

Soils and foliar nutrient analysis of *Chamaecyparis lawsoniana* and *Thuja plicata* in southwestern Oregon

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Surface mineral soil and foliage associated with *Chamaecyparis lawsoniana* (A. Murr.) Parl. and *Thuja plicata* Donn ex D. Don were sampled at six sites in southwestern Oregon. Total soil nitrogen concentrations ranged from 0.08 to 0.37%. Percentage exchangeable concentrations of other soil nutrients were 0.0002–0.0020 P, 0.014–0.224 Ca, 0.002–0.018 K, and 0.002–0.023 Mg. Foliage of *Chamaecyparis* contained 0.9–1.9% N, 0.11–0.23% P, 0.8–1.9% Ca, 0.67–1.20% K, and 0.11–0.26% Mg. Foliage of *Thuja* contained 0.9–1.6% N, 0.12–0.24% P, 1.1–2.0% Ca, 0.52–0.95% K, and 0.06–0.23% Mg. Overall, foliage of *Chamaecyparis* contained significantly higher concentrations of K, and tended to have lower Ca:Mg ratios than that of *Thuja*. Concentrations of soil nutrients showed no obvious relation to species occurrence on a study-wide basis. Within sites where the two species grew together, however, *Thuja* was associated with higher soil Ca:Mg ratios and foliar Ca, and *Chamaecyparis* was associated with higher levels of soil K and foliar N. Foliar nutrient concentrations showed little relation to concentrations in soil, although low soil Ca, P, and Mg concentrations were reflected in foliage at some sites. Soils in the study area have higher Ca:Mg ratios and more available N than soils over much of *Chamaecyparis*' range. Given the apparent nutritional requirements of *Thuja*, it seems unlikely that it will significantly replace *Chamaecyparis* killed by root rot.

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Les auteurs ont échantillonné le sol minéral de surface et le feuillage de *Chamaecyparis lawsoniana* (A. Murr.) Parl. et de *Thuja plicata* Donn ex D. Don dans six stations du sud-est de l'Orégon. Les concentrations en azote total du sol étaient de 0,08 à 0,37%; celles de P disponible et des éléments échangeables s'élevaient à 0,0002–0,0020 P, 0,014–0,224 Ca, 0,002–0,018 K et 0,002–0,023 Mg. Le feuillage de *Chamaecyparis* renfermait 0,9–1,9% N, 0,11–0,23% P, 0,8–1,9% Ca, 0,67–1,20% K et 0,11–0,26% Mg; celui de *Thuja* renfermait 0,9–1,6% N, 0,12–0,24% P, 1,1–2,0% Ca, 0,52–0,95% K et 0,06–0,23% Mg. Dans l'ensemble, le feuillage de *Chamaecyparis* était significativement plus riche en potassium que celui de *Thuja*, mais son ratio Ca:Mg était généralement plus faible. En considérant l'ensemble des stations, la distribution des espèces ne semble pas être liée aux concentrations des éléments du sol. Toutefois, à l'intérieur des stations où croissent les deux espèces, *Thuja* est associé à un ratio Ca:Mg du sol plus élevé et à une concentration foliaire de Ca plus grande, tandis que *Chamaecyparis* est associé à un plus haut niveau en K du sol, et son feuillage a une teneur plus élevée en azote. Peu de relations ont été observées entre les teneurs en éléments du feuillage et les concentrations dans le sol, si ce n'est que les faibles concentrations en Ca, P et Mg du sol se traduisaient au niveau des concentrations foliaires dans certaines stations. Les sols de la région étudiée ont des rapports Ca:Mg plus élevés et renferment plus d'azote disponible que les sols en général de l'aire de distribution de *Chamaecyparis*. Etant donné les besoins apparents en éléments de *Thuja*, il est peu probable que cette espèce puisse remplacer d'une façon significative le *Chamaecyparis* tué par la pourriture des racines.

[Traduit par le journal]

Introduction

Chamaecyparis lawsoniana (A. Murr.) Parl (Port Orford cedar) and *Thuja plicata* Donn ex D. Don (western red cedar), members of the Cupressaceae, grow together infrequently in southwestern Oregon and northwestern California. Both species are ecologically versatile, occurring within several vegetation zones and plant communities, and on a variety of parent materials (Franklin and Dyness 1973; Hawk 1977; Meyer and Amaranthus 1979). *Chamaecyparis* is largely restricted

to a narrow coastal strip in southwestern Oregon and northwestern California; in contrast, *Thuja* grows over much of the Pacific Northwest, British Columbia, and southern Alaska (Fowells 1965). Climatic requirements (i.e., sufficient precipitation, high humidity, moderate growing-season temperature) appear to explain, directly or indirectly, much of the geographical distribution of *Thuja* (Packee 1976; Sharpe 1974; Sudworth 1907), and at least the eastern and southern range boundaries of *Chamaecyparis* (Zobel and Hawk 1980). The cause of the northern range limit of *Chamaecyparis* remains obscure, although it may relate to phenological limitations or a geologic discontinuity (Zobel 1983; Zobel and Hawk 1980). Both species grow best in

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TABLE 1. Site characteristics

Site name	Site code	Elevation (m)	Parent material	Predominant tree age (years)	1979 annual precipitation (mm)	1979 mean annual temperature (°C)
Camas Mountain						
Wayside	CM	450	Sedimentary	0–125	903(1557) ^a	12.7(12.8) ^a
Coos County						
Forest	CC	400	Basalt	0–55	1643 ^b	11.8
Ash Swamp	AS	670	Sedimentary	35–60	1431 ^c	12.3
Squaw Lake	SL	640	Sedimentary	65–85	1431 ^c	12.3
POCRNA ^d	POC	300	Alluvium/sedimentary ^c	40–80	1431 ^c	12.3
CRFRNA ^f	CRF	520	Sedimentary	0–130	1431 ^c	12.3

^aClimatic data are for Roseburg and Dora (in parentheses) (Anonymous 1979); actual precipitation is probably intermediate between these two stations.

