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The Environment of Chamaecyparis lawsoniana

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ABSTRACT: The environment of *Chamaecyparis lawsoniana* (A. Murr.) Parl. was measured at 10 or more sites in Oregon and California which represent six different plant communities. Water is probably the factor most limiting the species' distribution. Most populations have late summer predawn xylem pressure potentials above −11 bars. The eastern range boundary coincides with a rapid decrease in the ratio of precipitation to evaporation. The species is usually confined to wet ultramafic parent materials except at high elevations and in the N. Its southern limit may coincide with absence of consistently wet ultramafics. Success of *Chamaecyparis* on ultramafics may result from failure of *Pseudotsuga* and other competitors to cope with the chemical composition and saturation of these substrates. Foliar nutrient concentrations of *C. lawsoniana* are lower on ultramafics than on other soils, but have a high Ca:Mg ratio. Mycorrhizae show no differences associated with soil type. Despite a large temperature range in the habitat of *C. lawsoniana,* temperature does not seem to limit the species directly. Mean annual air temperatures range from 4.4-10.9 C. Especially at the northern end of the range, temperatures decrease more slowly in late summer than outside the range. Soils are cool, with little annual variation in areas with seepage.

Chamaecyparis lawsoniana seems to be restricted by different aspects of the environment than are most dominant species with which it grows. Variations in temperature and parent material within its range are responsible for large changes in vegetation type without excluding the *Chamaecyparis.* Yet the changes in water availability which limit *C. lawsoniana* often do not produce discontinuities in the other vegetation present.

INTRODUCTION

Chamaecyparis lawsoniana (A. Murr.) Parl. (Cupressaceae), Port Orford cedar, is endemic to the Klamath Mountain region of Oregon and California. It is of interest because: (1) It has a paradoxical distribution, being restricted to a limited geographic range but occurring on many diverse habitats (Fowells, 1965); (2) exploitation and a nonendemic root rot are rapidly decimating the natural forests; (3) the wood is very valuable; and (4) as *Chamaecyparis* also grows in temperate habitats in Japan and Taiwan, comparison with studies of those species may clarify the meaning of our results.

The distribution, vegetation, topographic and geologic relationships of *Chamaecyparis lawsoniana* forests are known in some detail (Whittaker, 1960; Griffin and Critchfield, 1972; Hawk, 1977). Other ecological descriptions of this species (Fowells, 1965) are mostly general. This study sampled several aspects of the environment of *C. lawsoniana.* Sampling sites included extreme as well as typical conditions for the species. Air and soil temperatures, humidity, depth to water table, degree of shading of tree reproduction, effects of prolonged drought, and xylem pressure potential and foliar nutrient concentrations of the plants were measured. Our results can help define reasons for the range restriction of *C. lawsoniana,* as well as the environment where it may be best managed.

GENERAL ENVIRONMENT OF THE SPECIES' RANGE

Chamaecyparis lawsoniana receives moderately high precipitation. In southernmost Oregon, the eastern range boundary coincides approximately with the 1000-mm (40-inch) isohyet (U.S. Dep. Agric., 1964), and in California most stands receive at least 1500 mm (Rantz, 1968). East of its range, rainfall is less and evaporative stress is greater, as shown by the flora (Waring, 1969) and by moisture

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indices for valley weather stations (Thornthwaite Associates, 1964; Johnsgard, 1963; Walter *et al.,* 1975). Disjunct inland populations in California have at least 1250 mm precipitation. The range of *C. lawsoniana* has a definite droughty season, but it is less severe than farther S and E (Walter *et al.,* 1975).

Across the northern end of the range, climatic data show no abrupt changes. South of the range along the coast there are areas with precipitation and evaporation equal to those where *Chamaecyparis lawsoniana* grows.

The region is a diverse geological mosaic including extensive ultramafic outcrops (Calif. Div. Mines Geol., 1964; Dott, 1971; Baldwin and Beaulieu, 1973). At low elevations *Chamaecyparis lawsoniana* usually grows on parent material which is at least partly ultramafic (Hawk, 1977). An exception is on Eocene sedimentary rocks at the northern end of the range. At high elevations, *C. lawsoniana* occupies a wider diversity of parent materials.

STUDY AREAS

Ten primary study sites (Fig. 1, Table 1) were chosen from forests where *Chamaecyparis lawsoniana* is relatively important (Hawk, 1977). The sites represent the range of the species in terms of soil, vegetation, elevation and geography. They include five of eight major communities and one of six minor ones (Hawk, 1977), and represent all four vegetation zones (Franklin and Dyrness, 1973) where

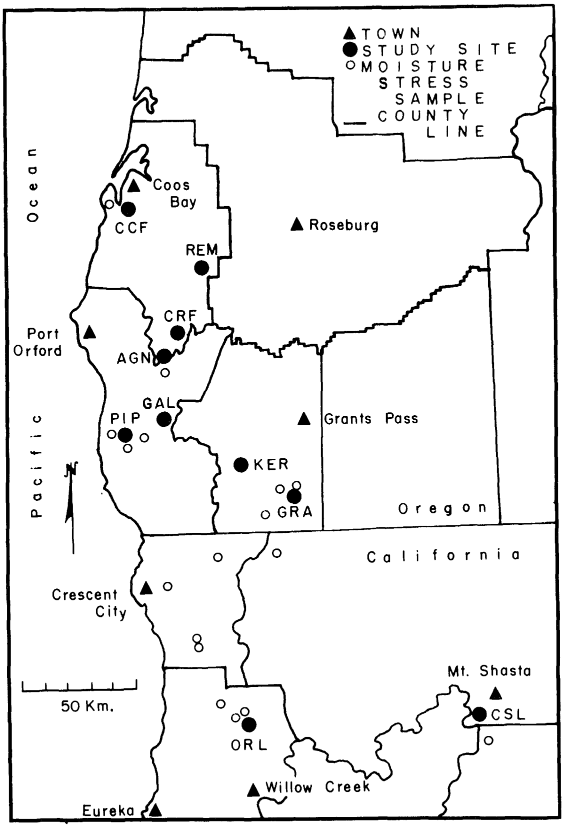

Fig. 1.—Location of 10 primary study sites and the secondary sites used for sampling plant moisture stress

