AN ABSTRACT OF THE THESIS OF

JOHN ERDMANN KUSER for the DOCTOR OF PHILOSOPHY
(Name) (Degree)

in FOREST SCIENCE presented on May 2, 1980
(Major) (Date)

Title: PROVENANCE VARIATION IN WESTERN HEMLOCK (TSUGA HETEROPHYLLA (RAF.) SARG.) SEEDLINGS

Signature redacted for privacy.

Abstract approved: Kim K. Ching

A range-wide sample of 22[1] provenances of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) showed much variation in several characteristics. Variation in seed weight was significant, but not correlated with seed source latitude, elevation, or distance from the ocean. Variation in the frequency of 4-cotyledon seedlings was significant at regional, provenance, and family levels, with the greatest frequency occurring in a high-elevation Rocky Mountain population.

In an outdoor common-garden experiment at Corvallis, significant variation at both provenance and family levels occurred in bud-set and bud-burst dates and cold hardiness. In a growth chamber experiment, seedlings maintained in continuous growth for a three-month test period showed significant variation influenced both by environment (air and soil temperature) and seed source. Variation among provenances and between families within provenance was highly significant, with the latter averaging up to one-half the former for most responses.

[1]22 provenances were used in the study of seed weight, 20 in tests of phenology and cold hardiness, and 21 in tests of growth responses under controlled environments.

Seedlings of northern, high-elevation, or Rocky Mountain provenances set and burst bud earlier and survived early frost and winter cold better than seedlings of southern, low-elevation, or coastal provenances. The latter groups grew faster than the former on the average, but there were some conspicuous exceptions; growth responses were not as highly correlated with seed source latitude, elevation, or distance from the ocean as were phenological responses and cold hardiness. Coastal provenances showed strong north-south clines in phenological responses, cold hardiness, and growth responses.

Rocky Mountain hemlock populations appeared to differ from coastal populations in growth rate, shoot:root ratio, and frequency of 4-cotyledon seedlings.

Provenance Variation in Western Hemlock (*Tsuga heterophylla* (Raf.) Sarg.) Seedlings

by

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A Thesis

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed May 12, 1980

Commencement June 1980

ACKNOWLEDGMENTS

My most profound and sincere thanks to my wife, Eleanor, for her unfailing support and good humor during three years of work on this project.

My grateful thanks to my major professor, Dr. Kim Ching, for his knowledgeable advice on provenance work in forest genetics, his introductions to many people in this field in the Pacific Northwest, and his knowledge of how to get things done. My thanks also to Dr. Tom Adams, who substituted during Dr. Ching's absence and was instrumental in teaching me sequential steps of analysis. Grateful thanks to the other members of my committee, Dr. David Butler, Dr. Kenton Chambers, Dr. Denis Lavender, and Dr. Chester Youngberg.

I shall remain always deeply indebted to the people of the State of Oregon, who through Oregon State University assisted me with a Ching Scholarship and a graduate research assistantship which helped me to pursue this study.

My thanks to the members of the Western Hemlock Tree Improvement Committee of the Industrial Forestry Association who helped me with this study. In particular, to Dr. Donald Lester, of Crown Zellerbach, who provided seed of 2 provenances, made computer time available, and reviewed manuscripts; to Dr. Jess Daniels, of Weyerhaeuser, who made suggestions for the design of the study and provided seed of 4 provenances; and to Drs. Roger Timmis and Ken Chisholm, of Weyerhaeuser, who lent essential testing equipment. Thanks to Messrs. Phil Hahn, of Georgia-Pacific; Archie Selders, of ITT-Rayonier; Jack Wanek, of the Oregon State Forestry Department; and Troy Moore, of Publishers Paper, who all contributed seed. Thanks to Mr. Cal Carpenter, of the U.S.

Forest Service, who showed me Idaho hemlocks and collected cones of 2 provenances; to Mr. Jim Rydelius, of Simpson Timber, who showed me California hemlocks and later collected cones; and to Mr. Don Richardson, who showed me one of the southernmost natural stands of western hemlock and collected cones from it.

Special thanks to Dr. Michael Meagher, of the B. C. Forestry Service, who extended his hospitality on Vancouver Island, took me on a tour of the Duncan, B. C. container nursery and provided instructions on the latest methods of growing hemlock seedlings, and also seed of 4 provenances. Thanks to Mr. Al Harris, of the U. S. Forest Service, who sent seed of 2 Alaska provenances; and to Mr. Mel Parker, of St. Regis Paper, for seed. Grateful thanks to Mr. Don Oliver, of the U. S. Forest Service, who provided seed, supplies, and advice on growing hemlock, and allowed me to use his cone sacks, cone drying rack, cone tumbler, and seed cleaner.

Thanks to Dr. Robert K. Campbell, of the U. S. Forest Service, for his suggestions on the design of the study and his review of manuscripts. Thanks to Mr. Paul Arons and Ms. Sandy Beder, of Crown Zellerbach, and Mr. Dennis Muscato, Oregon State University, for help with computer analysis of data. And finally my thanks to my fellow doctoral student, Mr. (now Dr.) Tim White, who showed me how to do some things a little better.

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CHAPTER 1

INTRODUCTION

Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) has recently achieved long-deserved recognition as an important timber and pulp species. On about 2,000,000 hectares along the Pacific coast from Oregon to Alaska (McCullough 1977, Rottink 1977), hemlock out-yields Douglas-fir and produces nearly as valuable wood (Tustin 1977). For certain uses such as interior molding and paneling, and for pulp, hemlock is more desirable. It is more shade-tolerant than Douglas-fir, and can produce more m^3/ha/yr where conditions are suitable for it.

Because of belated acknowledgment of hemlock's importance, relatively few experiments have been done to determine its genecological patterns of variation. In Britain, Buszewicz and Holmes (1960) studied the relationship of seed size to latitude of origin of 14 provenances, and Lines and Mitchell (1969) compared heights of 18 provenances 10 years after planting on 16 different sites, finding an Alaska strain tallest in Scotland and a Leaburg, Oregon provenance tallest in England. In Canada, Meagher (1976) reported a study of seedlings of 17 British Columbia provenances from seed collected along a west-east transect from sea level to 1,500 m at about 49°N; he compared bud-set and bud-burst dates and growth of the seedlings. In the U. S., no planting trials or seedling studies have been reported. Irgens-Moller began a study of seedlings of 4 Canadian and 2 U. S. provenances in 1973 at Oregon State University, but never completed it. Sakai and Weiser

(1973) reported significant differences in cold tolerance of winter-cut twigs of 3 coastal provenances and 1 Rocky Mountain provenance.

Purpose of Study

It appeared that the first step toward gaining an understanding of genecological patterns of variation in such characteristics as growth rate and cold tolerance should be a range-wide study, extensive rather than intensive, to find the range of variation present in the species, the geographic patterns associated with it, and the amount of variation occurring within local populations. This idea was proposed to the members of the Western Hemlock Tree Improvement Committee of the Industrial Forestry Association (I. F. A.), who responded with enthusiasm for the project, ideas on what to investigate, and offers of seed. They suggested that growth rate and winter hardiness were the two most important traits requiring investigation within the commercial range of the species. It was known or suspected that southern hemlock provenances grew faster but were less hardy than northern provenances, and it was thought that provenances from high elevations in the Cascade Mountains had superior cold resistance. The I. F. A. members were familiar with provenance differences in Douglas-fir, and their own experience in growing hemlock had led them to believe that provenance variation in this species was generally analogous.

My interest in the species' variation and the extent to which it had been able to adapt itself to a wide range of environments indicated a study inclining slightly more toward probing the full scope of variation in the species, and slightly less toward in-depth study of local variation. Granted availability of a finite space in which a finite number of seedlings could be tested, our choices were to test 2 or 3 families from each of 20 to 25 provenances from throughout the range of western hemlock, or 10 families from each of 6 provenances in the Pacific Northwest. Eventually it was agreed that the whole species should be investigated, but that provenances in western Washington and Oregon would be sampled more intensively.

In summary, the purpose of the study was to develop useful information on comparative growth rates and cold hardiness of different western hemlock provenances, and estimate average amounts of variation in these traits present in local populations. This information can now serve as a basis for 1) further research on how far from the latitude and elevation of genetic origin western hemlock seedlings can be successfully moved, 2) deciding where to search for the most promising genetic material in terms of desired traits for each hemlock-growing area, and 3) further research to determine the full extent of variation present in specific provenances of interest.

Explanation of Format

This thesis follows a new format. It is structured around two publications, one already accepted and the other in final draft for submission. Chapter 2 consists of revised copy accepted by FOREST SCIENCE, and Chapter 3 is my final draft given to the Forest Research Laboratory editor for editing and submission to CANADIAN JOURNAL OF FOREST RESEARCH. Several photographs, text references to them, and references to appendices have been added here to the publication versions of these chapters for the sake of greater depth and completeness.

CHAPTER 2

Provenance Variation in Phenology and Cold Hardiness of Western Hemlock Seedlings[1]

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ABSTRACT. Seedlings from a range-wide sample of 20 western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] provenances showed much variation in phenology and cold hardiness at Corvallis, Oregon. Seedlings of northern, high-elevation, or Rocky Mountain provenances set and burst bud earlier and survived early frost and winter cold better than seedlings of southern, low-elevation, or coastal provenances. A strong north-south cline was found in the variation among coastal provenances. A sample of three families per provenance revealed four cases of marked intraprovenance variation, two in bud-set date and two in cold survival.

ADDITIONAL KEY WORDS. Bud burst, bud set, *Tsuga heterophylla*.

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[1]Accepted January 29 for publication by FOREST SCIENCE substantially as is. Figures 2, 3, 5, and 6, and text references to them, have been added here.

INTRODUCTION

Despite commercial importance of western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], few experiments have been done to determine its genecological patterns of variation in growth rate or cold tolerance. Comparing the suitability of 18 provenances for planting at 16 sites in Britain, Lines and Mitchell (1969) found the Leaburg, Oregon, strain superior for warmer or more sheltered sites but Juneau, Alaska, seedlings better in the north. Sakai and Weiser (1973), working with winter-cut twigs, reported differences in cold tolerance between one Rocky Mountain and three coastal provenances; and Meagher (1976) compared bud-set and bud-burst dates and cold tolerance of 17 provenances along a west-east transect from sea level to 1,500 m at about 49°N in British Columbia.

We undertook a range-wide provenance study of western hemlock to determine the extent of variation in cold tolerance and phenology within the species and compare intraprovenance with interprovenance variation. This seemed a logical first step toward establishing seed transfer rules for western hemlock. Our experiment also served as a preliminary screening preceding a series of planting trials to be conducted by the Western Hemlock Tree Improvement Committee of the Industrial Forestry Association (I.F.A.).

MATERIALS AND METHODS

Our provenance testing strategy was to sample (1) a latitudinal transect along the Pacific coast, to test for north-south differences; (2) high-elevation seed sources in the Cascade Mountains, to test for differences between these and lower sources; and (3) sources in the Rocky Mountains to test for differences due to lower precipitation and greater temperature extremes. Six sources were paired to compare bud set, bud burst, and cold survival for high _vs._ low elevations (No. 6 _vs._ 15, 8 _vs._ 16, and 18 _vs._ 19). We collected at closer intervals in commercial areas of the species' range between 41° and 53°N and wider intervals at range extremes and in disjunct areas. Although unable to obtain seed from the northern extreme at 61°, we did collect seed from 14 provenances in coastal areas between 38° and 59° and three provenances each in the Cascades and Rockies (Fig. 1, Table 1).

In October 1977, individual cone collections were made from three to 10 trees at least 400 m apart from each provenance. Seed was extracted and cleaned in December. In a few cases, fresh cones were not available, so stored seed identified by parent tree was obtained from I.F.A. cooperators.

Seed was sown at Corvallis, Oregon, in February 1978 in racks of 50-ml Leach tubes filled with a commercial 1:1 peat-vermiculite mix. Enough was sown to provide 40 seedlings of each family, three families per provenance (except No. 14, for which only mixed seed was available and No. 18, in which chalcids had destroyed the seed of one family). Two seeds per tube were placed on top of the mix, covered with 0.5 cm of No. 2 chicken grit, well watered, covered with clear plastic, and placed in the greenhouse. Ten days later, when germinants began to appear, the plastic was removed. After the first true leaves appeared and seedlings had been thinned to one per tube, soluble 20-19-18 fertilizer (2.5 g/l) was added to the water weekly. The pH of the nutrient solution was adjusted to 4.5 by addition of H_3PO_4. Every fourth week, the seedlings were watered with 0.001 M $FeSO_4$ instead of nutrient solution. Extra water was given as necessary.

In May, the seedlings were divided into four replicates of 10 seedlings per family, or about 550 seedlings each (allowing for mortality and missing families), and moved to a 50-percent shade house outdoors where they remained through the following winter. No supplementary light was provided. As soon as the first seedlings began to show signs of dormancy by slowing growth, turning dark green, and setting buds (Figure 2, Figure 3), we counted the seedlings in each family that had set terminal buds and calculated the percentage of bud set for each family on seven different dates (Appendix 4).

In late November, after a severe cold spell had damaged some seedlings of the two southernmost provenances, we counted the seedlings in each family which showed visible leaf and shoot-tip browning. On December 12, we examined the injured seedlings to determine extent of damage to leaves, buds, basal bark, and roots.

In January 1979, when the seedlings of remaining provenances were presumably at maximal hardiness, we tested two seedlings of each provenance at six different temperatures in a freezing chamber to determine the range of killing temperatures to use on larger lots. Starting at 0°C, we lowered the temperature by 5°C/h to a pre-set minimum, held it 2 h, then raised it by 20°C/h back to 0°C. After determining the range of killing temperatures, we ran trials on three of the four 550-seedling replicates in February, using minima of -17.5°C on one and -30°C on two. All treated seedlings were scored as alive or dead on May 14.

The fourth replicate, which served as a control, wintered in the lath house at ambient temperatures and was scored for survival in May. It was also used for spring bud-burst counting on three different dates. Bud burst was recorded by family within provenance.

Statistical Analysis.--Bud-set data for each family were converted by interpolation into 50-percent dates, and the dates for 54 families in 18 provenances were subjected to analysis of variance. Cold-survival percentage values were transformed to angles of equal information in degrees (Bliss 1937) for use in regression analysis. Bud-burst data were converted to 50-percent dates by provenance only because winter losses and availability of only one replicate had reduced seedling numbers too low for reliable estimation by family. Regressions of bud-set and bud-burst dates and cold survival values against latitude of origin were calculated for coastal provenances. Data for the high vs. low pairs were subjected to chi-square homogeneity analysis (Steele and Torrie 1960).