^bClimatic data are for North Bend, 15 km north at sea level.

^cClimatic data are for Powers, at 230-m elevation, and 15 to 20 km north of the sites.

^dPort Orford cedar Research Natural Area.

^eParent materials correspond to plots in the order POr/POp.

^fCoquille River Falls Research Natural Area.

relatively moist, protected habitats and require abundant soil moisture at the southern end of their ranges. Although their southern range boundaries coincide closely, they seldom grow together on the same site. We suspected that differences in nutrient relationships contribute to local segregation and different northern limits for the two species; Imper (1981) investigated the possibility. Understanding these habitat differences is also important for predicting the degree to which *Thuja* may replace *Chamaecyparis* where the latter is being eliminated by a fatal root rot (Roth *et al.* 1972).

This paper reports soil and foliar nutrient concentrations for *Chamaecyparis* and *Thuja* growing at six sites near the southern end of the Oregon Coast Range, including three which support both species, and relates these nutrient concentrations to the species distributions.

Study areas

Twelve plots were sampled at six sites in southwestern Oregon (Tables 1 and 2, Fig. 1). Our choice of sites was limited by the uncommon occurrence of *Thuja* within *Chamaecyparis*' range. Emphasis was placed on sampling where the trees occurred in their highest concentration and where both young and older trees were present. Some sites were sampled because of the clear segregation of the two trees on a local scale, enabling comparison of soils within a short distance. The sites ranged from having dense *Thuja* and little or no *Chamaecyparis* at Coos County Forest and Camas Mountain, to common *Chamaecyparis* with no *Thuja* at the Coquille River Falls Research Natural Area.

All sites fall within the *Tsuga heterophylla* vegetation zone (Franklin and Dyrness 1973). Sites at Ash Swamp, Squaw Lake, and the Coquille River Falls and Port Orford cedar Research Natural areas, well within the northern portion of *Chamaecyparis*' range, have vegetation similar to either

the *Tsuga heterophylla* – *Chamaecyparis lawsoniana*/*Polystichum munitum* – *Oxalis oregana* community or the *Tsuga heterophylla* – *Chamaecyparis lawsoniana*/*Rhododendron macrophyllum* – *Gaultheria shallon* community defined by Hawk (1977). Sites at Coos County Forest and Camas Mountain are similar to the *Tsuga heterophylla*/*Gaultheria shallon* – *Polystichum munitum* association described by Franklin and Dyrness (1973) for the Oregon Cascades. Weather data from four stations encompassing the study area are included in Table 1. The site at Camas Mountain is driest, and has the largest annual temperature fluctuation, being separated from the coast by part of the Coast Range. The site at Coos County Forest is most affected by marine fog and precipitation patterns, since it is located on a ridge which directly overlooks Coos Bay. The remaining sites, near the southern end of the Coquille River Valley, are influenced by moist air driven down the valley during the summer by northwesterly winds off the ocean.

Camas Mountain (CM)

The plot near Camas Mountain was located in a relatively dense stand of *Thuja* on an old-stream terrace, apparently east of the range of *Chamaecyparis*. Parent material is probably sedimentary rock of the Flournoy formation (Baldwin 1974).

Coos County Forest (CC)

This plot was located on an outcrop of marine basalt within surrounding Roseburg formation sediments. The site lies close to the northern limit of *Chamaecyparis*. Although absent from mature forests in the area, some *Chamaecyparis* did occur adjacent to the CC plot (CC(adj.)) and was sampled for foliar analyses.

Ash Swamp (AS)

Ash Swamp is an old floodplain of the south fork of the Coquille River. *Thuja* is restricted to stream banks (plot ASr-1) and lower parts of the swamp (plot ASr-2). *Chamaecyparis* generally occurs throughout but is most important on higher ground (plot ASp). Parent material in the swamp is

Quaternary alluvium. Surrounding hills are underlain by sedimentary rocks of the Tyee and Flournoy formations. Soils are well developed. The water table in July and September 1979, and January 1980 was always deeper than 1 m in the ASP plot, but varied from over a metre deep (July) to above ground (January) in the ASr-2 plot, which had gleyed soil.

