Coquille Falls RNA

BOT. GAZ. **144**(1):92–103. 1983.
© 1983 by The University of Chicago. All rights reserved.
0006-8071/83/4401-0012$02.00

TWIG ELONGATION PATTERNS OF CHAMAECYPARIS LAWSONIANA

DONALD B. ZOBEL

Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331

Twig elongation was measured during two growing seasons for 12 native populations of saplings of *Chamaecyparis lawsoniana* and for co-occurring saplings of *Pseudotsuga menziesii, Tsuga heterophylla,* or *Abies concolor* at some sites. Growth of lateral branches of *C. lawsoniana* was always early, and sometimes completed more quickly, on the hot and open sites but was always late and brief on the colder ones; moderate coastal sites had more prolonged elongation centered in midsummer. The rate of growth increased with the rise in daytime air temperature in the spring, with populations at cold sites responding most to rising temperature. Rates of growth after the peak were not related to temperature. Early growth cessation of populations in open, hot sites occurred despite their high predawn water potentials. Twig elongation of Pinaceae associated with *C. lawsoniana* was of shorter duration than for *Chamaecyparis. Pseudotsuga* in the mixed-evergreen zone was more responsive to temperature than was *C. lawsoniana.* Phenology of rooted cuttings of four populations of *C. lawsoniana* grown in a garden varied much less than did saplings studied in the field; no phenological differences were significant. Genetic variability of phenology of *C. lawsoniana* is smaller than that of competing Pinaceae. Its phenological pattern appears to be important in restricting *C. lawsoniana* to sites with dependable summer moisture and perhaps in determining its northern range limit.

Introduction

Chamaecyparis lawsoniana (A. Murr.) Parl., Port-Orford-cedar (Cupressaceae), has a limited range in southwestern Oregon and northwestern California. Within its small distribution, this tree appears to be ecologically quite versatile, growing in many plant communities on several soil types over a wide range of elevation (ZOBEL, in press). Temperatures vary greatly within its range (ZOBEL and HAWK 1980), from high summer maxima and a large diurnal range to little daily range and a muted annual cycle; high elevation areas have short growing seasons with winter snowpack. To occupy such diverse environments, *C. lawsoniana* probably must vary its phenology.

Timing of shoot elongation varies considerably among different conifer species on the same site in the Pacific Northwest and also varies among native populations of the same species (BUCKLAND 1956; WALTERS and SOOS 1963; WILLIAMS 1968; ZOBEL 1975). Species of Pinaceae which grow with *C. lawsoniana* have been extensively studied in culture (CAMPBELL and SORENSEN 1973, 1978; CAMPBELL 1974; NIENSTAEDT 1974; CAMPBELL and SUGANO 1975, 1979; POLLARD, TEICH, and LOGAN 1975; CANNELL, THOMPSON, and LINES 1976; CANNELL and WILLETT 1976; EMMINGHAM 1977; WHITE, CHING, and WALTERS 1979; KUSER and CHING 1980; REHFELDT and WYKOFF 1981). Their phenology and the way it changes with environment vary genetically among populations in relation to latitude, distance from the coast, and native climate and vary with the conditions in which the experiment was conducted. Twig phenology varies in a pattern similar to frost resistance and contributes to avoidance of frost damage. Other patterns of phenological variation in these Pinaceae have also been interpreted as having adaptive value.

Information about twig elongation of *C. lawsoniana* is scanty, apparently limited to a survey of many conifers in England (MITCHELL 1965). Its anatomy and the relative timing of events in the apical meristem were described briefly by AL-SHERIFI (1952), and twig development was studied by ROUANE (1973, 1979). Variation in vegetative phenology among populations of *Chamaecyparis* spp. has not been described. Genetic variation of phenology or factors controlling vegetative phenology appear not to have been studied for any member of the Cupressaceae.

A basic difference between *C. lawsoniana* and most of its competitors is, as in all Cupressaceae, the lack of bud scales (AL-SHERIFI 1952; DE LAUBENFELS 1953) with no preformation of next year's shoot; the season of cell formation coincides with that of cell enlargement (AL-SHERIFI 1952), as in *C. nootkatensis* (OWENS and MOLDER 1974). Whereas the growth of preformed shoots of mature Pinaceae depends considerably on the environment of the previous growing season (KOZLOWSKI 1971), twig elongation of *Chamaecyparis* probably does not. Twig expansion of Cupressaceae takes longer than that of associated Pinaceae (WALTERS and SOOS 1963; MITCHELL 1965; WILLIAMS 1968). Twig elongation and leaf expansion of Pinaceae do not coincide precisely; in contrast, elongation of the leaf-sheathed twig of *Chamaecyparis* closely reflects the display of new leaves.

I describe the variability in growth pattern of native saplings of *C. lawsoniana* and major competing conifers on a variety of sites and relate this

Manuscript received March 1982; revised manuscript received October 1982.

to the site environment. In addition, phenology of rooted cuttings from several sources in a common environment is described to help establish the degree to which variation observed in the field is genetically based.

Methods

Native populations

Twig elongation was measured on several trees in 12 populations at 10 sites (fig. 1, table 1). All trees grew in understory conditions, except at Coos County Forest, where the trees measured were on disturbed soil in the open. Most sample trees were 1.5–3 m tall, some up to several meters. On each sample tree, three healthy lateral branches were chosen; the terminal was also measured, except on trees which were too tall or lacked an obvious leader (mostly *Tsuga heterophylla*). Each branch was marked with acrylic paint several centimeters behind its terminus. The distance from the paint mark to the end of the longest branchlet beyond it was measured to the nearest millimeter approximately monthly, from early spring until fall. At high elevation stands, access was not possible until after growth started in 1975. Where the 1975 growth was satisfactory, the same branches were reused. Data from branches with less than 20 mm growth were used only for the slowest growing sites. Pinaceae were measured similarly. Trees were remeasured in September 1977 and October 1978 (six populations) to determine total elongation for those years.

Thermographs recorded air temperature at 1 m and soil temperature at −20 cm in the habitat of the saplings at 10 sites. Xylem pressure potential was measured at least once late each season (and several times at some sites) on trees of similar size in the same stands, using a pressure chamber. Percentage of "full light" had been determined on many saplings per site (Zobel and Hawk 1980). Ages of trees of similar size (table 1) were determined by counting stem cross sections at the soil surface (Hawk and Zobel, unpublished data).

