# Habitat relationships of *Chamaecyparis nootkatensis* in southern Washington, Oregon, and California

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*Chamaecyparis nootkatensis* is uncommon south of Mount Rainier, Washington. It occurs almost exclusively above 1100 m elevation and occasionally reaches timberline. Populations are generally adjacent to open habitats such as meadows, rocky ridges, avalanche tracks, bogs, and lakeshores. The species rarely grows in extensive tracts of closed-canopy forest. In 75 sample plots, 387 vascular species occurred, including indicators of both very wet and dry environments. Judging from the accompanying flora, the topographic locations occupied, and water potential data, *C. nootkatensis* can grow throughout much of the range of moisture conditions present at high elevations in the Cascade Mountains from central Oregon north. *Chamaecyparis nootkatensis* varies in growth form from a shrub to a tree 50 m tall. Layering produced the majority of small stems on most sites; it facilitates expansion both on open sites and of shrub-form plants in the forest. *Chamaecyparis nootkatensis* establishes some seedlings and is shade tolerant enough to survive under moderately dense canopies, but forest-grown seedlings fail to develop a strong upright trunk. Most trees on forest sites appear to have established following disturbance.

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*Chamaecyparis nootkatensis* n'est pas commune au sud du Mont Rainier, Washington. Elle se trouve presqu'exclusivement audessus de 1100 m d'altitude et, occasionnellement, elle atteint la limite des arbres. Les populations sont généralement adjacentes aux habitats ouverts tels prairies, crêtes rocheuses, traces d'avalanche, bords de lacs et tourbières. L'espèce croît rarement sur des étendues extensives de forêt dont la voûte de feuillage est close. Dans 75 parcelles expérimentale l'on a dénombré 387 espèces de plantes vasculaires, incluant des espèces indicatrices de milieux très humides et secs. Si l'on en juge par la flore d'accompagnement, par les sites topographiques occupés et par les données sur le potentiel hydrique, *C. nootkatensis* peut croître dans la plupart des conditions d'humidité présentes aux fortes élévations des Monts Cascade, du centre au nord de l'Orégon. *Chamaecyparis nootkatensis* varie, dans les formes de croissance, de l'arbrisseau à l'arbre d'une hauteur de 50 m. Le marcottage produit la majorité des petites tiges, chez la plupart des sites. Il facilite l'expansion tant pour les sites ouverts que pour les arbrisseaux en forêt. *Chamaecyparis nootkatensis* établit quelques plants et tolère l'ombre suffisamment pour survivre sous des voûtes de feuillage modérément denses, mais les jeunes plants croissant en milieu forestier sont incapables de développer un tronc droit et fort. La plupart des arbres de cette espèce en milieu forestier semblent s'être établis suite à un dérangement.

[Traduit par la revue]

### Introduction

Chamaecyparis nootkatensis (D. Don) Spach, Alaska cedar, occurs from southeast Alaska to the Siskiyou Mountains of extreme northern California but is uncommon south of Mount Rainier, Washington. The species is locally abundant and widely distributed in the coastal mountains of southeastern Alaska and British Columbia (Brooke et al. 1970; Harris and Farr 1974; Krajina 1970), and in both the Olympic Mountains and Cascade Mountains of northern Washington (del Moral and Watson 1978; del Moral et al. 1976; Douglas 1971; Fonda and Bliss 1969; Franklin and Dyrness 1973). It is widespread in forests around Mount Rainier (Franklin et al. 1979; Hemstrom and Franklin 1982) but occurs infrequently in the southern Washington Cascades (Franklin 1966). Chamaecyparis nootkatensis is locally common on many mountain peaks in the western part of the central Oregon Cascades but is absent from the High Cascades south of Mount Jefferson (Hickman 1968). It grows at a few disjunct locations in the Siskiyou Mountains (Griffin and Critchfield 1972; Mason 1941), and at one location in the Aldrich Mountains, 200 km east of its nearest occurrence in the Oregon Cascades (Frenkel 1974).

In the northern part of its range, *Chamaecyparis nootkatensis* occurs on sites ranging from bogs to rocky ridges. At the edge of bogs, *C. nootkatensis* forms dense thickets through layering (Neiland 1971). *Chamaecyparis nootkatensis* extends to timberline and can form krummholz and tree islands (Arno Printed in Canada / Imprimé au Canada

1977; Brooke *et al.* 1970; Douglas 1972; Douglas and Bliss 1977; Franklin and Dyrness 1973). It also grows on avalanche tracks (Fonda and Bliss 1969).

South of Mount Rainier, *C. nootkatensis* also occupies a variety of sites. It forms a major component of some stands on both very wet sites (Dyrness *et al.* 1974; Franklin 1966) and relatively dry, rocky ridges (Hickman 1968, 1970). It occurs primarily as shrubby thickets on very rocky, wet sites in the Siskiyou Mountains (Siemens 1972). In the Aldrich Mountains, *C. nootkatensis* is confined to the head of a sheltered, north-facing drainage (Frenkel 1974).

Chamaecyparis nootkatensis grows in a cool, wet maritime climate with a pronounced winter precipitation maximum. In general, precipitation decreases across its range from north to south, especially in summer. In the study area, *C. nootkatensis* occurs primarily in the upper *Abies amabilis* and *Tsuga mertensiana* vegetation zones (Franklin and Dyrness 1973). At such high elevations deep winter snowpacks accumulate and often do not melt until early summer. Winters are cool, but extreme low temperatures are rare. Summers can have long dry periods, especially in the Siskiyou Mountains and southern Oregon Cascades. The Aldrich Mountain trees probably receive substantially less precipitation than any other population.

The Cascade Range, within the study area, is formed almost exclusively of volcanic rocks (Baldwin 1976). Parent materials range from deep, coarse pumice, through volcanic ash, to decomposition products of massive volcanic rocks. The



FIG. 1. Map of study area showing the distribution of *Chamaecyparis nootkatensis* and the location of sampled stands.  $\bullet$ , sample sites. Areas of relatively continuous distribution (on appropriate habitats) are encircled by broken lines. +, isolated locations.

Oregon Cascades can be divided into the High Cascades, of relatively recent origin, and the older Western Cascades (Baldwin 1976; Franklin and Dyrness 1973). The High Cascades have relatively gentle topography formed from lava

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flows and pumice deposits that are punctuated by prominent volcanic peaks. In contrast, the Western Cascades are lower in elevation, with generally steep topography. The relatively stable, high-elevation, erosional landscape occurring in the Goat



FIG. 2. Detrended correspondence analysis ordination of all 75 stands sampled (axes 1 and 2). Stand groups used in presenting results are separated by lines and numbered. The stands in Washington are circled, stands in the Siskiyou Mountains are enclosed by squares, and the two stands from the Aldrich Mountains are underlined; others are from the Cascade Range in Oregon.