Squaw Lake (SL)

The forest near Squaw Lake also showed segregation of the species. Most of the area is dominated by *Chamaecyparis* and *Pseudotsuga*, but relatively pure stands of *Thuja* grow at the base of the slope (plots SLr-1, SLr-2) and higher on the slope in areas where the soil is wetter and heavier textured (plot SLr-3). *Chamaecyparis* (plot SLp) also grows under conditions similar to that present in the nearby SLr-3 plot (i.e., a steep hillside drainage); the primary distinctions between the two plots were the coarser-textured soil and the virtual absence of *Thuja* in the SLp plot. Some nutrient analyses were also made of the soil just adjacent to the SLp plot (SLp(adj.)) which was of heavier texture (surface texture is sandy clay loam), and coincided with the occurrence of *Thuja* farthest upslope at this site. Parent material at the site is sedimentary rock of the Tyee formation. Soil profiles were most developed in the SLr-3 plot and adjacent to the SLp plot, and least developed in the SLp and SLr-2 plots.

Port Orford cedar Research Natural Area (POC)

Thuja occurs in scattered clumps along drainages (plot POr) and, rarely, higher on the slopes. *Chamaecyparis* occurs throughout but was sampled in a relatively dense stand near the top of a vertically convex slope (plot POP). Soil in plot POr consisted of pockets of sandy alluvium between boulders, overlain by a thick litter layer. Parent material at POP was Jurassic-aged sediments of the Galice formation.

Coquille River Falls Research Natural Area (CRF)

This old-growth forest is representative of those supporting the best growth of *Chamaecyparis* (Zobel and Hawk 1980). There is no evidence of *Thuja* within the Natural Area. Parent material is the same as at nearby Squaw Lake.

Methods

Soils

Samples were collected beneath 4 to 10 trees per plot (*n*, Table 3) in September 1979. Each sample consisted of soil collected from 0–10 cm deep at four locations evenly spaced around a circle one-half the distance from the trunk to the edge of the canopy. Soil temperature at 10 cm was measured at two of the four locations per tree, at the times of soil collection. Field moisture content was determined gravimetrically (8 h, 105°C). Soils were air dried at room temperature, lightly crushed, and passed through a 2-mm mesh screen. Sub-samples were ground to pass a 0.30-mm (No. 50) mesh screen, digested by a modified semimicro-Kjeldahl method (Bremner 1965a), and analyzed for N concentration with an HNU ammonia-sensing electrode (Anonymous 1978).

Portions of all samples from each plot were bulked before determination of other nutrient concentrations. Exchangeable and total Ca, K, and Mg concentrations were measured by atomic absorption by the Forestry Sciences Laboratory, U.S. Forest Service, Corvallis, OR. Exchangeable P was deter-

TABLE 2. Study-plot characteristics

Plot designation	Species sampled ^a	Aspect	Slope (%)	Textural class, AI horizon ^a	Mean soil moisture ^b (%)	Mean soil temperature ^b (°C)	Basal area (m ² /ha) ^a						
							Chla	Thpl	Alru	Psme	Tshe	Abgr	
CM	Thpl	NE	10	L	18	15.9	—	16	—	—	69	1	13
CC	Thpl	S	60	vgL	36	15.6	—	14	2	29	24	—	—
ASr-1	Thpl	—	0	SCL	49	11.6	(Sampled on a plotless basis)						
ASr-2	Thpl + Chla	—	0	CL	64	11.2	42	10	37	t ^c	—	—	—
ASp	Chla	—	0	CL	25	11.5	35	—	—	41	—	—	—
SLr-1	Thpl + Chla	—	0	gSL	23	12.9	65 ^c	67	22	1	9	—	—
SLr-2	Thpl + Chla	SW	5	SL	23	12.4	5	96	58	—	—	—	—
SLr-3	Thpl	NW	70	CL	32	12.0	—	11	9	—	10	—	—
SLp	Chla	NW	70	SL	32	12.5	22	t	13	—	7	—	—
POr	Thpl	NW	60	SL	18	13.9	—	24	—	40	t	18	—
POP	Chla + Thpl	N	60	vgL	27	14.0	70	3	6	9	8	11	—
CRF	Chla	NW	45	SCL	28	13.9	104	—	—	47	15	—	—

^aAbbreviations: Thpl, *Thuja plicata*; Chla, *Chamaecyparis lawsoniana*; Alru, *Alnus rubra*; Psme, *Pseudotsuga menziesii*; Tshe, *Tsuga heterophylla*; Abgr, *Abies grandis*; t, less than 0.5 m²/ha; g, gravelly; vg, very gravelly; S, sandy; C, clay; L, loam.
^bSamples collected in September; least significant difference (0.05 level) for moisture values = 7.2; for temperature values = 0.6.
^cAll basal area in one tree.

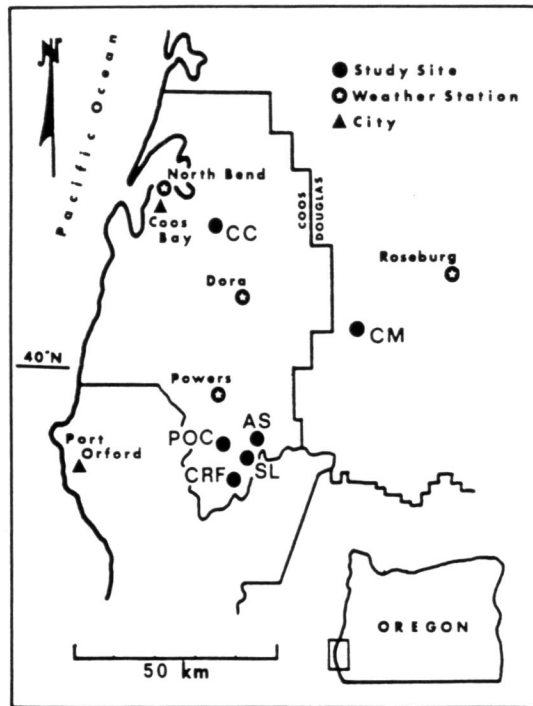


FIG. 1. Location of study sites, weather stations, and major cities (see Table 1 for key to site abbreviations).

mined by the Bray method by the Oregon State University Soils Testing Laboratory, Corvallis, OR.