C. lawsoniana grows. We include the one *Picea sitchensis* zone site within the similar *Tsuga heterophylla* zone. All measurements were made wherever possible on these 10 sites. In addition, a Douglas-fir terrace community (Grayback Creek Terrace) was used for shade and intensive measurements of xylem pressure potential (P). Mixed pine communities near Agness Pass and Pine Point were sampled

TABLE 1.—Characteristics of 10 primary sample sites. Zones and communities are those of Hawk (1977)

Site name	Site abbreviation	Elevation (m)	Parent material	Zone
Coos County Forest	CCF	70	Sedimentary	Tshe*
Remote	REM	500	Sedimentary	Tshe
Coquille River Falls	CRF	520	Sedimentary	Tshe
Agness Pass	AGN	850	Ultramafic	ME
Pine Point	PIP	620	Ultramafic	ME
Orleans	ORL	830	Other	ME
Kerby	KER	360	Ultramafic	ME
Game Lake	GAL	1280	Ultramafic +Other	Abco
Castle Lake	CSL	1520	Other	Abco
Grayback	GRA	1420	Other	Abco

TABLE 1.—(continued)

Site name	Community	Approximate precipitation (mm)[1]	Dominant trees	Dominant tree age	Tree reproduction
Coos County Forest	Sandstone	1500	Chla* Psme Pisi	65	none ....
Remote	Swordfern	1800	Psme Chla Tshe	100	Tshe* Chla ....
Coquille River Falls	Swordfern	2300	Chla Psme Tshe	450+	Tshe Chla ....
Agness Pass	Tanoak	2700	Chla Pila Psme	110	Chla Pila Psme
Pine Point	Tanoak	2300	Chla Psme Pila	230	Chla ....
Orleans	Tanoak	2000	Chla Psme	370	Chla ....
Kerby	Mixed Pine	1500	Chla Psme Pije	300	Chla Psme Pije
Game Lake	White Fir	2800	Chla Psme	170	Chla Abco
Castle Lake	White Fir	1500	Chla Abco Pimo	300+	Chla ....
Grayback	Mixed Fir	1100	Chla Psme Abco	450+	Chla Abco ....

* Abbreviations: Trees: Chla = *Chamaecyparis lawsoniana,* Tshe = *Tsuga heterophylla,* Psme = *Pseudotsuga menziesii,* Pisi = *Picea sitchensis,* Pila = *Pinus lambertiana,* Pije = *Pinus jeffreyi,* Abco = *Abies concolor,* Pimo = *Pinus monticola*

Zone: ME = Mixed Evergreen

[1] From Rantz (1968), U. S. Dep. Agric. (1964)

similarly. Xylem pressure potential was measured in late summer on several other sites (Fig. 1).

The Remote, Coos County Forest and Coquille River Falls sites occur on Eocene sedimentary rocks (Baldwin and Beaulieu, 1973). Agness Pass, Pine Point and Kerby occur on pure ultramafic materials, the former two on serpentinite and the latter on peridotite (Wells *et al.,* 1949; Dott, 1971). The other four sites have "other" parent material: Game Lake is a mixture of diorite and serpentinite; Orleans and Castle Lake are on nonultramafic igneous rocks, but appear to be in the path of erosion and drainage from ultramafics (Calif. Div. Mines Geol., 1964); and Grayback is on diorite (Wells, 1940). On-site identifications confirmed the information from geologic maps.

METHODS

Measurements were made on or near 1-3 m saplings of *Chamaecyparis lawsoniana* because saplings are more sensitive indicators of some environmental stresses than are larger trees (Waring and Cleary, 1967). Environmental measurements in several studies in the Pacific Northwest have used trees of this size (Waring, 1969; Minore, 1972; Zobel *et al.,* 1976). Where other conifer reproduction was important, we made corresponding measurements on other species. Nearly all trees sampled were growing under typical stand conditions. The exception, Coos County Forest, had no tree reproduction; there shade and soil temperatures were sampled systematically under the stand, and trees on a disturbed area were sampled for xylem pressure potential and foliar nutrition.

Temperature.—Air and soil temperatures were recorded continuously on 31-day charts. The air temperature sensor was beneath an insulated A-frame shield 1 m above the ground, in the edge of the crown of a single *Chamaecyparis* sapling. The soil temperature probe was buried 20 cm deep in the root zone of the same or an adjacent tree, outside the shade of the air sensor shelter. Thermographs were recalibrated each month. Records extend from late September 1974 to late September 1976 (except for instrument failure or lack of access due to snowpack).

Air temperature means were determined separately for day and night, day length being that of the 15th of the month. Daily average soil temperatures were read off the charts. Day and soil temperatures were used to determine a "Temperature Growth Index" (TGI) for each day. This index weights temperatures by their effect on dry weight of *Pseudotsuga menziesii* seedlings. It is the same as "Optimum Temperature Days" of Cleary and Waring (1969), and should be a suitable index of the influence of temperature on assimilation. We calculated total TGI for each month.

The representativeness of the soil temperature sample was checked by spot readings in the root zones of several saplings in summer, and at some sites in winter.

Shade.—Ozalid paper sensors (Friend, 1961) were calibrated using a Kipp solarimeter. One sensor was clipped horizontally to a top branch of each of 2-24 saplings of each major conifer species at each site. Species were sampled in approximate proportion to their density. Sensors were left in place for one full, clear midsummer day. Notes were made on tree vigor. Sensors were placed on a few saplings which had recently died. Sensors were simultaneously exposed in the nearest large opening to give "full light" values, and data were converted to a percentage of "full light" for that day.

Humidity.—To quantify the range of atmospheric humidity encountered by the species, the Kerby and Coos County Forest sites were chosen as the probable extremes. Hygrothermographs with hair humidity sensors were operated in shelters 10 cm above the ground at these sites periodically throughout the summer of 1976.

They provided a total record for 30 days, of which 16 were sampled in common.

Water table depth.—In June 1976, a soil auger was used to locate the water table at all sites (if within 90 cm of the soil surface or the bottom of a soil pit). Pipes were placed in holes with free water, and the depth recorded monthly through September 1976.

Xylem pressure potential.—Most sampling was designed to determine the minimum soil-induced potential encountered by 1-3 m tall saplings of *Chamaecyparis lawsoniana*. Xylem pressure potential (P) was measured before dawn in late August of each year, following the logic of Waring and Cleary (1967). In 1974 and 1975, 130 and 160 *Chamaecyparis* saplings, and ca. 80 of other species each year, were sampled at both the primary and additional sites (Fig. 1). In 1976 only primary sites were measured. At edges of some *Chamaecyparis* stands, transects of measurements determined whether the edge corresponded with a decrease in P.