Rocks and on parts of Mount Rainier has no counterpart in the Oregon Cascades.

In this paper we (i) document the range of site characteristics and vegetation types associated with *Chamaecyparis nootkatensis* south of Mount Rainier, (ii) examine the dynamics of *C. nootkatensis* populations, and (iii) evaluate the factors that may control the abundance and distribution of this species.

# Methods

During summer 1979 we visited as many as possible of the known and probable locations of *Chamaecyparis nootkatensis* south of Mount Rainier. We briefly described site characteristics and vegetation for all locations examined. We quantitatively sampled 75 stands distributed over the study area (Fig. 1) and representing at least the major types of sites and stand structures occurring within major geographical divisions of the study area. No stand sampled showed evidence of human disturbance.

Within each stand we layed out a 500-m<sup>2</sup> plot (20  $\times$  25 m) in a representative location. We assigned each vascular species a canopy cover value based on an examination of the entire plot. Although sampling extended over a 3-month period, almost all herbs on these sites are in leaf throughout the summer; thus time of sampling should not greatly affect coverage data. For each tree species we recorded cover estimates for (i) trees > ca. 10 m tall (canopy trees on forest sites) and (ii) smaller trees (reproduction on forest sites and the canopy on some open sites). We also estimated total cover for all large trees, all small trees, shrubs >2 m tall, smaller shrubs, herbs, moss, lichens, litter, rock, and mineral soil. In each plot we dug a shallow soil pit and estimated soil texture by horizon and percent of rock in the top 20-30 cm of soil. We recorded slope angle and inclination, topographic position, and elevation. In most stands, a distinct line occurred on the tree trunks below which fruticose lichens abruptly decrease in abundance, its location being related to snowpack depth (Long 1976); we recorded height of this "lichen line" as an index of snow depth.

We tallied trees in the plot in classes <0.3 m tall, 0.3-1 m tall, 1-2 m tall, >2 m tall but < 5 cm diameter at breast height (DBH), and then by 5 cm diameter classes. Where small trees were abundant, we recorded them only in four 25-m<sup>2</sup> plots, one in each corner of the main plot. We kept a separate tally for *C. nootkatensis* stems that clearly originated by layering and seedlings of *C. nootkatensis*, which

 
 TABLE 1. Correlations (r values) between stand attributes and ordination axes for the stand ordination

Stand attribute	Axis 1	Axis 2
Elevation	0.48*	0.12
Latitude	-0.25	0.71*
Aspect	0.23	0.34
Topographic position	0.58*	-0.30
Slope angle	0.16	-0.54*
Moisture index (high = $dry$ )	0.65*	-0.06
Lichen snow line	-0.08	0.38*

NOTE: Aspect is rated from 1 = N - NE to 5 = S - SW; topographic position is rated as 1 = streambottom, 2 = lower slope, 3 = midslope, 4 = upper slope, 5 = ridge top. The moisture index is derived by combining aspect and topographic position. Other attributes are explained further in the text.  $* = p \le 0.001$ .

have distinct juvenile foliage for the first few years. At most sites we took increment cores from one to a few canopy trees and subcanopy *C. nootkatensis.* Cores were taken as close to ground level as possible (ca. 20-40 cm) and counted with a dissecting microscope. Many older trees had heart rot, making age determinations impossible. Because we had no data to allow an adjustment for coring height, our values represent minimum tree ages.

Near the end of an approximately 1-month dry period during fall 1979, we used a pressure chamber to examine predawn xylem pressure potential of trees on what we considered to be a dry site in the central Oregon Cascades.

# Data analysis

To examine patterns of variation within the species composition data, we employed detrended correspondence analysis, the most appropriate ordination technique for vegetation data (Gauch *et al.* 1981; Hill and Gauch 1980); it simultaneously produces both stand and species ordinations. The analysis was performed using the program DECORANA (Hill and Gauch 1980) on octave-transformed species cover data, from all stands and from various subsets of the stands, in order to examine patterns in different geographical areas.

We correlated stand positions on an ordination axis with site characteristics and major vegetation attributes. We rated slope aspect on a 1 to 5 scale from N-NE to S-SW. Topographic position was rated as follows: 1, stream bottom; 2, lower slope; 3, midslope; 4, upper slope; and 5, ridge top. To derive a moisture index we added the values for aspect and topographic position, which we adjusted upward one unit for stands with very shallow soil.

Using the ordination as a guide, we divided the 75 stands into 10 groups that appear to represent different environments, and also divided the common species into groups.

Almost all plants were identified in the field; uncertain specimens were collected and verified by comparison with herbarium specimens. A few specimens (especially *Carex*) could not be identified to species. Some species pairs could not be distinguished consistently in the field, especially in the vegetative condition, and were combined for data analysis: *Bromus orcuttianus* and *B. vulgaris*, *Erythronium montanum* and *E. grandiflorum*, *Lilium columbianum* and *L. washingtonianum*, *Osmorhiza chilensis* and *O. purpurea*, and *Viola orbiculata* and *V. sempervirens*. *Abies grandis* and *A. concolor*, and *A. procera* and *A. magnifica* intergrade within the study area; we combined species within each pair for analysis. Species nomenclature follows Hitchcock and Cronquist (1973) except for those present only in the Siskiyou Mountains or southern Cascades; these follow Munz and Keck (1973).

#### Results

# Distribution pattern

We examined most areas occupied by *Chamaecyparis noot*katensis south of Mount Rainier (Fig. 1). The species is much

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FIG. 3. Species ordination derived from detrended correspondence analysis using all 75 stands and 200 species. Only the most important species are indicated; they are the same as those in Table 3. Species names are indicated by the first three letters of the genus followed by the first three letters of the specific name. Lines separate species groups which are lettered A - G.