Foliage

Trees sampled for foliage were often, but not always, the same as those sampled for soils. Samples were collected in September 1979, from one to five trees per species per plot (n , Table 4), depending on the availability and accessibility of healthy foliage. Samples consisted of the apical 2 dm collected from at least four branches; whenever possible branches which extended in four opposing directions were sampled. Limited accessibility of foliage necessitated sampling trees of different size and age so that height of the sample in the canopy varied. Foliage was air dried at room temperature and stripped of its scaly leaves. Some fine, brittle branchlets were included in the samples of both species. Leaves were finely ground, and samples from individual trees were analyzed for total N concentration by the method used for soils.

Foliage samples from trees larger than and smaller than 15 cm dbh (diameter at breast height) were kept separate; samples from all trees of each diameter class were combined by species and analyzed for other nutrient concentrations. Concentrations of Ca, K, and Mg were determined by the method used for soils. P concentration was determined by the molybdate blue method, using a Technicon analyzer (Technicon industrial method 334-74W/B), by the Department of Soil Science, Oregon State University, Corvallis, OR. All foliar and soil analyses were converted to an oven-dried (8 h, 105°C) basis.

Statistical analyses

The least significant difference was used to test differences among soil total N concentrations. Statistical comparisons for other soil nutrients were not possible owing to the small sample number after bulking. Significance of differences in foliar nutrient concentrations were determined with t -tests.

Results

Soil analyses

Exchangeable P and Mg, and total N concentrations, showed no obvious relation to species occurrence; differences in soil Ca and K levels were variable, but seemed related to species occurrence within individual study sites (Table 3). Exchangeable Ca was highest in plots where *Thuja* was most important locally (i.e., ASr-2 > ASp; SLr-1, 2, and 3 > SLp; POR > POP), and was considerably higher at CM than at CRF. The four plots where *Thuja* was absent or rare (ASp, CRF, SLp, and POP) were among the five lowest in total soil Ca concentration. Ca:Mg ratios showed an even stronger relationship to local distribution; with one exception, *Thuja* was most important on soils with higher exchangeable Ca:Mg ratios when comparisons were made between plots within a site.

In contrast, plots dominated by *Chamaecyparis* had slightly greater exchangeable soil K than *Thuja*-dominated plots at the same site (i.e., ASp > ASr-2 > ASr-1; SLp > SLr-2 and 3; POP > POR), and soils in which *Chamaecyparis* did not occur (CM, ASr-1, SLr-3, POR) were four of the five lowest in exchangeable soil K.

Concentrations of the exchangeable cations showed little overall relation to their total concentrations, and sites with high total K had relatively low exchangeable levels. Correlation coefficients between total and exchangeable concentrations were 0.10, -0.44, and 0.12 for Ca, K, and Mg, respectively.

Foliar analyses

Most differences in foliar nutrient concentrations between *Thuja* and *Chamaecyparis* appeared only on a local basis (Table 4). There were two exceptions: when all samples were considered, K was significantly higher in *Chamaecyparis* ($P = 0.01$) and Ca:Mg ratios appeared to be lower ($P = 0.10$). However, the range for both values overlapped considerably between species. In plots where the two occurred together (POP, ASr-2, SLp) or very close (CC), foliar N and K were consistently higher in *Chamaecyparis*, while Ca levels were lower.

Soil-foliar relationships

Foliar concentrations showed little correlation with soil nutrient levels on a study-wide basis, although soil Ca:Mg ratios were reflected by that of foliage from trees less than 15 cm dbh ($r = 0.93$ and 0.73 for *Thuja*

TABLE 3. Soil (0–10 cm) nutrient concentrations and Ca:Mg ratios

Plot designation	n	%N ^a (Tot)	%P (Ex)	%CA		%K		%Mg		Ca:Mg (Ex)
				Ex	Tot	Ex	Tot	Ex	Tot	
CM	10	0.08	0.0007	0.082	0.31	0.007	0.18	0.005	0.18	16.4
CC	10	0.31	0.0003	0.075	0.24	0.018	0.15	0.022	1.28	3.4
ASr-1	4	0.23	0.0004	0.024	0.43	0.007	0.32	0.017	0.76	1.4
ASr-2	5	0.37	0.0006	0.210	0.68	0.012	0.52	0.022	0.58	9.5
ASp	10	0.14	0.0008	0.101	0.24	0.013	0.30	0.013	0.49	7.8
SLr-1	5	0.15	0.0017	0.224	0.90	0.016	0.25	0.022	0.84	10.2
SLr-2	5	0.12	0.0008	0.218	0.85	0.010	0.19	0.023	0.82	9.5
SLr-3	10	0.11	0.0008	0.218	0.62	0.006	0.18	0.021	0.89	10.4
SLp	10	0.12	0.0013	0.098	0.30	0.015	0.20	0.016	0.87	6.1
SLp(adj.) ^b	1	—	0.0020	0.021	0.14	0.012	0.19	0.002	0.47	10.5
POr	6	0.11	0.0017	0.036	2.81	0.002	1.20	0.010	3.26	3.6
POp	10	0.27	0.0002	0.014	0.10	0.006	0.37	0.004	0.95	3.5
CRF	10	0.15	0.0016	0.039	0.20	0.013	0.18	0.008	0.40	4.9

NOTE: Values are for composites of *n* samples, except %N, which is the mean for *n* soil samples; Ex, exchangeable; Tot, total concentration.