Sampling was usually between 1 AM and dawn, using a pressure chamber (Scholander *et al.*, 1965). Data are presented as negative bars (1 bar = 10^5 Pa); the more negative the value, the more limited is water for the plant. Daily change in P was measured at three sites.

Foliar nutrient content.—Foliage was collected in October from 2-10 saplings of *Chamaecyparis lawsoniana* and, at some sites, 2-8 of each other conifer. All green foliage was collected from one large branch from the upper crown. Leaves only were collected from Pinaceae, and leaves with their enclosed small twigs were stripped from *Chamaecyparis*. All trees were in natural stand conditions except at Coos County Forest.

Foliage was analyzed by the Department of Horticulture at Oregon State University (Chaplin and Dixon, 1974) for total N, K, P, Ca, Mg, Mn, Fe, Cu, B, Zn and Al. Comparisons of *Chamaecyparis* with *Tsuga heterophylla* were made for two sedimentary soils and, with *Pseudotsuga menziesii*, on three sites with ultramafic and one with sedimentary rocks.

Mycorrhizal condition.—Litter and roots were collected from all plots except Remote and Coquille River Falls. Roots were inspected microscopically for mycorrhizal formation and spores of hypogeous fungi from the litter identified.

Drought effects.—Effects of a severe drought were assessed in late August 1977. Water table depth, predawn P, soil temperature and twig elongation of understory saplings since the previous September were measured and extent of foliar chlorosis was estimated.

RESULTS

Air temperature.—The habitats of *Chamaecyparis lawsoniana* varied greatly in air temperature (Fig. 2, Table 2). The more inland sites had a more continental temperature regime. The frostless season in 1975 varied from 52 days at Castle Lake to 255 days at Coos County Forest (Table 2). Extreme temperatures were —15 C at Castle Lake and 46 C at Kerby.

Abies concolor zone stands had surprisingly high summer night temperatures; the monthly average minimum at Grayback in August 1975 was 12.2 C, the highest of all areas.

Our study probably included most of the temperature range where *Chamaecyparis lawsoniana* grows. Temperatures at Kerby are probably as high as anywhere in the range. Although the species occurs higher than at Castle Lake, this dense stand in a creek bottom, with copious surface seepage in the summer, probably is one of the coldest.

Temperatures in the range of *Chamaecyparis*, especially the northern end, decrease less from midsummer to September than they do elsewhere in the Pacific Northwest. This pattern was quantified as the "October drop index," the ratio of "the temperature decrease from September to October" to "the total decrease from the warmest month to October" (Table 2). A high index, indicating a relatively hot September, is characteristic of weather stations of the Oregon coast (index = 0.75) (U.S. Dep. Comm., 1975), and especially of our five northern sites (a mean of 0.92). The southern sites had a mean index of 0.65. In contrast, stands sampled in a similar manner in the Oregon Cascades (Zobel, 1975; Zobel *et al.*, 1976) had a much lower index (0.18 to 0.46) than do the appropriate weather stations (0.65).

Marine air masses moving off the ocean may synchronize major temperature changes throughout the range. The pattern of temperature change was inspected for agreement among sites, in terms of the direction of the changes in day temperature from one period to the next. Most sites, especially the northern montane sites and Orleans, changed in parallel with Remote, which had the most complete record. Sites separated from the ocean by a major mountain range showed less agreement (5-11% of major temperature changes did not coincide with those at Remote). Surprisingly, the most different site was Coos County Forest, close to Remote but near the coast. Local coastal phenomena, such as fog during hot weather inland, affect it but not other sites.

Soil temperature.—Five sites represent much of the variability in soil temperature (Fig. 3). Soil temperature variation among sites is sometimes not associated with the pattern of air temperature (Table 2). Seepage at the sensor location

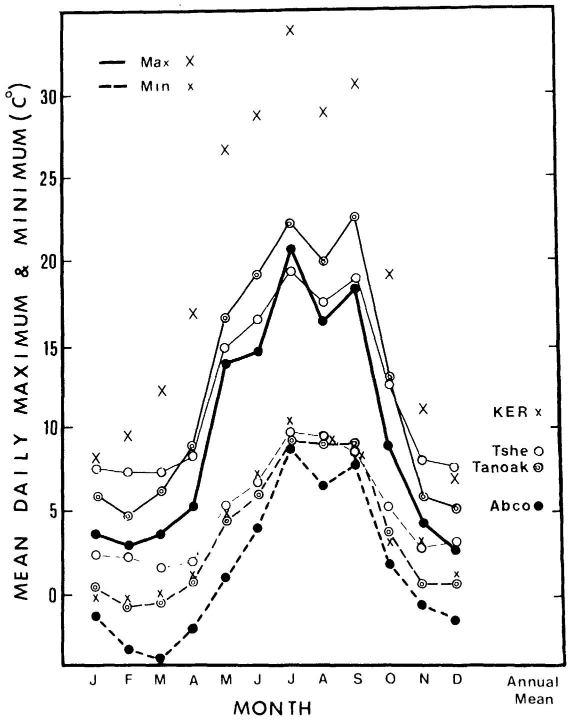

Fig. 2.—Actual mean daily maximum and minimum temperatures (C), and annual mean temperature by zone. Mixed Evergreen zone data are presented separately for the Tanoak community and for the Mixed Pine community at KER (X). Abco represents the *Abies concolor* zone; Tshe is the *Tsuga heterophylla* zone

TABLE 2.—Temperature characteristics of primary study sites. "Warmest month" and "coldest month" data are means of the mean maxima and minima of air, and the mean monthly temperature of soil, for the appropriate months in both years of the study. "Normal," "October drop index" and "Temperature Growth Index" are defined in the text. Community and zone abbreviations identified in Table 1. NA = insufficient data available