Common environment study

Branches were collected in summer 1974 from several trees in four populations of *Chamaecyparis lawsoniana* (fig. 1, table 2). They were rooted on a mist bench until May 1975 and transplanted to potting soil in the greenhouse until the experiment began in March 1976. Four replications of all populations were planted outside in plant beds, with the potting soil and root mass undisturbed, but the pot was removed. The 12 plants per replication were placed in three rows, each row containing one plant of each source, with sources in random order. All plants were watered regularly. Unseasonal cold just after transplanting caused discoloration of the top surface of some foliage, but all plants and most branches recovered.

Elongation of the terminal and two lateral branches of each plant was measured in the same manner as for field saplings, from March 17 to October 26, 1976, approximately every 2 wk. The same plants were remeasured from March 29 to November 13, 1978.

Data analysis

Each length measurement was converted to the percentage of that year's total growth of that twig. Dates were converted to year day: January 1 = 1, June 1 = 152, September 1 = 244.

Data from lateral and terminal twigs were analyzed separately. For lateral twigs, an equation was computed for each tree, and site averages were computed from individual tree values. For terminals, with only one sample per tree, one equation was computed for each site. Data for a given tree (or site, for terminals) for 1 yr were summarized by calculating an empirical logistic relationship between percentage of growth completed and time: $P = 100/(1 + e^{a+bx})$, where P = percentage of growth completed, a and b = coefficients calculated for each case, and x = year day of the observation. Each tree was characterized for a given year by (1) the value of coefficient b, a more negative value reflecting a faster relative rate of elongation, i.e., a shorter period required for development; and (2) X_{50}, the date at which the equation indicates that elongation is half completed, expressing the timing of elongation. In the text and tables, the value of coefficient b will be referred to as "duration of elongation" and X_{50}, as "earliness." To check the assumption that the data fitted a logistic curve, the estimated percentage of growth was compared with actual growth on a given date for several of the data sets.

All statistical tests were made at the .05 significance level. Significance of differences among several sites or sources of cuttings was tested by analysis of variance. When overall site differences were significant, differences among individual sites were tested with Duncan's new multiple-range test. Differences between years for the same trees were tested using a paired t-test. Least-squares regressions were used to relate growth parameters to each other and to temperature variables.

Results

Native populations

Timing of growth of lateral branches.—Duration and earliness of elongation of *Chamaecyparis* varied considerably among populations (fig. 2, table 3). Elongation continued during much of the growing season and appeared to be approximately a linear function of time during the middle part of the season.

Analysis of variance showed highly significant variation among sites in both years for both duration and earliness (table 3). In 1975, saplings from sites in the *Tsuga heterophylla* zone and denser mixed-evergreen zone forests grew for a longer period (less negative *b* coefficients) than those from the open mixed-evergreen sites and the *Abies concolor* zone. In 1976, duration of elongation was less distinctly different; trees in the *A. concolor* zone again grew most briefly, but the order among lower elevation sites differed from 1975, with saplings from open mixed-evergreen forests growing for as long or longer than those in the more dense forests. In both years, growth was earliest at Kerby and latest in the *A. concolor* zone and the dense forest at Agness Pass.

Differences between years varied with site. When the same trees were compared, elongation at Agness Pass, the mixed-pine community at Pine Point, Kerby, and Grayback lasted longer in 1976

