Geographic Variation in Douglas-fir from the Coastal Ranges of California

I. Seed, Seedling Growth and Hardiness Characteristics

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Introduction

Coastal Douglas-fir (Pseudotsuga *menziesii* (Mirb.) Franco var. *menziesii)* is a component of many forest types throughout its range from British Columbia to northern California, and there is ample evidence of adaptive variation in growth rate and hardiness. Most provenance studies have been carried out in Europe where, for climatic reasons, emphasis has been placed on Washington and British Co-

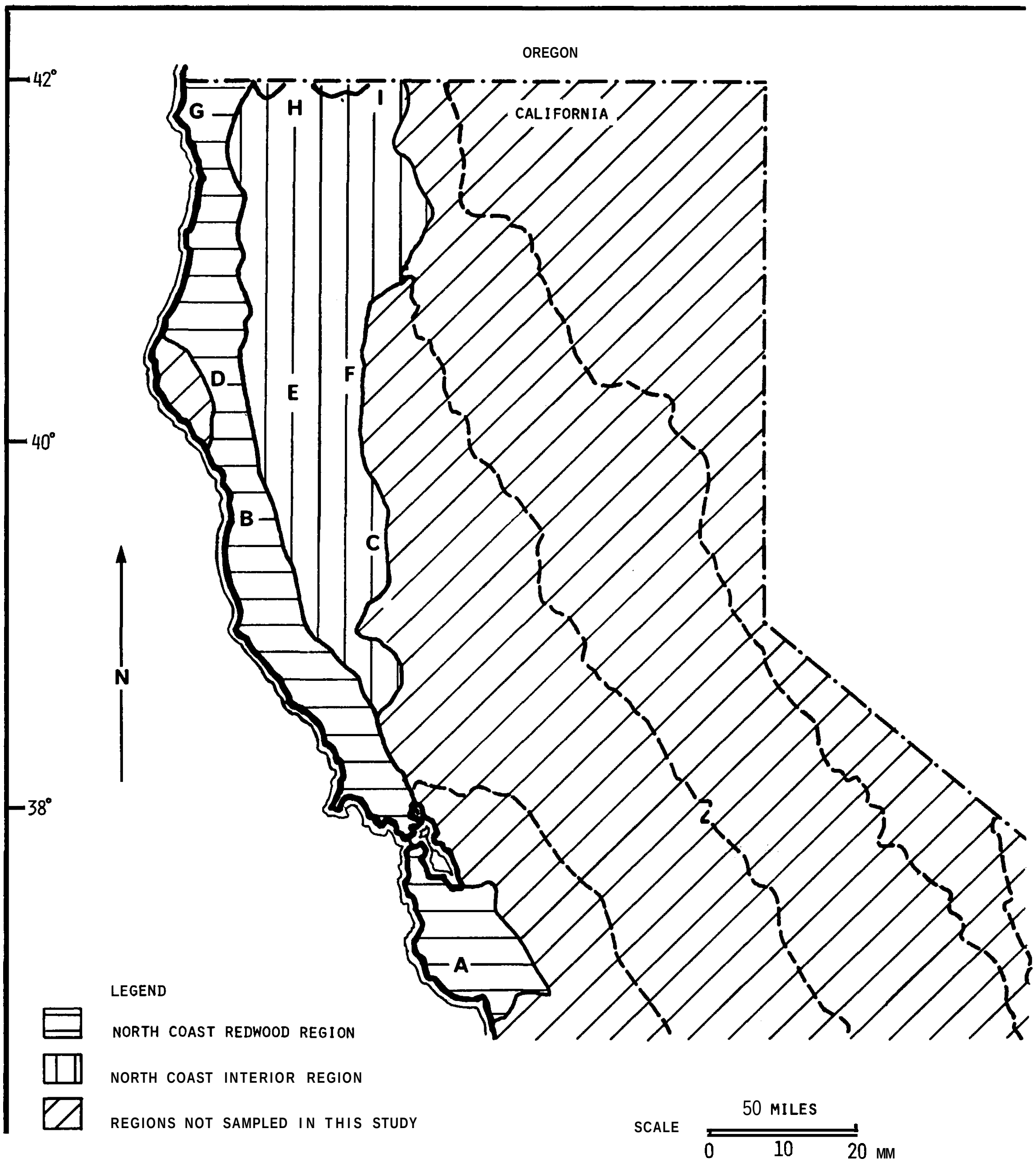

Figure 1. — Physiographic and climatic regions of northern California (after Californian Tree Seed Zone Map, Buck *et* al. (1970),), showing sampling locations (A...... I).

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lumbia sources (Schober 1963, Hattemer and König 1975). In the western United States major trials (Rowe and Ching 1973, Silen 1964) have also concentrated on more northerly sources. The IUFRO collection (Birot 1972, Kleinschmit *et al.* 1974) did include a number of samples from northern California, but low elevation coastal fog-belt sites were not well represented. Sweet (1965) found that, in New Zealand, seedlings from such sites grew faster than those from more inland locations and higher latitudes.

This paper reports an investigation of variation in seed characteristics, seedling growth and phenology, response to moisture stress, and resistance to winter cold damage, exhibited by Douglas-fir from the coastal ranges of northern California.