Zone	Community	Site	..........Air temperatures..........					......Soil temperatures......			Temperature Growth Index	
			Mean annual (C)	Frostless season 1975 (days)	Minimum coldest month ....(C)........	Maximum warmest month	October drop index (units)	Annual ....(C)..................	Coldest month	Warmest month	Total annual (units)	June to Sept. (%)
Tshe	Sandstone	CCF	8.9	255	+2.2	17.7	0.74	9.8	6.8	13.2	126	48
	Swordfern	REM	8.2	197	+0.8	19.0	1.00	8.3	4.1	13.2	108	56
		CRF	8.4	185	+0.8	22.7	0.93	7.9	4.0	12.2	107	58
	Zone Mean		8.5	......	+1.3	19.8	0.91	8.7	5.0	12.9	114	54
M E	Tanoak	AGN	6.9	155	−2.1	25.2	0.98	7.6	3.6	13.5	95	67
		PIP	8.8	124	−0.3	23.5	0.97	9.2	5.4	13.7	119	57
		ORL	7.5	NA	−1.0	22.2	0.65	6.9	5.1	9.1	86	61
	Community Mean		7.7	......	−0.8	23.6	0.87	7.9	4.7	12.1	100	62
	Mixed Pine	KER	10.9	233	−0.4	34.9	0.55	11.3	8.3	15.0	153	52
	Zone Mean		8.5	......	−0.7	26.4	0.79	8.8	5.6	12.8	113	60
Abco	White fir	GAL	NA	NA	−1.6	20.1	0.72	NA	NA	12.3	67	76
		CSL	4.4	52	−6.7	23.6	0.51	3.9	0.4	9.0	52	86
	Mixed fir	GRA	5.7	NA	−2.7	18.4	0.84	4.8	1.4	9.3	58	77
	Zone Mean		5.2	......	NA	20.7	0.69	4.4	0.9	10.2	59	80

moderated winter minima, summer maxima or both (*e.g.*, Kerby, Orleans, Castle Lake, Fig. 3). Coos County Forest and Coquille River Falls illustrate a difference between coastal and montane stands with a dense canopy but without seepage (Fig. 3). All sites except Coos County Forest had maximum soil temperatures in September, apparently reflecting the warm September characteristic of the range of *Chamaecyparis*.

Soils in our plots were generally cold (Fig. 3); for example, Castle Lake exceeded a mean of 5 C only 4 months of the year. On the other hand, soil temperature approached freezing only in the *Abies concolor* zone, where —0.5 C was recorded at all three sites. Snowpack at these sites may usually prevent freezing.

At several sites, soil temperature was measured below several conifer saplings. *Pinus jeffreyi, Pseudotsuga menziesii* and *Abies concolor* average over a half-degree warmer in summer than the *Chamaecyparis* on the same sites. However, with the large tree-to-tree variation, t-tests show only *P. jeffreyi* to be significantly higher (3.4 C). The few winter measurements made at Kerby indicate that *P. jeffreyi* and *Pseudotsuga* have significantly cooler soil then. The association of *Chamaecyparis lawsoniana* with seepage should explain the difference.

Summer soil temperatures varied by 1.7-8 C among *Chamaecyparis* saplings within a site. The thermograph sensor had soil temperatures ranging from 0.7 above the mean of *Chamaecyparis* to about 1.5 C below; however, none significantly differed from the mean. Since temperature of the wet soil in other seasons probably varies much less within the site than in summer, the annual means at the sensors were probably within 1 C of the average for all trees.

Temperature growth index.—Annual accumulation of TGI varied ca. threefold from Castle Lake to Kerby (Table 2). The *Tsuga* zone had twice the units of the *Abies* zone. However, only half accumulated during the summer, compared to 80% in the *Abies* zone (Table 2, Fig. 4), which had essentially none from December through April. The *Tsuga* zone and the Tanoak communities were similar from April through October (Fig. 4). Coastal sites were the highest within

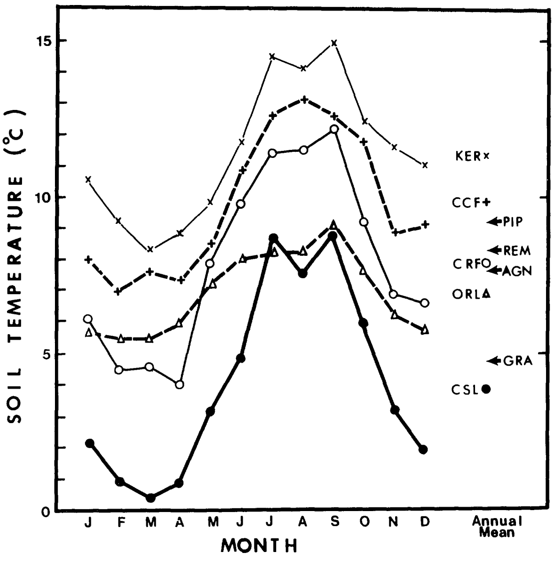

Fig. 3.—Mean monthly soil temperature (C) for five sites, with mean annual soil temperature for nine sites

each zone (Table 2). Maximum accumulations in September reflected the peak soil temperature and the high air temperature.

Shading of tree reproduction.—Chamaecyparis saplings grew in both very shaded and quite open conditions (Table 3). *Tsuga heterophylla* zone stands provided deep shade. In *Abies concolor* zone communities, the saplings received more light. Mixed Evergreen zone sites varied from quite shaded to open (in the Mixed Pine community) (Table 3). In all zones, reproduction occurs in the open on clear-cuts near natural forest.

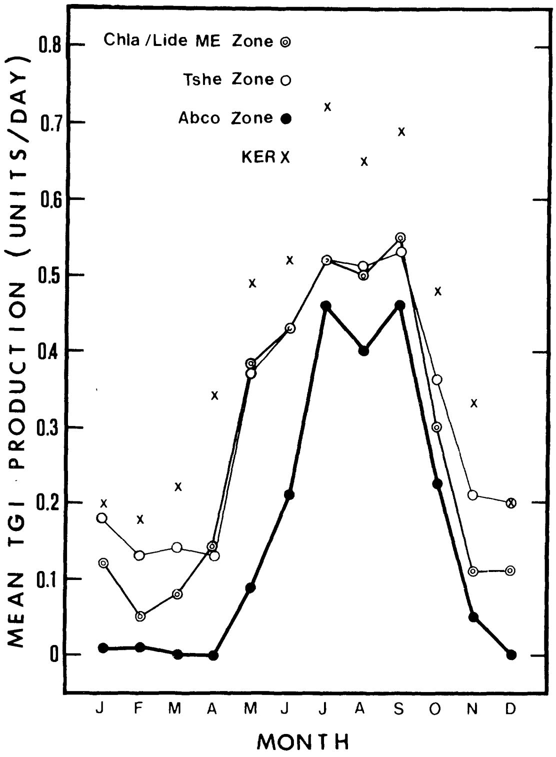

Fig. 4.—Mean daily production of Temperature Growth Index units by zone. Mixed Evergreen zone data are presented separately for the Tanoak community (Chla/Lide) and the Mixed Pine community at KER. For abbreviations, *see* Figure 2