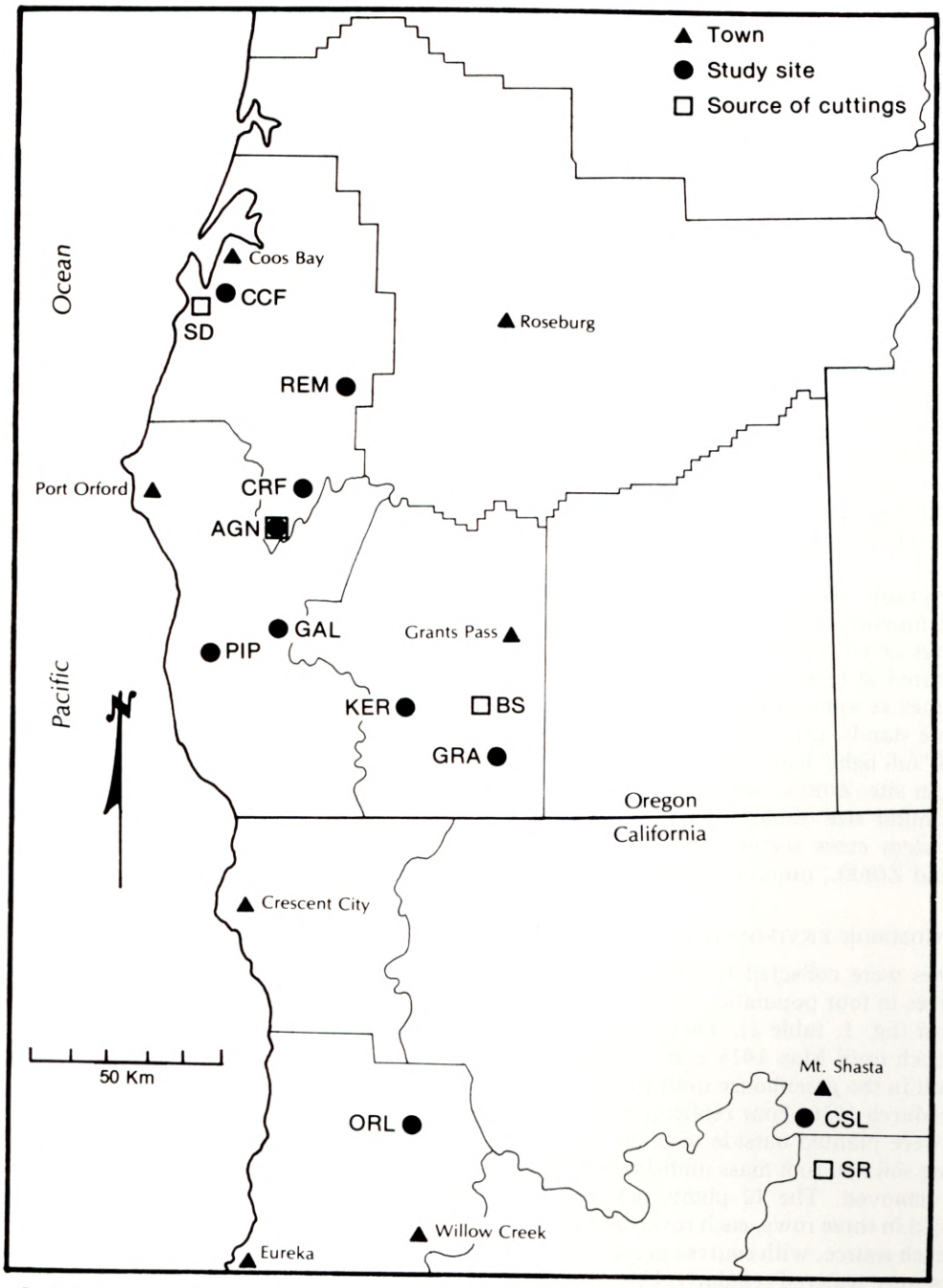

FIG. 1.—Locations of study sites and of sources of rooted cuttings. See tables 1 and 2 for abbreviations and description.

TABLE 1

SITE CHARACTERISTICS OF FIELD PLOTS

SITE	ABBREVIATION	VEGETATION ZONE	COMMUNITY	ELEVATION (m)	AIR TEMPERATURE (°C) May Mean	May Daily range	July Mean	July Daily range	UNDERSTORY LIGHT (%)	STAND AGE (yr)	MEAN AGE OF 2-m SAPLING (yr)	YEARS OF MEASUREMENT 1975	1976	OTHER SPECIES SAMPLED	No. *Chamaecyparis* BRANCHES SAMPLED (lateral/terminal)
Coos County Forest...	CCF	Pisi	Sandstone	70	10.1	8.3	13.3	8.1	(Open)	...	7	[a]	X	Psme	15/5
Remote.....	REM	Tshe	Swordfern	500	9.4	8.5	13.7	8.9	.6	100	23	X	X	Tshe	6/0
Coquille River Falls ..	CRF	Tshe	Swordfern	520	10.2	11.4	14.6	13.2	.7	450+	23	X	X	Tshe	14/5
Agness Pass.....	AGN	ME	Mixed pine	900	...	...	...	...	39.3	180	39	[a]	X	Psme	13/4
	AGN	ME	Tanoak	850	8.4	13.8	14.5	15.9	9.9	110	47	X	X	Psme	15/4
Pine Point	PIP	ME	Mixed pine	580	...	...	...	...	35.1	150	39	X	X	Psme	15/5
	PIP	ME	Tanoak	620	11.3	11.2	14.4	11.7	2.9	230	47	X	X	...	12/3
Orleans.....	ORL	ME	Tanoak	830	8.7	11.5	16.2	11.4	1.5	370	47	[a]	X	...	17/5
Kerby	KER	ME	Mixed pine	360	14.7	21.8	21.6	24.4	42.0	300	39	X	X	Psme	15/4
Game Lake	GAL	Abco	White fir	1,280	...	...	14.2	9.9	2.0	170	44	X	X	...	18/5
Castle Lake.....	CSL	Abco	White fir	1,520	5.6	15.7	13.8	17.2	2.6	300+	44	[a]	X	...	16/4
Grayback.....	GRA	Abco	Mixed fir	1,420	6.8	9.8	13.8	8.7	5.5	450+	41	[a]	X	Abco	17/6

NOTE.—Zones are according to FRANKLIN and DYRNESS (1973), communities to HAWK (1977). Temperature and light data were collected as described by ZOBEL and HAWK (1980). Age of 2-m saplings is from a regression line for the community (HAWK and ZOBEL, unpublished data). Abbreviations are: Pisi = *Picae sitchensis*, Tshe = *Tsuga heterophylla*, ME = mixed evergreen, Abco = *Abies concolor*, Psme = *Pseudotsuga menziesii*.

[a] Sampled partial year only.

TABLE 2

SITE CHARACTERISTICS AT THE SOURCES OF ROOTED CUTTINGS

SITE	ABBREVIATION	ELEVATION (m)	VEGETATION ZONE	MEAN TEMPERATURE[a] (°C)		
				Annual	May	July
Seven Devils	SD	140	Pisi	11.2	11.6	14.6
Agness Pass	AGN	850	ME	6.9	8.4	14.5
Brewer Spruce Research Natural Area	BS	1,300	Abco	7.2	8.0	15.0
Sacramento River	SR	580	ME	12.2	16.5	25.3

NOTE.—See table 1 for zone abbreviations and fig. 1 for locations.

[a] Weather Bureau data for Seven Devils are from Bandon and North Bend, Oreg.; for Sacramento River, from Mount Shasta and Shasta Dam, Calif. Data for Brewer Spruce are estimated from data at Grayback (table 1).

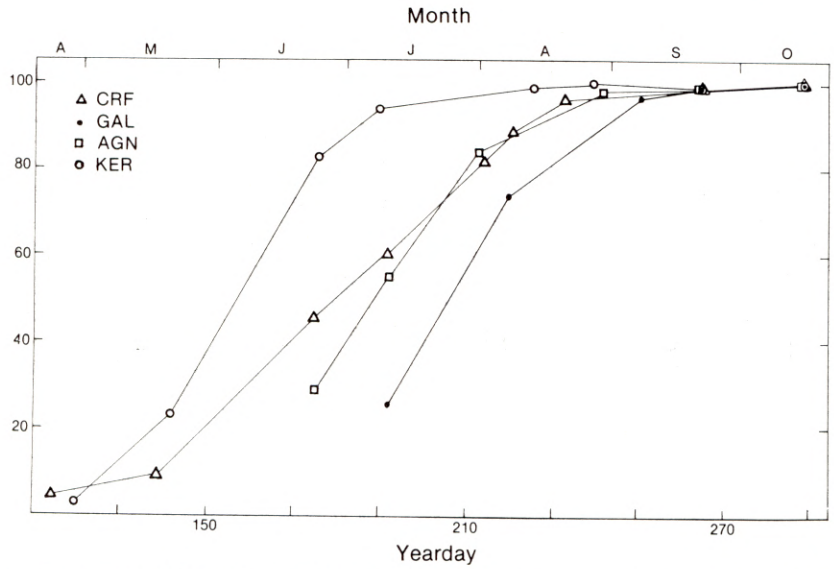

FIG. 2.—Cumulative percentage of elongation in 1975 of lateral branches of four populations, illustrating differences in duration and earliness of elongation. See table 1 for site abbreviations.