The region sampled is defined by the Pacific Ocean to west, Sacramento Valley to the east, in the north by the Oregon border (Lat. 42^{0} N) and the south by Monterey Bay (Lat. 37^{0} N). *(Figure 1).* In the north and north-easterly direction the boundary is arbitrary in that the Douglas-fir distribution is continuous into southern Oregon and the northern Sierra Nevada. In other directions, it is delineated by the species' range discounting several small isolated populations to the south (Griffin 1964).

The area consists of two distinct though contiguous mountain regions — the Klamath Mountains and California Coast Range. These differ in age, geologic character and complexity, height and east-west extent (Whittaker 1960).

Climate

Topography is the over riding determinant of the climate, and in contrast to the more usual latitudinal gradient, isotherms parallel the north-south alignment of the outer coast ranges (Sprague 1941).

The immediate coastal area and seaward facing slopes have a true marine climate marked by moderate temperatures with small diurnal and annual range, and the more easterly (interior) ranges experience more continental conditions (Visher 1954). Growing season precipitation is extremely limited, but advectional fog adds significantly to soil moisture along the coast (Azevedo and Morgan 1974). The fog also reduces air temperature, and increases humidity.

Within this pattern climate varies with elevation though the relationship is not consistent over the whole study area. Baker (1944) reported that, for the Klamath Mountains and inner Coast Ranges mean temperature of the hottest month decreased by 1.7^{0} F/1000 ft., but, because of the influence of fog, mean temperature actually increased with elevation on the seaward slopes.

Occurrence of Douglas-fir

Excluding small sub-alpine areas the forest vegetation may be broadly classified into two types (Daubenmire 1969) co-incident with the North Coast Redwood and North Coast Interior regions designated by the Forest Tree Seed Committee of the Society of American Foresters (Buck *et al.* 1970) *(Figure 1).* Douglas-fir is an important component of both types — successional to coast redwood in the former, and the major climax dominant in the latter.

Sampling

Sampling was designed to cover the species' distribution in terms of latitude, elevation and distance from the ocean. Since the steepest environmental gradients run east-west collections were made at up to three locations along an east-west transect at each of four latitudinal intervals *(Figure 1, Table 1).* The varying number of locations sampled in each transect reflects the greater environmental range of the species in the northern part of the study area. At each location the altitudinal range of the Douglas-fir was sampled — ideally with collections from two trees per elevational interval of 250 ft. Each sample point at a particular elevation is referred to as a stand. Collections were made over a four week period in August, 1971.

Assessment Methods

1. *Seed Characteristics*

Each seedlot was dewinged, cleaned in an air column, counted and weighed to determine mean seed weight. Prior to weighing a cutting test was used to confirm that at least 80% of the seed were full. One hundred seeds from each lot were moist stratified for four weeks at 2^{0} C, and germinated under an 8-hour light (27^{0} C)/16-hour dark (18^{0} C) regime. Percentage germination after seven days was taken as a measure of germination rate.

2. *Response to Moisture Stress*

Because of the effect of advectional fog on soil moisture (Azevedo and Morgan 1974) it is likely that the post-germination micro-environment in the inner ranges differs from that nearer the coast with respect to moisture conditions. The hypothesis that this is reflected by source-related variation in response to moisture stress was tested under nursery conditions.

Following moist stratification seeds were germinated and pricked out into two-inch styroblock containers when the radicles were approximately 1 cm long. Because of the danger of undefined interaction with watering regimes fertilizer was not added to the soil, and growth was dependent upon nutrients available in the forest top soil/sand (3 : 1) medium.

Table 1. — Origin of Seed Samples (Locations grouped according to Latitude).

Location		Lat. (N) °	Lat. (N) '	Long. (W) °	Long. (W) '	Distance from Ocean(miles)	Average Location Indices+ Elevation (ft.)	Average Location Indices+ Elevation Range Sampled (ft.)	Stands No.	Parent Trees Total No.
Gasquet	(G)*	41	47	124	00	7	1847	3500	10	19
Happy Camp	(H)	41	52	123	28	36	2437	3450	15	34
Mt. Ashland	(I)	41	56	122	47	74	3238	3200	11	26
Humboldt Redwood State Park	(D)*	40	14	124	00	16	1490	2900	12	22
Forest Glen	(E)	40	23	123	23	42	3532	2250	8	14
Harrison Gulch	(F)	40	20	123	00	58	3567	1750	4	9
Jackson State Forest	(B)*	39	32	123	36	11	1250	2450	10	19
Bear Creek (Mendocino N.F.)	(C)	39	17	122	50	50	3290	2250	6	11
Santa Cruz	(A)*	37	08	122	11	5	1292	2650	9	27

* Located in North Coast Redwood Region. (Buck *et al.* 1970).

+ For location indices of individual families see Griffin (1974) unpubl.

A split-plot design was adopted with three watering regimes as main treatments, twice replicated, and 181 families as sub-treatments in 6-seedling plots.