RESULTS

Bud Set.--Analysis of variance for bud-set dates showed that interprovenance differences were highly significant, $F = 23.57^{**}$[1]. Coastal provenances showed a continuous north-south trend in bud-set dates of seedlings (Fig. 4), with those from the extreme north reaching 100% set before those from the extreme south had even slowed growth (Figure 5; Appendix 4). The 50% bud-set level occurred among seedlings of No. 14 on July 24 and progressed to more southerly

[1]$^{**} = P < 0.05$.

provenances at a rate of about 4 days per degree of latitude of origin, reaching No. 1 on October 9. The two southernmost provenances never reached 100-percent set; on November 10, 24 percent of No. 1 and 10 percent of No. 2 had not yet set terminal buds.

Seedlings from Cascade and Rocky Mountain sources set bud earlier than those from equivalent latitudes along the Pacific coast. In the Cascade series, No. 17 seedlings (from 1,300 m) set bud markedly earlier than those from Nos. 15 and 16 (from 900 m). In the Rockies series, No. 19 seedlings (from 1,400 m in Idaho) were the first of all provenances to set bud (Figure 6). Chi-square comparisons of bud-set for high *vs.* low pairs showed significant differences (Table 2).

The time spread between earliest and latest provenance means for 50-percent bud-set dates in our shade house was 83 days (91 days from earliest family in earliest provenance to latest family in latest provenance). Within provenances, the time spread between earliest and latest families' 50-percent bud-set dates averaged 10 days, with the commonest spreads between 6 and 10 days and the longest spreads 34 days (No. 2), 30 days (No. 19), and 20 days (No. 18).

Bud Burst.--Seedlings of coastal provenances showed a north-south trend in bud-burst dates (Fig. 7), beginning April 16 with No. 14, progressing to more southerly provenances at a rate of about 2 days per degree of latitude of origin, reaching No. 4 on May 6. No meaningful bud-burst data could be taken for Nos. 1, 2, 3, and 5 because few or none of their seedlings had survived the winter.

Seedlings from the Cascades and the Rockies burst bud earlier in the spring than did those from similar latitudes along the coast

(Fig. 7). Those of Nos. 19 and 20, both from 1,400 m in the Rockies, were the first of all provenances to flush new growth. Chi-square comparisons of bud-burst dates for high *vs.* low pairs showed significant differences for two of three pairs (Table 2).

The time spread between earliest and latest provenance means for 50-percent bud-burst dates in our shade house was 36 days. Differences in bud-burst dates between provenances were not as great as those for bud set but were comparable in terms of length of the bud-burst period (Appendix 5).

Cold Hardiness.--Northern, high-elevation, and Rocky Mountain provenances survived better in four cold tests of progressively increasing severity (Appendix 6). The November freeze revealed clinal differences in fall frost hardiness among the southernmost coastal provenances. Only 12 percent of No. 1 and 39 percent of No. 2 seedlings survived; seedlings in Nos. 3-6 showed occasional slight leaf browning and shoot-tip dieback; and seedlings in Nos. 7-20 had no discernible injury.

Examination of tissues of injured California seedlings (Nos. 1 and 2) showed that nearly all had dead bark or roots whereas the few Northwest seedlings (Nos. 3-6) with browned leaves were otherwise uninjured. Within Nos. 1 and 2, significant differences in survival were apparent between families: the three families of No. 1 averaged 3-, 14-, and 19-percent survival; chi-square comparison of numbers of healthy *vs.* injured seedlings showed the family with 3-percent survival to be significantly less hardy ($\chi^2 = 6.3^*$)[1]. The three families of No. 2 averaged 20-, 26-, and 70-percent survival; chi-square

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[1] $^* = P < 0.05$.

comparison similarly showed the family with 70-percent survival to be significantly hardier ($\chi^2 = 15.7^{**}$)[1].

Survival through the whole winter in the shade house at ambient temperatures was correlated with latitude of origin of coastal provenances (Fig. 8). Cascade and Rocky Mountain seedlings survived better than those from comparable latitudes along the coast. The -17.5°C test gave results essentially similar to those of the ambient winter. Chi-square comparisons of survival through -17.5°C for high *vs.* low pairs showed significant differences (Table 2).

The -30°C test discriminated among the hardiest provenances, which had survived other tests nearly intact. Survival was 65 percent for No. 14, 40 percent for Nos. 13 and 20, 8 percent for No. 19, 2 percent for Nos. 10 and 11, and 0 percent for all others. The three families of No. 20 exhibited striking diversity in survival--0, 50, and 70 percent (20 seedlings each, $\chi^2 = 20.1^{**}$[1] for comparison of the least hardy family to the other two).

DISCUSSION

Data for bud set, bud burst, and cold hardiness of western hemlock show latitudinal clines similar to those for other species with extended north-south ranges. In eastern hemlock [*Tsuga canadensis* (L.) Carr.], Nienstaedt and Olson (1961) reported clinal variation of length of growing period of seedlings associated with length of frost-free growing season of seed source. In Sitka spruce

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[1]** = $P < 0.01$.

[Picea sitchensis (Bong.) Carr.], Burley (1966) reported an essentially continuous relationship between time of bud formation and latitude of seed origin. In Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco], Campbell and Sorensen (1973) reported source-dependent north-south clines in mean date of bud set and in frost sensitivity of seedlings growing at Corvallis.

Because western hemlock's distribution along the Pacific coast is continuous, except in the extreme south, it is reasonable to assume that the evolutionary response to environmental factors which vary gradually with latitude has been clinal. The factors causing divergent selection pressure between north and south are probably dates of first fall and last spring freezes and severity of midwinter temperatures.

Bud set, an early symptom of dormancy, is probably influenced by the specific day length insufficient to keep each provenance in active growth. Pollard et al. (1975) found that photoperiods critical for sustained growth in Sitka spruce were up to 4 h shorter for southern than northern provenances. Western hemlock's coastal range overlaps that of Sitka spruce, and it is possible that the two species have developed similar photoperiodic adaptations.

Bud-set timing apparently is closely linked with fall frost hardiness in hemlock, as it is in Douglas-fir (Campbell and Sorensen 1973). For example, one family in No. 2, which set bud 17 days earlier than its provenance average, showed significantly less November freeze injury than the other two No. 2 families (Appendix 8). One family in No. 1, which set bud 5 days later than its provenance average, showed significantly greater injury than the other two No. 1 families. From these instances, it seems plausible that bud-set dates of families or clones within a provenance could be used to estimate resistance to fall frost. But the same criterion does not apply to resistance to extreme low temperatures later in the winter. One family in No. 20 set bud 2 days earlier than its provenance average; yet no seedlings from this family survived the -30°C freeze cycle, although 24 of 40 seedlings of the other two families survived.

In terms of bud set, bud burst, and cold hardiness, western hemlock's genetic response apparently have been the same to increasing latitude and elevation. If we assume that temperature decreases with both latitude and elevation, this is what would be expected if the selective effects of both are mediated by temperature. The advantages of earlier bud set and greater cold hardiness for northern and montane populations are obvious; that of earlier bud burst is less so. It may be that spring warmup at high latitudes and elevations is less likely to be followed by late frost, as Burley (1966) suggested. Perhaps bud-burst timing is selectively neutral but genetically linked or pleiotropic to bud set; Cannell and Willett (1975) reported that northerly and inland montane provenances of Sitka spruce begin to produce primordia earlier than southerly and coastal provenances. If this is so in hemlock, buds of northern and high-elevation provenances may overwinter in a more advanced state.

Although it is generally agreed that bud-set dates fall into a geographic pattern, some workers have found comparable patterns in bud burst and others have not. Kraus and Lines (1976) and Burley (1966) found no overall pattern in Sitka spruce flushing; Meagher (1976) found no pattern in western hemlock flushing, but the provenances he tested did not vary widely in latitude, as did ours.

For those concerned with growing western hemlock, the differences in cold hardiness noted seem to require using a seed zone approach with this species. Such zones might be determined by multiple regression of latitude, elevation, and distance inland, combined with administrative factors. Preliminary, we recommend not moving seedlings more than 2° north of their genetic origin nor more than 400 m above elevation of origin. The amount of between-family variation within provenances augurs feasibility of within-provenance selection of families having the desired hardiness characteristics.

TABLE I. Geographic locations of 20 western hemlock provenances tested.

No.	Name	Latitude (°N.)	Elevation (m)	Distance from ocean (km)
		Coastal		
1	Stewart's Point, Calif.	38° 38'	200	10
2	Korbel, Calif.	40° 57'	700	20
3	Coos Bay, Oreg.	43° 30'	500	10
4	Alsea, Oreg.	44° 30'	700	40
5	Netarts Bay, Oreg.	45° 26'	200	10
6	Elk Rock, Wash.	46° 02'	500	140
7	Grays Harbor, Wash.	46° 55'	100	10
8	Snoqualmie, Wash.	47° 35'	200	200
9	Neah Bay, Wash.	48° 22'	100	10
10	Nootka Sound, B.C.	49° 50'	400	10
11	Mahatta River, B.C.	50° 24'	100	10
12	Queen Charlotte Is., B.C.	52° 56'	300	10
13	Naukati Bay, Alaska	55° 55'	100	10
14	Auke Bay, Alaska	58° 23'	100	10
		Cascade Mountains		
15	Cougar (Mt. St. Helens), Wash.	46° 22'	900	120
16	Carbon Ranger Sta. (Mt. Rainier), Wash.	46° 59'	900	170
17	Molalla (Mt. Hood), Oreg.	45° 10'	1,300	160
		Rocky Mountains		
18	Priest River, Idaho	48° 21'	700	570
19	Priest River, Idaho	48° 21'	1,400	570
20	Salmo-Creston Summit, B.C.	49° 08'	1,400	570

TABLE II. Chi-square homogeneity tests of responses of three western hemlock provenance pairs differing in source elevation.

Provenance no.	Bud set		Bud burst		Survival (−17.5°C)	
	Set	Total	Burst	Total	Alive	Total
6[a]	74	142	6	18	3	21
15[a]	97	146	13	28	21	22
	χ^2 =	5.75*[c]	χ^2 =	0.72	χ^2 =	28.56***[c]
8[a]	76	137	9	20	10	20
16[a]	119	147	19	25	19	22
	χ^2 =	21.23***	χ^2 =	4.65*	χ^2 =	6.45*
18[b]	26	80	8	18	9	12
19[b]	71	120	21	26	18	18
	χ^2 =	18.40***	χ^2 =	6.37*	χ^2 =	22.10***

[a]Buds set as of Sep. 8, 1978, and burst as of Apr. 29, 1979, in Corvallis shade house.

[b]Buds set as of Aug. 2, 1978, and burst as of Apr. 29, 1979, in Corvallis shade house.

[c]* = $P < 0.05$.
*** = $P < 0.005$.

Figure 1. Range of western hemlock (U. S. Forest Service 1965), with locations of provenances tested.

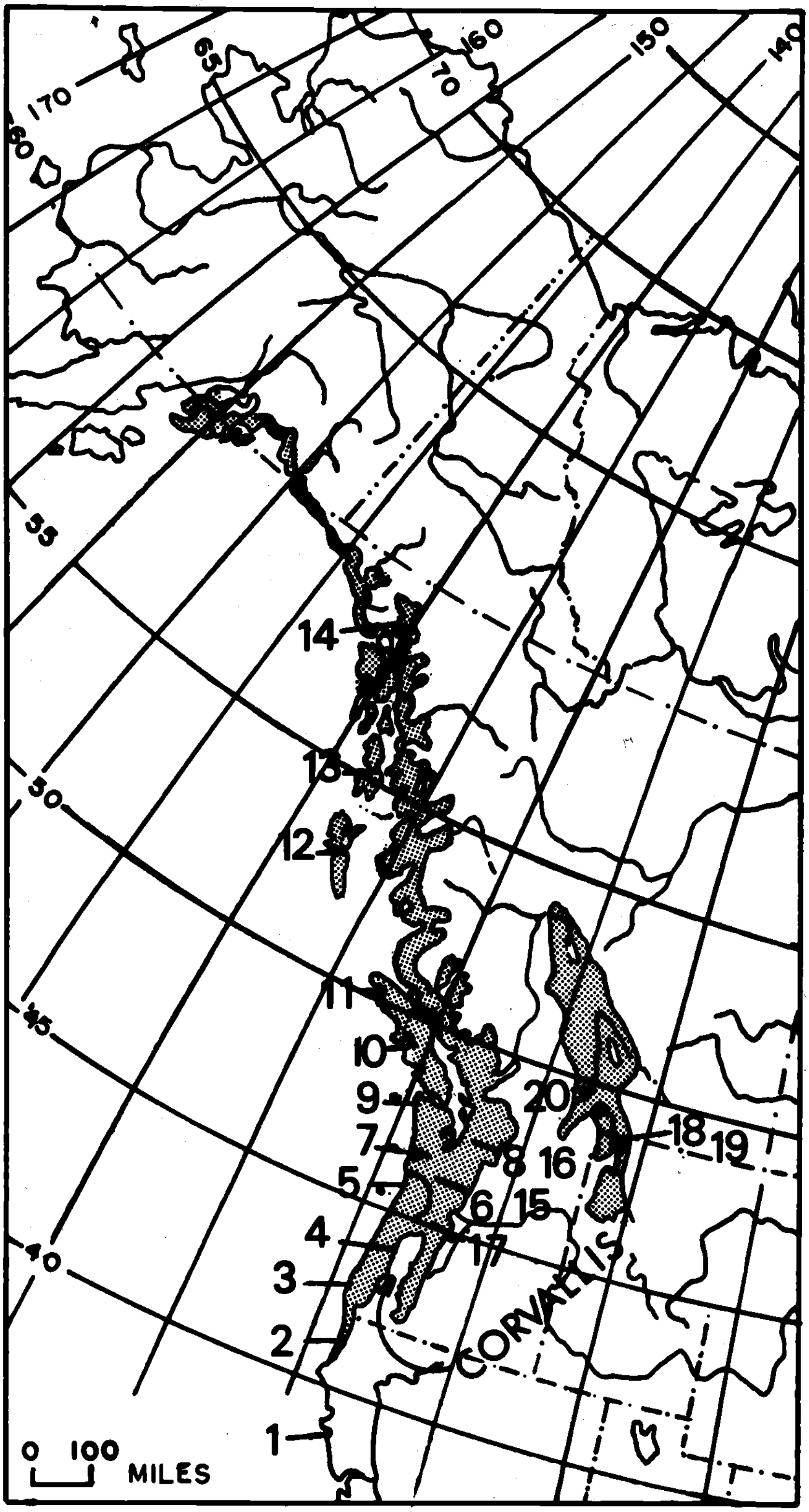


Figure 2. Terminal of western hemlock seedling (Molalla, Oregon provenance) in active growth, showing the drooping tip which characterizes this species. Photographed August 28, 1978.

Figure 3. Terminal of western hemlock seedling (Priest River, Idaho 1,400 m provenance) with bud set, large distal leaves surrounding bud, and stem partially straightened. Photographed August 28, 1978.