TABLE 3

DURATION OF ELONGATION[a] AND EARLINESS OF ELONGATION[b] FOR NATURAL SAPLINGS OF CHAMAECYPARIS

SITE	ZONE[c]	DURATION		EARLINESS	
		1975	1976	1975	1976
Coos County Forest[d]	Pisi	. . .	−.0538abc	. . .	164a
Remote	Tshe	−.0559a	−.0612bcd	184bc	179b
Coquille River Falls	Tshe	−.0489a	−.0533abc	179b	184bcd
Agness Pass	ME	−.0632ab	−.0522ab	188c	195ef
Pine Point	ME	−.0541a	−.0538abc	177b	185bcd
Orleans	ME	−.0625ab	−.0544bcd	181b	181bc
Kerby[e]	ME	−.0761bc	−.0531abc	155a	162a
Agness Pass[e]	ME	. . .	−.0535abc	. . .	188cde
Pine Point[e]	ME	−.0658bc	−.0489a	169a	186bcd
Game Lake	Abco	−.0817cd	−.0616bcd	205d	198f
Castle Lake	Abco	. . .	−.0636d	. . .	191def
Grayback	Abco	−.0973d	−.0622cd	202d	196f

NOTE.—A more negative value of *b* indicates a briefer period of elongation. Items in the same column with the same letter are not significantly different from each other.

[a] Expressed by the average value of *b*.

[b] Expressed by the year day at which growth was half completed.

[c] For key to abbreviations, see table 1.

[d] Open-grown saplings. Others are in natural forest.

[e] Mixed-pine community. Other populations in this zone are in the Tanoak community, with a dense canopy.

than in 1975. Growth was later in 1976 at Coquille River Falls, Agness Pass, and the mixed-pine community at Pine Point, and earlier at Grayback.

Correlations between duration and earliness of growth of individual trees within sites were usually low, although the fastest trees grew significantly earlier at two sites in the mixed-evergreen zone in 1976. Duration and earliness of growth did not vary consistently among sites (r = .42 and .48 for the 2 yr, both nonsignificant). Even the sign of the correlation between duration and earliness of elongation was not consistent within sites, vegetation zones, or years.

The logistic equation used to calculate duration and earliness of elongation fitted the data well. The correlation between actual values of growth on a sample day and that predicted from the logistic equation varied from .990 to .996 for five sites for which it was computed.

AMOUNT OF GROWTH.—Total annual lateral twig elongation of *Chamaecyparis* varied significantly among sites (table 4). At some sites, trees consistently grew much (Pine Point [mixed pine], Grayback), and at others, little (Kerby, Castle Lake). The relative elongation at some sites varied considerably among years (Game Lake). Sites with much twig elongation occurred in all zones, and there were no overall significant differences among zones. Trees in the open at Coos County Forest grew much more than those in natural forest elsewhere but less than interspersed *Pseudotsuga* (table 4).

The total annual elongation was not correlated with either duration or earliness of growth; i.e., trees on sites with the most growth were neither consistently late nor early, nor did they generally use a longer or shorter part of the growing season than did those trees on sites with less growth.

GROWTH OF TERMINAL SHOOTS.—Duration and earliness of elongation did not differ significantly between lateral branches and terminal shoots from the same sites. Total elongation of terminals varied more within sites than it did for laterals, and differences among sites (table 4) were not significant. There was no significant overall difference between total elongation of laterals and terminals on the same site when compared over the 34 site-by-year combinations for which data were available for understory populations.

RELATIONSHIP WITH MEAN ANNUAL TEMPERATURE.—In both years, elongation was earlier at sites with higher mean annual temperature (fig. 3). The relationship of duration of elongation to mean temperature was not consistent from year to year; in 1975, hottest and coldest sites elongated for the shortest time, but there was little difference in 1976. Total elongation was small at the hottest and coldest sites but otherwise was quite variable and not well correlated with mean annual temperature (r^2 of .22).

RELATIONSHIPS WITH CONCURRENT ENVIRONMENT.—Growth accelerated with increasing temperatures. The increase in average percentage of elongation per day for a measurement period was correlated with the increase in mean day temperature during the period (fig. 4), until the peak rate was reached. Mean day temperature had a higher correlation with elongation than did mean night temperature or a temperature growth index which incorporates both soil and daytime air temperature (CLEARY and WARING 1969). In some cases, decreases in mean day temperatures were associated with a lower rate of growth during a period; in others, growth rate was not lower during cold periods, including the three points which are badly out of line on figure 4. Linear regressions relating percentage of growth per day to mean day temperature were highly significant for all zones (table 5). The effect of a given temperature change on increasing growth of *Abies* zone trees ("slope" in table 5) was significantly greater than that in the other zones. The intercept value for the regression equation did not differ significantly among zones.

Mixed-evergreen zone trees reached moderate to high growth rates at higher temperatures than *Tsuga* zone trees, while *Abies* zone trees usually reached comparable rates at lower temperatures (fig. 4). There was almost no growth during periods with mean day temperature below 5 C (fig. 4). However, the temperature for zero growth, extrapolated from regression lines, is lower for the *Tsuga* zone than for other zones (table 5). Trees at Kerby reacted just as others in its zone; early growth there appeared to be entirely due to the earlier rise of temperature (ZOBEL and HAWK 1980) and not to a different reaction of the population to temperature. The decline in periodic growth rate after its maximum was not correlated with temperature; in most trees, growth rates dropped while temperature was still rising.

Soil temperature had no obvious relationship with timing of growth initiation. Growth occurred with average soil temperature as low as 3–4 C at sites in all zones, although at some sites the soil never was that cold. Soil temperature at first growth at Kerby was 8–9 C, and at Coos County Forest, Orleans, and Pine Point it was 6–7 C.

