aA	720bA
22.1–	5,870–	110–	2,270–	530–	570–
92.3aA	6,320aA	140aA	3,160bA	620aA	690bA
45.4aA	5,480aA	100aA	3,040bA	630aA	690bA
27.7aA	5,870aA	130aA	3,010bA	590aA	620bA
36.0(23.5)Z	4,960(1,630)Z	100(80)Z	4,110(1,480)Z	740(260)Z	870(310)Z
32.6aAX	3,250aAZ	40aAX	7,540aAX	1,100aBZ	2,140aBZ
29.1aAX	2,830aAZ	70aAX	6,660abBZ	980abAZ	1,390bBZ
23.3aAX	3,160aAZ	90abBX	5,010abcBZ	850abAZ	990bcBZ
26.5–	3,050–	120–	3,640–	640–	770
29.2aA	3,250aB	130abcB	4,140bcbA	710abA	810cdA
51.9aA	3,270aB	190abcA	3,290cbB	600abA	690cdA
24.0–	2,850–	170–	2,080–	480–	510–
67.6aA	3,290aB	240abcB	2,950cbB	550abB	630cbB
18.3–	3,090–	180–	1,700–	410–	420–
46.5aA	3,270aB	220abcB	1,880dB	440bB	470cbB
14.6–	3,380–	160–	1,520–	380–	360–
15.9aA	3,660aB	210abcA	1,800dB	430bB	400dB
22.7–	3,310–	140–	1,510–	360–	350–
30.0aA	3,930aB	270abcA	1,730dB	410bB	400dA
24.7aA	3,240aB	400bcA	1,450dB	360bB	410dA
39.8aA	4,290aA	440cA	1,530dB	440bA	500cdA
32.7(15.1)X	3,240(640)Z	170(120)X	3,230(1,910)Z	600(270)X	740(430)Z

Numbers in each column followed by the same upper case letter (X or Z) are not significantly different when comparing similar tissue age and tissue type between the two species (Scheffes, $p < 0.01$).

*Mean $\pm$ one standard deviation.

Table 2. Element concentrations for bole tissues for *A. amabilis* and *T. mertensiana* (mean ± one standard deviation).

Species	Tissue type*	Al	Cu	Mn
		ppm		
Tsuga mertensiana	Heartwood	20aA+	1.5abA	170aA
		(10)	(0.8)	(30)
	Sapwood	10	0.9aA	100aA
		(0)	(0.1)	(30)
	Live bark	300bA	1.7abA	470bA
		(190)	(0.2)	(160)
	Dead bark	180abA	1.9bA	240aA
		(90)	(0.2)	(130)
Abies amabilis	Heartwood	10aA	0.8aB	120aB
		(0)	(0.1)	(30)
	Sapwood	10aA	1.1aA	80aA
		(0)	(0.4)	(20)
	Live bark	120aA	1.7bA	420bA
		(140)	(0.4)	(120)
	Dead bark	150aA	2.7cB	340bA
		(140)	(0.7)	(140)

* All samples obtained at breast height diameter.
+ Numbers in each column followed by the same lower case letter (a) are not significantly different between tissue types within each species (Student-Newman-Keuls, $p < 0.05$). Numbers in each column followed by the same upper case letter (A) are not significantly different when comparing similar tissue types between the two species (Student-Newman-Keuls, $p < 0.05$).

Ca/Al ratios in tissues

The Ca/Al ratios of root, bole and canopy tissues of both species are presented in Table 4. *Tsuga mertensiana* always had lower Ca/Al ratios than *A. amabilis* when similar tissue types were compared. The lowest Ca/Al ratios were measured in < 2 mm roots for both species.

Element interactions

Comparison of changes between Ca, Mn, P and Al by root diameters and types showed no pattern in root phloem tissue. A positive correlation coefficient ($r = 0.82, p < 0.01$) occurred between Fe and Al concentrations in root phloem tissue. Significant positive correlation coefficients existed between Al and Mn ($r = 0.83, p < 0.01$), Al and Ca ($r = 0.78, p < 0.02$), and Al and Fe ($r = 0.97, p < 0.0001$) but not between Al and P and Mg within root xylem tissue across all root diameters.