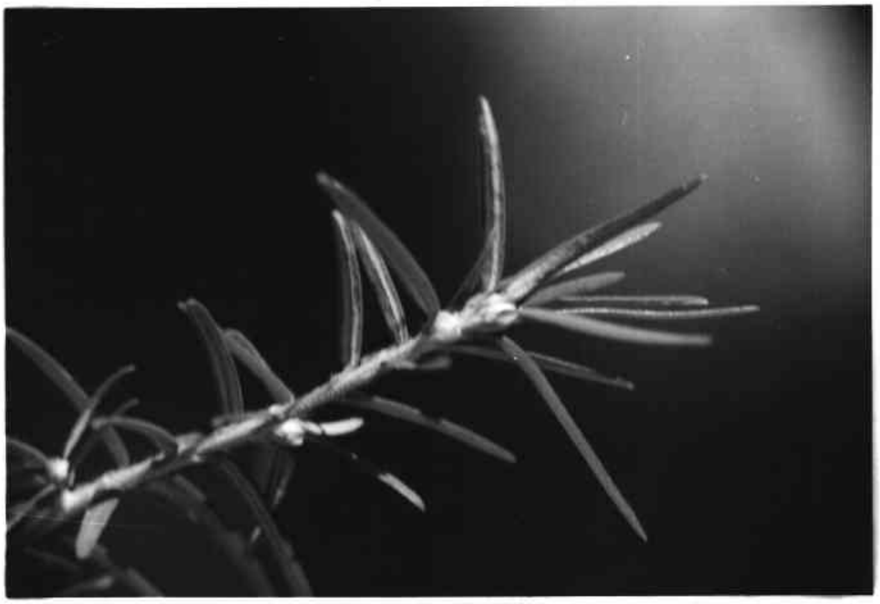


Figure 4. Relationship between latitude of seed origin and date on which 50 percent of terminal buds were set at Corvallis, Oregon, for 20 western hemlock provenances.

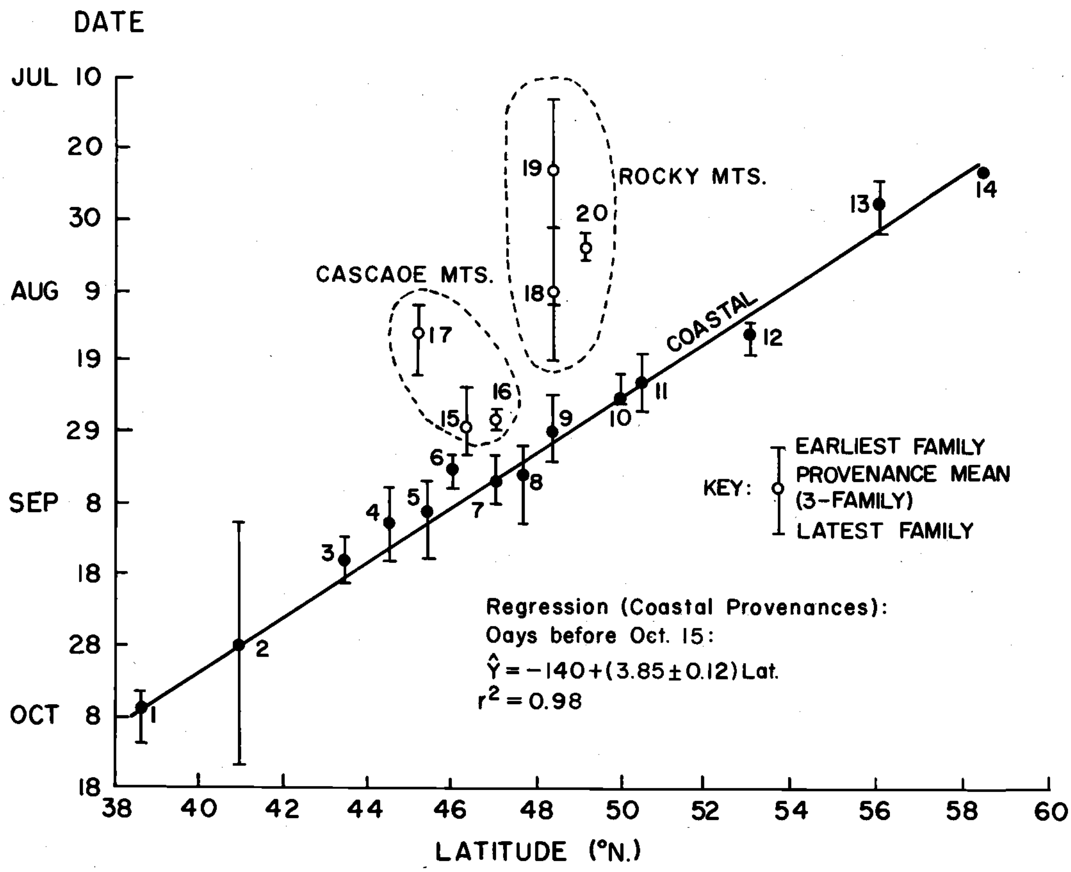


Figure 5. Difference in bud-set timing of western hemlock seedlings associated with provenance latitude: left, Stewart's Point California; right, Auke Bay, Alaska. Photographed August 28, 1978.

Figure 6. Difference in bud-set timing of western hemlock seedlings associated with provenance elevation: left, Priest River, Idaho (700 m) seedling still in active growth; right Priest River, Idaho (1,400 m) seedling with buds set. Photographed August 28, 1978.

Figure 7. Relationship between latitude of seed origin and date on which 50 percent of buds had burst at Corvallis, Oregon, for 16 western hemlock provenances.

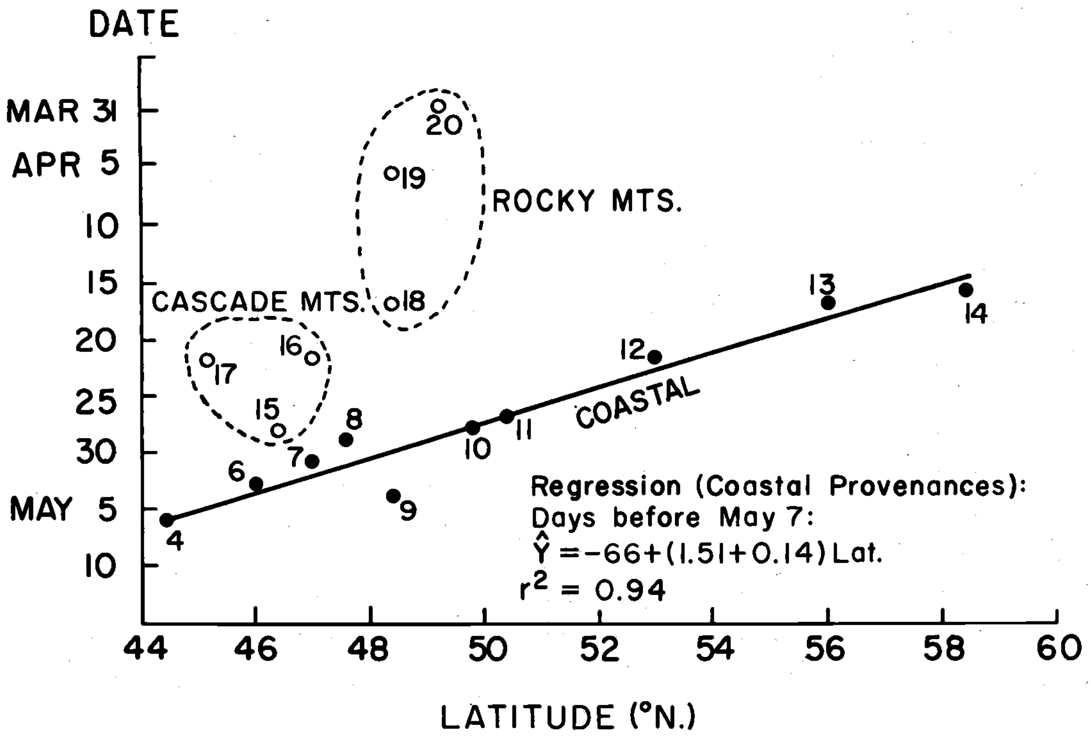
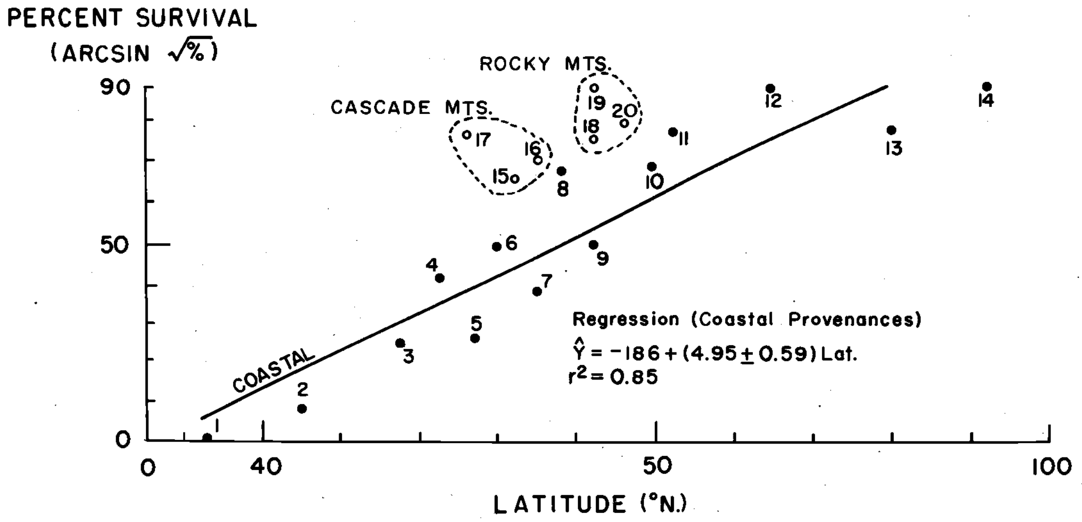


Figure 8. Relationship between latitude of seed origin and outdoor survival of western hemlock seedlings of 20 provenances through 1978-79 winter at Corvallis, Oregon.



CHAPTER 3

PROVENANCE VARIATION IN SEED WEIGHT, COTYLEDON NUMBER, AND GROWTH RATE OF WESTERN HEMLOCK SEEDLINGS

ABSTRACT. A range-wide sample of 21 provenances of western hemlock [Tsuga heterophylla (Raf.) Sarg.] showed significant variation in seed weight, frequency of 4-cotyledon seedlings, and growth rates of seedlings under continuous growth in controlled environments. Growth responses were strongly influenced by environment (air and soil temperature) and seed source. Variation among provenances and between families was highly significant, with the latter averaging up to one-half the former for most responses. Seedlings of southern and low or medium elevation provenances grew faster, in general, than seedlings of northern or high elevation provenances, but there were marked exceptions to these rules. A strong north-south cline was found in the variation among coastal provenances. Rocky Mountain hemlock populations from high elevations differed from coastal populations in cotyledon number, growth rate, and shoot/root ratio.

INTRODUCTION

Despite the commercial importance of western hemlock [Tsuga heterophylla (Raf.) Sarg.], few studies have been done to determine its genecological patterns of variation. Buszewicz and Holmes (1960) reported on the relationship of seed size to the latitude of origin of 14 provenances. Lines and Mitchell (1969) compared the suitability of 18 provenances for planting at 16 test sites in Britain; and Meager (1976) compared height, height/diameter ratio, and number of branches of seedlings from 17 sources along a west-east transect from sea level to 1,500 m in British Columbia.

We undertook a range-wide provenance study to determine the extent of genetic variation in western hemlock growth rates, and to compare intra-provenance variation with inter-provenance variation. Comparative phenology and cold hardiness of the same provenances were also investigated in this study and are reported elsewhere (Kuser and Ching 1980). Our experiments served as a preliminary investigation of provenance variation preceding a series of planting trials to be conducted by the Western Hemlock Tree Improvement Committee of the Industrial Forestry Association (I.F.A.).

MATERIALS AND METHODS

Experimental Design.

In October 1977, cones or seed were obtained from 21 locations (Table III. Figure 9). Our provenance testing strategy was to sample 1) a latitudinal transect along the Pacific Coast (locations 1-15) to test for north-south differences, 2) high elevation sources on the west slope of the Cascade Mountains (locations 16-18) to compare with lower sources at similar latitudes, and 3) sources in the Rocky Mountains (locations 19-21) to test against the others for differences due to lower precipitation and greater temperature extremes. Provenances in the commercial range of the species along the coast were sampled at closer intervals than those at range extremes and in disjunct areas.

Provenances were represented by seed from each of 3 parent trees in all locations except No. 15, for which only a bulked collection from several parent trees was available. Seed was extracted, cleaned to remove empty seeds and 100-seed weights from each parent tree were determined. Seed of each family was then sown in 50-ml Leach tubes filled with a commercial 1:1 peat-vermiculite mix. After most seedlings had germinated, cotyledon numbers were counted. The seedlings were grown for the first two months in the greenhouse.

To determine whether families and provenances were different in growth responses, seedlings from two families of each provenance were tested in 12 controlled environments for a three month period of continuous growth during which no seedlings were allowed to go dormant. Two environmental factors, air and soil temperature, were varied, with 4 levels of constant air temperature and 3 levels of constant soil temperature. We chose air temperatures of 12°, 16°, 20°, and 24°C in order to bracket the 18°C optimum growth temperature for hemlock seedlings reported by Brix (1971), and we chose soil temperatures of 12°, 16°, and 20°C because Lavender and Overton (1972) had found that Douglas-fir seedlings responded significantly to soil temperature differences in this range. The 3 soil temperatures were maintained by water-baths in each of 4 growth rooms programmed for the 4 air temperatures. Two-month-old seedlings in tubes were placed in sand-filled trays in these water-baths. Twenty of the provenances were represented by 4 seedlings from each of 2 families (there was not enough room for the originally planned 3 families), and the remaining provenance by 4 seedlings from the bulked collection. Seedlings were placed at random in the trays without regard to their family or provenance.

Light was supplied by 2.5 m cool-white fluorescent tubes and 150-watt incandescent bulbs; the light intensity as measured at seedling crown level with a Westin Illumination Meter (Model 765) held horizontally was approximately 700 ft-c. The photoperiod was 16 h, with lights on from 1800 to 1000 to maintain the programmed temperature during the night and avoid overheating during the day. Once a week the seedlings were watered with a nutrient solution (2.5 g/l of 20-19-18, acidified with H_3PO_4 to pH of 4.5), drained to prevent accumulation of salts, and rotated in the water-baths. Every fourth week the seedlings were watered with 0.001 M $FeSO_4$ instead of nutrient solution.

At the end of the growth chamber test period, height and total branch length (including all secondary branches) of each seedling were separately measured to the nearest centimeter. Then, shoot and root were clipped apart at the soil line, dried 48 h at 65°C and weighed separately.

Statistical Analysis.