A pressure bomb (Waring and Cleary 1967) was used to monitor pre-dawn plant moisture stress on control seedlings planted systematically throughout each main plot, and seedlings were re-watered to saturation when values exceeded 30, 60 or 90 p.s.i. respectively for the three stress regimes. These regimes were maintained from early June through September, and all seedlings periodically scored for the presence of terminal buds. Many seedlings made more than one growth flush, and buds were considered to have burst if at least one needle had emerged through the scales. The date of final bud set for each seedling was expressed as the number of days from pricking out (April 12th). At the end of the growing season, total height and hypocotyl length were measured, and epicotyl length determined by subtraction.

Date of final bud set and epicotyl length were used as indices of response to stress. As expected watering regime effects were significant (Griffin 1974 unpubl.), and preliminary analyses showed that seed-source related differences were most clearly demonstrated through the contrast of performance under the low (30 p.s.i.) and moderate (60 p.s.i.) regimes. Families from the inner ranges set their final buds relatively earlier under the moderate stress regime, and grew relatively less than coastal families. This effect was quantified by deriving two new variables:

a) Bud Sensitivity to Stress — the difference in mean time to final terminal bud set between seedlings of the same family grown under each regime.

b) Height Growth Sensitivity — the difference in mean epicotyl length expressed as a percentage of the low stress value. The latter variable reflects the proportional loss of height growth potential due to the stress response.

3. *Growth and Phenology*

Family mean performance over all watering regimes (36 seedlings per family) was used for analysis of geographic variation in time to terminal bud set, total height and its components, hypocotyl and epicotyl lengths. Mean cotyledon number was determined from 18 seedlings per family.

All seedlings were assessed for flushing date during the spring of the second growing season, and the character expressed as days from March 16th when the first seedling flushed. Those which had been damaged by fall frost, winter cold, or insects, were excluded. Separate observations were made for terminal and lateral buds, but since a number of seedlings did not have well developed lateral branches, and since where both were present dates appeared closely correlated, only the terminal bud data is presented.

4. *Cold Hardiness*

The trial was exposed to a period of abnormally cold weather in December, 1972, with a minimum temperature of —7° F. Most seedlings were covered with snow and escaped injury, but parts of the 30 p.s.i. stress main-plots were exposed, and needle discoloration and death were apparent on some seedlings within two weeks. As all seedlings were not equally exposed the following criteria were adopted in deciding whether to assess damage in a particular sub-plot: The three sub-plots within each container section were assessed if it, together with at least one adjacent section, contained two or more damaged seedlings. Although the method was biased against sections which contained only hardy families, this was considered preferable to the possibility of including families that had in fact been under snow cover. 970 seedlings from 119 of the families were assessable by these criteria.

Each seedling within assessed sub-plots was scored on a scale 0 (no damage) —4 (dead), but as this provided no more information than a simpler analysis of the frequency of damaged seedlings, only the latter is presented.

Results

Family mean values for all variables except cold hardiness were subjected to nested analysis of variance. The latter observations required a different analysis because of their unbalanced nature.

Preliminary analysis showed that, for the majority of variables, the major contrast was between the four coastal fog-belt locations (A, B, D, G) and the five from the interior (C, E, F, H, I) *(Figure 1)* so classification into these two regions was added to locations, stands and families as levels in the analysis *(Table 2)*.

Table 2. — Variance component estimates, significance levels, and selected companent ratios for 10 characters.

Character	Components				Ratios		
	S^2_R	S^2_L	S^2_S	S^2_F	$\frac{R}{L + S}$	$\frac{R + L + S}{F}$	$\frac{L + S}{F}$
Seed Weight	0.090*	0.030**	0.014	0.12	2.05	1.09	0.37
Germination Rate	129.4*	52.2*	62.3	345.0	1.13	0.71	0.33
Cotyledon No.	0.08*	0.027**	0.024	0.14	1.56	0.86	0.36
Hypocotyl Length	0.029**	0.003	0.019**	0.030	1.38	1.70	0.73
Total Height	0.034**	0	0.005**	0.007	6.41	5.60	0.71
Epicotyl Length	0.1035**	0.0039**	0.0029*	0.011	15.22	10.03	0.62
Terminal budset	962.6**	33.2**	25.2**	83.0	16.48	12.30	0.70
Bud Sensitivity	0.052**	0	0.014	0.168	3.71	0.39	0.08
Height Sensitivity	148.6**	0	40.5	318.0	3.67	0.59	0.13
Terminal budburst	1.07	10.00**	1.67*	8.20	0.09	1.60	1.42

Convention used throughout paper: * — Sig. at 5%, ** — Sig. at 1%.

Source of Variation	d.f.	E.M.S.
Regions (R)	1	$\sigma^2_F + 2.50\ \sigma^2_S + 22.95\ \sigma^2_L + 90.36\ \sigma^2_R$
Locations (L)	7	$\sigma^2_F + 2.39\ \sigma^2_S + 19.29\ \sigma^2_L$
Stands (S)	76	$\sigma^2_F + 2.10\ \sigma^2_S$
Families (F)	96	σ^2_F
TOTAL	180	

Table 3. — Regional and location means for ten seed and seedling characteristics.