^aLeast significant difference (0.05 level) for nitrogen values = 0.04.

^bSampled adjacent to SLp within extension of *Thuja* to top of slope.

TABLE 4. Foliage nutrient levels and Ca:Mg ratios for trees less than 15 cm dbh, and greater than 15 cm dbh (marked by asterisk)

Species	Plot designation	n	%N	%P	%Ca	%K	%Mg	Ca:Mg
<i>T. plicata</i>	CM	3	1.05	0.12	1.66	0.56	0.13	12.8
		2*	1.20	0.13	1.48	0.70	0.06	24.7
	CC	5	1.11	0.12	1.66	0.52	0.23	7.2
	ASr-1	1	1.60	0.24	1.63	0.89	0.22	7.4
		2*	1.11	0.17	1.37	0.77	0.13	10.6
	ASr-2	1	1.08	0.14	1.98	0.54	0.17	11.6
		2*	1.08	0.13	1.49	0.67	0.12	12.4
	SLr-1	2*	1.22	0.16	1.87	0.74	0.16	11.7
	SLr-3	1	1.28	0.13	1.82	0.51	0.19	9.6
		1*	1.01	0.14	1.56	0.53	0.13	12.0
	SLp	1	1.34	0.20	1.18	0.81	0.14	8.4
	POr	3	1.25	0.16	1.20	0.95	0.15	8.0
	POp	2	0.94	0.13	1.14	0.55	0.15	7.6
<i>C. lawsoniana</i>	CC(adj.) ^a	2	1.31	0.12	1.34	0.67	0.20	6.7
	ASr-2	1	1.39	0.11	1.15	0.81	0.11	10.4
		1*	1.40	0.15	1.46	1.00	0.15	9.7
	ASp	2	1.19	0.16	1.38	0.88	0.18	7.7
		2*	1.25	0.16	1.46	0.95	0.19	7.7
	SLp	2	1.85	0.23	0.83	1.20	0.16	5.2
		2*	1.50	0.16	1.46	0.88	0.16	9.1
	POp	3	1.03	0.11	1.07	0.78	0.13	8.2
	CRF	4	0.90	0.11	1.86	0.78	0.26	7.2

NOTE: Values are for bulked samples from *n* trees, except %N which is mean for *n* trees sampled.

^aFoliage sampled adjacent to CC plot; similar conditions.

and *Chamaecyparis*, respectively). Nutrients with the best correlations between soil and foliar concentrations for *Thuja* were Ca ($r = 0.66$) and Mg ($r = 0.51$), and for *Chamaecyparis* they were P ($r = 0.41$) and Mg ($r = 0.37$).

In many cases, however, low soil nutrient concentrations and local differences in soil concentrations were reflected in foliar concentrations. Low levels of soil Ca and P at POp, and soil Mg at CM were associated with relatively low foliar levels in trees sampled at

TABLE 5. Foliage nutrient levels and Ca:Mg ratios reported for *Thuja plicata* and *Chamaecyparis lawsoniana*

Species	Footnote	%N	%P	%Ca	%K	%Mg	Ca:Mg
<i>T. plicata</i>	a	0.73	0.13	1.16	0.52	0.10	11.6
	b	1.27	0.06	1.78	0.52	0.71	2.5
	c	1.13	0.08	1.33	0.53	0.96	1.4
	d	1.22	0.10	1.05	0.38	0.16	6.6
	e	<1.5	0.13	0.10-0.20	0.39-0.78	0.06-0.18	—
	*	0.9-1.6	0.12-0.24	1.1-2.0	0.52-0.95	0.06-0.23	7.2-24.7
<i>C. lawsoniana</i>	d	0.92	0.06	1.02	0.30	0.19	5.4
	f	0.61-1.14	0.06-0.15	0.50-2.02	0.27-0.71	0.11-0.37	2.3-11.7
	g	0.57-1.22	0.09-0.21	0.54-1.24	0.53-0.84	0.11-0.30	2.2-11.3
	h	0.55-1.39	0.12-0.24	0.51-0.92	0.72-0.90	—	—
	i	1.70	0.34	0.59	0.59	0.17	3.5
	j	0.59	0.06	—	—	—	—
	k	2.49	0.26	—	—	—	—
	l	0.61-0.67	0.06-0.07	0.83-1.00	0.27-0.42	0.24-0.37	2.3-3.7
	m	0.57	0.09	1.11	0.58	0.30	3.7
	n	0.98	0.09	0.80	0.66	0.18	4.4
	*	0.9-1.9	0.11-0.23	0.8-1.9	0.67-1.20	0.11-0.26	5.2-10.4

*Range of values for this study.

^aBeaton *et al.* (1965) in British Columbia; five 58-year-old trees.