One-way analyses of variance were performed on 100-seed weights and mean cotyledon numbers (Steele and Torrie 1960). Chi-square homogeneity analysis was used to determine whether family, provenance and regional differences in the proportions of 4-cotyledon seedlings were significant. The growth chamber experiment was a split-split-plot design with air temperatures as main plots, soil temperatures as sub-plots, and provenances as sub-sub-plots. The experiment was replicated twice over time in the same growth rooms. In the second replicate, different air temperatures were assigned to each room, and soil temperature locations within each room were different. Analysis of variance for a split-split-plot design was used; estimated variance components were tested for significance and compared for relative contributions to total variation. In computing expected mean squares, provenances were considered to be random on the basis that they constituted a reasonably good sampling of the species, from which we could draw inferences about the whole species.

Regression analyses were used to determine whether patterns of variation were associated with environment of provenance origin, as measured by latitude, elevation, or distance from the Pacific Ocean.

RESULTS

Seed Weight.

Variation among provenances means in 100-seed weight was significant (Table IV). However, correlations of 100-seed weight with latitude, elevation, or distance from the ocean were all low. The highest obtained was with distance from the ocean, $r = -0.17$. This is not significantly different from 0 at $P < 0.05$ (Appendix 3).

Cotyledon Number.

The average cotyledon number for seedling of all provenances was 3.10; 87.3 percent of seedlings had 3 cotyledons, 11.4 percent had 4, and 1.3 percent had only 2. Analysis of variance showed that variation in average cotyledon number among provenance means was not significant. But a chi-square heterogeneity test showed that differences in frequency of 4-cotyledon seedlings (*vs.* 2- and 3-cotyledon combined) were significant (Table V) within the coastal and Rocky

Mountain regions, and among regions. Among the coastal populations, 4-cotyledon frequency ranged from 5 percent in provenance 10 to 19 percent in provenance 3; among Rocky Mountain populations, it ranged from 12 percent in provenance 21 to 24 percent in provenance 20, and in one family of the latter it reached 37 percent.

Growth Responses.

Growth of western hemlock seedlings appeared to be strongly influenced by both growth environment and seed source (Table VI). Air temperature and soil temperature had significant effects ($P < 0.05$ or less) on almost all growth responses. In addition, significant interaction variation between these two factors was found for total branch length and shoot and root dry weight, indicating that changes in growth rates over varying soil temperatures may not be consistent at varying air temperatures. For all traits measured, variation among provenances and between families within provenance was highly significant ($P < 0.01$). The estimated between-family, within-provenance variance components were roughly half as great as the among-provenance components (Table VI, component percents). The highest ratio of maximum within-provenance variance to the total of all within-provenance variances for any response was 0.33. This was low enough to justify assuming that variation was distributed equally within all provenances (Pearson and Hartley 1966). Interaction effects between seed sources and environments were sometimes significant, but accounted for only minor percentages of total variation. Examination of provenance rank changes for three responses, in which source X treatment interactions were significant, showed only one change consistent between replicates and persistent through sub-plots: provenance No. 2 changed rank from 5th to 2nd in branch length and shoot dry weight as air temperatures increased from 12° to 24°C. All other provenance rank changes in responses showing interactions either showed no set pattern or were negligible.

Seedlings of all provenances made their greatest mean growth in height and branch length at 24°C air/16°C soil temperature but mean dry weight of shoots and roots was greatest at 20°C/20°C (Table VII). At 3 of the 4 air temperatures we tested, mean shoot and root growth were greatest in 16°C soil.

To determine if differences in growth responses of provenances were associated with environmental differences among locations of their geographic origin, provenance means (over all 12 air-soil temperature combinations) (Table VIII) were regressed on source latitude, elevation, and distance from the ocean. In addition to the four responses originally measured, three derived ones were also regressed. These were shoot size (height plus total branch length), biomass (shoot and root dry weights combined), and shoot/root ratio (shoot weight divided by root weight). Because shoot/root ratios are influenced by seedling size (Ledig et al. 1970), they were adjusted for differences in shoot dry weight on the basis of Ledig's plot for Douglas-fir grown under low light and high moisture (no data for hemlock are reported).

Eight independent variables were tested in these regressions: provenance latitude (L), elevation (E), and distance from the ocean (K), their squared terms (L^2, E^2, and K^2), and two interactions (LE and KE). LK and LKE were not allowed to enter the regressions because of confounding of L and K in the closely-grouped Rocky Mountain populations sampled. SAS Stepwise Regression (Helwig 1978) was used, with variables required to meet $P < 0.50$ for entry into the model and $P < 0.05$ to remain. Latitude of origin, either linear or squared, proved to have a significant effect ($P < 0.01$) on all 7 responses (Table IX), and the interaction term elevation X distance from ocean was significant ($P < 0.05$) for three responses. The regressions indicate that, in general, southern, lowland, or coastal provenances grew faster under our conditions than northern, high elevation, or Rocky Mountain provenances.

Regressions for only the provenances along the coastal transect (Nos. 1-15) showed that responses were significantly affected by latitude and the interaction term latitude X elevation. Latitude was always significant ($P < 0.01$); LE was significant in three responses ($P < 0.05$), and nearly significant in three others ($P < 0.25$). Latitude was strongly and negatively correlated with growth responses, as illustrated by plots of shoot size or shoot/root ratio *vs.* latitude of origin (Figure 10, Figure 11). It is interesting to note that the two coastal provenances which fall outside the 99 percent confidence band are from disjunct range areas. Reasoning that lack of genetic contact with other populations might allow the disjuncts to behave abberrantly, we removed provenances 1 and 13 from the regressions. We found that r^2 values for the 13 contiguous populations were much higher (Table X), while slopes and intercepts were not significantly affected.

Comparisons of mean provenance responses of high *vs.* low elevation pairs (Nos. 7 *vs.* 17, 9 *vs.* 18, 19 *vs.* 20) showed that, although low elevation seedlings grew larger on the average than their high elevation counterparts, differences (as measured by t tests) were not significant. This was partly because of large standard deviations resulting from pooling across 4 air temperatures. Comparisons of high vs. low pairs' responses within each of the 12 air/soil temperature combinations yielded significant t values ($P < 0.05$) about one-third of the time. Analysis of variance of biomass of high vs. low seedlings showed that the difference in elevation of origin was significant at 12°C/16°C ($P < 0.005$), but less so at 16°C/16°C and 24°C/16°C ($P < 0.06$, $P < 0.07$, respectively). While the general pattern was for high elevation provenances to grow more slowly, this was not true in every case. One Cascade Mountains provenance (No. 16) produced robust, fast growing seedlings which ranked first in mean biomass and fifth in mean shoot size among all provenances tested (Table VI).

The two 1,400 m Rocky Mountains provenances (Nos. 20, 21) grew relatively slowly for their latitude in terms of height and branch length, and about averagely for their latitude in biomass. They had very low adjusted (Ledig et al. 1970) shoot/root ratios (Figure 11), well outside 99% prediction limits of the regression for coastal provenances. The 700 m provenance (No. 19) grew averagely for its latitude in terms of height and branch length, but heavier in biomass than coastal provenances from similar latitudes.

DISCUSSION

Many conifers show an increase in seed weight toward drier parts of their range. Sorensen (1978) found this to be true for Douglas-fir, with seed weight increasing along a transect from the Coast Range to central Oregon. Buszewicz and Holmes (1960) reported that hemlock seed weight increased to the south, with less seeds to the pound from Oregon collections than from lots collected in Alkaska. Interestingly, we did not find any consistent relationships between seed weight and latitude, elevation, or distance from the ocean (Appendix 3).

The greater number of 4-cotyledon seedlings in Rocky Mountain populations may be a feature of drought adaptation. Precipitation at Priest River, Idaho (the collection area for Nos. 19 and 20) averages 824 mm yearly (NOAA 1971-1973), compared to 1,000-3,800 mm yearly in the coastal hemlock range (U.S. Forest Service 1965). Increases in cotyledon number towards drier parts of their range have been reported in at least three other conifers: loblolly pine in a disjunct area with precipitation two-thirds that of the main range was found by Knauf and Bilan (1977) to have a significantly greater number of cotyledons; the noble fir/California red fir complex was reported by Franklin and Greathouse (1968) to have higher cotyledon numbers southward; and lodgepole pine was reported by Maschning (1970) to show the same phenomenon.

Our finding that seedlings grew taller at 24° than at 20°C air temperature, but heavier at 20°C air temperature parallels the results of Lavender and Overton (1972) with Douglas-fir, in which they reported the tallest seedlings at 30°C air temperature but the heaviest at 24°C air temperature. Apparently the optimum temperature for biomass production is lower than that for height. The taller growth of seedlings at 24°C air temperature appears different at first glance from Brix's (1971) results, in which he reported greater stem length at 18°C. But since Brix did not vary soil temperatures, and our seedlings were taller at 24°C air temperature only in combination with 16°C soil temperature, our results reveal the effect of air temperature X soil temperature interaction.

Our finding that seedlings of southern provenances of western hemlock grew faster, in general, than those northern provenances, parallels results for juvenile growth of eastern white pine (King and Nienstaedt 1969), Sitka spruce in Europe (IUFRO 1976), lodgepole pine in New Zealand (IUFRO 1976), and interior Douglas-fir in Nebraska (Read and Sprackling 1976). A different pattern prevails in coastal Douglas-fir (Ching and Bever 1960, Ching and Hinz 1978) and Scotch pine (Dittmar 1977), where provenances from central or west-central portions of the species' ranges have usually have grown fastest because southerly provenances are adapted more for drought resistance than for rapid growth. Wright (1976) sums up these cold/warm and dry/moist clines for many forest tree species.

An unexpected finding was that growth responses of seedlings from two disjunct areas along the coastal transect (Nos. 1 and 13) deviated farther from the regression pattern than responses of seedlings from the contiguous range (Figure 10, Figure 11). These two populations are separated from the contiguous hemlock population by 60 km or more, and may each have evolved in their own directions. Perhaps different selection pressures have resulted in populations with genetic makeups deviating from the clinal pattern. No. 1, from the farthest south naturally occurring western hemlock population, may have evolved in response to the longer summer droughts which occur in its enclave than in the main range to the north. No. 13, which occupies an island area protected by a relatively wide strait from severe cold accompanying occasional outbreaks of Arctic air on the mainland, may have been freer to evolve for rapid growth.

Several of the provenances we tested showed marked between-family variation. One family of provenance 3 outgrew the other in shoot size by an average of 41 percent across all air and soil temperature combinations, and ranked first among 41 families in almost all measured responses under almost all conditions. Similar wide variation existed in some of the same provenances with respect to phenology and cold hardiness (Kuser and Ching 1980).

It appears that high-elevation Rocky Mountain provenances have evolved several adaptations to continental climate: greater frequency of 4-cotyledon seedlings, lower shoot/root ratio, and slower growth rates than coastal hemlock. They also possess greater cold hardiness (Sakai and Weiser 1973, Kuser and Ching 1980) and differ in phenology (Kuser and Ching 1980), exhibiting earlier bud-set and bud-burst than any coastal populations. Still, the Rocky Mountain and coastal hemlock populations do not seem as well differentiated as analogous Douglas-fir populations (which can be distinguished at a glance), so it may be that hemlock has not occupied its present range for as long a time. Alternatively, it may not have been equally able to develop new genotypes to take advantage of differing environments. Perhaps this is why hemlock's range does not extend as far south and east in the Rocky Mountain biogeoclimatic zone as does that of Dogulas-fir.

Table III. Geographic locations of 21 western hemlock provenances tested.

No.	Name	Latitude (°N)	Elevation (m)	Distance from ocean (km)
		COASTAL		
1	Stewart's Point, Calif.	38°38'	200	10
2	Korbel, Calif.	40°57'	700	20
3	Coos Bay, Oreg.	43°30'	500	10
4	Alsea, Oreg.	44°30'	700	40
5	Siletz, Oreg.	44°41'	100	10
6	Netarts Bay, Oreg.	45°26'	200	10
7	Elk Rock, Wash.	46°02'	500	140
8	Grays Harbor, Wash.	46°55'	100	10
9	Snoqualmie, Wash.	47°35'	200	200
10	Neah Bay, Wash.	48°22'	100	10
11	Nootka Sound, B. C.	49°45'	400	10
12	Mahatta River, B. C.	50°24'	100	10
13	Queen Charlotte Is., B. C.	52°56'	300	10
14	Naukati Bay, Alaska	55°55'	100	10
15	Auke Bay, Alaska	58°23'	100	10
		CASCADE MOUNTAINS		
16	Molalla (Mt. Hood), Oreg.	45°10'	1,300	160
17	Cougar (Mt. St. Helens), Wash.	46°22'	900	120
18	Carbon Ranger Station (Mt. Rainier), Wash.	46°59'	900	170

Table III. (cont.)

No.	Name	Latitude (°N)	Elevation (m)	Distance from ocean (km)
		ROCKY MOUNTAINS		
19	Priest River, Idaho	48°21'	700	570
20	Priest River, Idaho	48°21'	1,400	570
21	Salmo-Creston Summit, B. C.	49°08'	1,400	570

Table IV. Analysis of variance of 100-seed weights for 20[1] western hemlock provenances.

Source of Variation	df	SS	MS	F
Among provenances	19	64.505	3.395	6.06[2]
Within provenances	40	22.411	0.560	

[1]Only 20 of 22 provenances were used, because 2 provenances did not contain 3 families each.

[2]$P < 0.005$.

Table V. Chi-square homogeneity tests of frequency of 4-cotyledon hemlock seedlings in coastal, Cascade Mountain, and Rocky Mountain populations sampled.

Population	Frequency of 4-cotyledon seedlings	N	Heterogeneity Chi-square Within Region	(df)	Among Regions (df)
Coastal	0.11	1,674	36.09***[1]	(11)	-
Cascade Mountain	0.11	337	3.16	(1)	-
Rocky Mountain	0.15	401	14.09	(2)	-
	0.123[2]	2,412			9.35** (2)

[1]** P < 0.01.
*** P < 0.005.

[2]Unweighted mean of regional frequencies.

Table VI. Summary of analysis of variance of 4 growth responses among 21 hemlock provenances (41 families).