Region/ Location	Seed Weight (mg)	Germination % at 7 days	Cotyledon No.	Hypocotyl Length (cm)	Total Height (cm)	Epicotyl Length (cm)	Days to Bud Set	Bud Sensitivity (days)	Height Growth Sensitivity %	Days to Budburst
Coast: A	11.76abc[1])	30.3a	6.78a	1.28a	3.62a	2.33a	145.6a	4.2a	18.2ab	23.9b
B	10.37ab	40.7ab	6.81ab	1,27a	3.67a	2.49a	143.9a	5.5a	19.4ab	31.6a
D	12.46abcd	45.3abc	7.27bc	1.42ab	3.36b	1.94b	133.9a	3.0a	26.2ab	25.4b
G	9.61a	49.3abc	6.86ab	1.27a	3.71a	2.43a	145.5a	2.1a	13.2a	33.1a
Weighted Mean	11.51	40.5	6.93	1.31	3.60	2.28	142.3	3.7	19.4	27.9
Interior: C	12.74abcd	46.5abc	7.39c	1.39ab	2.63cd	1.25c	102.7bc	13.4a	37.1ab	27.5ab
E	13.91bcd	71.0c	7.10abc	1.57b	2.74c	1.17c	104.3b	20.5a	42.1b	25.2b
F	17.98d	66.6c	7.55c	1.69b	2.70cd	1.00c	93.1bc	14.7a	41.7b	26.3b
H	13.62bcd	52.1bc	7.32c	1.54b	2.71c	1.17c	102.0bc	14.7a	35.7ab	24.5b
I	14.82d	59.5bc	7.43c	1.61b	2.59d	0.98c	89.7c	16.8a	34.0ab	24.8b
Weighted Mean	14.28	57.7	7.35	1.56	2.67	1.11	98.2	15.7	36.9	25.2
Region Contrast (F-test)	*	*	*	**	**	**	**	**	**	n.s.
Grand Mean	12.72	49.4	7.15	1.44	3.10	1.62	119.4	9.4	28.5	26.5

[1]) For each characteristic, means with a letter in common do not differ significantly at the 5% level Scheffé Test).

Seed weight, epicotyl length, and total height, were analysed following square root transformation and the natural logarithm was appropriate in the case of bud sensitivity. In the latter case it was also necessary to add a constant term to each observation to eliminate negative values. Untransformed data were used for other characters. After analysis contrasts were calculated on transformed means and these were back-transformed for presentation *(Table 3)*.

Significance levels shown in *Table 2* were based on approximate F-tests using Satterthwaite's procedure (Ostle 1963), and since unequal size classes were involved, Scheffés test (Snedecor and Cochran 1967) was used for the multipe mean comparisons (Gill 1973).

Correlation of Characters

Before discussing the observed variation patterns it is useful to consider the degree of inter-correlation among characters *(Table 4)*. Of the 45 coefficients, 39 were significant at the 1% level — some relationships were expected because of inter-dependence of measurement methods, and others have greater biological significance. Seed weight, cotyledon number and hypocotyl length are moderately correlated expressions of embryo size. The hypocotyl forms a significant component of seedling height at the end of the growing season (46% over-all and 58% interior region seedlings, *Table 3*), so total height is influenced by seed size effects and is a less desirable index of growth per se than epicotyl length. Further discussion of growth will be restricted to the latter variable.

Epicotyl growth is strongly correlated with date of bud set (r = +0.93), but the relationship between bud burst and bud set is not strong, indicating the possibility of selection for various phenological combinations.

Cold Hardiness

Seedlings were classified by seed-source location and time of final bud set, and the percentage of damaged seedlings per class tabulated *(Table 5)*. Only classes containing an arbitrary minimum sample of 10 seedlings are shown. Chi-squared tests were used to judge the significance of class differences in frequency of damaged seedlings. There was a strong correlation between location mean date of bud set *(Table 3)* and percentage of damaged seedlings (r = +0.93) in agreement with the findings of Bialobok and Mejnartowicz (1970), and Campbell and Sorensen (1973), but cold hardiness also varied independently of bud set date (Campbell and Sorensen 1973) since seedlings which had set buds on a given date showed the same general pattern of interlocation variation as the combined analysis over all dates.

The point is best illustrated by the data for day 124 *(Table 5)*. Within locations there was not a strong association between the date at which a seedling set its terminal bud and its subsequent cold hardiness, although for the three locations, where damage varied significantly according to date (H, B, C), seedlings which set buds earliest were the most hardy.

Variation Patterns

All characters except date of bud burst differed significantly between regions *(Table 3)*. Compared with interior samples, coastal seeds were lighter and germinated more slowly. Coastal seedlings had fewer cotyledons, shorter hypocotyls, but greater epicotyl growth; grew for a longer period before setting buds; showed less bud and height sensitivity to moisture stress, and were less cold hardy.

According to the aproximate F-tests *(Table 2)*, 6 char-

Table 4. — Correlation matrix for family mean values of 10 seed and seedlings characteristics.