No soil-induced low water potentials correlated with the different growth regimes described here. Xylem pressure potentials measured in 1975–1976 were not very severe (ZOBEL and HAWK 1980) and were lowest when growth was almost complete. Predawn values were -10 bars or less only at the mixed-pine community at Agness Pass in 1975. At Kerby, growth stopped very early, and a decrease in soil moisture at this hot site might seem a logical cause; however, in seven measurements over 3 yr, predawn xylem pressure potentials never averaged drier than -8 bars (ZOBEL and HAWK 1980). However, midday plant water potential became more

TABLE 4

TOTAL ELONGATION (mm) OF TWIGS SAMPLED IN EACH POPULATION BY YEAR

	CHAMAECYPARIS						OTHER SPECIES				
	Laterals				Terminals		Laterals				
SITE	1975	1976	1977	1978	1975	1976	Species	1975	1976	1977	1978
Coos County Forest[a]	. . .	159	154		. . .	432	Psme[b]	. . .	272	250	204
Remote	52a	54b	40bcd	. . .	. . .	16	Tshe	41	65	69	. . .
Coquille River Falls	32bc	43bcd	53ab	. . .	28	28	Tshe	38	40	39	39
Agness Pass	23cd	37cde	32cd	47bc	16	30	Psme	. . .	33	35	43
Pine Point	28bcd	41bcde	41bc	40c	19	36	. . .	. . .	. . .	. . .	. . .
Orleans	37b	48bc	42bcd	65ab	24	43	. . .	. . .	. . .	. . .	. . .
Kerby[c]	29bc	29de	26de	. . .	38	31	Psme	39	32	47	43
Agness Pass[c]	. . .	32de	16e	32c	. . .	24	Psme	. . .	40	47	45
Pine Point[c]	38b	72a	51ab	36c	39	62	Psme	32	38	49	57
Game Lake	19d	49bc	56ab	82a	13	39	. . .	. . .	. . .	. . .	. . .
Castle Lake	. . .	26e	28de	. . .	. . .	19	. . .	. . .	. . .	. . .	. . .
Grayback	37b	52bc	64a	. . .	27	47	Abco	42	64	61	. . .
Tshe[b] Zone mean	42.0	48.5	46.5	. . .	. . .	22.0	. . .	. . .	. . .	. . .	. . .
ME Zone mean	31.2	43.2	34.7	51.0	27.2	37.7	. . .	. . .	. . .	. . .	. . .
Abco Zone mean	28.0	42.3	49.3	. . .	. . .	35.0	. . .	. . .	. . .	. . .	. . .

NOTE.—Means in the same column with the same letter are not significantly different.

[a] Trees in the open; data excluded from means and statistical tests.

[b] See table 1 for abbreviations.

[c] Populations in the open mixed-pine community.

severe than −15 bars at Kerby by mid-July in 1975 and may have influenced growth termination at the open, less humid sites.

GROWTH OF ASSOCIATED PINACEAE.—Although only some phenological differences between Pinaceae and *Chamaecyparis* were significant (table 6), Pinaceae almost always grew for a shorter period than the cedar, and *Pseudotsuga* and *Abies* grew earlier than cedar. In contrast, cedar reached 50% elongation earlier than *Tsuga*. Among the Pinaceae, as for cedar, there was no consistent relationship between earliness and duration of elongation of single trees within a site.

Tsuga reacted to rising air temperature similarly

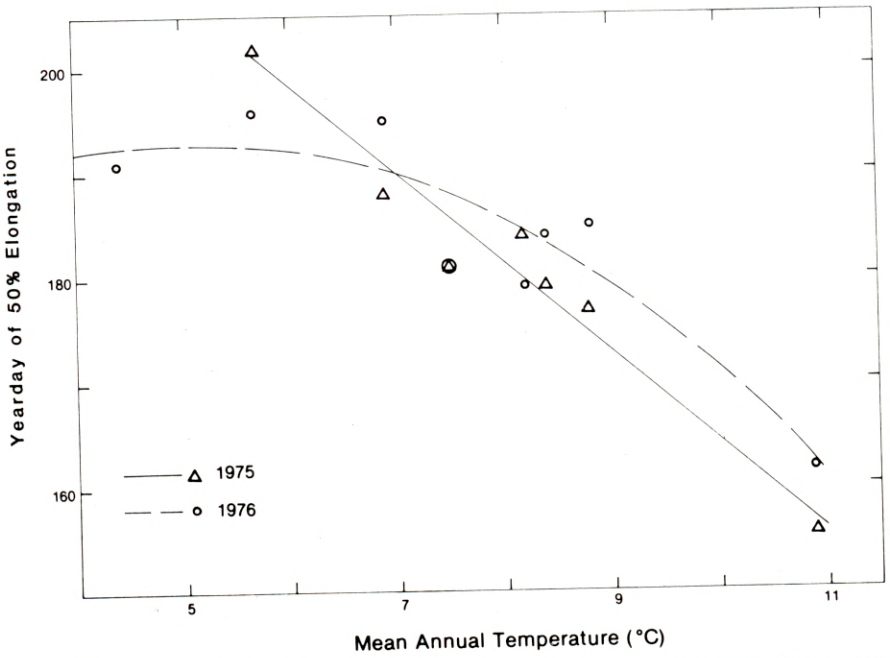

FIG. 3.—The relationship of earliness of growth (X_{50}) to mean annual temperature (MAT) at field sites. *1975:* $X_{50} = 248.8 - 8.43$ (MAT); no. = 7, $r^2 = .90$. *1976:* $X_{50} = 170.1 + 9.16$ (MAT) $- 0.91$ (MAT)^2; no. = 8, $r^2 = .84$.