Source of variation	df	Test against line no.	Expected mean squares	a. HEIGHT				b. TOTAL BRANCH LENGTH			
				m.s.	F^a	component value	component %	m.s.	F^a	component value	component %
Air temperatures	3	2	$\sigma_e^2 + 21\sigma_\beta^2 + 63\sigma_\alpha^2 + 252\phi_A$	8,426	11.0*	30.38	57.8	101,985	26.6**	389.5	57.6
Error "a"	3	-	$\sigma_e^2 + 21\sigma_\beta^2 + 63\sigma_\alpha^2$	768	7.3*	-	-	3,841	6.72*	-	-
Soil temperatures	2	5	$\sigma_e^2 + 21\sigma_\beta^2 + 336\phi_S$	1,053	9.9**	2.82	5.4	19,263	33.7**	55.6	8.2
Air T x Soil T	6	5	$\sigma_e^2 + 21\sigma_\beta^2 + 84\phi_{AS}$	273	2.58 n.s.	1.99	3.8	2,028	3.55*	17.3	2.6
Error "b"	8	-	$\sigma_e^2 + 21\sigma_\beta^2$	106	13.1**	-	-	572	5.50*	-	-
Provenances	20	7	$\sigma_e^2 + 24\sigma_{F(P)}^2 + 48\sigma_P^2$	471	4.71**	7.73	14.7	6,725	4.35**	107.9	16.0
Families in prov's.	20	14	$\sigma_e^2 + 24\sigma_{F(P)}^2$	100	12.3**	3.83	7.3	1,546	14.9**	60.1	8.9
Air T x Prov.	60	9	$\sigma_e^2 + 6\sigma_{AF(P)}^2 + 12\sigma_{AP}^2$	17.3	1.57*	0.52	1.0	417	2.22**	19.0	2.8
Air T x Fam. (Prov.)	60	14	$\sigma_e^2 + 6\sigma_{AF(P)}^2$	11.0	1.35*	0.48	0.9	188	1.81**	14.1	2.1
Soil T x Prov.	40	11	$\sigma_e^2 + 8\sigma_{SF(P)}^2 + 16\sigma_{SP}^2$	15.1	1.98*	0.47	0.9	159	1.13 n.s.	1.1	0.2
Soil T x Fam. (Prov.)	40	14	$\sigma_e^2 + 8\sigma_{SF(P)}^2$	7.63	0.94 n.s.	0	0	141	1.36 n.s.	4.7	0.7
Air T x Soil T x Prov.	120	13	$\sigma_e^2 + 2\sigma_{ASF(P)}^2 + 4\sigma_{ASP}^2$	11.6	1.38 n.s.	0.80	1.5	133	1.28 n.s.	7.2	1.1
Air T x Soil T x Fam. (Prov.)	120	14	$\sigma_e^2 + 2\sigma_{ASF(P)}^2$	8.39	1.03 n.s.	0.14	0.3	104	1.00 m.s.	0	0
Error "c"	3,261	-	σ_e^2	8.11	-	-	-	104	-	-	-
Replicate	1	2	$\sigma_e^2 + 21\sigma_\beta^2 + 63\sigma_\alpha^2 + 504\sigma_r^2$	2,468	3.21 n.s.	3.37	6.4	1,890	0.5 n.s.	0	0
TOTAL	3,765					52.53	100.0			676.5	100.2

[a] * $P < 0.05$.
** $P < 0.01$.

Table VI. (cont.)

Source of variation		Test against line no.	Expected mean squares	c. SHOOT DRY WEIGHT m.s. $x10^3$	F^a	component value $x10^3$	%	d. ROOT DRY WEIGHT m.s. $x10^5$	F	component value $x10^5$	%
Air temperature	3	2	$\sigma_e^2 + 21\sigma_\beta^2 + 63\sigma_\alpha^2 + 252\phi_A$	11,700	38.0**	45.2	33.1	39,170	4.18 n.s.	118	19.3
Error "a"	3	-	$\sigma_e^2 + 21\sigma_\beta^2 + 63\sigma_\alpha^2$	308	0.71 n.s.	-	-	9,380	7.82**	-	-
Soil temperatures	2	5	$\sigma_e^2 + 21\sigma_\beta^2 + 336\phi_S$	5,070	11.8**	13.8	10.1	18,800	15.7**	52	8.5
Ait T x Soil T	6	5	$\sigma_e^2 + 21\sigma_\beta^2 + 84\phi_{AS}$	699	1.55 n.s.	2.8	2.0	7,240	6.03*	72	11.8
Error "b"	8	-	$\sigma_e^2 + 21\sigma_\beta^2$	431	14.37**	-	-	1,200	6.25**	-	-
Provenances	20	7	$\sigma_e^2 + 24\sigma_{F(P)}^2 + 48\sigma_P^2$	2,132	5.47**	36.3	26.6	10,580	5.11**	117	29.0
Families in prov's.	20	14	$\sigma_e^2 + 24\sigma_{F(P)}^2$	390	13.0**	15.0	11.0	2,070	10.8**	78	12.8
Air T x Prov.	60	9	$\sigma_e^2 + 6\sigma_{AF(P)}^2 + 12\sigma_{AP}^2$	77	1.31 n.s.	1.4	1.0	356	0.94 n.s.	0	0
Air T x Fam. (Prov.)	60	14	$\sigma_e^2 + 6\sigma_{AF(P)}^2$	59	1.97 **	4.8	3.5	379	1.97**	31	5.1
Soil T x Prov.	40	11	$\sigma_e^2 + 8\sigma_{SF(P)}^2 + 16\sigma_{SP}^2$	86	1.95*	2.6	1.9	562	2.48**	21	3.4
Soil T x Fam. (Prov.)	40	14	$\sigma_e^2 + 8\sigma_{SF(P)}^2$	44	1.47*	1.7	1.2	227	1.18 n.s.	4	0.6
Air T x Soil T x Prov.	120	13	$\sigma_e^2 + 2\sigma_{ASF(P)}^2 + 4\sigma_{ASP}^2$	68	1.70**	7.0	5.1	374	1.56**	34	5.6
Air T x Soil T x Fam. (Prov.)	120	14	$\sigma_e^2 + 2\sigma_{ASF(P)}^2$	40	1.33*	5.1	3.7	240	1.25*	24	3.9
Error "c"	3,261	-	σ_e^2	30	-	-	-	192	-	-	-
Replicate	1	2	$\sigma_e^2 + 21\sigma_\beta^2 + 63\sigma_\alpha^2 + 504\sigma_r^2$	748	2.43 n.s.	0.9	0.7	3,350	0.36 n.s.	0	0
TOTAL	3,765					136.8	99.9			611	100.9

[a]* $P < 0.05$.
**$P < 0.01$.

Table VII. Mean responses of hemlock seedlings to 4 air temperatures and 3 soil temperatures (ignoring provenance and family differences).

Response	Air Temp. 12°C			Air Temp. 16°C		
	Soil 12°	Soil 16°	Soil 20°	Soil 12°	Soil 16°	Soil 20°
Height, cm	8.59	11.90	11.64	13.53	14.55	15.37
Total branch length, cm	6.76	15.01	14.21	17.29	23.63	25.64
Dry shoot weight, mg	256	430	328	382	520	492
Dry root weight, mg	82	100	87	104	154	122

Response	Air Temp. 20°C			Air Temp. 24°C		
	Soil 12°	Soil 16°	Soil 20°	Soil 12°	Soil 16°	Soil 20°
Height, cm	15.54	17.12	16.57	17.39	18.60	16.58
Total branch length, cm	25.81	33.36	35.79	33.01	39.54	33.17
Dry shoot weight, mg	476	576	650	547	630	555
Dry root weight, mg	116	132	159	123	136	117

Table VIII. Mean growth responses (over all 12 air-soil temperature combinations) of 21 western hemlock provenances.

No.	Height (cm)	Branch length (cm)	Shoot size (cm)	Shoot dry wt. (mg)	Root dry wt. (mg)	Biomass (mg)	Shoot/root ratio[1]
1	15.03	25.53	40.57	556	135	691	4.34
2	16.55	33.19	49.74	614	143	758	4.85
3	17.18	36.95	54.13	642	152	794	4.71
4	17.03	31.50	48.53	647	159	806	4.60
5	15.98	29.14	45.12	583	133	716	4.80
6	14.36	26.95	41.31	417	96	513	4.17
7	15.49	25.16	40.65	489	117	606	4.32
8	13.61	23.01	36.62	404	91	495	4.20
9	14.40	24.79	39.19	472	112	584	4.25
10	13.30	22.77	36.07	395	94	489	4.13
11	15.12	25.38	40.50	473	121	594	4.15
12	13.42	20.17	33.59	367	89	456	4.21
13	16.12	32.42	48.54	584	141	725	4.58
14	12.90	17.73	30.63	367	94	461	3.95
15	9.22	9.06	18.28	240	65	305	3.02
16	15.90	31.19	47.09	652	156	808	4.70
17	14.62	24.58	39.20	467	118	585	4.01
18	12.35	19.34	31.69	378	97	475	3.70
19	15.96	24.58	40.54	525	136	661	4.01
20	14.06	17.55	31.61	388	110	498	3.19
21	13.75	15.05	28.80	357	106	463	3.00

[1]Adjusted (Ledig et al. 1970).

Table IX. Regressions of mean growth responses of 21 western hemlock provenances against parameters of provenance origin (e.g., latitude, elevation, and distance from Pacific Ocean).

Response	Fitted Regression Equation	r^2
Height, cm	$y = 21.0 - (0.0028 \pm 0.0007)\ L^2$	0.45
Branch length, cm	$y = 48.5 - (0.0099 \pm 0.0026)\ L^2 - (9.97 \pm 4.65)\ KE$	0.53
Shoot size, cm	$y = 68.7 - (0.0124 \pm 0.0031)\ L^2 - (9.89 \pm 5.60)\ KE$	0.52
Shoot dry weight, mg	$y = 1276 - (6.8 \pm 4.4)\ L$	0.43
Root dry weight, mg	$y = 198 - (0.035 \pm 0.011)\ L^2$	0.37
Biomass, mg	$y = 1557 - (20.2 \pm 5.4)\ L$	0.42
Shoot/root ratio	$y = 5.81 - (0.00066 \pm 0.00016)\ L^2 - (1.34 \pm 0.30)\ KE$	0.68

L = latitude, decimal, °N.

K = distance from Pacific Ocean, km x 10^{-3}.

E = elevation, m x 10^{-3}.

Table X. Regressions of mean growth responses of seedlings of 13 contiguous coastal provenances of western hemlock against latitude and elevation of provenance origin.

Response	Fitted Regression Equation	r^2
Height, cm	$y = 33.0 - (0.39 \pm 0.06)\ L$	0.77
Branch length, cm	$y = 92.3 - (1.40 \pm 0.21)\ L$	0.81
Shoot size, cm	$y = 122.9 - (1.74 \pm 0.22)\ L$	0.85
Shoot dry wt., mg	$y = 1179 - (16.1 \pm 4.2)\ L + (4.6 \pm 2.0)\ LE$	0.81
Root dry wt., mg	$y = 223 - (2.7 \pm 1.0)\ L + (1.5 \pm 0.5)\ LE$	0.78
Biomass, mg	$y = 1402 - (18.8 \pm 5.2)\ L + (6.1 \pm 2.5)\ LE$	0.81
Shoot/root ratio	$y = 8.41 - (0.087 \pm 0.013)\ L$	0.81

L = latitude, decimal, °N.

E = elevation, m x 10^{-3}.

Figure 9. Range of western hemlock (U. S. Forest Service 1965), with locations of provenances tested.

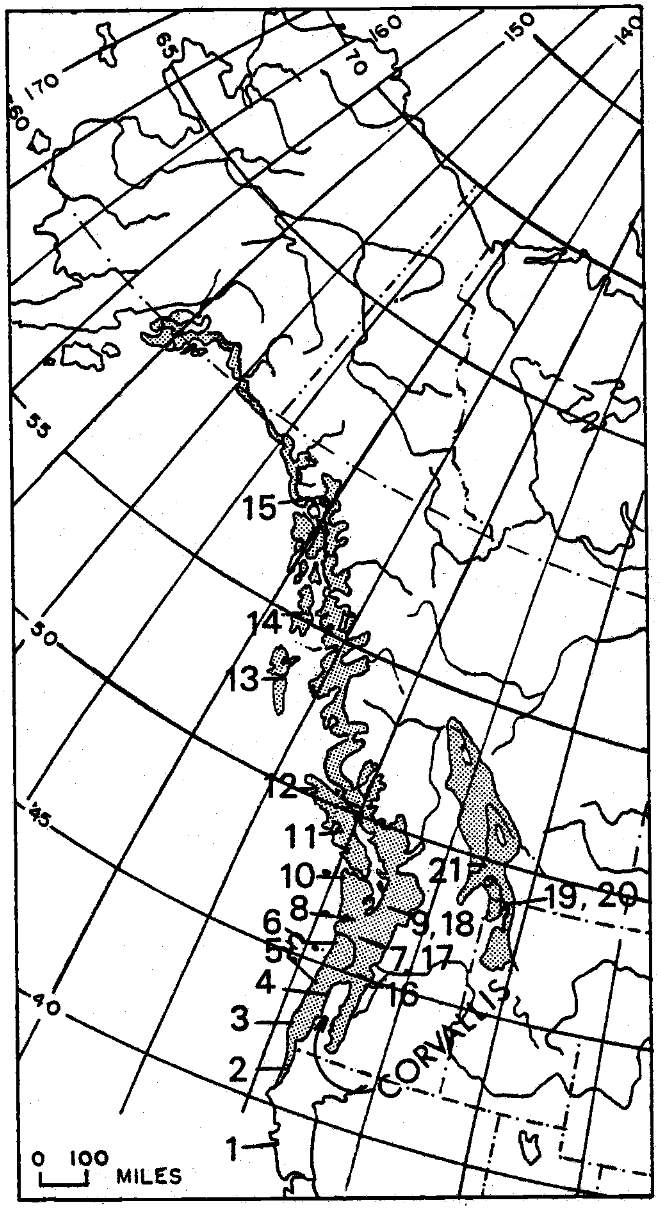


Figure 10. Relationship of mean shoot size of seedlings of coastal provenances of western hemlock to latitude of origin.