Character	1	2	3	4	5	6	7	8	9
Seed Weight (1)									
Germination Rate (2)	.25								
Cotyledon No. (3)	.56	.18							
Hypocotyl Length (4)	.68	.46	.44						
Total Height (5)	—.23	—.21	—.34	—.11					
Epicotyl Length (6)	—.46	—.36	—.47	—.47	.93				
Budset (7)	—.53	—.41	—.51	—.51	.83	.93			
Bud Sensitivity (8)	.21	.22	.08	.21	—.42	—.45	—.39		
Height Sensitivity (9)	.21	.22	.08	.26	—.39	—.44	—.41	.62	
Bud burst (10)	—.30	—.07	—.14	—.27	.37	.42	.36	—.17	—.24

Critical $r_{(0.01\ 179\ \mathrm{d.f.})} = \pm 0.19$.

Table 5. — Percentage of cold damaged seedlings by seed-source location and time of final bud set*.

Location	No. <59 % Ass-essed	No. <59 % Dam-aged	Days to final bud set from April 12th: 91—124 N	91—124 %	125—138 N	125—138 %	139—152 N	139—152 %	153—159 N	153—159 %	All dates N	All dates %
Coast												
A			29	79	19	74	46	77	17	87	128	82
B			37	51	22	86	64	84	21	81	155	75
D			58	60	15	72	41	56	10	60	133	60
G			27	33	11	54	44	61			96	56
Combined:			151	57	67	75	195	71	48	79	512	69
Interior												
C	16	0	30	43							55	33
E	19	0	40	8							79	5
F	14	0	15	20							41	17
H	40	10	83	17	19	21	14	14			163	14
I	38	8	61	10							118	8
Combined:	127	5	229	17	19	21	14	14			456	13

Contrasts:		χ^2
a) All Dates — between regions		308**
within coast region		24.9**
within interior region		20.6**
b) Between dates in locations	— H	8.50*
(where significant)	B	16.31**
	C	9.76**
c) Between locations in dates	— 124 days	84**
(where significant)	138 days	49**
	152 days	42**

* Only classes with $\geqslant$10 seedlings are tabulated. The "All Dates" column includes additional seedlings that set buds at other dates.

acters also differed significantly between locations in regions, though the Scheffé tests (*Table 3*) did not always demonstrate the pairwise contrasts. Date of bud burst was the only character varying more between locations than regions, both the earliest (A) and the latest (G) being coastal.

Compared with other coastal locations (D) was distinguished by heavier seed, more cotyledons, earlier bud set and less epicotyl growth. Buds also burst earlier than those from adjacent locations to the north (G) or south (B), but timing was similar to that from the most southerly coastal source (A). Of all locations (D) showed most intermediacy between the regional groups, but for cold hardiness and growth rate there was clearly a greater affinity with other coastal sources.

Cold hardiness was the only character varying clinally with latitude (*Table 5*). 82% of exposed seedlings from (A) were damaged compared with 56% from (G) — a 5.6% increase in hardiness per degree increase in latitude. The cline was not apparent in the interior region, though the most southerly location (C) again had the greatest percentage of damaged seedlings.

No other characters showed significant single location contrasts within the interior region, though when the two most easterly locations (F, I) were compared with the other three (C, E, H) they showed earlier bud set and less epicotyl growth.

The data for characters showing a significant stand-within-location component were re-analysed to determine whether differences were demonstrable over the whole study area, and whether a relationship with elevation was apparent. Cold hardiness data was treated by grouping seedlings into 500 ft. elevation classes and testing for homogeneity of number damaged per class (*Figure 2*).