	Stand group									
	1	2	3	4	5	6	7	8	9	
Elevation (m)	1381	1545	1286	1475	1472	1606	1609	1829	1518	
Slope angle (°)	22	21	6	14	24	21	25	21	7	
Lichen snow line (m)	2.9	2.8	2.9	3.3	2.2	2.4	2.8	3.7	3.2	
% rock in surface soil	38	19	9	18	32	51	90	15	8	
Litter depth (cm)	3.6	4.3	4.4	3.6	4.4	1.9	1.4	0.8	4.1	
% cover of rock	2.6	1.8	0.4	0.6	3.1	22.3	45.0	3.0	0.1	
% cover of mineral soil	1.1	0.6	0.5	0.1	1.1	16.9	3.2	10.0	0.1	
% cover of overstory trees	45	56	70	67	71	28	4	3	51	
% cover of smaller trees	14	28	34	34	40	37	43	47	33	
% cover of shrubs	74	14	63	15	22	23	40	5	49	
% cover of herbs	85	75	47	10	31	51	24	80	39	
% cover of bryophytes	3	3	17	11	8	9	4	8	19	
No. of tree species	2.8	4.2	5.1	4.2	4.8	5.4	4.8	4.0	4.8	
No. of shrub species	8.0	5.3	6.9	2.4	6.5	5.3	11.8	4.0	6.2	
No. of herbaceous species	33.5	36.8	23.9	11.4	26.7	36.3	25.2	35.7	11.1	
Cover of species group A	79	3	9	0	0	0	0	0	0	
Cover of species group B	68	59	19	1	9	1	3	1	1	
Cover of species group C	8	3	40	3	1	1	0	13	25	
Cover of species group D	4	25	29	18	15	8	8	7	23	
Cover of species group E	14	20	3	2	22	14	14	1	2	
Cover of species group F	0	0	0	0	2	23	9	4	0	
Cover of species group G	1	1	2	3	3	15	1	15	20	
Maximum canopy height (m)	39	38	35	38	37	15	11	11	27	
Total tree basal area (m <sup>2</sup> /ha)	71	77	91	104	83	19	7	12	80	
C. nootkatensis basal area (m²/ha)	46	31	40	33	19	6	3	3	16	

TABLE 2. Characteristics of stand groups (averaged for all stands within a group)

NOTE: Cover for species groups is the total cover of all shrub and herbaceous species defined within a group in Fig. 3. Stand groups are shown in Fig. 2.

TABLE 3. Average cover by stand group for species which occurred in 7 or more of the 75 stands and also had >1% cove	er
in at least one group	

	Stand group									
	group	1	2	3	4	5	6	7	8	9
Trees										
Abies amabilis										
0	С	16.8	21.5	21.7	41.0	12.3	0	0	2.3	20.4
S	С	6.6	9.5	28.6	31.0	12.9	1.2	0	5.0	18.9
Abies grandis and A. concolor										
0	E	0	7.0	0	0	7.5	2.3	0.8	0	0
S	E	0	1.7	0	0	1.2	3.3	7.7	0	0
Abies lasiocarpa	-									
0	G	0	0	0	0.4	0.7	2.0	0	0.3	1.4
S	G	0	0.1	0.1	0.1	1.2	7.2	0	13.2	0.4
Adles procera and A. magnifica	Б	26	4.5	0	0	0.2	0.4	1.4	0	0
S S	E	2.0	4.5	0	0	8.3	0.4	1.4	0	0
Chamacounaris nootkatansis	E	0	0.2	0.1	0	1.4	2.2	0.0	0	0
O	л	26.8	38 1	31 /	16.6	22.0	12 7	2.0	0.2	16.0
Š	D	20.8	70	1.4	2 4	22.0	21.6	2.0	26.3	7.0
Picea engelmannii	D	7.0	1.9	1.0	2.4	24.2	21.0	25.0	20.5	1.9
0	C	0	0	79	0	0	0	0	0	29
Š	Č	Ő	Ő	0.8	Ő	Ő	Ő	0	0	0.2
Pseudotsuga menziesii	U U	U	0	0.0	0	0	0	U	U	0.2
0	E	0.3	1.5	1.4	2.8	13.6	0.8	0	0	0
S	E	0	0.3	0	0	0.6	0.6	0.2	0	0
Tsuga heterophylla										
0	С	3.8	0	12.9	13.4	2.1	0.2	0	0	1.3
S	С	0.6	0.7	1.2	1.4	0.4	0	0	0	0.1
Tsuga mertensiana										
0	G	0.6	1.2	4.1	0	10.6	7.9	0	0	17.1
S	G	0	0.4	1.4	1.2	0.9	5.1	1.0	2.0	6.3
Shrubs										
Acer circinatum	Α	12.6	0.1	0	0	0.2	0	0	0	0
Acer glabrum	E	4.6	0	0	0	0.6	0.9	1.4	0	0
Alnus sinuata	A	12.8	0.2	5.9	0	0	0	0.2	0.3	0.1
Amelanchier alnifolia	F	0	0	0	0	0.3	1.5	1.3	0	0
Arctostaphylos nevadensis	F	0	0	0	0	0.4	10.8	2.2	0	0
Berberis nervosa	E	0.1	0.1	0	0	2.1	0	0	0	0
Menziesia jerruginea Optopanar horridum		20 0	0 2	8.2	0.2	0	0	0	0	2.0
Pachistima myrsinitas	A E	20.0	0.5	0	0	22	2 4	1.0	02	0
Rhododendron albiflorum	Ē	0	0.2	10	02	2.2	5.4	1.0	0.2	15.9
Ribes bracteosum	Δ	16	01	0.4	0.2	0	0	0	0.2	0
Ribes lacustre	B	4.8	15	0.4	0	03	0.2	0	0	0
Rubus parviflorus	B	4.9	0.3	0.2	Ő	0.2	0.2	01	õ	Ő
Rubus spectabilis	Ā	3.1	0	1.3	õ	0	Õ	0	õ	Ő
Taxus brevifolia	E	0	0	0	0	3.7	0.1	5.2	0	0
Vaccinium alaskaense	С	2.1	0.2	7.1	0	0	0	0	0	1.5
Vaccinium membranaceum	D	0.8	10.2	17.8	12.6	9.6	6.6	7.0	2.0	15.3
Vaccinium ovalifolium	С	0.2	0	14.9	2.4	0	0	0	0	2.1
Vaccinium scoparium	G	0	0	0	0	0	0	0	1.3	3.6
Herbs and subshrubs										
Achlys triphylla	В	5.9	8.0	1.6	0	1.0	0	0	0	0
Actaea rubra	В	1.8	3.0	0.1	0	0.1	0	0	0	0
Adenocaulon bicolor	E	0.1	2.8	0	0	0.7	0	0.1	0	0
Anemone deltoidea	E	0.3	1.8	0.6	0	0.5	0	0.4	0	0
Anemone lyallii	E	0.1	1.6	0	0	0.5	0.2	0.2	0	0.1
Antennaria racemosa	F	0	0	0	0	0.4	1.4	1.4	0	0
Arnica latijolia	D	0.9	2.2	2.4	0.2	0.5	0	0.4	2.7	0.7
Asarum cauaatum	В	7.2	4.1	0	0	0.1	0	0	0	0
Aster leaopnyllus	F	10 1	0.3	1 2	0	0.2	0.6	0.1	1.0	0
Anyrium juix-jemina Promus prouttianus and P mila-	A	10.1	1.4	1.3	0	0	0	0	0	0
Campanula scouleri	E	0.8	1./	0.1	0	0.9	0.2	0.2	0	0
Carex pensylvanica	F	0	0	0	0	0.4	4 1	0 1	0.2	0
- perception and a second second		0	0	0	0	0.2	4.1	0.1	0.2	0