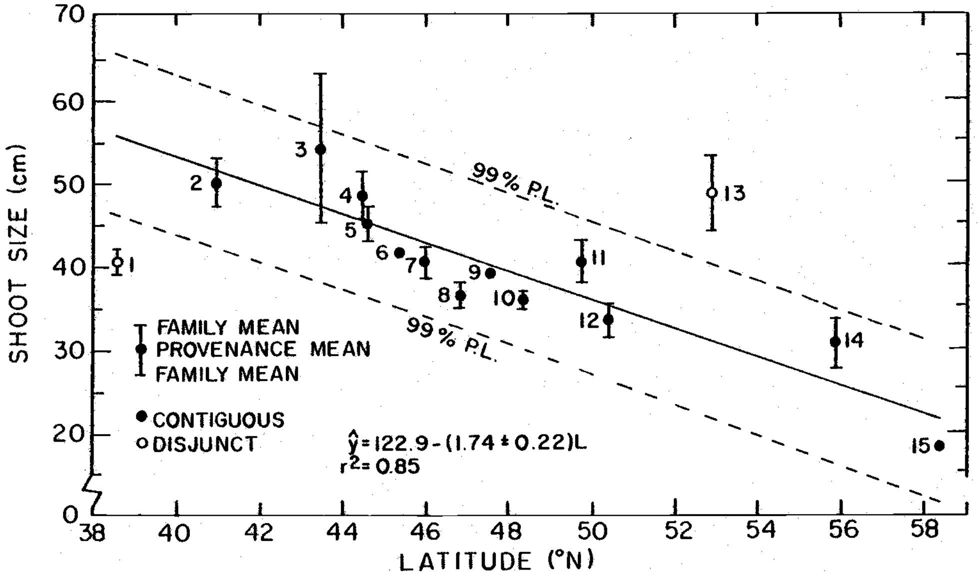
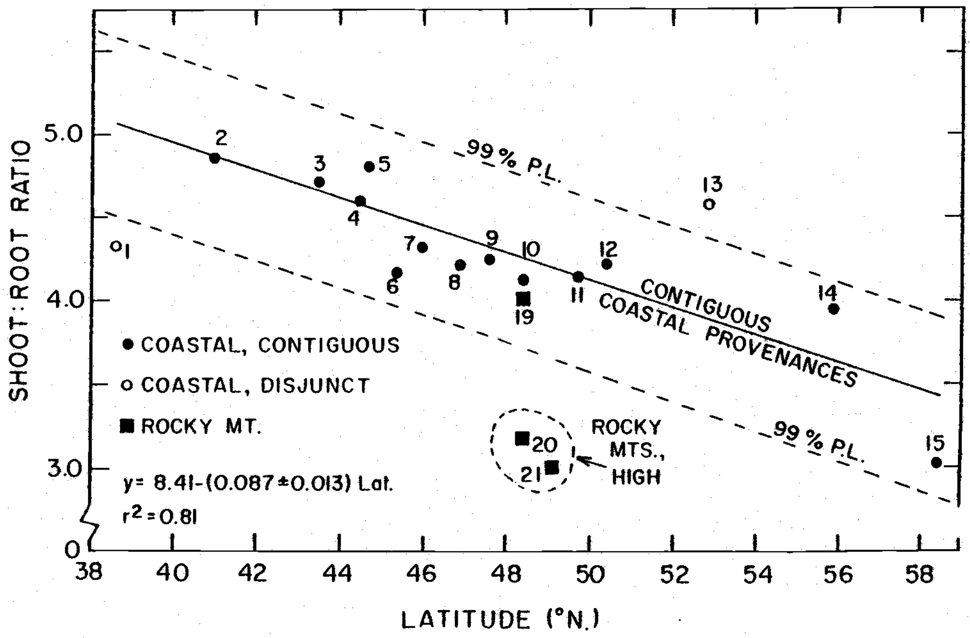


Figure 11. Relationship of adjusted mean shoot/root ratios of western hemlock seedlings of latitude of provenance origin.



CHAPTER 4

INTEGRATING RESULTS ON PHENOLOGY, HARDINESS, AND GROWTH RATE: CONCLUSIONS

1) Cumulative effect of differences in growing season length and differing growth rates.

Southern provenances burst bud later in the spring than northern provenances did in our common garden test at Corvallis, but set bud much later in the summer or fall (Chapter 2); as a result, the southern provenances remained in active growth over a longer period of time. They also grew faster, on the average, in our controlled environment experiments, than northern provenances did (Chapter 3). If these two effects are additive in the field (i.e., if they are not offset by reversal of the growth rate differential under longer natural photoperiods at high latitudes), southern provenances should grow considerably faster than northern provenances, up to latitudes where the former suffer low-temperature injury. At least, this should be true of seedlings; the extent to which the difference applies to trees of any age may depend on juvenile:mature correlation.

2) Differences in hardiness *vs*. differences in growth rate; need and feasibility of zonal selection.

The slopes of the regressions for growth rate and cold hardiness in coastal provenances of western hemlock seedlings are opposite. Because of danger of winter injury, seedlings should not be moved too far north of their latitude of genetic origin (Chapter 2). On the other hand, if planting trials validate our guess that southern provenances will grow faster, it would be desirable to use seed from as far south as possible in order to maximize yield. Hemlock growers may be caught in a dilemma between need for adequate hardiness and desirability of rapid growth.

The way out of the dilemma appears to be use of a seed zone approach with this species, accompanied by planting trials in each seed zone to screen within-zone selections and determine which ones of promising selections from outside the zone will perform well in it. Reasoning from differences in juvenile characteristics which we found, we expect that there is opportunity for gain from selections from both inside and outside seed zones. Several provenances we tested seemed to combine the merits of hardiness and rapid growth, so should be worth testing in more than one zone. In addition, there appeared to be enough between-family-within-provenance variation, on the average, to make plus tree searches within each zone rewarding.

The reader or researcher should bear in mind that the trees we tested were first-year seedlings, and that 10-, 20-, or 60-year results of planting trials will be different. We cannot foretell exactly how different they will be - that is why they are necessary.

In the next chapter, detailed suggestions are made for 1) an intensive search for variation in each area where hemlock is a crop tree, and 2) planting trials of certain provenances which appear to have desirable qualities.

CHAPTER 5

RECOMMENDATIONS FOR FURTHER RESEARCH

Four major areas for short term research are suggested, three others are possible, and one overridingly important area for long term research is suggested. Short term research should be directed to 1) superior provenance areas, 2) genetic differences due to elevation, 3) family-within-provenance variation, and 4) clonal variation. Other possible short term projects are 5) cold tolerance at -35° and -40°C, 6) hybridization, and 7) geographic variation in needle length and color. The long term research area is 8) planting trials. Each area is briefly outlined below.

A. Short term studies

1. Superior provenance areas

It would be interesting to investigate reasons for the rapid growth of seedlings from the Queen Charlotte Islands (52°56' N) and from Molalla, Oregon (1,300 m) despite the general rule that seedlings of northern and high-elevation provenances are slower growing. The unexpectedly fast growth of the 2 families tested from each of these provenances should be authenticated by testing seedlings from other parent trees in these areas, to make sure whether the superiority of the seedlings tested is representative of their provenance averages or was caused by sampling error due to the small number of families tested. If the superiority is real, i.e., if most parent trees in the sampled stands produce unexpectedly fast-growing seedlings, what of other stands in the same general areas? Are the Queen Charlotte Islands and the Cascade foothills south of Mt. Hood "plus" genetic areas for western hemlock? And what of the Coos Bay area, where one family we tested grew 41% faster than the other and ranked highest among all families in nearly all growth responses under nearly all conditions tested? What are the characteristics of seedlings from other parent trees in this and other stands in the Coos Bay area?

Seed from several additional parent trees of the Molalla, Queen Charlotte Is., and Coos Bay provenances (other than the parent trees tested in this study) is available in the Forest Research Laboratory freezer at Oregon State University.

The question naturally arises as to the degree of correlation between the juvenile differences we observed and eventual rotation-age differences. We think the chances of success are good enough to warrant some progeny testing of different trees and stands within the "juvenile plus" areas, but warn the reader again that the only positive proof of long-term superiority is long-term planting trials.

2. Genetic differences due to elevation.

Our tests of paired high vs. low elevation provenances showed that seedlings of high elevation origin set and burst bud earlier and were more cold-tolerant than seedlings of low elevation origin (Chapter 2), but usually grew more slowly (Chapter 3) although seedlings of one high elevation provenance grew very fast. Further research needs to be done to determine whether the response differences are clinal, as we found was the case with response differences associated with latitude.

A researcher could collect seed at intervals along elevational transects in areas where hemlock occupies a wide range of elevations within a short distance, as McGee did with red oak (McGee 1974).

Three areas suggested for elevational transects are 1) from Leaburg, Oregon to Willamette Pass, 2) Mt. Baker, Washington, from the upper limit of western hemlock down to sea level along the Nooksack River, and 3) Priest River Experimental Forest, Idaho, from 700 m to 1,400 m along the "J" road.

3. Family-within-provenance variation.

In our experiments we assumed, in comparing intraprovenance variation (20-21 df) with interprovenance variation (19-20 df), that intraprovenance (family-within-provenance) variation was equally distributed in all the provenances we tested. This assumption is probably approximately but not exactly true, i.e., some provenances may be more variable than others.

Local variation in phenology, cold hardiness, and growth rate should be investigated by experiments similar to ours in each seed zone (roughly every 2° of latitude and every 500 m of elevation) where hemlock is a crop tree. From 5 to 10 different stands per zone, and from 5 to 10 different parent trees per stand, should be tested.

4. Clonal variation.

Variation between provenances and variation between families within provenances were studied on our experiments. The next level of variation is that among clones within families. Many wild plant species depend partially or entirely on natural reproduction of superior clones by various sorts of apomixis (Grant 1971), thus preserving the full benefit of non-additive as well as additive genetic variation from generation to generation. Among cultivated plants, many fruit trees and ornamentals are propagated as clones because the ratio of benefit to cost justifies it. In forest tree species, the Japanese plant clonal sugi (Cryptomeria japonica), while the New Zealanders are experimenting with cutting propagation of Monterey pine (Pinus radiata), and work on clonal redwood (Sequoia sempervirens) has been carried on for a number of years in California. Caution must be observed here not to risk epidemic disease or pest outbreak by concentrating on too few clones.

5. Cold tolerance at -35° and -40°C.

Laboratory freeze cycles with minima of -35° and -40°C were attempted in this study, but were unsuccessful because of compressor icing which caused rapid temperature fluctuations killing all tested seedlings, whereas the normal freeze cycle used (Chapter 2) might not have killed them. Sakai and Weiser (1973) reported that twigs, leaves, and buds of Alaska and Idaho hemlock sampled in midwinter were hardy to -35° or -40°C, but they did not test seedlings, and they did not sample the utter extremes of range in latitude or elevation to determine the limits of western hemlock's hardiness.

Further freeze cycle tests need to be performed on seedlings of different provenances to define hardiness limits of the species more exactly. Some should be made at the time of maximal hardiness of seedlings overwintering outdoors, probably in January. The large scale freeze trials conducted in this study were made in late February, after hardiness had begun to wane, and survival of some provenances was less than in the preliminary small-scale trials run in January (Appendix 9).

6. Hybridization.

The genus Tsuga is divided into two subgenera, Eutsuga and Hesperopeuce. Attempts by Meagher (1976) and Sorensen (Meagher 1976) to cross western hemlock (Eutsuga) with mountain hemlock T. (Hesperopeuce) mertensiana were unsuccessful, although Taylor (1972) investigated putative natural hybrids between these two species and concluded that introgression of mountain hemlock genes for two polyphenolic pigments, not found in typical western hemlock, may have occurred. It seems more likely that some of the Eutsuga series (which includes all of Tsuga except T. mertensiana) may be allopatric semispecies which could be crossed. Several are commercially valuable forest trees, including T. canadensis of the eastern U. S. and Canada, T. sieboldii of Japan, T. chiensis var. formosana of Taiwan, and T. dumosa of the Himalayas. All these are diploids with n = 12 (Sax and Sax 1933, Santamour 1963, Ho and Owens 1974).

Because western hemlock (T. heterophylla) is a larger, faster-growing tree than any of the others, it seems possible that genes for improving these qualities in other hemlocks might be obtained from it.

7. Geographic variation in needle length and color.

Hemlocks growing in natural stands at the south end of the species' range along the coast appear to have relatively long needles (personal observation), while those at the north have relatively short needles. The same difference appeared between seedlings of southernmost and northernmost provenances in our growth room experiment (Figure 10), indicating that the difference subjectively observed in the field was real and probably genetically caused. Similar difference in needle length did not appear to exist between high and low elevation Idaho hemlocks, although needles of the former were almost as cold-tolerant as those from Auke Bay, Alaska. Possibly selection for short needles is so weak in hemlock that it is swamped by migration over short distances, as with white fir (Hamrick 1976), but is able to produce differences between the north and south ends of the range. The nature of the adaptation of needle length to environment could be studied, and it would be a challenge to make a quantitative study of the relative magnitudes of $\underline{s}$ (selection) and $\underline{m}$ (migration) for needle length.

Seedlings of the northernmost and highest-elevation provenances tested in our study became dark green as they set terminal buds in preparation for dormancy. On the other hand, seedlings of the southernmost provenances remained light or medium green throughout the winter. Color differences among coastal provenances appeared to be clinal. Dark green color has been noted by Cheung (1975) as an indicator of dormancy. Variation in color among provenances might be caused by different levels of dormancy-inducing hormones, different levels of development of wax coating on needles, or different chlorophyll/carotenoid molar ratios. This could be studied. It might also be possible to use degree of color change as a non-destructive indicator of relative hardiness to early cold, as has been suggested for budset (Campbell and Sorensen 1973).

B. Long term studies.

8. Planting trials.

Planting trials conducted over relatively long periods in terms of rotation age (such as 20, 30, or 50 years) are the most reliable means of determining which provenances, families, or clones of western hemlock are desirable for growing in each seed zone. Furthermore, they are the only way to obtain data on juvenile/mature correlation of performance of families or clones selected because of superior juvenile characteristics. Preliminarily, it seems desirable to establish trial plots in each zone where hemlock is a crop tree, at perhaps 2° intervals of latitude and 500 m intervals of elevation.

Planting trials should include the following: a) family tests, i.e., progeny of plus trees selected within the seed zone, b) clone tests, i.e., ramets of plus trees selected within the seed zone, and c) seedlings and clonal ramets of plus trees from promising provenances outside the seed zone, e.g., Queen Charlotte Islands at Neah Bay. Planting trials should also include a random sampling of the gene pool at each site, for use as a base against which to compare the performance of selected progeny at each age of measurement up to full rotation.

Figure 12. Difference in needle length of western hemlock seedlings associated with provenance latitude: left, Auke Bay (near Juneau), Alaska; right, Stewart's Point (Sonoma County), California. Photographed November 6, 1978.

CHAPTER 6

CULTURAL NOTES

1. Tests of container media for hemlock.

Before beginning our provenance experiments, it seemed desirable to compare growth of hemlock seedlings in several media available for use in containers, on the premise that vigorous seedling growth would more readily reveal genetic differences. Three soils were compared:

"Black soil"--the standard dark forest soil used at Forest Research Laboratory for Douglas-fir and other species. It was obtained from the FRL soil bin.

"Red soil"--a gravelly soil dug from a roadbank under hemlock trees on U. S. 34 about 1/2 mile up Marys Peak from where the road leaves the Willamette Valley floor. This appeared to be a subsoil from one of the Tyee formation series, dumped in its present location and graded to a high, steep bank on the downhill side of the road. It was thickly colonized by western hemlock seedlings 20-40 cm high. Before being used, it was well mixed to insure dispersion of mycorrhizal inoculum, then screened (1/2").

A pre-blended, pre-moistened peat-vermiculite mixture (Lite Gro, McConkey Co., Sumner, WA) used for hemlock by the U. S. Forest Service nursery, Beaver Creek, OR.

Ninety 50-ml Leach tubes were washed and sterilized with hot detergent and NaOCl in a top-loading washing machine. Thirty were then filled with each soil medium, and planted with 2 seeds each from U. S.

Forest Service hemlock parent tree Alsea No. 152, covered with 0.25 cm No. 2 chicken grit, watered, and covered with clear plastic until the seed germinated. The seedlings were grown in the greenhouse and shade house for 8 months.