Intra-location differentiation was weak compared to that

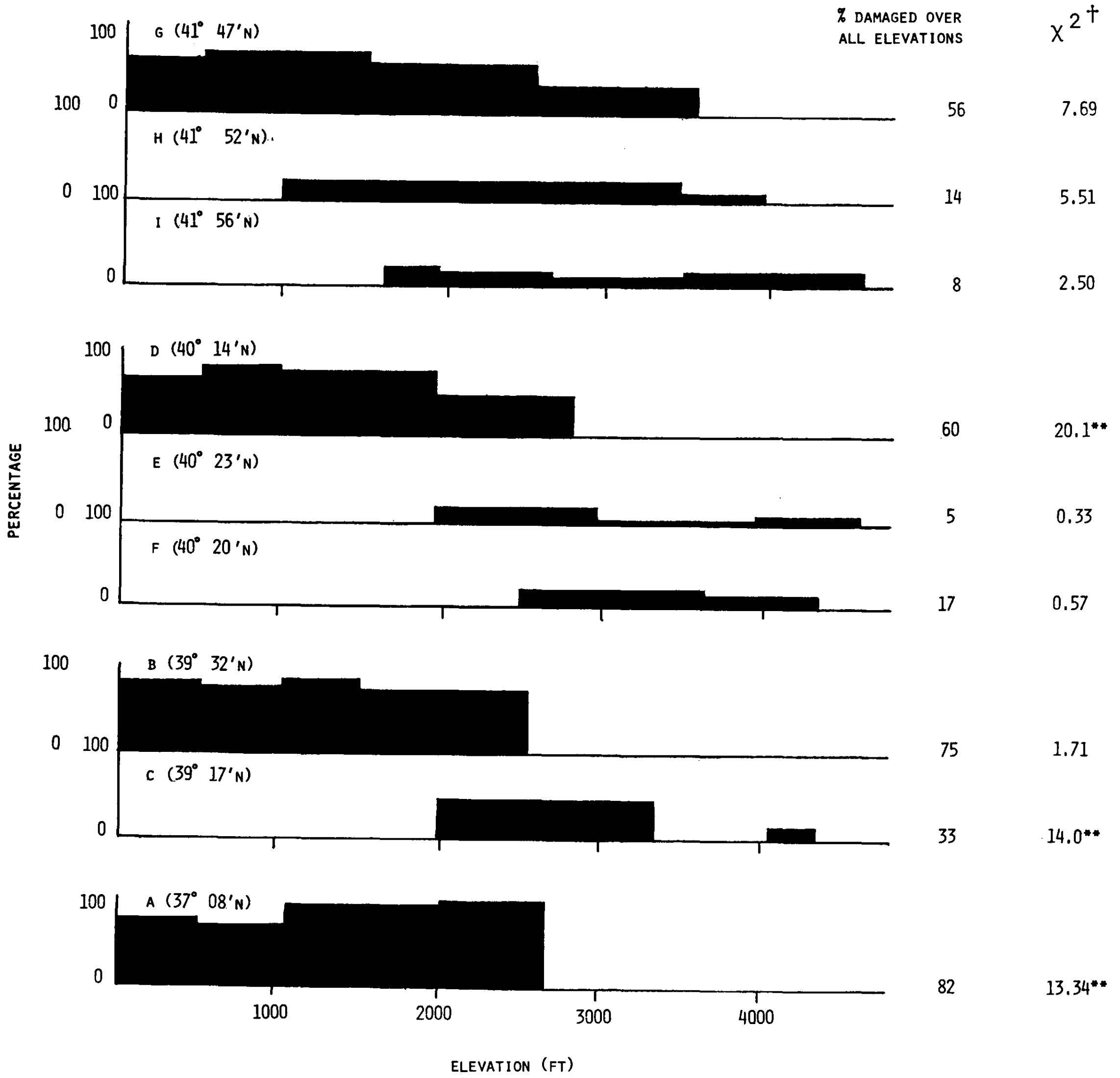

Figure 2. — Percentage of seedlings showing cold damage symptoms by elevation classes within locations.
† Chi-squared value for test of homogeneity of proportion damage per elevation class.

on a broad geographic scale, with growth and hardiness showing the most consistent variation patterns. For 8 of the 9 locations elevation was negatively correlated with time of bud set and epicotyl length, though only significantly so for 3 and 2 locations respectively. When trees within regions were combined the correlation between epicotyl length and elevation was more apparent for those from the interior region ($r = -0.42^{**}$) than from the coast ($r = -0.21^{ns}$). A trend to increased hardiness with elevation was also apparent *(Figure 2)* except for the two most southerly coastal locations (A, B). At (A) the highest elevation seedlings showed significantly more damage, though even the most hardy class contained 70% of damaged plants.

Variation in time of bud burst was quite heterogeneous over locations. At (D) there was significant stand-to-stand variation unrelated to elevation; at (A) a weak negative correlation with elevation ($r = -0.41^{*}$); and at (E) a positive correlation ($r = +0.62^{*}$). Elsewhere no pattern was apparent.

It is clear that the distribution of total geographic variation among sampling levels is not the same for all characters. The ratios of variance component estimates *(Table 2)* are used to illustrate the point. S^2_R, S^2_L and S^2_S represent geographic variation which may or may not be habitat correlated, while S^2_F is the residual between family within stand component.

Epicotyl length and terminal bud set show much greater regional differentiation $(\frac{R}{L+S} > 15)$ than seed related characteristics $(\frac{R}{L+S} = 1 < 2)$, and the greater degree of adaptation of growth to environment can also be inferred from the geographic: within stand ratio. $\frac{(R+L+S)}{F} > 10$ for epicotyl length and bud set c.f. values of $\leqslant 1$ for seed weight, germination rate, and cotyledon number. If the regional component is removed all characters vary more within stands than between, but $\frac{(L+S)}{F}$ is about twice as great for the former pair of characters as for the latter group.

Two other variation patterns are apparent: time of bud burst has more geographic than within stand variation

($\frac{R + L + S}{F} = 1.6$), but a very small regional component in the numerator; and bud and height sensitivity to moisture stress are most variable within stands ($\frac{R + L + S}{F} < 1$) with geographic variation being almost wholely regional. Since the sensitivity variables are rather arbitrary indices of response, subject to large sampling error, it is not surprising that only broad scale regional variation is demonstrable.

Discussion

The Douglas-fir population in northern California varies genetically for all characteristics assessed, with a predominant pattern of strong east-west differentiation and weak to non-significant variation with latitude and elevation. There are, however, substantial differences in the patterns exhibited by various characteristics, particularly between components of the annual cycle of growth and dormancy, and the seed related variables.

The strong regional differentiation of the growth characteristics corresponds to the climatic variation pattern. This relationship is explored in greater detail in a separate paper, but the data presented in *Table 6* is adequate for discussion of the salient factors.