^bGessel *et al.* (1951) in Washington; one 11-year-old healthy tree.

^cGessel *et al.* (1951) in Washington; three 100-year-old healthy trees.

^dOvington (1956) at Bedgebury, England; composite of five 20-year-old trees.

^eWalker *et al.* (1955); deficiency levels for seedlings in culture.

^fZobel and Hawk (1980); range of values for saplings at ten sites throughout *Chamaecyparis*' range.

^gPlocher (1977); range of values for seedlings at four sites within the northern part of *Chamaecyparis*' range.

^hYoungberg (1958); range of values for whole seedlings in three forest nurseries in Washington and Oregon.

ⁱZobel and Liu (1979); sixteen 1 1/2-year-old nursery seedlings in Taiwan.

^jLeyton (1955); twenty 15-year-old trees from a heathland plantation in England.

^kLeyton (1955); same as footnote j but treated with heather mulch.

^lZobel and Hawk (1980); range of values for saplings at three sites on ultramafic soils.

^mPlocher (1977); single bulked sample from seedlings growing in ultramafic soil.

ⁿUnpublished data from McNabb, reported in Plocher (1977), for *Chamaecyparis* in ultramafic soil.

those sites. In general, Ca levels in *Thuja* foliage reflected local changes in this availability in the soil (i.e., ASr-2 > ASr-1; SLr-1 and 3 > SLp; POr > POP).

Discussion

Relation of soil-nutrient availability to other soils in the region

Availability of N in forest soils of southwestern Oregon may be generally lower than in soils farther north. Total soil N concentration may be used as an approximate estimate of N availability (Bremner 1965b; Geist 1977) and, for these soils, was closely related to N mineralized by aerobic incubation ($r = 0.94$ in September (Imper 1981)). Total soil N in this study ranged from 0.08 to 0.37%. Other values reported for southwestern Oregon range from 0.03 to 0.24%, often for soils under *Chamaecyparis* (Bullard 1957; Meyer and Amaranthus 1979; Plocher 1977). In contrast, Franklin and Dyrness (1973) reported 0.5% as representative of the *Picea sitchensis* zone near the coast, in which *Thuja* is common. Bollen and Lu (1968) and Franklin *et al.* (1968) found a minimum of 0.53% N in soils along the central Oregon coast under pure

coniferous stands, with much higher levels in soils of mixed broadleaf-coniferous stands. Bullard (1957) reported a range of 0.19 to 0.64% N for coastal Oregon soils, and Tarrant (1948) reported a mean of 0.4% N for five forest soils in western Oregon and Washington.

Concentrations of soil K, P, Ca, and Mg in this study showed no consistent differences from values for soils of coniferous forests north of the range of *Chamaecyparis* in western Oregon (Bullard 1957; Franklin *et al.* 1968) or British Columbia (Feller 1977).

Nutrient availability in this portion of *Chamaecyparis*' range may exceed that in its range farther south, which occurs predominately on ultramafic soils (Hawk 1977). Ultramafic soils are normally low in N, Ca, and P, and high in Mg (Walker 1954). Our values for soil N, P, K, and Ca are generally higher, and soil Mg values are generally lower than reported for ultramafic forest soils in southwestern Oregon and northwestern California, some of which support *Chamaecyparis* (Meyer and Amaranthus 1979; Plocher 1977; Whittaker 1960). In particular, these sources report soil Ca:Mg ratios of 0.1 to 0.9, well below any found in this study (Table 4). In addition, *Chamaecyparis* on

ultramafic soils has lower foliar N, K, and P, and higher foliar Mg levels than trees growing on other soils, such as the sedimentary-derived soil at Coquille River Falls Research Natural Area (Plocher 1977; Zobel and Hawk 1980). Our data support this difference; concentrations of foliar N, K, and P, as well as foliar Ca, are clearly high, and foliar Mg concentrations are low, compared with data reported for *Chamaecyparis* growing on ultramafic substrates (footnotes *l-n*, Table 5).

The following conclusion seems reasonable, based on the data available. Soil sampled in this study, representative of where *Thuja* occurs within *Chamaecyparis*' range, appear to be intermediate between the relatively infertile ultramafic soils in southwestern Oregon and soils farther north, more characteristic of *Thuja*'s range. Availability of N in the range of *Chamaecyparis* appears to be low compared with other forest soils in the Pacific Northwest. Nutrients (including N but excluding Mg) are more available in the study area than over a majority of *Chamaecyparis*' range.

Factors related to species distribution

Distribution of *Chamaecyparis* and *Thuja* within individual sites did appear to be related to differences in soil Ca:Mg ratios, and, to a lesser extent, Ca concentrations. Some serpentine-adapted plants require less Ca than nonadapted plants (Main 1974). Foliar data from other sources indicate that *Chamaecyparis* often has considerably lower Ca levels than *Thuja* (Table 5), although both species have higher foliar Ca concentrations than most other conifers (Ovington 1956; Zobel and Liu 1979). Abundant soil Ca seems to be important to *Thuja* (Gessel *et al.* 1951; Krajina 1970), and *Thuja* has been associated with relatively high soil Ca:Mg ratios elsewhere (Feller 1977). Its affiliation with abundant Ca may be related to its reported preference for soils in which nitrification is vigorous (Krajina 1970).