TABLE 3.—Light reaching live conifer saplings in sampling areas as a percent of that in the open on the same clear midsummer day. *See* Table 1 for key to abbreviations

				Percent of full light (No. trees)				
Zone	Community	No. sites	All species	Chla	Tshe	Psme	All pines	Abco
Tshe	Sandstone	1	0.9*	....	..	....	....	..
	Swordfern	2	0.6	0.7(16)	0.6(28)	....	....	..
ME	Tanoak	3	4.0	2.9(37)	..	9.5(2)	8.7(6)	..
	Mixed pine	3	38.6	37.1(30)	..	44.8(20)	33.3(15)	..
	Terrace	1	3.8	3.4(5)	..	4.9(2)	....	..
Abco	White fir	2	2.3	2.1(43)	..	....	1.2(2)	3.6(10)
	Mixed fir	1	5.5	5.4(17)	..	....	....	5.7(5)

* No tree reproduction. Data from 16 systematically located points

Other species of conifers were compared to *Chamaecyparis* on the same sites (Table 3). *Pseudotsuga menziesii, Pinus jeffreyi* and *Calocedrus decurrens* grew on considerably less-shaded microsites, averaging over 5% more light. Other species were much more similar to *Chamaecyparis.*

At Coquille River Falls and Castle Lake some dead and near-dead *Chamaecyparis* were sampled. They received 0.2-0.4%, compared to 0.7 and 2.5% of full light for the live ones. Apparently the species' shade tolerance is exceeded in parts of some communities. Vigor of live saplings was rated as "good" or "fair." One might expect the good seedlings to be less shaded in closed stands, but more shaded in open ones, than those with fair vigor. This occurred at one open and four closed sites, but the reverse was true at two shaded sites.

Humidity.—Humidity at Coos County Forest and Kerby showed the expected difference. For all sample days, Coos County Forest had 86.4%, and Kerby, 63.4% relative humidity. Comparing only days in both samples increased the difference, means being 88.4 and 59.9%. Since part of the sampling period was rainy, the normal summer difference between sites may be even greater.

Vapor pressure deficit (VPD), a function of both temperature and relative humidity, is more directly related to transpiration. On the driest sample days, the mean VPD was 4.1 mb at Coos County Forest and 23.5 mb at Kerby. Maxima were 10 mb at Coos County, and 47.5 mb at Kerby.

Water table depth.—In June 1976 a water table was located at all except three northern plots, Coos County Forest, Coquille River Falls and Agness Pass. Depths to the water table varied from 2-69 cm. At Castle Lake, Orleans and Kerby, seepage was obvious and rapid. Game Lake and Grayback had obvious seepage only in some spots, and at Remote only one small area had a shallow water table. On ultramafic substrates, at Kerby and Pine Point, the water table was perched above a very dense layer of fine clay; this is probably the case for many ultramafic areas, considering the high P values in most of these stands (*see* next section).

The pattern of change of water table depth in summer 1976 varied, rising at some sites while dropping at others. Two wells at one site often varied in their depth and pattern of change. At several wells, the variation exceeded 50 cm. At Kerby, however, the level changed only 1.5 cm.

Xylem pressure potential.—Most populations of *Chamaecyparis lawsoniana* experienced high xylem pressure potential (P) (Table 4), with site means below

TABLE 4.—Summary by plant community of the minimum predawn xylem pressure potentials (P) recorded. Some sites were measured only 1 year; others were measured for 3. Means ($\bar{X}$) and ranges (R) are computed over the several sites measured in one community. Data for years of greater than minimum P are not included. The "minimum values" presented are site values, each the mean of several trees of each species. Data are negative bars. Abbreviations are defined in Table 1

				P							
				Chla		Tshe		Psme		Abco	
Zone	Plant community	No. sites	No. site-years	$\bar{X}$	R	$\bar{X}$	R	$\bar{X}$	R	$\bar{X}$	R
Tshe	Sand dune	1	1	6		..		....		..	
	Blacklock	1	1	5		5		....		..	
	Sandstone	1	2	9		..		....		..	
	Swordfern	2	3	8	(8-8)	8	(7-8)	....		..	
Mixed evergreen	Tanoak	9	18	9	(7-11)	..		....		..	
	Mixed pine (A)	2	5	18	(17-18)	..		18	(17-18)	..	
	Mixed pine (B)	7	16	8	(7-10)	..		13	(7-17)	..	
	Terrace	2	5	23	(20-25)	..		18	(17-18)	..	
Abco	White fir	6	14	8	(7-9)	..		....		8	(7-10)
	Mixed fir	4	8	8	(7-9)	..		....		8	(7-9)

—10 bars only in the Mixed Evergreen zone. High P might be expected from the restriction of *C. lawsoniana* to areas of seepage in the southern part of its range, and from the marine influence evident at the northern end of the range.

There were exceptions to this generalization. Trees in two open Mixed Pine communities (separated as "A" in Table 4) had moderately low P values in 1974, even after a wet early July. These stands were on more exposed topography than the nearby Agness Pass and Pine Point thermograph sites (Table 1), located in Tanoak vegetation. Both areas were more exposed to marine air and fog than the other samples of the Mixed Pine community. Other sites in this open, xeric-appearing community ("B," Table 4) had P no lower than more obviously mesic forests.

A second exception, dense low elevation stream terrace communities in the Mixed Evergreen zone, had low P values (Table 4). The possible compensating factors here might be high humidity near the stream and cold air flow down the valley at night. But, considering the usual high P values of *Chamaecyparis,* its size, reproductive success and even presence in these stands are surprising.

Conifers besides *Chamaecyparis* had similar P except in the Mixed Evergreen zone (Table 4), where they usually occur on more convex topography or drier microsites (Fig. 5). At Castle Creek, 9 km S of the Castle Lake site, a pure, closed stand of *Chamaecyparis* was confined to the bottom of a small drainage, with reproduction of other species scattered up the slope. At Kerby, several species grew intermixed, but all *Chamaecyparis* except one were in areas with seepage, while other species were mostly in drier microsites. Data for 2 years at these sites were similar. On four other transects, *Chamaecyparis* also disappeared where predawn P dropped to ca. —11 bars.