Comparison of average element concentrations of all foliage ages for *T.*

Zn	Ca	Fe	K	Mg	P
ppm					
20.1aA	840aA	40aA	1,450bA	200aA	320bA
(3.2)	(330)	(30)	(200)	(70)	(160)
18.2abA	510aA	30aA	980abA	90aA	90aA
(5.6)	(80)	(10)	(560)	(20)	(70)
12.4bA	6,820bA	30aA	2,460cA	390bA	590cA
(3.9)	(4,380)	(10)	(560)	(110)	(120)
5.8cA	2,940aA	20aA	640aA	150aA	260abA
(1.6)	(1,180)	(10)	(130)	(50)	(100)
21.9aA	580aB	30abA	990aB	120aB	30aB
(4.9)	(90)	(10)	(290)	(50)	(50)
30.5aB	520aA	80aB	970aA	80aA	60aA
(12.2)	(110)	(40)	(180)	(10)	(40)
13.8aA	3,900bA	20bA	1,990bA	300bA	380bB
(2.4)	(810)	(0)	(270)	(60)	(130)
37.0aB	3,550bA	80aB	1,470aB	210cA	360bA
(25.6)	(1,070)	(60)	(600)	(60)	(120)

mertensiana and *A. amabilis* resulted in significant positive correlation coefficients betweeen Al and Mg ($r = 0.71$, $p < 0.0001$), and Al and Mn ($r = 0.98$, $p < 0.0001$). Significant but low correlations were found between Al and P ($r = 0.49, p < 0.01$), Ca and Fe ($r = 0.64, p < 0.0005$), Mg and Fe ($r = 0.50, p < 0.01$), and P and Fe ($r = 0.51, p < 0.01$) in foliage. Unlike roots, poor correlation coefficients occurred between Al and Ca, and between Al and Fe in foliage.

Discussion

Aluminum concentrations in *T. mertensiana* tissues suggest that mountain hemlock is an Al accumulator and not just tolerant of high Al levels. Amaury de Medeiros and Haridasan (1985) suggested that Al accumulating woody species have foliar Al concentrations of 1.0–1.8% (never lower than 0.9%) while nonaccumulating species range from 0.01–0.06% (never higher than 0.08%). Based on this classification, *T. mertensiana* foliage Al concentrations (500 to 1120 ppm) falls between the ranges for accumulators and nonaccumulators while *A. amabilis* is classified as an Al nonaccumulator (110 to 260 ppm). Chenery and Sporne (1976) defined Al accumulator plants as those having > 1000 ppm Al in their shoots. Older foliage of *T. mertensiana* would fit in this latter category as an Al accumulator.

Table 3. Element concentrations for roots by tissue type for *A. amabilis* and *T. mertensiana* (mean ± one standard deviation).

Species	Root diameter (mm)	Root tissue type	Al	Cu
			ppm	
Tsuga mertensiana	< 1	Phloem + Xylem	1,320aA (640)	7.8abA (2.9)
	1–2	Phloem	910bA (380)	10.4aA (4.6)
		Xylem	180cA (120)	5.6bcA (3.0)
	> 2–5	Phloem	490dA (110)	3.6cA (1.4)
		Xylem	40cA (20)	1.7cA (1.2)
	> 5–10	Phloem	410dA (130)	2.8cA (1.1)
		Xylem	40cA (20)	1.5cA (1.3)
	> 10	Phloem	370dA (130)	3.8cA (1.9)
		Xylem	30cA (10)	1.4cA (0.5)
Abies amabilis	< 1	Phloem + Xylem	730aB (190)	7.4aA (1.2)
	1–2	Phloem	430bB (120)	7.3aA (0.8)
		Xylem	90cdA (40)	5.4abA (2.1)
	> 2–5	Phloem	420bA (180)	4.1bcA (1.4)
		Xylem	50cdA (20)	3.1bcdB (1.0)
	> 5–10	Phloem	240cB (110)	2.3cdA (1.3)
		Xylem	20dB (10)	1.1dA (1.0)
	> 10	Phloem	190cdA (50)	2.2cdA (1.3)
		Xylem	20dA (10)	1.4dA (1.0)

+Numbers in each column followed by the same lower case letter (a) are not significantly different when comparing root diameter classes and root tissue type within each species (Student-Newman-Keuls, $p < 0.05$). Numbers in each column followed by the same upper case letter (A) are not significantly different when comparing similar root diameter and tissue type between the two species (Student-Newman-Keuls, $p < 0.05$).