Comparative results noted from time to time were as follows:

Length of roots at time of thinning seedlings:

Black soil--2.5-5.0 cm

Red soil--7.5 cm

Peat-vermiculite--5.0-7.5 cm

Losses before seedlings reached 5 cm high:

Black soil--3%

Red soil--3%

Peat-vermiculite--0%

Age 10 weeks:

Seedlings in peat-vermiculite noticeably larger than others and beginning to branch.

Age 4 months:

Black soil--4-7 cm high

Red soil--7-8 cm high

Peat-vermiculite--9-12 cm high

Age 38 weeks (Figure 11):

Black soil--8 cm high x 8 cm wide

Red soil--12 cm high x 12 cm wide

Peat-vermiculite--15 cm high x 15 cm wide

The peat-vermiculite mixture tested was judged most suitable for our purpose, and used.

2. Problems with commercial peat-vermiculite.

Approximately 3,000 seedlings were started in February, 1978, grown in the greenhouse until May, and then moved to the 50% shade house outdoors. Late in June, when the first hot, dry weather occurred, brown needles, chlorosis, and necrosis were observed on some seedlings, in spite of frequent watering. In each subsequent hot spell, more seedlings developed such symptoms. The pattern was for injury to appear two or three days after the beginning of hot weather, and then remain static during more moderate weather between hot spells.

On July 18 it was noted that the soil at the bottom-hole of a tube containing a dying seedling had a pH of 6.0, while that at the bottom of a tube containing a healthy seedling had a pH of 4.5. On July 22, the same soil pH difference was observed again, between another pair of tubes (one sick seedling, one healthy). During the next two weeks, tests on tubes containing 18 healthy seedlings revealed pH levels of 4.5 to 5.3, while tubes containing 13 sickly or dead seedlings had levels of 5.2 to 7.5 (Appendix 10). It was clear that pH was closely and negatively correlated with seedling health.

It is common knowledge that commercial peat-vermiculite mixes sometimes contain ground dolomite limestone, although the Beaver Creek nursery (source of our peat-vermiculite) was supposedly using a limestone-free formulation. Samples of our medium from tubes containing a dead seedling and a healthy seedling were tested by the Oregon State University soil testing laboratory, and it was found that the Ca^{++} level in the tube containing the dead seedling was over six times that in the tube containing the healthy seedling (Appendix 11). The remedy was determined by consultation with the U. S. Forest Service nursery at Beaver Creek, the B. C. Forest Service, and Dr. P. Owston of the PNW Forest and Range Experiment Station. It involved two treatments: 1) acidification of the irrigation water to pH 4.5 by addition of H_3PO_4 (Jaramillo and Owston 1977), and 2) reduction of pH of the medium and precipitation of Ca^{++} by periodic application of $FeSO_4$. We found that the B. C. Forest Service apply nutrient solution to hemlock seedlings once a week for three weeks, then on the fourth week they substitute 0.001 m $FeSO_4$ solution. We did the same and had no further problems.

3. Recommended medium and nutrients.

For hemlock seedlings being grown in Leach tubes, good results can be obtained with a 1:1 peat-vermiculite mixture. The researcher can either blend the ingredients himself, or purchase a commercial peat-vermiculite mixture which is ground to suitable fineness and contains enough moisture to handle well. Peat-vermiculite is probably the best medium to use for most purposes, provided that pH is controlled by acidification of irrigation water (suggested pH 4.5), and Ca^{++} (if possibly present) is controlled by precipitation with sulfate ion at regular intervals. One further caution about peat-vermiculite: the researcher who uses it must make sure that it is sufficiently moist before being placed into containers, because if it is too dry it is nearly impossible to wet it after it is in the containers. Water will "channel" through it without wetting most of it, and seedling mortality will result.

4. Miscellaneous.

Botrytis is a serious problem at many hemlock-growing facilities, because the drooping growth habit of hemlock seedlings makes them tangle together in a mat, holding dampness and facilitating spread of the fungus. We were able to keep our seedlings far enough apart not to tangle, and observed no instances of *Botrytis*.

Stratification is a needless waste of time and effort which are better directed elsewhere. Western hemlock germinates adequately without it (Ching 1958); among the provenances we tested germination was substantially complete within four weeks.

Time and effort can also be saved by use of clear plastic to cover racks of tubes after sowing and watering. The plastic holds moisture and obviates necessity for frequent watering until germination. As soon as germinants begin to appear, the plastic should be removed.

Figure 13. 38-week old western hemlock seedlings grown in three different media: left, black forest soil; middle, red gravelly soil; right, peat-vermiculite. Sown December 5, 1977 and photographed August 28, 1978.

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APPENDICES

Appendix 1. Cone Length, Cone Weight, and Cone Scale Width (Unweighted Average of Family Data for 13 Provenances).

Prov. Name	# of Fam's.	Weight (g)	Std. Dev. (g)	Length (mm)	Std. Dev. (mm)	Scale Width (mm)	Std. Dev. (mm)
Stewart's Pt.	3	0.262	0.093	17.68	2.11	6.11	0.13
Korbel	7	0.313	0.083	19.00	2.25	5.99	0.88
Coos Bay	10	0.448	0.098	20.75	1.86	7.01	0.71
Alsea	4	0.526	0.099	22.80	1.92	6.95	0.18
Siletz	3	0.342	0.081	18.26	1.29	7.12	0.46
Grays Hbr.	9	0.304	0.059	17.43	0.79	6.18	0.80
Mahatta R.	10	0.372	0.075	20.47	1.58	6.46	0.62
Q. Ch. Is.	10	0.290	0.081	17.85	2.28	6.53	0.94
Naukati B.	4	0.352	0.149	19.33	2.86	6.21	0.76
Molalla	8	0.431	0.045	21.94	1.23	6.90	0.54
Priest 700	3	0.423	0.088	24.42	2.14	6.44	0.82
Priest 1,400	3	0.261	0.066	19.20	0.58	6.13	0.34
Salmo-Cr.	4	0.285	0.066	20.48	2.05	5.80	0.30

Appendix 2. Seed Weight (Unweighted Average of Family Data for 22 Provenances).

Provenance Name	# of Fam.	Weight (mg)	Std. Dev.
Stewart's Point	3	196	34
Korbel	7	206	38
Coos Bay	10	248	43
Alsea	4	203	15
Siletz	3	179	19
Netarts Bay	3	166	21
Elk Rock	4	192	27
Grays Harbor	9	173	34
Snoqualmie	4	211	16
Neah Bay	3	178	11
Nootka Sound	10	274	33
Mahatta River	10	225	32
Q. Charlotte Is.	10	204	30
Naukati Bay	4	238	51
Auke Bay	mix	160	--
Molalla	8	221	19
Cougar	4	224	36
Carbon Ranger Station	4	229	22
Troy, Montana	3	198	10
Priest R. (700 m)	2	198	17
Priest R. (1,400 m)	3	184	3
Salmo-Creston	4	183	6
MEAN		204	24

Appendix 3. Correlations of Cone Weight, Seed Weight, Shoot Size, Biomass, Latitude, Elevation, and Distance from the Pacific Ocean.

Correlation Between	df	r	t	$t_{.05}$
Cone Weight and Seed Weight	11	0.46	1.94	2.201
Cone Weight and Shoot Size	11	0.56	2.24*	2.201
Cone Weight and Biomass	11	0.57	2.30*	2.201
Cone Weight and Latitude, Coastal Provenances Only	7	-0.07	0.23	2.365
Seed Weight and Shoot Size	19	0.31	1.42	2.093
Seed Weight and Biomass	19	0.30	1.38	2.093
Seed Weight and Latitude, Coastal Provenances Only	13	0.03	0.11	2.160
Seed Weight and Latitude, Coastal Provenances Only, Seed Obtained from IFA	4	-0.17	0.34	2.776
Seed Weight and Latitude, Coastal Provenances Only, Seed I Extracted and Cleaned	7	0.32	0.89	2.365
Seed Weight and Elevation	19	0.10	0.44	2.093
Seed Weight and Distance from Pacific Ocean	19	-0.17	0.76	2.093

Below are two correlations known to be good--compare t values:

Shoot Size and Latitude, Coastal Provenances Only	13	0.66	3.17**	2.160
Shoot Size and Biomass	19	0.94	11.71***	2.093

Appendix 4. Terminal Buds Set: Percent by Family on Seven Dates, Family 50% Dates, and Provenance Means in Calendar and Sequential Dates (Days Before Oct. 15).

Provenance	Fam.	7/18	8/2	8/23	9/8	9/29	10/17	11/10	50% Date	Prov. Mean (Cal.)	Prov. Mean (Seq.)
Stewart's Pt.	1	0.00	0.00	0.00	0.00	0.44	0.62	0.67	Oct. 5		
	2	0.00	0.00	0.00	0.00	0.39	0.72	0.79	Oct. 5	10/7	8
	3	0.00	0.00	0.00	0.00	0.18	0.62	0.82	Oct. 12		
Korbel	4	0.00	0.00	0.00	0.04	0.22	0.54	0.82	Oct. 15		
	5	0.00	0.00	0.00	0.15	0.42	0.60	0.89	Oct. 7	10/1	14
	6	0.00	0.00	0.10	0.47	0.73	0.75	1.00	Sep. 11		
Coos Bay	3	0.00	0.00	0.02	0.40	0.86	0.97	1.00	Sep. 13		
	5	0.00	0.00	0.00	0.23	0.73	0.90	1.00	Sep. 19	9/16	29
	10	0.00	0.00	0.00	0.22	0.89	0.89	1.00	Sep. 17		
Alsea	1	0.00	0.00	0.00	0.39	0.97	0.98	1.00	Sep. 12		
	2	0.00	0.00	0.00	0.57	0.97	1.00	1.00	Sep. 6	9/11	34
	3	0.00	0.00	0.00	0.25	0.92	0.98	1.00	Sep. 16		
Netarts Bay	2	0.00	0.00	0.03	0.27	0.88	0.97	1.00	Sep. 16		
	4	0.00	0.00	0.02	0.62	0.90	0.92	1.00	Sep. 5	9/10	35
	8	0.00	0.00	0.05	0.50	0.84	0.88	1.00	Sep. 8		
Elk Rock	4250	0.00	0.00	0.29	0.50	0.92	1.00	1.00	Sep. 2		
	4280	0.00	0.00	0.16	0.44	0.89	0.98	1.00	Sep. 6	9/3	42
	4283	0.00	0.00	0.32	0.62	0.97	0.98	1.00	Sep. 1		
Grays Harbor	4	0.00	0.00	0.04	0.50	0.93	1.00	1.00	Sep. 8		
	6	0.00	0.00	0.09	0.85	0.97	1.00	1.00	Sep. 1	9/5	40
	7	0.00	0.00	0.09	0.61	0.97	1.00	1.00	Sep. 5		

Appendix 4. (cont.)

Provenance	Fam.	7/18	8/2	8/23	9/8	9/29	10/17	11/10	50% Date	Prov. Mean (Cal.)	Prov. Mean (Seq.)
Snoqualmie	4843	0.00	0.00	0.04	0.44	0.92	0.98	1.00	Sep. 11		
	4845	0.00	0.00	0.16	0.76	1.00	1.00	1.00	Sep. 1	9/4	41
	4847	0.00	0.00	0.15	0.78	1.00	1.00	1.00	Sep. 1		
Neah Bay	1	0.00	0.00	0.21	0.66	1.00	1.00	1.00	Sep. 2		
	3	0.00	0.00	0.33	0.80	0.91	0.96	1.00	Aug. 29	8/29	47
	6	0.00	0.00	0.46	0.90	1.00	1.00	1.00	Aug. 24		
Nootka Sd.	38	0.00	0.00	0.43	0.90	1.00	1.00	1.00	Aug. 25		
	45	0.00	0.00	0.44	0.98	1.00	1.00	1.00	Aug. 25	8/24	52
	46	0.00	0.00	0.56	0.98	1.00	1.00	1.00	Aug. 21		
Mahatta R.	7	0.00	0.00	0.64	1.00	1.00	1.00	1.00	Aug. 18		
	9	0.00	0.00	0.65	0.97	1.00	1.00	1.00	Aug. 18	8/21	55
	10	0.00	0.00	0.42	0.92	0.95	0.95	1.00	Aug. 26		
Q. Char. Is.	803	0.00	0.10	0.62	1.00	1.00	1.00	1.00	Aug. 18		
	817	0.06	0.10	0.78	1.00	1.00	1.00	1.00	Aug. 14	8/16	60
	828	0.00	0.20	0.67	1.00	1.00	1.00	1.00	Aug. 15		
Naukati Bay	1	0.24	0.52	0.85	1.00	1.00	1.00	1.00	Aug. 1		
	2	0.34	0.70	0.91	1.00	1.00	1.00	1.00	Jul. 25	7/28	79
	3	0.42	0.55	0.96	1.00	1.00	1.00	1.00	Jul. 27		
Auke Bay	-	0.40	0.65	1.00	1.00	1.00	1.00	1.00	Jul. 24	7/24	83
Molalla (Mt. Hood)	4	0.00	0.32	0.74	1.00	1.00	1.00	1.00	Aug. 11		
	5	0.00	0.05	0.59	1.00	1.00	1.00	1.00	Aug. 19	8/17	59
	6	0.00	0.00	0.56	0.98	1.00	1.00	1.00	Aug. 21		

Appendix 4. (cont.)

Provenance	Fam.	7/18	8/2	8/23	9/8	9/29	10/17	11/10	50% Date	Prov. Mean (Cal.)	Prov. Mean (Seq.)
Cougar	6266	0.00	0.00	0.41	0.71	1.00	1.00	1.00	Aug. 26		
(Mt. S.H.)	6274	0.00	0.00	0.26	0.68	1.00	1.00	1.00	Sep. 1	8/27	49
	6278	0.00	0.00	0.51	0.84	0.97	0.97	1.00	Aug. 23		
Carbon R.S.	6804	0.00	0.00	0.36	0.85	0.98	1.00	1.00	Aug. 28		
(Mt. Rnr.)	6807	0.00	0.00	0.33	0.97	1.00	1.00	1.00	Aug. 27	8/27	49
	6810	0.00	0.00	0.40	1.00	1.00	1.00	1.00	Aug. 26		
Priest R.	2	0.16	0.55	0.90	1.00	1.00	1.00	1.00	Jul. 31		
(700 m)	3	0.00	0.10	0.60	1.00	1.00	1.00	1.00	Aug. 19	8/9	67
Priest R.	4	0.02	0.28	0.74	0.98	1.00	1.00	1.00	Aug. 12		
(1400 m)	5	0.56	0.80	1.00	1.00	1.00	1.00	1.00	Jul. 14	7/23	84
	6	0.54	0.70	1.00	1.00	1.00	1.00	1.00	Jul. 13		
Salmo-Creston	1	0.18	0.45	0.82	1.00	1.00	1.00	1.00	Aug. 5		
	2	0.42	0.52	0.88	1.00	1.00	1.00	1.00	Aug. 1	8/3	73
	3	0.14	0.48	0.82	0.95	1.00	1.00	1.00	Aug. 3		

Appendix 5. Bud Burst: Percent by Provenance on Three Dates; Provenance 50% Dates, Calendar and Sequential (Days Before May 7).