Daily patterns of P were measured during 2 days each at Kerby, Grayback Creek Terrace and in the Mixed Pine community at Agness Pass. P of *Chamaecyparis* was usually from 7-10 bars lower in midday than at its highest. The daily change in *Pseudotsuga* usually averaged 2.0 bars more than for *Chamaecyparis.* On 1 day at

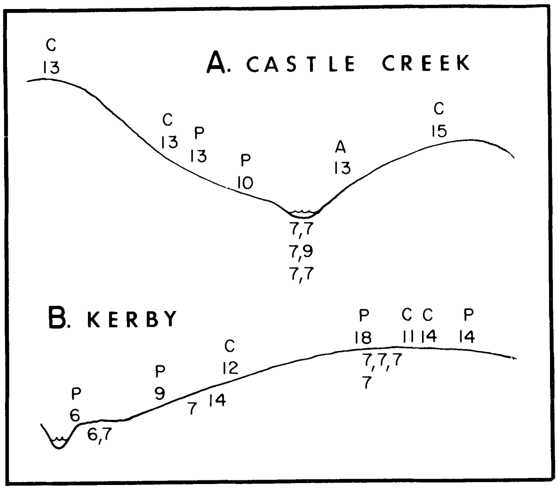

Fig. 5.—Transects of late summer predawn xylem pressure potential at two sites. Each value represents the average value for one tree, from 2 years of sampling. Values below the topographic profile are for *Chamaecyparis lawsoniana;* values above the profile are for other species (C = *Calocedrus decurrens,* P = *Pseudotsuga menziesii,* A = *Abies concolor*). All values are in negative bars

the Grayback Creek Terrace, *Chamaecyparis* fell only 3 bars from its predawn value of —19, while *Pseudotsuga,* beginning at —14, dropped 10 bars. One day at Kerby, when vapor pressure deficit reached 44 mb, P of *Chamaecyparis* changed the same as for *Pseudotsuga.* Thus, *Chamaecyparis* controlled P as effectively as *Pseudotsuga* under these conditions. This is apparently not always the case. At the open Agness Pass stand, drought which continued into October 1974 killed the older half of the foliage on *Chamaecyparis,* but did not affect *Pseudotsuga* and the pines.

Data for xylem pressure potential and shading were compared to see if the more exposed trees had lower P. Differences which occurred in three stands were small, usually only ca. 1 bar.

Drought effects.—In late August 1977, no extreme effects were noted from the severe drought of 1976-1977. Very few trees in or near the plots died. Most water tables were similar to or higher than in 1976. Soil temperatures at 20 cm were higher than previously recorded at only two sites. Estimated percentages of chlorotic foliage varied. Ten populations appeared no different than in previous years while four had 15-19% yellow foliage, and looked less healthy than before. These trees were in the open except at Castle Lake. Damage at the open site at Agness Pass was less severe than during 1974.

Very low P in the growing season of 1977 should have reduced twig elongation since the previous autumn. *Chamaecyparis,* having no winter buds and a long growing season, apparently forms most new tissue in the summer of elongation and probably grows mostly at the expense of current photosynthate. This is in contrast to most temperate Pinaceae, with preformed shoots which use much stored carbohydrate (Kozlowski, 1971). Elongation of individual lateral branches was compared for the 1976 and 1977 growing seasons (unpublished data). It was significantly lower in 1977 only at two open sites where previous P values had been moderately low, and at Kerby. In contrast, *Pseudotsuga* grew more at those sites in 1977. Growth of *Tsuga* and *Abies* saplings did not differ between years.

Thus, effects of the drought of 1976-1977 were minimal except at open sites which previously had low xylem pressure potential, and at the hottest site. Heavy rainfall in or just before the growing season (160-180% of normal in May 1977) probably prevented major damage to *Chamaecyparis.*

Foliar nutrient concentration.—Foliar concentrations of all macronutrients, Fe and B in *Chamaecyparis* reflected the type of parent material (Table 5). Nitrogen, P and K were lower in trees from ultramafic rocks than on the other soils. Trees from "Other" soils were higher in Ca and B, but lower in Fe than those from sedimentary and ultramafic types. The four sites with some ultramafic materials, plus Orleans (with possible ultramafic influence), had higher Mg than the other five. No relationship with parent material was evident for Al, Cu, Mn or Zn.

The ratio of Ca:Mg varied from 2.3-11.7 in *Chamaecyparis;* trees from ultramafic rocks or those sites with apparent influence from them had the lowest ratios, and trees in the *Abies* zone communities on nonultramafic rocks had the highest. Differences among Ca:Mg ratios were due primarily to differences in Mg content, but both relatively low Mg and high Ca contributed to the high ratios at Grayback and Castle Lake. The lowest Ca:Mg ratio for an individual of *Chamaecyparis* was 1.2.

Both *Tsuga heterophylla* and *Chamaecyparis* were sampled on two sedimentary soils. *Tsuga* had more P, Mn, B, Cu and Al, and less Ca and Zn (Table 5). Its P concentration was twice that of *Chamaecyparis* (and of *Pseudotsuga*) on any soil. *Tsuga*'s Ca:Mg ratio was only half that of *Chamaecyparis* (but still above 2), due to its lower content of Ca.

TABLE 5.—Field foliar nutrient concentrations from saplings sampled in October. Abbreviations are defined in Table 1; n = number of trees sampled