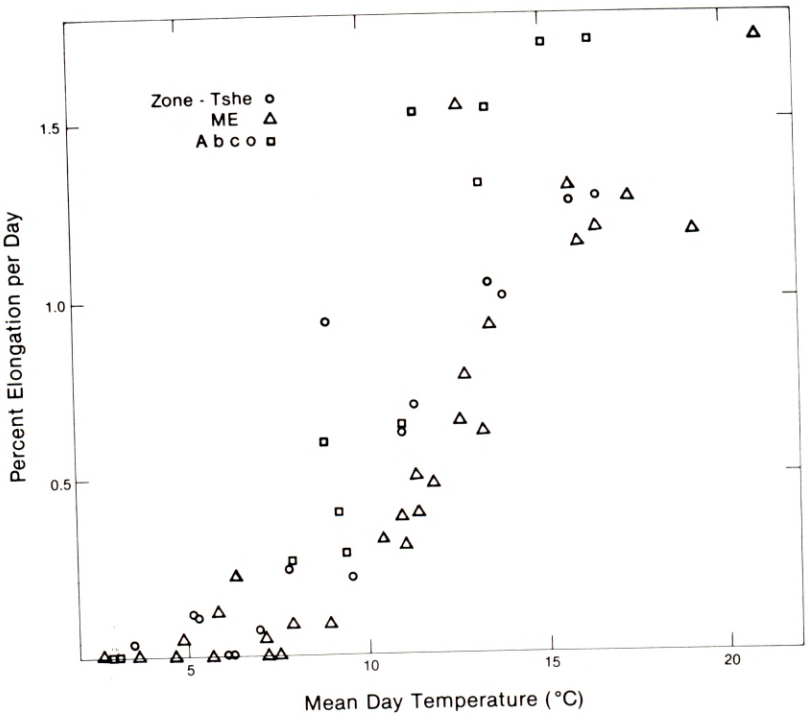

FIG. 4.—Relationship between percentage of elongation of lateral branches of *Chamaecyparis* per day during a sampling period and the mean daytime temperature during that period. Data are only for those periods before and including peak elongation. Rates of later periods show little relationship to temperature. Characteristics of linear regressions for these data are given in table 5.

to *Chamaecyparis* but was less closely related to temperature (table 5). Growth of *Pseudotsuga* in the mixed-evergreen zone started at a higher temperature but increased more rapidly than that of *Chamaecyparis* as temperature rose (table 5).

Common environment study

Analysis of variance indicated that in 1976 neither duration nor earliness of elongation varied significantly among the four sources of cuttings (table 7). Growth in 1978 slowed drastically in midseason and later accelerated again, a pattern different from that assumed by the model used to calculate values for duration and earliness for 1976. However, since measurements were made once every 2 wk, the actual date of 50% growth could be estimated accurately, and duration of growth was estimated by the number of days required for growth from 5% to 95% (table 7). Again, sources did not differ significantly in either attribute.

Total growth of sources differed in 1976, the coastal source growing most and the high elevation, least (table 7). Sources were not significantly different in 1978. Within the plant bed, duration of elongation of individual trees was not significantly correlated with earliness, except for the Seven Devils trees, for which slower growing trees reached 50% elongation earlier. Total growth was seldom related significantly to duration or earliness in comparisons among sources or among trees within

TABLE 5

Relationship of average elongation rate (% of length per day) for a site with average day temperature (°C) for that site, for all periods before and including the peak elongation rate

Zone and species	No. periods with data	Intercept (A)	Slope (B)	r^2	Temperature at time of growth initiation (°C)
Tsuga heterophylla:					
Chamaecyparis	12	−.487	.108	.84	4.5
Tsuga	13	−.560	.116	.37	4.8
Mixed evergreen:					
Chamaecyparis	25	−.715	.114	.82	6.2
Pseudotsuga	9	−1.271	.171	.88	7.4
Abies concolor:					
Chamaecyparis	12	−1.180	.194	.74	6.1

Note.—Regressions were calculated only for periods with nonzero elongation; all were significant. Elongation rate = $A + B$ (mean temperature).

TABLE 6

Duration and earliness of elongation for Pinaceae measured in field plots

Species and site	Duration		Earliness	
	1975	1976	1975	1976
Tsuga heterophylla:				
Remote	−.0735N	−.0808N	190N	184N
Coquille River Falls	−.0861S	−.0825S	190L	193L
Pseudotsuga menziesii:				
Coos County Forest	. . .	−.0707S	. . .	161N
Agness Pass	−.0843N	−.0558N	175N	180E
Kerby[a]	−.0863N	−.0701S	154N	147E
Agness Pass[a]	. . .	−.0555N	. . .	173N
Pine Point[a]	−.0761S	−.0488N	176L	169E
Abies concolor:				
Grayback	−.0819N	−.1024S	183E	184E

Note.—Letters indicate which values differ significantly from those of *Chamaecyparis* at the same site: S = shorter duration of growth (more negative b value) for the Pinaceae, E = Pinaceae earlier, L = later, N = no significant difference.

[a] Populations in the mixed-pine community.

sources. Total growth of terminal shoots varied similarly to laterals, both among sources in 1976 and by showing no significant differences in 1978.

Discussion

Elongation of *Chamaecyparis lawsoniana* takes longer than that of associated Pinaceae, both in the forest and in cultivation (MITCHELL 1965). The same holds for *Thuja plicata* (Cupressaceae) (BUCKLAND 1956; WALTERS and SOOS 1963; WILLIAMS 1968). Environment during the current growing season probably affects both initiation and enlargement of stem units of *Chamaecyparis;* in most mature conifers, initiation occurs in the bud during the previous growing season and is affected by the environment at that time, whereas enlargement occurs during the current season. Cell division inside conifer buds responds to environment (CANNELL et al. 1976) and may be more sensitive than is elongation of the resulting shoot (BAXTER and CANNELL 1978). The apex of *Chamaecyparis,* without bud scales, is probably even more sensitive. The protection of a bud apparently allows apices to initiate new stem units in a wider range of environmental conditions than an unprotected meristem could (CANNELL et al. 1976), suggesting that *Chamaecyparis* has a lower potential for elongation than associated Pinaceae.

Twigs of Pinaceae usually elongated for a shorter period than native *Chamaecyparis,* although the difference was significant in only six of 14 comparisons. *Tsuga* grew at the same time or later, and the other species at the same time or earlier than did *Chamaecyparis*. Deployment of new foliage of these Pinaceae is further accelerated because their leaves expand as a brush, reaching a large size before the twig itself elongates much.

Timing of conifer twig elongation responds to spring temperature, winter chilling, photoperiod, and water relations (WORRALL 1973; NIENSTAEDT 1974; CANNELL et al. 1976). Air temperature seems to be the primary factor inducing growth of most species. Soil temperature is suggested to be important for *Pseudotsuga* (EMMINGHAM 1977), but other factors probably are more important in delaying the start of growth (CAMPBELL and SORENSEN 1978). Photoperiod probably has a minimal effect in the spring if chilling has been adequate (NIENSTAEDT 1974; CAMPBELL and SUGANO 1979). The delay of elongation of *Chamaecyparis* in the *Abies* zone is probably due to low air temperatures. However, the effect of air temperature on increasing rates of growth (fig. 4, table 5) is suspect, once growth begins to accelerate rapidly. A linear increase with time during rapid elongation and the failure of some rather cool periods to prevent further growth acceleration (fig. 4) suggest that temperature may have little control once growth becomes rapid. Variable soil temperature associated with growth initiation makes it unlikely that *C. lawsoniana* responds to rising soil temperature. Although short photoperiod stops indeterminate shoot elongation of young seedlings of Pinaceae (HEIDE 1974*a,* 1974*b;* POLLARD et al. 1975; CANNELL et al. 1976), VAARTAJA (1957) found no photoperiod response for *Thuja plicata*. My results suggest that photoperiod does not control elongation of *C. lawsoniana*.