TABLE 3. (concluded)

	Spacias	Stand group									
	group	1	2	3	4	5	6	7	8	9	
Chimaphila umbellata	Е	0.1	1.0	0.1	1.0	3.1	2.8	0.3	0	0.1	
Circaea alpina	В	3.1	0.7	0	0	0	0	0.1	0	0	
Clintonia uniflora	В	4.3	10.5	8.9	0.2	2.0	0.1	0.4	0	0.1	
Cornus canadensis	С	0.5	0.2	4.1	0	0	0	0	0	0	
Dicentra formosa	E	3.1	0.6	0	0	0.2	0.1	0	0	0	
Disporum hookeri	В	3.5	2.0	0	0	0.2	0.1	0.4	0	0	
Elymus glaucus	G	0.1	0.1	0	0	0	0.3	0.3	3.3	0	
Fragaria vesca	E	0	0.2	0.3	0	0.4	1.3	0	0	0	
Galium oreganum	В	0.9	1.7	0.1	0	0.2	0	0	0	0	
Galium triflorum	В	1.1	0.8	0.3	0	0.2	0	0.2	0.2	0	
Gaultheria humifusa	С	0	0	0.2	0.1	0	0	0	0	1.9	
Goodyera oblongifolia	D	0.3	1.0	0.4	0.4	0.7	0.3	0.5	0	0.4	
Heuchera micrantha	E	0.1	0	0	0	1.0	0.3	2.2	0	0	
Hieracium albiflorum	E	0.3	0.4	0.1	0	0.5	1.1	0	0.3	0	
Hydrophyllum tenuipes	Α	14.4	0.4	0	0	0	0	0	0	0	
Ligusticum grayi	G	0.3	0.2	0.1	0	0.1	0.5	0.2	1.2	0	
Linnaea borealis	E	0.1	4.1	1.7	0.2	1.4	0	0	0	0	
Lomatium martindalei	F	0	0	0	0	0.1	1.3	0	0.3	0	
Lupinus latifolius	G	0	0.1	0	0	0.1	0.8	0	7.7	0.6	
Mitella breweri	С	1.5	0.2	0.3	0.1	0.2	0	0	2.3	0.1	
Mitella caulescens	Α	1.1	0.1	0	0	0	0	0	0	0	
Mitella trifida	E	0	0.4	0	0	0.5	2.1	0	0	0	
Montia sibirica	В	3.6	1.0	0	0	0.1	0	0	0	0	
Nothochelone nemorosa	E	0.1	0.1	0	0.1	0.9	0.8	1.8	0	0	
Osmorhiza chilensis and O. purpurea	E	1.8	1.9	0.1	0.1	0.8	0.2	0.1	0.8	0	
Pedicularis racemosa	G	0.1	0.4	0.5	0.8	0.9	2.4	0	1.0	0.3	
Phlox diffusa	F	0	0	0	0	0.1	0.8	1.1	2.7	0	
Polystichum munitum	E	1.3	0.5	0.1	0.1	1.0	0.1	0.3	0	0	
Pteridium aquilinum	В	0.9	2.1	0.4	0	0.6	0	0	0	0	
Pyrola secunda	D	0.2	1.9	1.6	1.1	0.8	0.2	0.1	0.2	1.0	
Rubus lasiococcus	D	1.2	7.8	5.1	3.1	2.5	0.4	0	1.7	5.6	
Sedum oregonense	F	0	0	0	0	0.1	2.1	2.4	0	0	
Senecio triangularis	C	0.9	0.3	0.4	0	0.1	0.1	0	1.0	0	
Smilacina racemosa	E	1.1	0.6	0	0	0.4	0.3	0.3	0	0	
Smilacina stellata	B	9.1	8.9	1.7	0.1	2.7	0	0.9	0	0	
Streptopus amplexifolius	В	0.5	2.1	0.4	0	0	0	0	0	0.1	
Streptopus roseus	C	1.6	1.2	2.4	0.2	0	0	0	0	0.5	
Tiarella trifoliata var. unifoliata	В	8.5	7.0	4.9	0.6	0.6	0	0	0	0.7	
Trillium ovatum	В	2.0	1.1	0.3	0.2	0.5	0.1	0.2	0	0	
Valeriana sitchensis	C	0.8	0.4	1.1	0	0.2	0.4	0	8.0	0.5	
vancouveria hexandra	В	3.6	2.6	0.1	0 2	0.2	0	0.1	0	0	
veratrum viriae	C	0.6	0.3	0.4	0.2	0.1	0 1	0 1	1.5	0.3	
Viola glabella	В	2.0	1.1	0.1	0 0	0.4	0.1	0.1	0.3	1 4	
Viola ordiculata and V. sempervirens	D C	0.7	1./	1.9	0.8	1.2	11.0	0	1 5	1.4	
легорпушит tenax	G	0.1	0	1.2	2.0	1.8	11.0	0	1.5	19.2	

NOTE: Stand groups are defined in the text and indicated on the ordination (Fig. 2). Group 10 is not considered because it had only two stands. The species group as shown in Fig. 4 is indicated after each species' name. Tree cover is indicated separately for the overstory (O) and smaller individuals (S).

more common in the Goat Rocks than elsewhere in the study area. *Chamaecyparis nootkatensis* occupies a wide range of sites in the Goat Rocks and on the higher ridges between the Goat Rocks and Mount St. Helens, including deep pumice soils, from which it is absent farther south.

Near Mount Hood, Oregon, *Chamaecyparis nootkatensis* is uncommon and occurs primarily on wet sites; it increases in abundance south of the Clackamas River (Fig. 1). The vast majority of *C. nootkatensis* in Oregon grow on an extensive system of ridges and peaks approximately 1500 to 1700 m high in the Western Cascades between the Clackamas and McKenzie rivers. The species occurs on rocky ridges, meadow margins, avalanche tracks, seeps, streamsides, and lake margins, usually above 1100 m elevation. It is rare in closed-canopy forest far from nonforested habitats. Drainages and saddles between the peaks and ridges are low enough that the distribution is highly fragmented. Some high-elevation areas lack the species. Many of these are heavily forested, but others have habitat more appropriate for *C. nootkatensis*.