Zone	Site	Parent material	Species Code	n	N	K	P	Ca	Mg	Ca:Mg	Mn	Fe	Cu	B	Zn	Al
					percent					ratio	ppm					
Tshe	REM	Sed	CHLA	2	0.99	0.56	0.15	1.01	0.21	4.8	525	301	9.5	24	35	233
			TSHE	8*	1.02	0.68	0.28	0.50	0.18	2.8	888	329	15.0	31	17	547
	CCF**	Sed	CHLA	5	1.14	0.68	0.12	0.50	0.11	4.4	367	162	3.6	9	76	188
			PSME	5	1.51	0.59	0.14	0.32	0.11	3.0	275	156	4.4	20	30	509
	CRF	Sed	CHLA	8	0.89	0.59	0.13	1.20	0.21	5.8	377	298	8.9	20	55	257
			TSHE	2	0.98	0.54	0.27	0.48	0.22	2.2	528	272	12.0	30	17	924
ME	AGN	Um	CHLA	10	0.67	0.41	0.07	0.88	0.24	3.7	400	308	13.6	18	54	286
			PSME	5	0.76	0.39	0.16	0.33	0.31	1.1	1368	159	3.8	28	15	172
	PIP	Um	CHLA	10	0.65	0.42	0.07	0.83	0.37	2.3	255	229	10.4	20	42	135
			PSME	5	0.99	0.35	0.11	0.25	0.50	0.5	297	194	2.2	57	13	70
	ORL	Other	CHLA	10	0.78	0.51	0.12	1.37	0.37	3.7	875	124	5.1	26	59	127
	KER	Um	CHLA	10	0.61	0.27	0.06	1.00	0.28	3.5	178	214	7.0	14	47	124
			PSME	5	0.74	0.29	0.11	0.27	0.43	0.6	409	111	1.4	22	12	67
Abco	GRA	Other	CHLA	10	0.92	0.71	0.15	1.08	0.12	9.2	620	187	17.2	27	46	298
	GAL	Um-other	CHLA	10	1.08	0.68	0.15	0.88	0.29	3.1	157	165	6.0	30	40	88
	CSL	Other	CHLA	10	1.09	0.51	0.09	2.02	0.17	11.7	377	102	4.2	32	41	116
Least Significant			PSME	....	.13	.16	.05	.14	.13	....	491	108	2.8	15	19	227
Difference			CHLA	....	.19	.18	.05	.47	.18	....	......	56	4.8	9	....	82
Mean		Sed	CHLA	15	0.99	0.62	0.13	0.94	0.18	5.2	393	253	7.2	17	59	231
			TSHE	10	1.01	0.65	0.28	0.50	0.19	2.6	816	318	14.4	31	17	622
Mean		Um	CHLA	30	0.64	0.37	0.07	0.90	0.30	3.0	278	250	10.3	17	48	182
			PSME	15	0.83	0.34	0.13	0.28	0.41	0.7	691	155	2.5	36	13	103
Mean		Other	CHLA	40	0.97	0.60	0.13	1.34	0.24	5.6	507	145	8.1	29	47	157
Mean	All	All	CHLA	85	0.86	0.52	0.11	1.11	0.25	4.4	406	201	8.7	23	49	179

* One bulked sample from eight trees

** Trees near the CCF site but growing in the open

Comparison of *Pseudotsuga* with *Chamaecyparis* on three ultramafic sites showed it to have higher P, Mn, B, Mg, and N than *Chamaecyparis,* and lower levels of Cu, Ca, Zn, Al and Fe. Ca:Mg ratios of *Pseudotsuga* were very low (1.1, 0.6, 0.5), with both higher Mg and lower Ca than *Chamaecyparis.* Several of these relationships were not repeated in the one *Pseudotsuga* sample from sedimentary soil at Coos County Forest (Table 5).

Mycorrhizal conditions.—With varied soil and climate, it seems reasonable that differences in mycorrhizal symbionts of *Chamaecyparis lawsoniana* might occur. Such was not the case for our samples. All roots examined had similar, normal mycorrhizal formation. All spores identified were of *Glomus macrocarpus* and *G. fasciculatus,* both common symbionts of *C. lawsoniana* (J. Trappe, pers. comm.).

DISCUSSION

Results of our short-term environmental sampling reflected the idiosyncracies of the sampling years. August, March and April were cooler than normal both years, and September was hotter. However, September being only slightly cooler than August and March being nearly as cold as February are both characteristics of regional weather station records, and appear to be real patterns in the environment of *Chamaecyparis lawsoniana.* The specific importance of a warm September to *C. lawsoniana* is not immediately obvious. The longer growing season may cause the tallest trees to occur in the N where the pattern is most obvious, although both water and nutrients are also favorable there. If *C. lawsoniana* is shallow-rooted, as are other *Chamaecyparis* (Sato, 1974; Korstian and Brush, 1931), buffering of soil temperature by seepage may be necessary to protect its roots.

The study years were probably too wet to determine the minimal xylem pressure potential experienced by *Chamaecyparis lawsoniana.* Only the Kerby-Grayback area had a whole summer drier than average, although the nearly rainless August 1974 probably overcame the effect of a wet early summer elsewhere. Table 4 should represent the general pattern after a uniformly dry summer, if not the absolute values.

Climate in the range of *Chamaecyparis lawsoniana* was generally milder than at sites sampled similarly in the central Cascades (Zobel, 1975; Zobel *et al.,* 1976). Air and soil temperatures at most sites were not as extreme. The annual range of monthly mean air temperatures varied 9-15 C (20 at Kerby), compared to 16-25 C in the Cascades. Maximum rates of TGI accumulation were lower than in the Cascades, although values for September were higher.

Compared to other western Oregon forests (Waring, 1969; Minore, 1972; Hawk and Zobel, 1974; Zobel *et al.,* 1976) xylem pressure potential of most *Chamaecyparis* populations was high. However, predawn P on Mixed Evergreen zone terraces was low even in a regional context.

Little information is available about nutrient requirements of *Chamaecyparis lawsoniana.* Compared to other northwestern conifers, our values for N and P were usually low, as was K at Kerby (C. T. Youngberg, pers. comm.). Levels of K, N, P and Ca have been correlated with growth of *C. lawsoniana* (Leyton, 1955; Plocher, 1977) and *C. obtusa* (Kawada *et al.,* 1973). Since foliar K and N were lowest on ultramafic parent materials, growth potential for *C. lawsoniana* is probably intrinsically lowest there also. The tree is smaller on ultramafics than on other soils (Hawk, 1977). However, the size of *C. lawsoniana* is reduced less by ultramafics than that of *Pseudotsuga* (Whittaker, 1960; Hawk, 1977), which accumulated less Ca and more Mg than *Chamaecyparis* in this study, giving it a very low Ca:Mg ratio.

In British Columbia, nutrient concentrations of *Thuja,* also in Cupressaceae, show generally the same relationships to those of *Pseudotsuga* and *Tsuga* than our *Chamaecyparis* does, N and P being lower, Ca being higher, and K and Mg being similar (Beaton *et al.,* 1965). However, our foliage had average N, P, and K at or below deficiency levels in greenhouse-grown *Thuja* (Walker *et al.,* 1955).