Bradshaw (1965) noted that plant characteristics are frequently determined by the most adverse conditions encountered, and that permanent genetic adjustment is necessary for survival since adaptive modifications would be operative too late if initiated by the environmental conditions to which they were adaptive. The shorter period of active growth, and hence epicotyl length, for interior seed sources corresponds to a reduced frost free period and increased annual temperature range relative to the coast. On average the first fall frost occurs 48 days later in the coastal region than in the interior *(Table 6)*, and the mean temperature of the coldest month is 48^{0} F c.f. 39^{0} F. In the test environment adaptation to this climatic variation was reflected in a regional mean difference of 44 days in the date of final bud set *(Table 3)*. There was a high correlation between time of bud set and epicotyl length ($r = 0.93$) *(Table 4)*, and the interior seedlings made only 49% of the growth of those from the coast.

Regional variation in cold hardiness *(Table 5)* is paralleled by a reduction in average winter temperature, but this does not provide an adequate explanation of the latitudinal cline in the hardiness of coastal populations. There were 5.6% fewer sensitive plants per degree increase in latitude, and the cline continues into Oregon and Washington (Campbell and Sorensen 1973), yet mean temperature of the coldest month at Santa Cruz (A) is only 2.7^{0} F warmer than at Crescent City (G), 4^{0} 39' further north. Possibly the cline has developed in response to periods of abnormally cold weather, the frequency of which would increase with latitude. The 1955 cold wave, which caused extensive damage to natural stands of Douglas-fir in the Pacific north-west (Duffield 1956, Daubenmire 1957) could be considered an example of such selection in action.

Seedlings from the interior ranges have a capacity for plastic response to moisture stress which has not evolved in the coastal population where summer moisture stress conditions are less severe (Azevedo and Morgan 1974). Intraspecific variation in plasticity of many Californian plant species has been demonstrated by Clausen *et al.* (1940) but the phenomenon has received little attention in the forest tree literature. Irgens-Moller (1967) found that seedling

Table 6. — Average Meteorological Data* for stations nearest to sample locations.

Sample Location	Weather Station	Station Elevation (ft.)	Days from Jan. 1st datum: Last Spring $<28^{0}$ F	Days from Jan. 1st datum: First Fall $<28^{0}$ F	Period $>28^{0}$ F	Mean Temperature (^{0} F): Annual	Mean Temperature (^{0} F): Hottest Month	Mean Temperature (^{0} F): Coldest Month	Mean Temperature (^{0} F): Ann. Range	Precipitation (in. ×100): Jan.—March	Precipitation (in. ×100): April—June	Precipitation (in. ×100): July—Sept.	Precipitation (in. ×100): Oct.—Dec.	Precipitation (in. ×100): Annual
G	Crescent City	40	10	360	350	52.6	58.2	46.4	11.8	3175	970	319	2537	7000
H	Happy Camp	1000	78	329	251	55.9	73.4	47.6	25.8	2298	533	124	1956	4911
I	Siskiyou Summit	4485	130	315	185	46.8	64.0	31.8	32.2	836	461	122	851	2270
D	Scotia	139	7	355	348	54.9	61.5	47.7	13.8	2271	573	63	1794	4701
E	Forest Glen	2340	125	288	163	51.2	68.4	35.5	32.9	2723	695	126	2001	5545
F	Platina	2260	104	298	194	55.6	75.3	37.1	38.2	1427	369	71	1548	3415
B	Fort Bragg	80	9	351	343	52.9	57.4	47.8	9.4	1910	463	78	1347	3798
C	Lake Pillsbury	1740	130	281	151	55.0	71.2	41.2	30.0	2533	359	69	2488	5449
A	Santa Cruz	125	27	349	322	57.1	63.2	49.1	14.1	1519	314	54	953	2840

* Derived from U.S. Weather Bureau records (1964; 1960—70).

Douglas-fir from the northern Rocky Mountains set buds after a single growth flush, no matter how favourable the growing conditions, whereas those from Arizona flushed repeatedly under long photoperiods. The latter was considered to be an adaptation to the relatively higher proportion of summer precipitation in Arizona. Comparable variation, attributed to adaptation to drought stress occurs in loblolly pine (Woessner 1972) and ponderosa pine (Squillace and Silen 1962).

The pattern of variation in time of bud burst confirms the conclusion (Sorensen 1967, Sweet 1965) that there is no simple relationship with spring climate, though variation is undoubtedly genetically determined (Munger and Morris 1936, Irgens-Moller 1966). The seedlots with earliest (A) and latest (G) average flushing dates are both of coastal origin from locations differing by 17 days in date to last spring frost *(Table 6)*, while interior location samples did not vary significantly though last frost dates differed by 52 days. Nevertheless a recent glasshouse study (Campbell 1974) did demonstrate genetic differentiation among Douglas-fir provenances in temperature requirements for bud burst, and also that date of last spring frost was a significant variable in the regression of provenance bud burst characteristics on habitat factors.

At present it can only be concluded that the meteorological records available inadequately describe the operational selection pressures. The possibility of significant provenance by test environment interaction should also be considered before the results are used in formulation of any seed transfer rules.