Mn	Zn	Ca	Fe	K	Mg	P
			ppm			
240abA	35.3aA	1,880abA	780aA	2,750abA	440aA	1,390aA
(180)	(8.7)	(650)	(440)	(1,140)	(110)	(520)
420abA	35.5aA	2,500abA	430bA	2,550abA	720aA	1,100abA
(220)	(11.2)	(970)	(340)	(700)	(460)	(270)
310abA	15.2bcA	1,270abA	80cA	2,430abA	470aA	910abA
(160)	(4.5)	(640)	(50)	(1,090)	(160)	(230)
640bA	29.4abA	3,270bA	160cA	3,150aA	730aA	1,090abA
(270)	(7.2)	(1,160)	(80)	(1,660)	(320)	(620)
230abA	9.3cA	780aA	30dA	1,370bA	310aA	410cA
(130)	(2.2)	(400)	(0)	(510)	(170)	(140)
520abA	20.5abcA	2,360abA	80cA	2,010abA	560aA	730bcA
(280)	(5.4)	(680)	(30)	(530)	(290)	(310)
200aA	5.5cA	640aA	30dA	1,240bA	200aA	350cA
(120)	(0.7)	(240)	(10)	(450)	(180)	(90)
420abA	30.8abA	3,520bA	130cA	1,500bA	420aA	460cA
(290)	(14.9)	(1,440)	(40)	(750)	(290)	(150)
160aA	7.4cA	710aA	20dA	880bA	160aA	200cA
(120)	(5.2)	(230)	(0)	(50)	(110)	(110)
300abA	32.6aA	1,820abA	680aA	3,550aA	650abB	1,480aA
(130)	(10.4)	(520)	(440)	(340)	(220)	(160)
470abA	30.8aA	2,750bcA	210bA	3,260aA	900bA	1,100bcA
(260)	(7.8)	(570)	(90)	(660)	(370)	(310)
290abA	17.3bcA	1,400aA	50bA	2,680abA	660abA	860cdA
(190)	(5.6)	(340)	(30)	(930)	(260)	(170)
560abA	30.2aA	3,290cA	330bA	3,230aA	870bA	1,210bA
(380)	(8.9)	(1,320)	(450)	(470)	(450)	(180)
240abA	7.9cA	890aA	30bA	1,930bcB	490abA	660defB
(190)	(2.4)	(290)	(30)	(360)	(140)	(140)
530abA	28.8aB	3,380cB	90bA	1,990bcA	600abA	710deA
(210)	(5.1)	(860)	(50)	(500)	(150)	(320)
210aA	8.0cB	850aA	20bA	1,990cA	300aA	360efA
(70)	(0.7)	(210)	(10)	(510)	(40)	(110)
620bA	31.9aA	3,690cA	80bA	1,780bcA	470abA	580defA
(310)	(5.8)	(1,030)	(30)	(680)	(200)	(260)
230abA	6.9cA	770aA	30bA	820cA	220aA	300fA
(130)	(2.1)	(300)	(10)	(430)	(110)	(90)

Table 4. Ca/Al ratios for above and belowground tissues for *A. amabilis* and *T. mertensiana.*

Tissue type	*A. amabilis*	*T. mertensiana*
Roots		
< 1 mm	2.5	1.4
1–2 mm (Phloem)	6.5	2.7
1–2 mm (Xylem)	15.5	7.0
> 2–5 mm (Phloem)	7.9	6.7
> 2–5 mm (Xylem)	17.2	17.4
> 5–10 mm (Phloem)	14.2	5.7
> 5–10 mm (Xylem)	40.7	17.3
> 10 mm (Phloem)	19.2	9.6
> 10 mm (Xylem)	40.3	26.3
Heartwood	44.6	38.0
Sapwood	47.5	56.6
Live Bark	32.0	22.4
Dead Bark	22.9	15.9
Foliage	24.2	4.3
Foliage bearing branches	15.9	4.2

These foliage Al concentrations are very similar to the Al values reported by Radwan & DeBell (1980) for western hemlock (*T. heterophylla*) in Washington (between 600 and 1000 ppm) and Gill & Lavender (1983) for western hemlock in Oregon and Washington (800 to 1400 ppm). Messenger (1975) reported high Al accumulation by eastern hemlock in contrast to some other tree species; however, the values reported for old (408 ppm) and new (266 ppm) foliage are lower than that measured for *T. mertensiana* old (1110 ppm) and new (500 ppm) foliage in this study. Mean foliar Al concentrations in pines (suggested to be Al accumulators by McCormick & Steiner 1978) varied from 693–1298 ppm (Humphreys & Truman 1964) which is similar to the 860 ppm average measured for *T. mertensiana* foliage in this study.

In this subalpine stand, whre the two species grow adjacent to one another, significantly higher levels of Al were accumulated in foliage, branch and root tissues by *T. mertensiana* than by *A. amabilis.* On an individual tree basis, *T. mertensiana* contributed more to the biocirculation of Al than *A. amabilis.* However, *A. amabilis* dominated the site on a stand level: the influence of *T mertensiana* would be more limited to the areas surrounding individual trees. Yet, since the influence of specific vegetation on soils can be considerable (Zinke & Crocker 1962; Alban 1982; Van Miegroet & Cole 1985) *T. mertensiana* has the potential to affect pedogenic processes and

future species composition of the site. Because the overstory is dominated by an Al tolerant *A. amabilis*, enhanced Al biocirculation by *T. mertensiana* does not appear to detrimentally affect stand growth. In some ecosystems, Al accumulators have been suggested to restrict the growth of other species not tolerant of high Al levels and therefore influence species succession (Messenger et al. 1978).