Comparisons of *Chamaecyparis* response to environment with that of first-year seedlings of Pinaceae, with indeterminate growth (CANNELL et al. 1976), may be more valid than comparison with older trees. Environmental control of growth of such juveniles also may differ from that of older seedlings (HEIDE 1974*b;* LOGAN and POLLARD 1975; POLLARD et al. 1975).

For *C. lawsoniana,* the amount of elongation could seldom be related to its duration or earliness. In contrast, final shoot length of most conifers is correlated with the rate of extension during midseason and to a lesser extent with its duration (WORRALL 1973; EMMINGHAM 1977; CAMPBELL and SORENSEN 1978), whereas indeterminate growth of young *Picea sitchensis* varies primarily with the duration of growth (POLLARD et al. 1975).

The variability of *Chamaecyparis* growth pat-

TABLE 7

MEAN VALUES FOR DURATION AND EARLINESS OF ELONGATION, AND TOTAL ELONGATION FOR LATERAL BRANCHES OF FOUR SOURCES OF ROOTED CUTTINGS GROWN IN CORVALLIS, OREGON, IN 1976 AND 1978

	1976			1978		
SOURCE	Duration (*b*-coefficient)	Earliness (year day)	Total (mm)	Duration (days)	Earliness (year day)	Total (mm)
Seven Devils.....	−.0520	207	130a	175	218	125a
Agness Pass.....	−.0540	211	86b	168	213	120a
Brewer Spruce	−.0565	209	50c	165	202	104a
Sacramento River	−.0592	211	81b	169	204	127a

NOTE.—For 1978, alternate estimates of speed and timing were used (see text). Neither duration nor earliness differed significantly among sources. Total = total elongation (mm). Values in the same column with different letters were significantly different.

terns in the field seems clearly adaptive. At the colder sites, growth was late and of limited duration; at Kerby, the hottest site, elongation was early, and in 1975, of short duration. Sites in the *Tsuga* and *Picea* zones have considerable fog and cloud, relatively high humidity, and temperatures that are relatively high in spring and fall but low all summer. At these sites, growth occurred over a longer period and reached its peak rate in midsummer.

Large differences among field populations and among seedlings transplanted to the greenhouse (PLOCHER 1977) suggested that populations of *C. lawsoniana* may differ genetically in their phenological response. However, phenological variation among cuttings from four contrasting habitats was small in 2 yr in a garden. Genetic variation in phenology of other conifers is apparently of considerable adaptive significance (CAMPBELL and SORENSEN 1973, 1978; CAMPBELL 1974; NIENSTAEDT 1974; EMMINGHAM 1977; WHITE et al. 1979). The genetic basis for the phenological repertoire of the widespread *Pseudotsuga* is especially complex (CAMPBELL and SUGANO 1979). Despite its morphological variability, expressed by its many horticultural varieties (DALLIMORE and JACKSON 1966), the genetic basis for phenology of *C. lawsoniana* seems relatively invariable.

Expression of genetic differences in phenology may depend on conditions of the test (CAMPBELL and SORENSEN 1978; CAMPBELL and SUGANO 1979); however, cuttings in this study grew as much in culture as did the best understory populations. While cuttings may have had incomplete chilling in 1976, they showed no differences in 1978 after two complete winters outside.

Its phenology probably contributes to the limited range of *C. lawsoniana*. Its usual requirement for a dependable, abundant water supply throughout the summer (HAWK 1977; ZOBEL and HAWK 1980) may be necessary to allow midsummer shoot production by its unprotected apex, its continual exposure of unhardened foliage, and its late seed germination (ZOBEL 1980). Also, reproductive structures, initiated in early summer and soon becoming exposed, continue to develop through the summer (ERSPAMER 1953; HASHIZUME 1973). Cellular development in unprotected small organs probably requires high plant water potentials.

Growth of *C. lawsoniana* is slower on most soils than that of *Pseudotsuga* (ZOBEL, in press), with which it must compete on most good sites. At the north end of its range, where *C. lawsoniana* grows best (and *Pseudotsuga* grows well on all soils), its prolonged shoot elongation may be necessary for the cedar to grow enough to compete. In this area, however, more northern coastal populations of *Pseudotsuga* and *Tsuga* inherently cease growth earlier and are more frost resistant (CAMPBELL and SORENSEN 1973; KUSER and CHING 1980), indicating that biologically important frost increases northward. A long growing season, perhaps necessary for *C. lawsoniana* to compete, may become impossible as one moves north.

Acknowledgments

I thank MILTON PLOCHER, JAMES THOMPSON, GLENN HAWK, SUSAN MASON, and KEITH REYNOLDS, who helped greatly in selecting sites and measuring trees. ROBERT CAMPBELL made useful suggestions about the manuscript. Financial support was primarily from National Science Foundation grants. Use of the Coquille River Falls and Brewer Spruce Research Natural Areas was with cooperation of the U.S. Department of Agriculture Forest Service and the Bureau of Land Management, respectively.

LITERATURE CITED

BAXTER, S. M., and M. G. R. CANNELL. 1978. Branch development on leaders of *Picea sitchensis*. Can. J. Forest Res. **8:**121–128.

BUCKLAND, D. C. 1956. Terminal shoot growth of four western conifers for a single growing season. Forestry Chron. **32:**397–399.

CAMPBELL, R. K. 1974. Use of phenology for examining provenance transfers in reforestation of Douglas-fir. J. Appl. Ecol. **11:**1069–1080.

CAMPBELL, R. K., and F. C. SORENSEN. 1973. Cold-acclimation in seedling Douglas-fir related to phenology and provenance. Ecology **54:**1148–1151.

———. 1978. Effect of test environment on expression of clines and on delimitation of seed zones in Douglas-fir. Theoret. Appl. Genet. **51:**233–246.

CAMPBELL, R. K., and A. I. SUGANO. 1975. Phenology of bud burst in Douglas-fir related to provenance, photoperiod, chilling, and flushing temperature. BOT. GAZ. **136:**290–298.