In the High Cascades, *Chamaecyparis nootkatensis* grows in wet sites and high-elevation tree islands north of Mount Jefferson in a small area with dissected topography, somewhat resembling the Western Cascades. It grows at higher elevations (1950 m) than occur in the nearby Western Cascades. South of the Mount Jefferson region, *C. nootkatensis* is absent in the High Cascades.

 
 TABLE 4. Extent of juvenile foliage and layering among small Chamaecyparis nootkatensis

	Trees <	< 0.3 m tall	Trees 0.3-2 m tall					
Stand group	Total no. of trees	% with juvenile foliage	Total no. of trees	% from layering				
1	20	85	136	52				
2	459	95	210	51				
3	100	77	88	23				
4	200	92	112	55				
5	673	83	968	62				
6	78	62	596	70				
7	3	100	325	93				
8	3	0	151	89				
9	305	82	459	57				
10	68	84	92	66				
All groups	1909	85	3137	65				

Abundance of *Chamaecyparis nootkatensis* decreases south of the McKenzie River (Fig. 1). It occupies a variety of sites including rocky ridges but is more restricted to northerly aspects. South of the North Umpqua River, *C. nootkatensis* occurs only in wet areas or on rocky, northerly exposures.

Siskiyou Mountain populations usually grow on very rocky north slopes that support only scattered small trees. Often, little or no soil covers the bedrock. In places *C. nootkatensis* occurs under open stands of large trees of other species. The distribution is highly fragmented, and many sites that appear appropriate are unoccupied.

The distribution in the Aldrich Mountains differs from that in other areas. The species is confined to dense forest in a wet seepage area in the head of a drainage.

#### Stand ordination patterns

Detrended correspondence analysis produced an ordination with good stand separation (Fig. 2). Moisture is the primary factor related to the first axis (Table 1). The first axis also is positively correlated with elevation (Table 1); dry ridges usually were higher than the wet sites.

The second ordination axis was correlated with latitude (Table 1, Fig. 2). Slope angle is negatively correlated with this axis primarily because Washington sites were flatter than more southern sites. A positive correlation with the lichen snow line reflects generally deeper snowpacks to the north.

## Associated species

In total, 387 vascular species were found in the 75 plots. *Chamaecyparis nootkatensis* is occasionally associated with most of the species occurring at higher elevations in the Cascades.

The species ordination shows the same basic gradients of variation as the stand ordination. Axis 1 ranges from indicators of very wet sites to those of very dry sites (Fig. 3). Axis 2 has mostly southern or low-elevation species at the bottom and northern or high-elevation species at the top; it represents a combined temperature – latitude gradient.

We have grouped together species that responded similarly within the range of sites sampled (Fig. 3). Group A contains mostly large shrubs of wet sites, including *Alnus sinuata*, *Oplopanax horridum*, and *Rubus spectabilis*; they are most abundant on wet avalanche tracks and stream bottoms. Group B contains species of the luxuriant herbaceous layers of wet to moist forests. Group C contains shrubs and herbs characteristic of northern or relatively cool sites. All shrubs in group C, but none in group A, are ericaceous.

Group D species are widely distributed in the stands sampled. Vaccinium membranaceum is the species most commonly associated with Chamaecyparis nootkatensis, occurring in 64 of 75 stands. It is followed by Abies amabilis and Rubus lasiococcus, which occur in 56 stands. All species in group D are abundant in the Cascades except C. nootkatensis.

Herbs common in mesic or drier forests occur in group E. The species on the right side of group E (Fig. 3) are frequent in meadows. The trees *Abies grandis* (including *A. concolor*), *Abies procera* (including *A. magnifica*), and *Pseudotsuga menziesii* occur in this group.

Group F contains species typical of open, dry, rocky sites (Fig. 3). *Phlox diffusa*, *Sedum oregonense*, and *Lomatium martindalei* occupy the rockiest open ridges, and presumably driest sites, at moderate to high elevations in the Cascades.

A mixture of high-elevation and open-site species constitute group G, including the subalpine conifers *Tsuga mertensiana* and *Abies lasiocarpa* (Fig. 3).

## Characteristics of stand groups

The variation among stands is fairly continuous, with few pronounced discontinuities with respect to both species composition and sites occupied. Nonetheless, we have divided the stands into groups (Fig. 2), using our overall knowledge of vegetation and sites associated with *C. nootkatensis*. Many characteristics vary among the groups (Tables 2 and 3).

Group 1 stands occur in seepage areas, generally along avalanche tracks. Most are on steep slopes (to 38°). The tree canopy is usually open with tall shrub thickets between trees. Oplopanax horridum, the most common shrub, is virtually restricted to these stands (Table 3). The herbaceous layer attains its highest cover here; most herb and shrub cover comes from species groups A and B (Table 2). Cover of small trees is low because of periodic snow movement and the dense herb and shrub layers. Chamaecyparis nootkatensis may be at an advantage on these sites relative to associated conifers because of its resistance to snow breakage and its ability to layer. The largest C. nootkatensis seen in the study area (210 cm diameter above its swollen base) was in stand 1 at the very brushy bottom of an avalanche track on Twin Buttes in the central Oregon Cascades. All stands in group 1 are in the Oregon Cascades except stand 11 (Fig. 2), at the terminus of an avalanche track in the Siskiyou Mountains.

Group 2 stands have luxuriant herb layers but limited shrub development (Table 2). The sites are generally moist, northfacing slopes in the Oregon Cascades. Most cover in these stands is contributed by species in group B, with a smaller amount from groups D and E (Table 2). Among the herbs, *Achlys triphylla, Clintonia uniflora, Rubus lasiococcus, Smilacina stellata,* and *Tiarella trifoliata* have the greatest cover; *Vaccinium membranaceum* is the only important shrub (Table 3).

Group 3 stands are as wet or wetter than those of group 2, are more northern in distribution, and generally occur on more level topography. Most stands are on lakeshores or stream bottoms with high cover of ericaceous shrubs (Tables 2 and 3). Herb-layer cover and diversity are much lower than in group 2, yet herbs are still prominent (56% cover), including many wet-site indicators (Tables 2 and 3).