Many foliar nutrient data are available for coastal *Pseudotsuga* north of the study area (van den Driessche, 1969). Our sample means for *Pseudotsuga* were at the lower end or below most reported values for N, P, K and Ca, even at Coos County Forest, and most were very high for Mg. Nitrogen concentration of *Pseudotsuga* from ultramafic areas was similar to natural stands in the Oregon Cascades (Zobel *et al.,* 1976) but below those on other soils in the eastern Siskiyou Mountains (Waring and Youngberg, 1972). Based on nutrient levels of *Pseudotsuga* saplings, the sites where they occur with *Chamaecyparis* apparently have limited supplies of available nutrients. In contrast, foliage of *Tsuga* at Remote and Coquille River Falls had concentrations just as high or higher than in British Columbia (Beaton *et al.,* 1965).

In general, foliar nutrient concentrations (Table 5) reflected the expected effect (Proctor and Woodell, 1975) of ultramafic substrates, with lower N, K and P, and higher Mg. However, Ca was not relatively as low as usual on serpentine soils.

Our results suggest hypotheses about which environmental factors limit the distribution of *Chamaecyparis lawsoniana.* Conditions which allow its presence, those that control its relative and absolute importance on a site, and those that control its growth may not be identical: *e.g.,* density and basal area of *C. lawsoniana* were greatest where trees were relatively short, specifically on mesic sites with ultramafic rocks (Hawk, 1977).

The species usually has readily available water throughout the year. Thus it is limited by the lower rainfall and greater evaporation E of its range. In the N, with a higher ratio of precipitation to evaporation and deeper soils, sufficient water is available over much of the landscape. Farther S and inland, the dry season is more intense, less area provides sufficient water, and stands are small, discontinuous and mostly in drainageways. Absence of *Chamaecyparis* from ridges and upper slopes (Hawk, 1977) is probably related to lack of water. An extensive slope above a site, with the associated seepage, also is important for *C. obtusa* (Sato, 1974). The coastal spots where the species does experience moderately low xylem pressure potentials have moister air and lower temperatures than inland.

The relative drought resistance of *Chamaecyparis obtusa* and *Cryptomeria japonica* seedlings depends on rooting depth, *Chamaecyparis obtusa* being more resistant where root penetration is limited (Satoo, 1956). This type of mechanism may aid *C. lawsoniana* where winter-saturated or skeletal soils limit its rooting depth, but cause its absence on nearby deeper or better-drained soils.

The restriction of the species to ultramafic soils at low elevations in the S probably reflects their dense clay layer, which keeps water available near the surface. On parent materials where *Pseudotsuga* is more abundant and vigorous, it probably uses the water necessary for *Chamaecyparis.* Only at high elevations or in the N does the ratio of available water to evapotranspiration appear sufficient to compensate for the competition.

In contrast to its eastern boundary, the latitudinal limits of *Chamaecyparis lawsoniana* coincide with no major macroclimatic change. However, the area to the S may lack suitable habitat for *Chamaecyparis* (J. Sawyer, pers. comm.), because major areas of ultramafic rocks are not associated with coastal mountains, major rivers or high elevations as they are farther N. The Eocene sediments which the species occupies at its northern limits are derived from older ranges to the S which include ultramafics (Snavely and Wagner, 1963). One wonders whether the northern limit reflects an ultramafic effect residual in the sediments, to which *Chamaecyparis* may respond more favorably than its competitors.

The occurrence of *Chamaecyparis lawsoniana* would probably be more restricted were it not for its tolerance to both shade and repeated fire (Hawk, 1977). Shade tolerance is confirmed by our measurements, as well as by earlier laboratory studies (Baker, 1945). Light is low enough in some stands to restrict reproduction of *Chamaecyparis;* however, this would not affect its overall distribution.

It seems unlikely that any parent material excludes *Chamaecyparis lawsoniana* if sufficient water is available. Its absence from a particular substrate is probably mediated by competition, as noted above (although no information about allelopathic effects is available). Low foliar levels of several macronutrients on ultramafic sites were associated with a reduction in height, but an increase in relative importance. Thus the change in importance apparently reflects an effect on competing species and does not indicate better conditions for the *Chamaecyparis.* Besides the nutrient problem, cold or saturated soils, common on some ultramafic sites, may reduce vigor of *Pseudotsuga.*

Axelrod (1976) suggests that, through geologic time, *Chamaecyparis lawsoniana* became restricted to the wet, mild climate of its present range. Our data confirm its usual requirement for dependable moisture and show that it is often further restricted to moist sites where the most common species grow poorly. Air temperatures, on the other hand, span a range including four vegetation zones. It seems unlikely that a requirement for "mild temperatures" now restricts *Chamaecyparis,* although the range may have less severe extremes than outside.

It is difficult to know the real biological significance of the environmental variability we measured. However, we can make some suggestions based on the covariation of vegetation and our measured factors. Pure ultramafic rocks resulted in distinctive vegetation types. More open communities on ultramafics occurred across the range of elevation where the species grows (Hawk, 1977), the substrate's influence overriding environmental change associated with elevation. The 5.5 C difference in mean annual temperature (and associated differences in other phenomena) was also associated with a large vegetation difference, spanning four zones. In contrast, late-summer, predawn xylem pressure potential (P) of *Chamaecyparis lawsoniana* varied considerably, but low P occurred in vegetation similar to that where P was high. Yet, to most populations of *Chamaecyparis* itself, a consistent abundance of water seems to be a critical necessity.

The above paragraph emphasizes the variability in vegetation and environment where *Chamaecyparis lawsoniana* grows. Within its range, its tolerance of some factors exceeds that of several more widespread conifers. Yet its geographic range is only a remnant of its former extent (Axelrod, 1976), and it survives in a very small part of the total environmental space occupied by western forests. *Chamaecyparis lawsoniana* is apparently restricted by different environmental dimensions than are the widespread northwestern conifers.

In summary, water seems to be particularly important in restricting *Chamaecyparis lawsoniana.* Its limits are probably not dependent on a direct effect of temperature. Soil type appears to control growth directly, and to control importance through the vigor of species which compete with *Chamaecyparis* for water.

Autecological studies on our sites should help to confirm (or discount) our hypotheses, clarify the relative importance of various environmental factors, and indicate what autecological processes these factors are affecting. However, the conditions we report may not be the critical limiting factors, which could occur as infrequent extremes. Furthermore, it is difficult to determine where the species is absent due to lack of seed source. Even so, the hypotheses we present seem logical and, until the effects of extremes are reported, are the most likely explanations we can develop.

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