Future management of these subalpine sites must consider the high soluble Al levels naturally present as part of the podzolization process. For successful replanting, future regeneration efforts will require identifying and selecting tree species tolerant of high Al levels, or those that do not increase the already high levels of soluble Al in these soil environments. The apparent Al tolerance of the subalpine vegetation at this site further suggests that these tree species would be little impacted by acid precipitation induced mobilization of Al.

Patterns of change in element concentrations with increasing foliage age differed for *T. mertensiana* and *A. amabilis*. *Tsuga mertensiana* foliage accumulated significant amounts of Al and Mn with increasing age while *A. amabilis* did not. These increases fit the generalization that Al toxicity is frequently associated with increased Mn uptake (Kabata-Pendias & Pendias 1984). Both elements are also associated with increased uptake in low pH situations. For all foliage ages, Al and Mn concentrations were significantly higher in *T. mertensiana* than *A. amabilis*. These differences show the vegetation differences in uptake of these nutrients.

Only for *T. mertensiana* did the increased Al accumulation in older foliage coincide with significant increases in Ca and Mn and significant decreases in Cu concentrations. Compared to a broad spectrum of plants, Mn concentrations reported for *T. mertensiana* and *A. amabilis* are present at excessive or toxic levels while Cu would be considered deficient (Kabata-Pendias & Pendias 1984). Manganese toxicity in conifers is not common. Levels of Mn that cause visual symptoms in Douglas-fir seedlings are generally much higher than those reported in this study or commonly measured in local forests (Beaton et al. 1965a; Radwan et al. 1979; Radwain & De Bell 1980; Gill & Lavender 1983). In solution culture, toxicity was observed for Douglas-fir seedlings when foliar Mn levels were higher than 8000 ppm and root levels were higher than 1400 ppm. In contrast, the decreases in Cu concentrations with increasing *T. mertensiana* foliage age occurred even though these levels are possibly already deficient (Oldenkamp & Smilde 1966).

The Mn, Fe, Mg, Ca and P concentrations reported here for foliage are similar to the values reported by Messenger (1975) for eastern hemlock and white spruce growing on well developed podzols; the only exception was the

lower Al concentrations in eastern hemlock and white spruce foliage. These values are also similar to those reported for western hemlock and Douglas-fir in the Pacific Northwest (Beaton et al. 1965ab; Radwan & DeBell 1980; Gill & Lavender 1983).

The concomitant increases in Ca and Al levels for *T. mertensiana* foliage do not follow the suggested reductions in Ca uptake hypothesized to occur in response to Al toxicity (Hüttermann 1983). When reductions in Ca uptake were measured by Schier (1985) for seedlings growing in Al solutions, Al toxicity also occurred. Even though aboveground tissues of *T. mertensiana* did not have reductions in Ca levels in response to Al, fine roots experienced decreased Ca with increased Al concentrations. This is also seen by the increases in Ca/Al ratios of bole tissues in contrast to fine roots. This suggests that even though roots tissues may show reduced Ca uptake with increasing Al levels, these ratios are not carried over into aboveground tissues. This may be explained by the fact that Al toxicity and associated reductions in Ca levels were measured in roots located in the deeper soil depths (Vogt et al. 1987). Since Al is sequestered in root tissues by soil horizon, the potential Al toxicity may also become localized at specific soil depths. The high levels of available Al found in the Bhs horizon soil appear to be contained in root tissues in that horizon and probably not contribute significantly to Al circulation by the total living biomass (see Vogt et al. 1987). Trees appear to avoid Al toxicity by obtaining nutrients in the upper horizons, where nutrient availability is greater and lower Al levels are present. Fine root distribution in this site (Vogt et al. 1981) supports this hypothesis since the majority (75%) of fine root biomass is found in the forest floor and E horizons.

These changes in Ca and Mn concentrations with increasing Al in foliage for mature forest trees differ sharply with results obtained with seedlings grown in solution culture (Schier 1985; Ryan et al. 1986a, b). The higher levels of Mn in *T. mertensiana* mature tree foliage contrasts with *T. heterophylla* seedlings foliage where Mn concentrations decreased as Al levels increased (Ryan et al. 1986a). Schier (1985) also reported that Al uptake decreased conifer seedling Mn, Mg and Zn uptake but had no effect on P levels. However, comparison of similar aged foliage for mature *A. amabilis* and *T. mertensiana* showed no significant difference in the Zn and P concentrations even though Al levels were significantly higher in *T. mertensiana*.