Provenance	Apr. 16	Apr. 29	May 14	50% Dates (Cal.)	50% Dates (Seq.)
Alsea	0.00	0.18	1.00	May 5	2
Elk Rock	0.06	0.38	0.88	May 3	4
Grays Harbor	0.00	0.43	0.57	May 1	6
Snoqualmie	0.00	0.50	0.94	Apr. 29	8
Neah Bay	0.00	0.36	0.81	May 4	3
Nootka Sound	0.04	0.54	1.00	Apr. 28	9
Mahatta River	0.08	0.56	0.92	Apr. 27	10
Queen Charlotte Is.	0.23	0.85	1.00	Apr. 22	15
Naukati Bay	0.48	0.91	1.00	Apr. 17	20
Auke Bay	0.50	1.00	1.00	Apr. 16	21
Molalla (Mt. Hood)	0.26	0.79	1.00	Apr. 22	15
Cougar (Mt. St. Helens)	0.16	0.52	0.96	Apr. 28	9
Carbon (Mt. Rainier)	0.21	0.79	0.92	Apr. 22	15
Priest River (700 m)	0.47	0.94	1.00	Apr. 17	20
Priest River (1,400 m)	0.81	1.00	1.00	Apr. 6	31
Salmo-Creston	0.93	1.00	1.00	Mar. 31	37

Appendix 6. Seedlings Surviving Four Low Temperature Tests; Data in Percent and in Arcsin $\sqrt{\%}$ (In Parentheses).

Provenance	Nov. Freeze	Amb. Win.	-17.5° C	-30°C
Stewart's	12 (19)	0 (0)	0 (0)	0 (0)
Korbel	39 (38)	2 (8)	0 (0)	0 (0)
Coos Bay	94 (79)	18 (25)	0 (0)	0 (0)
Alsea	98 (85)	44 (42)	4 (12)	0 (0)
Netarts Bay	98 (83)	19 (26)	14 (22)	0 (0)
Elk Rock	99 (87)	59 (50)	14 (22)	0 (0)
Grays Hbr.	100 (90)	40 (39)	14 (22)	0 (0)
Snoqualmie	100 (90)	86 (68)	50 (45)	0 (0)
Neah Bay	100 (90)	59 (50)	18 (25)	0 (0)
Nootka Sd.	100 (90)	87 (69)	59 (50)	2 (3)
Mahatta R.	100 (90)	96 (78)	100 (90)	2 (3)
Q. Char. Is.	100 (90)	100 (90)	81 (64)	0 (0)
Naukati B.	100 (90)	96 (78)	100 (90)	40 (39)
Auke Bay	100 (90)	100 (90)	100 (90)	65 (54)
Molalla	100 (90)	83 (66)	95 (77)	0 (0)
Cougar	100 (90)	89 (71)	86 (68)	0 (0)
Carbon	100 (90)	95 (77)	71 (57)	0 (0)
Pr. R., lo	100 (90)	94 (76)	75 (60)	0 (0)
Pr. R., hi	100 (90)	100 (90)	100 (90)	8 (16)
Salmo-Cr.	100 (90)	97 (80)	100 (90)	40 (39)

Regressions for survival (arcsin$\sqrt{\%}$) of coastal provenances (Nos. 1-15) with respect to latitude of origin.

Nov. Freeze: arcsin$\sqrt{\%}$ of survival = -363 + 9.92 (Lat.); r^2 = 0.94.

Appendix 6. (cont.)

Amb. Winter: $\arcsin\sqrt{\%}$ of survival = $-295 + 7.32$ (Lat.); $r^2 = 0.88$.

$-17.5°C$ Test: $\arcsin\sqrt{\%}$ of survival = $-314 + 7.33$ (Lat.); $r^2 = 0.81$.

$-30°C$ Test: $\arcsin\sqrt{\%}$ of survival = $-320 + 6.35$ (Lat.); $r^2 = 0.93$.

Appendix 7. Composite Cold Survival Through Four Low Temperature Tests.

$$\text{Composite Survival} = \frac{\Sigma(\text{Survival Through Four Tests}^{1})}{4}$$

Provenance	Composite Cold Survival Percent	Composite Cold Survival Arcsin $\sqrt{\%}$
Stewart's Point, California	0.03	0.10
Korbel, California	0.10	0.18
Coos Bay, Oregon	0.28	0.32
Alsea, Oregon	0.36	0.37
Netarts Bay, Oregon	0.32	0.35
Elk Rock, Washington	0.43	0.41
Grays Harbor, Washington	0.38	0.38
Snoqualmie, Washington	0.59	0.50
Neah Bay, Washington	0.44	0.42
Nootka Sound, British Columbia	0.62	0.52
Mahatta River, British Columbia	0.74	0.60
Queen Charlotte Is., British Columbia	0.70	0.57
Naukati Bay, Alaska	0.84	0.66
Auke Bay, Alaska	0.91	0.73
Molalla (Mt. Hood), Oregon	0.70	0.57
Cougar (Mt. St. Helens), Washington	0.69	0.56
Carbon (Mt. Rainier), Washington	0.66	0.54
Priest River, Idaho (700 m)	0.67	0.55
Priest River, Idaho (1,400 m)	0.77	0.61
Salmo-Creston Summit, British Columbia	0.84	0.66

For coastal provenances (Stewart's Point through Auke Bay), the correlation between composite cold survival and latitude is 0.97 ($r^2 = 0.94$).

[1]Appendix 6.

Appendix 8. Examples of Between-Family-Within-Provenance Variation: a) Korbel Family 6's Earlier Bud Set and Lesser Frost Injury; b) Stewart's Point Family 3's Later Bud Set and Greater Frost Injury.

a) Korbel, California

Buds Set on Sep. 29, 1978

	Set	Not Set	
Family 6	13	7	
Families 4, 5	17	53	$\chi^2 = 11.3$**[1]

Injury by Freeze on Nov. 14 and 15, 1978

	None	Slight	Moderate	
Family 6	14	2	4	
Families 4, 5	16	16	38	$\chi^2 = 15.7$**

b) Stewart's Point, California

Buds Set on Sep. 29, 1978

	Set	Not Set	
Family 3	5	27	
Families 1, 2	17	32	$\chi^2 = 5.7$*

Injury by Freeze on Nov. 14 and 15, 1978

	None	Slight	Moderate	
Family 3	1	7	24	
Families 1, 2	8	17	24	$\chi^2 = 6.3$*

[1]** $P < 0.01$.
* $P < 0.05$.

Appendix 9. Comparative Survival of Seedlings through −30°C, Freeze Cycles in Small-Scale Test Runs Performed in January, vs. Mass Trials Performed on February 14-17, 1979

Provenance	January Date	January Tested	January Survived	February % Survived
		COASTAL		
Coos Bay, Oregon	12	2	0	0
Alsea, Oregon	17	2	0	0
Netarts Bay, Oregon	17	2	0	0
Snoqualmie, Washington	19	2	2	0
Queen Charlotte Is., B. C.	24	2	2	0
Naukati Bay, Alaska	19	2	2	40
Auke Bay, Alaska	12	2	2	65
Auke Bay, Alaska	17	2	2	65
		CASCADE MOUNTAINS		
Molalla (Mt. Hood), Oregon	17	2	2	0
Carbon Ranger Station (Mt. Rainier), Washington	12	2	2	0
		ROCKY MOUNTAINS		
Priest R., Idaho (700 m)	24	2	2	0
Priest R., Idaho (1,400 m)	19	2	1	8
Priest R., Idaho (1,400 m)	24	1	1	8
Salmo-Creston Summit, B. C.	17	2	2	40

Appendix 10. Relationship of soil pH to seedling injury occurring in Summer 1978.

Date	Provenance	Healthy	Injured	pH ± 0.2 at Cell Drain-hole[1]
Jul. 18	Korbel		X	6.0
Jul. 18	Auke Bay	X		≤ 4.5
Jul. 22	Naukati Bay	X		5.0
Jul. 22	Stewart's Pt.		X	6.3
Jul. 22	Stewart's Pt.	X		≤ 4.5
Jul. 22	Korbel		X	6.0
Jul. 22	Korbel		X	6.0
Jul. 22	Stewart's Pt.		X	6.2
Jul. 22	Priest R. (700 m)	X		5.3
Jul. 22	Priest R. (1,400 m)	X		5.3
Jul. 22	Coos Bay		X	6.4
Jul. 22	Alsea	X		≤ 4.5
Jul. 22	Alsea	X		≤ 4.5
Jul. 25	Coos Bay		X	6.0
Jul. 25	Naukati Bay	X		5.2
Jul. 25	Nootka Sound		X	5.3
Jul. 26	Stewart's Pt.		X (dead)	7.5
Jul. 26	Stewart's Pt.	X		≤ 4.5
Jul. 26	Korbel		X (dead)	7.5
Jul. 27	Stewart's Pt.	X		≤ 4.5
Jul. 27	Stewart's Pt.		X (dead)	6.5

[1]Colorimetric method used does not indicate exact values below 4.5.

Appendix 10. (cont.)

Date	Provenance	Healthy	Injured	pH $\pm$ 0.2 at Cell Drain-hole[1]
Jul. 27	Stewart's Pt.		X (dead)	7.5
Jul. 27	Korbel		X (dead)	7.5
Jul. 31	Korbel		X	6.0
Jul. 31	Stewart's Pt.		X	6.0
Jul. 31	Neah Bay		X (dead)	6.0
Aug. 7	Netarts Bay	X		$\leq$ 4.5
Aug. 7	Netarts Bay		X	7.0
Aug. 10	Alsea	X		$\leq$ 4.5
Aug. 10	Korbel	X		$\leq$ 4.5
Aug. 10	Stewart's Pt.		X	6.0

pH Summary for 18 Injured Seedlings

Mean	6.43
Std. Dev.	0.67
Range	5.3-7.5

pH Summary for 13 Healthy Seedlings

Mean	4.72
Std. Dev.	0.34
Range	$\leq$ 4.5-5.3

[1]Colorimetric method used does not indicate exact values below 4.5

Appendix 10. (cont.)

Additional pH Tests

Material	pH ± 0.2
"Black Soil" (Chapter 6). Several tubes containing healthy Alsea 152 seedlings from our preliminary soil test were tested.	4.5
"Red Soil" (Chapter 6). Several tubes containing healthy Alsea 152 seedlings from our preliminary soil test were tested.	6.0[1]
Nutrient Solution (2.5 g/l of 20-19-18 in water from spigot in greenhouse or shade house).	6.0
Water from spigot in shade house.	6.5
Water from spigot in greenhouse.	6.7

[1]This appears contradictory in the light of the summaries of pH levels for healthy and injured seedlings on the previous page. However, the injury reported developed on seedlings growing in peat-vermiculite in the pH range of 5.2-7.5, while the "red soil" was mineral. Apparently, the same pH levels in the two different soils did not have the same effect.

Appendix 11. Analyses of Soils in Tubes Containing Healthy and Dead Seedlings Submitted Sep. 6, 1978 to Soil Testing Laboratory, Oregon State University.

Sample	Extractable Cations (meq/100 g) K	Ca	Mg	Nitrogen (NH_4 only)
Korbel, dead seedling, pH 6.0	3.9	57.6	24.8	413.30
Auke Bay, healthy seedling, pH 4.5	5.0	9.1	5.08	113.55

Appendix 12. List of Seed Cooperators

Provenance	Cooperator
Stewart's Point, Calif.	Don Richardson P.O. Box 1 Stewart's Point, CA 95480
Korbel, California	Jim Rydelius Simpson Timber Co. P.O. Drawer V Arcata, CA 95521
Coos Bay, Oregon	Jack Wanek Oregon State Forestry Department 2600 State Street Salem, OR 97310
Alsea, Oregon	Don Oliver U. S. Forest Service Beaver Creek, OR 97004
Siletz, Oregon	Phil Hahn Georgia-Pacific P.O. Box 1618 Eugene, OR 97401
Netarts Bay, Oregon	Don Lester Crown Zellerbach P.O. Box 368 Wilsonville, OR 97070
Elk Rock, Washington	Jess Daniels Weyerhaeuser Research Center 505 N. Pearl Street Centralia, WA 98531
Grays Harbor, Washington	Archie Selders ITT-Rayonier 409 E. Harvard Ave. Shelton, WA 98584
Snoqualmie, Washington	Jess Daniels Weyerhaeuser Research Center 505 N. Pearl Street Centralia, WA 98531
Neah Bay, Washington	Don Lester Crown Zellerbach P.O. Box 368 Wilsonville, OR 97070

Appendix 12. (cont.)

Provenance	Cooperator
Nootka Sound, B. C.	Mike Meagher B. C. Forestry Service 514 Government Street Victoria, B. C. V8V 1X5
Mahatta River, B. C.	Mike Meagher B. C. Forestry Service 514 Government Street Victoria, B. C. V8V 1X5
Queen Charlotte Is., B. C.	Mike Meagher B. C. Forestry Service 514 Government Street Victoria, B. C. V8V 1X5
Naukati Bay, Alaska	Al Harris U. S. Forest Service 709 W. 9th Street Juneau, AK 99802
Auke Bay, Alaska	Al Harris U. S. Forest Service 709 W. 9th Street Juneau, AK 99802
Cordova, Alaska[1]	Ed Ryberg, or Ray Weiss U. S. Forest Service P.O. Box 280 Cordova, AK 99574
Molalla, Oregon (Mt. Hood)	Troy Moore Publishers Paper 419 Main Street Oregon City, OR 97045
Cougar, Washington	Jess Daniels Weyerhaeuser Research Center 505 N. Pearl Street Centralia, WA 98531
Carbon Ranger Station, WA (Mt. Rainier)	Jess Daniels Weyerhaeuser Research Center 505 N. Pearl Street Centralia, WA 98531

[1]Seed from four trees in the Cordova and Montague Island areas was received a year late and consequently not used. It was given to Dr. Don Lester of Crown Zellerbach.

Appendix 12. (cont.)

Provenance	Cooperator
Glacier, Washington[1]	Ted Deer Georgia-Pacific 300 Laurel Street Bellingham, WA 98225
Priest River, Idaho Priest River, Idaho	Cal Carpenter U.S. Forest Service Priest River Experimental Forest Priest River, ID 83856
Salmo-Creston Summit, B. C.	Mike Meagher B. C. Forestry Service 514 Government Street Victoria, B. C. V8V 1X5
Troy, Montana[2]	Mel Parker St. Regis Paper Co. P.O. Box V-X Libby, MT 59923

[1]Because of a poor seed crop in the Mt. Baker area in 1977, we were unable to include this provenance in our experiments.

[2]Used only for seed weight study. The collection area was deemed too close to Priest River, ID and Salmo-Creston Summit, B. C.