Group 4 stands have sparse herb and shrub layers of low

Stand group	9	<0.3 m tall	0.3-2 m tall	>2 m tall and <15 cm DBH	15-50 cm DBH	>50 cm DBH
1	C. nootkatensis	1.8	12.4	7.6	3.1	2.5 -
	Other trees	14.9	11.7	5.7	2.4	2.1
2	C. nootkatensis	45.9	21.0	12.8	7.5	2.3
	Other trees	61.5	41.2	16.9	8.0	3.8
3	C. nootkatensis	14.3	12.6	3.6	5.9	3.1
	Other trees	471.4	251.2	77.2	21.2	4.6
4	C. nootkatensis	40.0	22.4	3.0	8.0	1.6
	Other trees	60.8	31.5	18.6	13.5	3.8
5	C. nootkatensis	62.9	64.5	30.8	9.2	0.7
	Other trees	60.8	31.5	18.6	13.5	3.8
6	C. nootkatensis	8.9	66.2	32.0	4.9	0
	Other trees	9.2	35.5	26.3	7.9	0.3
7	C. nootkatensis	0.6	65.0	33.0	1.6	0
	Other trees	3.6	16.6	16.2	4.0	0
8	C. nootkatensis	1.0	50.3	137.7	0	0
	Other trees	13.6	31.1	26.3	9.0	0
9	C. nootkatensis	38.2	57.4	24.1	8.8	0.6
	Other trees	278.3	111.3	22.7	24.0	4.1

 
 TABLE 5. Average number of Chamaecyparis nootkatensis and other trees by size class per 500-m<sup>2</sup> plot for the stand groups

diversity (Table 2). Most of the understory species are widely distributed forest plants (Tables 2 and 3). The dense-canopied *Tsuga heterophylla* and *Abies amabilis* have maximum cover in this group, which may account for the sparse understories.

The drier forests containing *Chamaecyparis nootkatensis* in Oregon constitute group 5 and occur on moderate to steep slopes of all aspects near mesic meadows or rock outcrops. The tree canopy is well developed; herb and shrub cover are moderate, mostly species from groups D and E (Table 2). No single herbaceous species has very much cover; *Vaccinium membranaceum* is the most important shrub (Table 3). Species typical of meadows and dry rock outcrops occur in some stands.

Stands in group 6 occur on dry, rocky ridge tops and upper slopes in the Oregon Cascades, at relatively high elevations (Table 2). The stands have very rocky, often shallow soils and considerable exposed bedrock (Table 2). Tree cover is intermittent; the trees are generally short and sometimes shrubby, but tree species diversity is high. In some stands, most trees are rooted in cracks in the bedrock. The herb layer is diverse, with fairly high average cover (Table 2), although some stands have only scattered herbs on exposed bedrock. Shrubs have moderate cover but are generally of low stature. Species group F, with its dry-site indicators, and to a lesser extent groups E and G are most important (Table 2). Many herbs in these stands are of widespread distribution east of the Cascades.

The five stands in group 7 comprise the majority sampled in the Siskiyou Mountains. Trees have low cover and basal area (Table 2) and tend to be shrubby, especially *Chamaecyparis nootkatensis*. The stands are all on moderate to steep northfacing slopes but range from 1370 to 2100 m elevation. Soils are extremely rocky and herb cover is low (Table 2). Many of the dominant species occurred only in the Siskiyou stands, for instance, *Quercus sadleriana*, the most abundant shrub.

Group 8 stands occur at high elevations in Washington and have the highest lichen line, indicating very deep snowpacks. Two (stands 63 and 64; Fig. 2) are in tree islands near timberline, the other in a fire induced meadow. All three have very high herb cover and diversity but low tree cover and the least shrub cover (Table 2). The herb layers are typical of subalpine meadows; forest herbs are much less abundant.

Stands in group 9 occur on gentle to moderate slopes of all aspects in Washington and the Oregon High Cascades. Cover of ericaceous shrubs is high (Tables 2 and 3). Herb diversity is low (Table 2), almost half the total cover being Xerophyllum tenax (Table 3). The cover is about equally from species groups C, D, and G (Table 2). Stand 73 occurs at 1950 m, a much higher elevation than the other stands in group 9. Cassiope mertensiana, Phyllodoce empetriformis, Vaccinium deliciosum, and Luetkea pectinata dominate the understory; few other species are present. Similar stands, without C. nootkatensis, are common in the High Cascades.

Both group 10 stands are in bogs, which are uncommon in our study area but represent a major habitat of *C. nootkatensis* farther north. Summary data are not presented because such stands are very heterogeneous. Herb cover and diversity are very high. Most of the few trees occur on raised ground.

# Origin of small Chamaecyparis

Chamaecyparis nootkatensis is recruited into populations both through layering and seed (Table 4). Of 1909 plants less than 0.3 m tall, 85% had juvenile foliage and thus definitely originated from seed. Only 9% of all *C. nootkatensis* less than 0.3 m tall were obviously layered; most stems which layer already exceed 0.3 m tall.

Of 3137 stems 0.3-2 m tall, 65% clearly resulted from layering (Table 4). The dry, open stands (groups 6-8) had the most layering. In many open and some forest stands, layering is virtually the only means of regeneration. Fewer stems taller than 2 m appear to have originated through layering, but evidence becomes obscured as plants grow.

#### Stand structure on open sites

The open sites (groups 1, 6-8) have fewer tree seedlings than forest sites (Table 5). On open sites there are more stems