Differences in Al and other element interactions between seedling and mature trees may be due to several factors:

— different species being compared
— differences in seedling and mature tree physiology
— that Al accumulating species have less or no toxic response to Al and

therefore lack the nutrient reductions of Al nonaccumulators
— organic acids in soil solution complex Al rendering it non-toxic to plants under natural conditions

Similar to foliage, significantly higher concentrations of Al were measured in *T. mertensiana* and *A. amabilis* branches. Unlike foliage, *A. amabilis* branches had significantly higher Ca, Mg, and P concentrations than similar aged *T. mertensiana* branches. It appears that branch tissue more than foliage reflected the commonly suggested reductions in Ca, Mg, and P resulting from high Al levels (Foy et al. 1978). No species differences were measured for branch concentrations of Fe and Zn while significantly higher Cu and Mn concentrations were measured in current year branches for *T. mertensiana.*

In general Cu and Fe were present in higher concentrations in branches than foliage tissues while Mn, P, Mg, and Ca occurred in higher concentrations in foliage for both species. Higher concentrations of some trace metals in branch tissue compared to foliage have been shown by Kabata-Pendias & Pendias (1984) and Heinrichs & Mayer (1980) for pines, spruce and beech. Accumulation of trace metals in woody tissues should result in lower circulation rates for them in the biological components; especially since only 27.5% of annual litterfall is branch tissue compared to 47.2% for foliage (Vogt et al. 1983). In spite of lower branch litterfall, higher trace metal concentrations in branch tissues resulted in similar inputs of Cu and Fe from foliage and branch litterfall (see Vogt et al. 1987). Even so, because branches decompose at slower rates than foliage (Vogt et al. 1983), accumulation of trace metals in branches will result in lower rates of biocycling of these elements.

For the two tree species, differences found between element levels in foliage, branch and root tissues were not evident in live bole tissues. No significant differences in Al levels occurred between *A. amabilis* and *T. mertensiana* when comparing similar types of bole tissues. These results suggest that foliage and roots selectively accumulate elements within their tissues and are better indicators of nutrient differents between species than the bole.

The relative importance of fine roots < 1 mm in diameter as sites of Al and Fe accumulation is quite apparent when comparing root and foliage element data. *Abies amabilis* had 3.6 times higher Al and 6.9 times higher Fe concentrations while *T. mertensiana* had 1.5 times higher Al and 9.3 times higher Fe concentrations in < 1 mm roots than in foliage. Aluminum concentrations found in *A. amabilis* very fine roots (730 ppm) are similar to the values reported by Mayer & Heinrichs (1981) for beech (680 ppm) growing on acid soil while the *T. mertensiana* value (1320 ppm) is similar to spruce

(1420 ppm) growing on acid soil. Even though the values appear similar, these Al levels for *T. mertensiana* and *A. amabilis* are minimum concentrations since roots were excavated from surface soil horizons. Mayer & Heinrichs (1981) reported a root Al value of 8640 ppm for maple growing in calcareous soil — which is similar to the stand level root Al concentration measured in the Bhs horizon (9300 ppm) (Vogt et al. 1987). Mayer & Heinrichs (1981) also measured accumulation of Cd and Zn in very fine roots which was not measured in our stand.

Comparison of *T. mertensiana* and *A. amabilis* roots by similar diameter and root tissue types showed that significant differencs in Al concentrations occurred in the < 1 mm and 1–2 mm root diameter classes. *Tsuga mertensiana* accumulated higher levels of Al in roots < 2 mm in diameter but once roots were > 2 mm in diameter no significant differences between tree species were apparent. Tree species differences in Al accumulation show up at the very fine root level where uptake and sequestering of Al occurs.

Heavy metal tolerance is often equated with the capacity to complex Al in cell walls of root tissues (Wagatsuma 1983) thus preventing Al uptake by the plant into metabolically active tissues where toxicity can occur. For both tree species, Al accumulated in root phloem tissues instead of root xylem. Part of the plant's resistance to Al toxicity may result from complexing metals in phloem tissues, reducing Al uptake in the xylem. This selective accumulation of Al in the phloem also means no direct relationship can be drawn between amounts of Al and amounts of other elements (except for Fe) present in the phloem. This contrasts the situation in root xylem where increased Al levels coincided with increased Ca, Mn and Fe levels, suggesting a direct relationship between these elements and Al movement within the xylem.

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