The seed related characteristics (weight, germination rate, and cotyledon number) show less geographic : within stand variation *(Table 2)*, though regional effects are still at least as great as the combined location and stand components. In part this may be due to non-genetic effects, as environmental conditions during seed development will have varied, but fast initial growth may also be adaptive to the drier conditions and shorter growing season in the interior ranges. Previous studies (Birot 1972 and Sweet 1965), confirm the smaller size of low elevation coastal seed, as do Allan (1961) and Owen (1957) for the slower germination rate of the latter.

The concept of environmental grain (Levins 1968) is useful for interpretation of the different variation patterns — a given environment being coarse-grained if spatial heterogeneity is great relative to tolerances of an individual genotype, and fine-grained in the reverse case. Phenology, growth and hardiness are components of the seasonal growth cycle, operative throughout a tree's life, and by which it responds to seasonal changes in micro-environment. The latter is largely determined by climate, a fine-grained element of the total environment relative to rates of gene flow in tree populations. However, the climatic selection pressure is not necessarily the same for each character, and pattern differences are sufficient to indicate that effects are not pleiotropic or even tightly linked. For example, the coastal population is relatively homogeneous for epicotyl length and time of bud set, but varies clinally for cold hardiness and ecotypically for bud burst.

Seed-related characteristics are expressed only during the first growing season, in an environment that may be extremely coarse-grained. Owen (1953) studied Douglas-fir seedling establishment in a "bald" near Corvallis, Oregon, and reported large variation in soil moisture, temperature, and light conditions depending upon proximity to the principal vegetation components — implying differences in selection pressures on the developing seedling. Selection for fitness at this stage may be further enhanced by competition (Tigerstedt 1967) as seed production may far exceed that necessary to maintain the population. The resulting inter-breeding population may be heterogeneous for seed related characteristics, though differing from other populations to the extent that average micro-site conditions vary.

The literature provides evidence of additional variation patterns. With respect to frequency of cortical monoterpene chemophenotypes (Zavarin and Snajberk 1975) the more southerly coastal populations have a greater affinity with those from the interior region than with those from the north coast. Thus Santa Cruz (A) was comparable to a population from Lakehead 60 km to the north east of Harrison Gulch (F), in marked contrast to the great difference in cold hardiness shown in the present study. While the greatest east-west change in chemophenotype frequency does correspond to the climatic transition between regions, any suggestion of discontinuity between regional populations becomes lost when characters other than growth and hardiness are considered. The data of Zavarin and Snajberk (1975), of El-Lakany and Sziklai (1971) for nuclear volume and DNA content, and of Sweet (1965) for growth, all suggest that the interior region population is intermediate between the coast and that from the Sierra Nevada, an observation compatible with the present finding of east-west differentiation between the interior region locations.

The most satisfactory concept of the northern Californian Douglas-fir population is that of a single gene pool within which a complex spectrum of selection pressure gradients have differentiated sub-populations expressing a comparable range of character combinations.

Since growth characters are closely adapted to climate, and the latter has shown great fluctuation over time, it is implicit that gene frequencies at a particular location cannot have remained static. Douglas-fir is wind pollinated and largely outcrossing (Sorensen 1971), and is thus well adapted to respond to changed selection pressures through gene flow between populations.

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Summary

181 wind-pollinated families of Douglas-fir from throughout the coastal ranges of northern California were raised in a nursery at Corvallis, Oregon and assessed for growth, phenology, cold hardiness, and response to moisture stress. Variation patterns for seed weight, germination rate and cotyledon number were also determined.

All characters varied genetically, and with the exception of date of bud burst the most significant contrast was between samples from the coastal fog-belt and those from the interior ranges. Coastal seed was relatively smaller and germinated more slowly, and seedlings had fewer cotyledons, less hypocotyl, but greater epicotyl growth; grew for a longer period before setting buds; showed less capacity to set buds in response to moisture stress; and were less cold hardy. Lesser variation patterns were associated with elevation and latitude. In spite of broad similarities in variation patterns, the distribution of variation among sampling levels was not the same for all characters. For example, time of bud set and epicotyl growth were closely associated with the regional difference in climate, the ratio

of geographic : within stand variation being >10, compared with values <1 for seed-related characters. Cold hardiness variation was also predominantly regional. Such differences indicate a variable complex of selection pressure gradients, and militate against any systematic distinction of the coastal and interior range populations.

Key words: Douglas-fir, provenance, adaptation, seed, growth rate, phenology, hardiness.

Zusammenfassung

In einem Versuch mit 181 Douglasien-Herkünften *(Pseudotsuga menziesii* (Mirb.) Franco) aus dem Küstengebiet Nord-Kaliforniens zeigten die Nachkommenschaften als Samen, im Keimlings- und später im Sämlingsstadium z. T. große Unterschiede. Die Samen aus dem Nebelgebiet in Küstennähe waren kleiner als diejenigen der Herkünfte mehr aus dem Innern des Landes und es dauerte länger bis sie keimten. Die Keimpflanzen der Küstenherkünfte hatten weniger Keimblätter und zeigten weniger Hypokotyl-, dagegen mehr Epikotylwachstum. Außerdem zeigten die Herkünfte aus dem Küsten-Nebelgebiet geringere Trockenresistenz und waren weniger frosthart.

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