The greatest K concentration and usually lower Ca:Mg ratios of *Chamaecyparis* foliage, in addition to local differences in soil nutrient concentrations, suggest a greater requirement for K and Mg than *Thuja* has. Some serpentine-adapted plants require higher external Mg levels to maintain internal levels (Main 1974). Absence of *Chamaecyparis* in the area sampled adjacent to the SLP plot (which had the lowest soil Mg content encountered, considerably lower than the nearby SLP soil) and at CM, suggests that Mg is limiting *Chamaecyparis* in these soils.

It is conceivable that Mg limitations may be partly responsible for *Chamaecyparis*' range limit. Low soil Mg at CM was accompanied by foliar levels in *Thuja* low enough to have caused deficiency symptoms in *Thuja* seedlings in culture (Table 5). The Ca:Mg ratio in both soil and *Thuja* foliage at CM is considerably

higher than any reported for *Chamaecyparis*, or for soils on which it occurs. CM was the only soil sampled which has developed on exclusively Flournoy formation sediments. The northeastern range boundary for *Chamaecyparis* coincides closely with the occurrence of Flournoy sediments as mapped by Baldwin (1974), and Hawk (1977), in his phytosociological study of *Chamaecyparis*, apparently found no significant occurrence on this geological formation. Although the Flournoy is geologically similar to, and often combined with, the Tyee formation, there is some question as to whether the two originated from the same source (Baldwin 1974). This evidence seems consistent with the hypothesis that a residual ultramafic influence in the Eocene sediments covering *Chamaecyparis*' northern range contributes to its occurrence there (Zobel and Hawk 1980). On the other hand, large chemical differences between the Tyee and Flournoy formations do not seem to have been described. Even so, in the absence of convincing evidence to account for its northern range limit, the effects of soil Mg status on *Chamaecyparis* seem worth investigating.

Although climatic differences between the CM site and *Chamaecyparis*' range may be responsible for the absence of *Chamaecyparis* at CM, this seems unlikely. The CM site was, climatically, the most extreme site studied. However, one observes a local pattern of distribution within *Chamaecyparis*' range in which *Thuja* invariably occupies more mesic, protected environments than *Chamaecyparis*, a pattern also reported elsewhere (Franklin and Dyrness 1973; Hawk 1977). This would seem to indicate that climatic factors may not be excluding *Chamaecyparis* from the CM site.

Occurrence of *Thuja* has been associated with relatively high levels of soil N (Alban 1969; Forristall and Gessel 1955; Krajina 1970; Larsen 1940). Little correlation was seen here, with *Thuja* occurring on soils with both the highest and lowest total N concentration.

Our data are not optimal for discriminating between the habitats of the two species because, at some sites, soil samples collected beneath both species were bulked before analysis. Of course, most soil and biological properties of a site are interrelated, and species distribution responds to factors other than those we studied. We cannot eliminate the possibility that distribution of the two species we studied is influenced by factors besides soil chemistry; of many possibilities, soil moisture seems the most likely to be important. Determining the causal relationships among properties of soil and the trees which occupy it is difficult, probably impossible (Major 1961). Perhaps we must be satisfied to demonstrate whether or not a relationship between species and soil does indeed exist.

In summary, the results of this and other studies suggest that *Thuja*, throughout much of its range, gen-

erally grows on soils which provide relatively large amounts of Ca and N, or which have relatively high Ca:Mg ratios. In contrast, *Chamaecyparis* often is dominant on less-fertile ultramafic soils, in which availability of N and Ca, and the Ca:Mg ratio, are usually relatively low. The sites studied here, where *Thuja* occurs together with *Chamaecyparis*, appear to be among the most fertile of *Chamaecyparis*' range. It seems unlikely, from a nutritional standpoint, that *Thuja* will ever replace *Chamaecyparis* over most of its range, even as *Chamaecyparis*' importance declines owing to spread of fatal root rot.