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S	tand				>2 m tall and			Γ	OBH (cm)	3		
] (g	No. roup)	Species	<0.3 m tall	0.3-2 m tall	< 10 cm DBH	10-20	20-30	30-40	40-50	50-60	60-70	70+
					50- to 1	35-year-ol	t stands					
72	( <b>0</b> )	C nootkatensis	10	70	J0= 10 T	7	2 stands 2	0	0	0	0	0
12	(9)	Ahies amabilis	90	6	49	4	2	1	1	0	0	0
		Tsuga mertensiana	3	4	10	6	0	0	0	0	0	0
		Other	1	2	5	5	4	1	0	0	0	0
21	(2)	C. nootkatensis	13	õ	2	5	9	3	0	Ő	õ	ŏ
	(_)	Abies amabilis	51	21	7	5	10	12	3	õ	õ	õ
		Other	0	2	Ó	õ	1	2	0	õ	õ	ŏ
29	(4)	C. nootkatensis	Õ	ō	6	9	12	5	1	õ	õ	ŏ
-	(.)	Abies amabilis	117	106	8	20	23	17	5	2	1	õ
		Other	0	0	õ	1	2	2	0	1	Ô	Õ
39	(5)	C. nootkatensis	3	27	26	18	9	2	0	0	0	0
	(0)	Abies amabilis	10	6	0	0	Ó	0	Ő	Ő	Ő	Õ
		Abies procera	0	4	6	7	8	6	3	Ō	1	1
					Stands	ca. 200 ve	ars old					
16	(2)	C. nootkatensis	75	10	0	1	4	1	2	1	1	0
	(_)	Abies amabilis	210	90	6	Ō	1	Ô	3	2	2	0
		Other	2	3	Ő	õ	Ô	õ	Ő	õ	ĩ	1
38	(5)	C. nootkatensis	10	0	õ	õ	1	8	2	Õ	Ô	Ô
50	(5)	Abies amabilis	18	15	7	2	2	1	2	õ	Ő	Ő
		Other	3	0	0	0	0	0	0	0	1	5
					Old	-growth sta	inds					
17	(2)	C nootkatensis	20	16	0	0	0	2	1	1	1	3
1 /	(2)	Ahies amahilis	15	20	18	12	3	1	1	1	î	0
		Tsuga heterophylla	1	20	0	0	ő	Ô	Ô	Ô	Ô	ŏ
25	(3)	C nootkatensis	15	37	Ő	õ	ŏ	ŏ	õ	õ	2	3
	(3)	Ahies amabilis	200	215	11	6	1	3	1	1	õ	1
68	(9)	C nootkatensis	10	210	0	Ő	1	3	4	3	Ő	Ô
00	()	Abies amabilis	240	115	27	15	13	12	Ó	õ	Ő	Ő
		Tsuga mertensiana	0	0	2	0	2	2	õ	Ő	õ	1
69	(9)	C nootkatensis	8	131	41	2	õ	ō	1	1	õ	Ô
0,	()	Abies amabilis	153	194	5	2	4	7	5	2	Õ	Õ
		Tsuga mertensiana	2	3	0	õ	Ö	Ó	õ	õ	1	3
41	(5)	C. nootkatensis	10	37	9	5	3	1	1	1	0	0
•••		Abies grandis	1	1	í	3	2	2	4	Ō	1	Ő
		Other	2	Ō	0	1	ĩ	ō	0	0	1	3
44	(5)	C. nootkatensis	305	32	73	15	9	1	3	Õ	Ō	0
	(0)	Abies grandis	5	0	4	5	1	4	2	2	1	0
		Other	0	0	0	0	0	1	1	1	0	0
45	(5)	C. nootkatensis	0	87	139	0	0	0	0	0	0	0
	(-)	Abies magnifica	3	8	7	7	2	2	0	0	1	0
		Picea breweriana	0	5	0	0	0	0	0	0	1	1
		Other	0	1	1	0	0	0	0	0	0	0

TABLE 6.	Tree size-class	distributions	for selected	stands. S	Stand groups	and stand	numbers a	re those	shown	on the	ordinations	(Figs.	2 and 3)	).
				Num	ber of stems	per 500-	m² plot							

0.3-2 than 0-0.3 m tall for most species and especially for *Chamaecyparis nootkatensis*; the reverse is true on forest sites.

The open, rocky sites in the Oregon Cascades (group 6) and Siskiyou Mountains (group 7) support several tree species, most of which regenerate to some extent because of microsite variability and an incomplete canopy (Table 5). *Chamaecyparis nootkatensis* seedlings do establish on exposed south-facing rock outcrops in the Cascades. Nonetheless, *C. nootkatensis* seedlings are few and most stems come from layering, which leads to clumping.

At high elevations in Washington, Chamaecyparis nootkatensis persists mainly by layering, as does Abies lasiocarpa (group 8, Tables 4 and 5). Abies lasiocarpa and Tsuga mertensiana grow taller and could slowly eliminate C. nootkatensis inside tree islands.

# Stand structure of closed forests

Among forest stands, density of all small trees is lower, but the density of small *Chamaecyparis nootkatensis* is higher in the more southern groups (2 and 5, Table 5). Most small trees in groups 3, 4, and 9 are *Abies amabilis*, the most abundant associate of *C. nootkatensis* in all forest groups.

We must use individual stands to examine stand development, because averages obscure the stand dynamics. No natu-



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FIG. 4. Tree height versus age for sites capable of supporting large trees (most plots in stand groups 1-6). The solid line separates the age-size combinations including *Chamaecyparis nootkatensis* from those where the species is absent. Only dominant and codominant trees of species other than *C. nootkatensis* are plotted.  $\bullet$ , dominant and codominant *C. nootkatensis*;  $\bigcirc$ , subcanopy *C. nootkatensis*; 1, *Abies amabilis*; 2, *Abies grandis*; 3, *Abies procera*; 4, *Larix occidentalis*; 5, *Picea engelmannii*; 6, *Pinus contorta*; 7, *Pseudotsuga menziesii*; 8, *Tsuga heterophylla*.

ral stands less than 50 years old were found. Those 50 to 135 years old show that shade-tolerant species, including *C. noot-katensis*, can establish soon after disturbance and dominate the canopy (stands 72, 21, 29; Table 6). *Abies amabilis* can grow faster and often overtops *C. nootkatensis*. In the dense pole stands (21 and 29), *C. nootkatensis* recruitment has largely stopped (Table 6) and many overtopped individuals have died. Less shade tolerant species are most common on large burns or drier sites (stand 39, Table 6). Most sites are near natural firebreaks and some *C. nootkatensis*, including small ones, commonly survive fire (e.g., larger trees in stand 72, Table 6).

Overtopping of *C. nootkatensis* continues in some stands of intermediate age (stand 16, Table 6). Where *C. nootkatensis* dominates the canopy (stand 38), *Abies amabilis* may have established later. In stands 16 and 38 regeneration was low for a long period but is now occurring, especially in canopy gaps. *Abies amabilis* dominates the regeneration, but *C. nootkatensis* seedlings also occur, especially on logs.

In old-growth stands the amount of *C. nootkatensis* regeneration varies. It does not establish as well as *A. amabilis* and often shows a pronounced gap in the size distribution (stands 17, 25, and 68; Table 6). Often *C. nootkatensis* seedlings fail to develop into trees and eventually die, or may spread by layering to form a shrub layer. For instance, stand 69 has numerous small *C. nootkatensis*, although seedlings are sparse (Table 6).