———. 1979. Genecology of bud-burst phenology in Douglas-fir: response to flushing temperature and chilling. BOT. GAZ. **140:**223–231.

CANNELL, M. G. R., S. THOMPSON, and R. LINES. 1976. An analysis of inherent differences in shoot growth within some north temperate conifers. Pages 173–205 *in* M. G. R. CANNELL and F. T. LAST, eds. Tree physiology and yield improvement. Academic Press, New York. 567 pp.

CANNELL, M. G. R., and S. C. WILLETT. 1976. Shoot growth phenology, dry matter distribution and root:shoot ratios of provenances of *Populus trichocarpa, Picea sitchensis* and *Pinus contorta* growing in Scotland. Silvae Genet. **25:**49–59.

CLEARY, B. D., and R. H. WARING. 1969. Temperature: collection of data and its analysis for the interpretation of plant growth and distribution. Can. J. Bot. **47:**167–173.

DALLIMORE, W., and A. B. JACKSON. 1966. A handbook of Coniferae and Ginkgoaceae. Revised by S. G. HARRISON. Edward Arnold, London. 729 pp.

DE LAUBENFELS, D. J. 1953. The external morphology of coniferous leaves. Phytomorphology **3:**1–20.

EMMINGHAM, W. H. 1977. Comparison of selected Douglas-fir seed sources for cambial and leader growth patterns in four western Oregon environments. Can. J. Forest Res. **7:**154–164.

ERSPAMER, J. L. 1953. Ontogeny and morphology of the microsporangia in certain genera of the Coniferales. Ph.D. diss.

University of California, Berkeley.

FRANKLIN, J. F., and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S. Dep. Agr. Forest Service Gen. Tech. Rep. PNW-8. 417 pp.

HASHIZUME, H. 1973. Studies on flower bud formation, flower sex differentiation, and their control in conifers. Bull. Tottori Univ. Forest. **7:**1–139. (English summary.)

HAWK, G. M. 1977. Comparative study of temperate *Chamaecyparis* forests. Ph.D. diss. Oregon State University, Corvallis.

HEIDE, O. M. 1974*a*. Growth and dormancy in Norway spruce ecotypes (*Picea abies*). I. Interaction of photoperiod and temperature. Physiol. Plantarum **30:**1–12.

———. 1974*b*. Growth and dormancy in Norway spruce ecotypes. II. After-effects of photoperiod and temperature on growth and development in subsequent years. Physiol. Plantarum **31:**131–139.

KOZLOWSKI, T. T. 1971. Growth and development of trees. Vol. **1.** Seed germination, ontogeny and shoot growth. Academic Press, New York. 443 pp.

KUSER, J. E., and K. K. CHING. 1980. Provenance variation in phenology and cold hardiness of western hemlock seedlings. Forest Sci. **26:**463–470.

LOGAN, K. T., and D. F. W. POLLARD. 1975. Mode of shoot growth in 12-year-old black spruce provenances. Can. J. Forest Res. **5:**539–540.

MITCHELL, A. F. 1965. The growth in early life of the leading shoot of some conifers. Forestry **38:**121–136.

NIENSTAEDT, H. 1974. Genetic variation in some phenological characteristics of forest trees. Pages 389–400 *in* H. LEITH, ed. Phenology and seasonality modeling. Springer, New York. 444 pp.

OWENS, J. N., and M. MOLDER. 1974. Cone initiation and development before dormancy in yellow cedar (*Chamaecyparis nootkatensis*). Can. J. Bot. **52:**2075–2084.

PLOCHER, M. D. 1977. Growth and nutrient content of *Chamaecyparis lawsoniana* seedlings from contrasting soils in Coos County, Oregon. Master's thesis. Oregon State University, Corvallis.

POLLARD, D. F. W., A. H. TEICH, and K. T. LOGAN. 1975. Seedling shoot and bud development in provenances of Sitka spruce, *Picea sitchensis* (Bong.). Carr. Can. J. Forest Res. **5:**18–25.

REHFELDT, G. E., and W. R. WYKOFF. 1981. Periodicity in shoot elongation among populations of *Pinus contorta* from the northern Rocky Mountains. Ann. Bot. **48:**371–377.

ROUANE, P. 1973. Etude comparée de la répartition des ramifications au cours de l'ontogenèse de quelques Cupressacées. Travaux Lab. Forest. Toulouse, tome 1, vol. **9,** art. 3. 277 pp.

———. 1979. Croissance des rameaux et différenciation chez *Chamaecyparis lawsoniana* (A. Murr.) Parl. (Cupressaceae). Bull. Soc. Bot. France **126:**133–137.

AL-SHERIFI, K. A. 1952. Histological studies on the shoot apices and leaves of certain Cupressaceae. Ph.D. diss. University of California, Berkeley.

VAARTAJA, O. 1957. Photoperiodic responses in seedlings of northern tree species. Can. J. Bot. **35:**133–138.

WALTERS, J., and J. SOOS. 1963. Shoot growth patterns of some British Columbia conifers. Forest Sci. **9:**73–85.

WHITE, T. L., K. K. CHING, and J. WALTERS. 1979. Effects of provenance, years and planting location on bud burst of Douglas-fir. Forest Sci. **25:**161–167.

WILLIAMS, C. B., JR. 1968. Seasonal height growth of upper-slope conifers. U.S. Dep. Agr. Forest Serv. Res. Paper PNW-62. 7 pp.

WORRALL, J. 1973. Seasonal, daily and hourly growth of height and radius in Norway spruce. Can. J. Forest Res. **3:**501–511.

ZOBEL, D. B. 1975. Local variation in intergrading *Abies grandis-Abies concolor* populations in the central Oregon Cascades. III. Timing of growth and stomatal characteristics in relation to environment. BOT. GAZ. **136:**63–71.

———. 1980. Effect of forest floor disturbance on seedling establishment of *Chamaecyparis lawsoniana*. Can. J. Forest Res. **10:**441–446.

———. In press. *Chamaecyparis lawsoniana,* Port-Orford-cedar. *In* Silvics of native and naturalized trees of the United States and Puerto Rico. Department of Agriculture, Forest Service, Washington, D.C.

ZOBEL, D. B., and G. M. HAWK. 1980. The environment of *Chamaecyparis lawsoniana*. Amer. Midland Natur. **103:**280–297.