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- ALBAN, D. H. 1969. The influence of western hemlock and western red cedar on soil properties. *Soil Sci. Soc. Am. Proc.* **33**: 453-457.
- ANONYMOUS. 1978. Analytical method guide. 9th ed. Orion Research Inc., Cambridge, MA.
- ANONYMOUS. 1979. Climatological data. U.S. National Oceanic and Atmospheric Administration, Washington, DC.
- BALDWIN, E. M. 1974. Eocene stratigraphy of southwestern Oregon. *Bull. Oreg. Dep. Geol. Miner. Ind.* No. 83.
- BEATON, J. D., A. MOSS, I. MACRAE, J. W. KONKIN, W. P. T. MCGHEE, and R. KOSIK. 1965. Observations on foliage nutrient content of several coniferous trees in British Columbia. *For. Chron.* **41**: 222-236.
- BOLLEN, W. B., and K. C. LU. 1968. Nitrogen transformations in soils beneath red alder and conifers. *In* Biology of alder. *Edited by* J. M. Trappe, J. F. Franklin, R. F. Tarrant, and G. M. Hansen. U.S. Department of Agriculture, Pacific Northwest Forest Range Experiment Station, Portland, OR. pp. 141-148.
- BREMNER, J. M. 1965a. Total nitrogen. *In* Methods of soil analysis. Part 2. *Agronomy*, **9**: 1149-1176.
- . 1965b. Nitrogen availability indexes. *In* Methods of soil analysis. Part 2. *Agronomy*, **9**: 1324-1345.
- BULLARD, W. E. (*Editor*). 1957. An introduction to the forest soils of the Douglas-fir region of the Pacific Northwest. Western Forestry and Conservation Association, Portland, OR.
- FELLER, M. C. 1977. Nutrient movement through western hemlock - western red cedar ecosystems in southwest British Columbia. *Ecology*, **58**: 1269-1283.
- FORRISTALL, F. F., and S. P. GESSEL. 1955. Soil properties related to forest cover type and productivity on the Lee forest, Snohomish County, Washington. *Soil Sci. Soc. Am. Proc.* **19**: 384-389.
- FOWELLS, H. A. 1965. Silvics of forest trees of the United States. U.S. Dep. Agric. Agric. Handb. No. 271.
- FRANKLIN, J. F., and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S. For. Serv. Gen. Tech. Rep. PNW-8.
- FRANKLIN, J. F., C. T. DYRNESS, D. G. MOORE, and R. F. TARRANT. 1968. Chemical soil properties under coastal Oregon stands of alder and conifers. *In* Biology of alder. *Edited by* J. M. Trappe, J. F. Franklin, R. F. Tarrant, and G. M. Hansen. U.S. Department of Agriculture, Pacific Northwest Forest Range Experiment Station, Portland, OR. pp. 157-172.
- GEIST, J. M. 1977. Nitrogen response relationships of some volcanic ash soils. *Soil Sci. Soc. Am. J.* **41**: 996-1000.
- GESSEL, S. P., R. B. WALKER, and P. G. HADDOCK. 1951. Preliminary report on mineral deficiencies in Douglas-fir and western red cedar. *Soil Sci. Soc. Am. Proc.* **15**: 364-369.
- HAWK, G. M. 1977. Comparative study of temperate *Chamaecyparis* forests. Ph.D. dissertation, Oregon State University, Corvallis, OR.
- IMPER, D. K. 1981. The relation of soil characteristics to growth and distribution of *Chamaecyparis lawsoniana* and *Thuja plicata* in southwestern Oregon. M.S. thesis, Oregon State University, Corvallis, OR.
- KRAJINA, V. J. (*Editor*). 1970. Ecology of forest trees in British Columbia. Ecology of Western North America. University of British Columbia Press, Victoria. pp. 1-146.
- LARSEN, J. A. 1940. Site factor variations and resources in temporary forest types in northern Idaho. *Ecol. Monogr.* **10**: 2-53.
- LEYTON, L. 1955. The influence of heather mulching on the growth and nutrient status of Lawson cypress. *Forestry*, **28**: 147-151.
- MAIN, J. L. 1974. Differential response to magnesium and calcium by native populations of *Agropyron spicatum*. *Am. J. Bot.* **61**: 931-944.
- MAJOR, J. 1961. Use in plant ecology of causation, physiology and a definition of vegetation. *Ecology*, **42**: 167-169.
- MEYER, L. C., and M. P. AMARANTHUS. 1979. Siskiyou National Forest soil resource inventory. U.S. Department of Agriculture Forest Service, Pacific Northwest Region, Portland, OR.
- OVINGTON, J. D. 1956. The composition of tree leaves. *Forestry*, **29**: 22-23.
- PACKEE, E. C. 1976. An ecological approach toward yield optimization through species allocation. Ph.D. thesis. University of Minnesota, Minneapolis, MN.
- PLOCHER, M. D. 1977. Growth and nutrient content of *Chamaecyparis lawsoniana* from contrasting soils in Coos County, Oregon. M.S. thesis, Oregon State University, Corvallis, OR.
- ROTH, L. F., H. H. BYNUM, and E. NELSON. 1972. *Phytophthora* root rot of Port Orford cedar. U.S. Dep. Agric. For. Serv. Pest Leaflet No. 131.
- SHARPE, G. W. 1974. Western red cedar. University of

- Washington Printing Co., Seattle, WA.
- SUDWORTH, G. B. 1907. Forest trees of the Pacific slope. U.S. Department of Agriculture Forest Service, Washington, DC.
- TARRANT, R. F. 1948. The role of organic matter as a source of nitrogen in Douglas-fir forest soils. U.S. For. Serv. Res. Note PNW-48.
- WALKER, R. B. 1954. The ecology of serpentine soils. II. Factors affecting plant growth on serpentine soils. *Ecology*, **35**: 259-266.
- WALKER, R. B., S. P. GESSEL, and P. G. HADDOCK. 1955. Greenhouse studies in mineral requirements of conifers: western red cedar. *For. Sci.* **1**: 51-60.
- WHITTAKER, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* **30**: 279-338.
- YOUNGBERG, C. T. 1958. The uptake of nutrients by western conifers in forest nurseries. *J. For.* **56**: 337-340.
- ZOBEL, D. B. 1983. Twig elongation patterns of *Chamaecyparis lawsoniana*. *Bot. Gaz. (Chicago)*, **144**: 92-103.
- ZOBEL, D. B., and G. M. HAWK. 1980. The environment of *Chamaecyparis lawsoniana*. *Am. Midl. Nat.* **103**: 280-297.
- ZOBEL, D. B., and V. T. LIU. 1979. Foliar nutrient concentrations of small *Chamaecyparis* in Taiwan. *Plant Soil*, **53**: 373-384.