Stands with little *Abies amabilis* tend to have relatively abundant and successful *Chamaecyparis nootkatensis* regeneration, in the Oregon Cascades (stand 41, Table 6) and the Aldrich Mountains (stand 44). Stands in the Aldrich Mountains had the most *C. nootkatensis* seedlings recorded. Many larger *C. nootkatensis* in these stands are fire scarred and partial burns may be common.

The two forest stands sampled in the Siskiyou Mountains have thickets of layered C. nootkatensis shrubs, but no seed-

lings, under tall *Abies magnifica* and *Picea breweriana* in one case (stand 45, Table 6) and *Chamaecyparis lawsoniana* and *Pseudotsuga menziesii* in the other. *Chamaecyparis nootkatensis* has the same growth form here as on nearby, open rock outcrops.

# Size-age relationships

Chamaecyparis nootkatensis grows more slowly than associated species. No C. nootkatensis sampled grew fast enough to occur above the solid line in Fig. 4, whereas many sampled trees of other species did. Subcanopy C. nootkatensis vary greatly in size relative to age (Fig. 4). Trees apparently survive long periods of suppression. On most dry sites C. nootkatensis appears to grow as rapidly as most other species, in contrast to the situation on better sites.

#### Xylem pressure potentials

On 13 October predawn xylem pressure potentials of 22 Chamaecyparis nootkatensis 0.4-10 m tall averaged -1.0 MPa and ranged from -0.4 to -1.5 MPa. The variability was not strongly associated with tree size or origin (seedling versus layering). Eight *Abies lasiocarpa* on the site averaged -1.3 MPa, range -1.0 to -1.6 MPa. This site (stand 52) is as dry as any sampled in the Cascades, judging from the ordination (Fig. 2) and its topographic position. On the same day, mid-afternoon xylem potential of *C. nootkatensis* reached -2.4 and averaged -1.7 MPa for 14 trees on another dry site nearby.

### Discussion

# Abiotic amplitude

From the central Oregon Cascades north, Chamaecyparis nootkatensis occurs over much of the range of site moisture conditions present at moderate to high elevations, a conclusion based on (i) the wide range of topographic positions occupied, (ii) the large number of associated species, which include wetand dry-site indicators, and (iii) predawn water potentials similar to those of relatively dry, higher elevation forests in the same region (Zobel et al. 1976). Its absence from most stands is probably not caused by low water availability alone. In the southern Oregon Cascades, Aldrich Mountains, and Siskiyou Mountains, most sites are too dry for the species, although some apparently favorable sites are unoccupied. The present populations may be relicts of those more widespread in moister times, which were reduced during the drier, warmer period 4000-8000 years ago (Arno 1977; Hansen 1961). The species may not as yet have colonized many sites that became suitable following the dry period.

Chamaecyparis nootkatensis is largely restricted to a wet, maritime climate, yet it occurs on dry locations within its range. It may effectively control its water loss. As predawn water potential declines during a dry period, minimal midday water potentials change little (Hickman 1970). Such conservative, protective, stomatal response would reduce  $CO_2$  uptake during long dry periods, but the resulting growth reduction may not be a serious problem.

The near absence of *C. nootkatensis*, and many associated species, from the High Cascades is probably related to the prevalence of deep pumiceous soils there.

The lower elevation limits of C. nootkatensis are abrupt but seem unlikely to be directly controlled by abiotic factors because (i) many of the largest and most vigorous trees occur at the lower elevational limits, (ii) regeneration is as good near the lower limits as elsewhere, and (*iii*) the tree grows well when planted at much lower elevations.

#### **Competitors**

Competition with *Thuja plicata* may set the lower elevational limit of *C. nootkatensis*. The upper limit of *T. plicata* corresponds almost exactly with the lower limit of *C. nootkatensis*; these two Cupressaceae have many characteristics in common but seldom grow together. In the transitional area, reproduction of *T. plicata* is usually more abundant and, although *C. nootkatensis* grows as rapidly there as anywhere, *T. plicata* tends to grow faster. The upper elevation limit of *Thuja plicata* appears to be controlled by temperature (Minore 1983).

Abundance of *Chamaecyparis nootkatensis* is sometimes best explained in terms of competing tree species. Within its range, *Abies amabilis* almost always occurs with *C. nootkatensis*, except on the driest sites, and is often more abundant than *C. nootkatensis*. It establishes with *C. nootkatensis* after disturbance, grows faster in the open, is better able to establish in the forest, and is more shade tolerant. On sites unsuitable for forest canopy development, *C. nootkatensis* has some advantages, largely as a result of its plastic growth form.

Besides A. amabilis, Tsuga mertensiana is the tree most commonly associated with C. nootkatensis. In most forests sampled, T. mertensiana is regenerating poorly. Tsuga mertensiana does establish well after disturbance and can outgrow C. nootkatensis; thus, it competes effectively for open spaces, especially at higher elevations.

Faster growing tree species also confine the distribution of *Chamaecyparis nootkatensis* in Alaska, where *Picea sitchensis* and *Tsuga heterophylla* dominate the more productive sites (Harris and Farr 1974). *Chamaecyparis lawsoniana* is similarly limited in parts of its range to low-productivity, ultramafic soils (Zobel and Hawk 1980).

## Growth-form characteristics

The main stems of *Chamaecyparis nootkatensis* are very flexible and form roots easily when in contact with soil. Such layering produces lateral spread, an advantage on open sites where seedlings are scarce. On forest sites, *C. nootkatensis* develops into a tall, erect tree, provided abundant overhead light is present, but in the shade, plants often become broad and asymmetric without a strong vertical leader. Asymmetrical shrubby individuals bend easily under snow accumulations, which induces further asymmetry; large asymmetrical stems often break under snow load.

## The role of Chamaecyparis nootkatensis on the landscape

The most consistent characteristic of *Chamaecyparis nootkatensis* populations is their proximity to moderate- to highelevation sites that lack, and probably cannot support, a closed tree canopy: rock outcrops, avalanche tracks, and the margins of meadows, lakes, and streams. Disturbance is necessary for *C. nootkatensis* to be more than a minor forest component, and the species is often rare or absent in forest stands far from open areas where a seed source is likely to persist following fire. On disturbed sites it must compete with faster growing species, but it grows well where stands do not fully stock rapidly.

The high elevation habitats of *C. nootkatensis* are disjunct and many apparently appropriate locations are unoccupied. Severe fires or long disturbance-free intervals could eliminate the species locally; recolonization from other areas may be very slow. Chamaecyparis nootkatensis is a stress tolerator in the sense of Grime (1977). The plants grow relatively slowly and can persist under a wide range of conditions, yet the species is largely displaced from the more productive sites within its range.

# Acknowledgments

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