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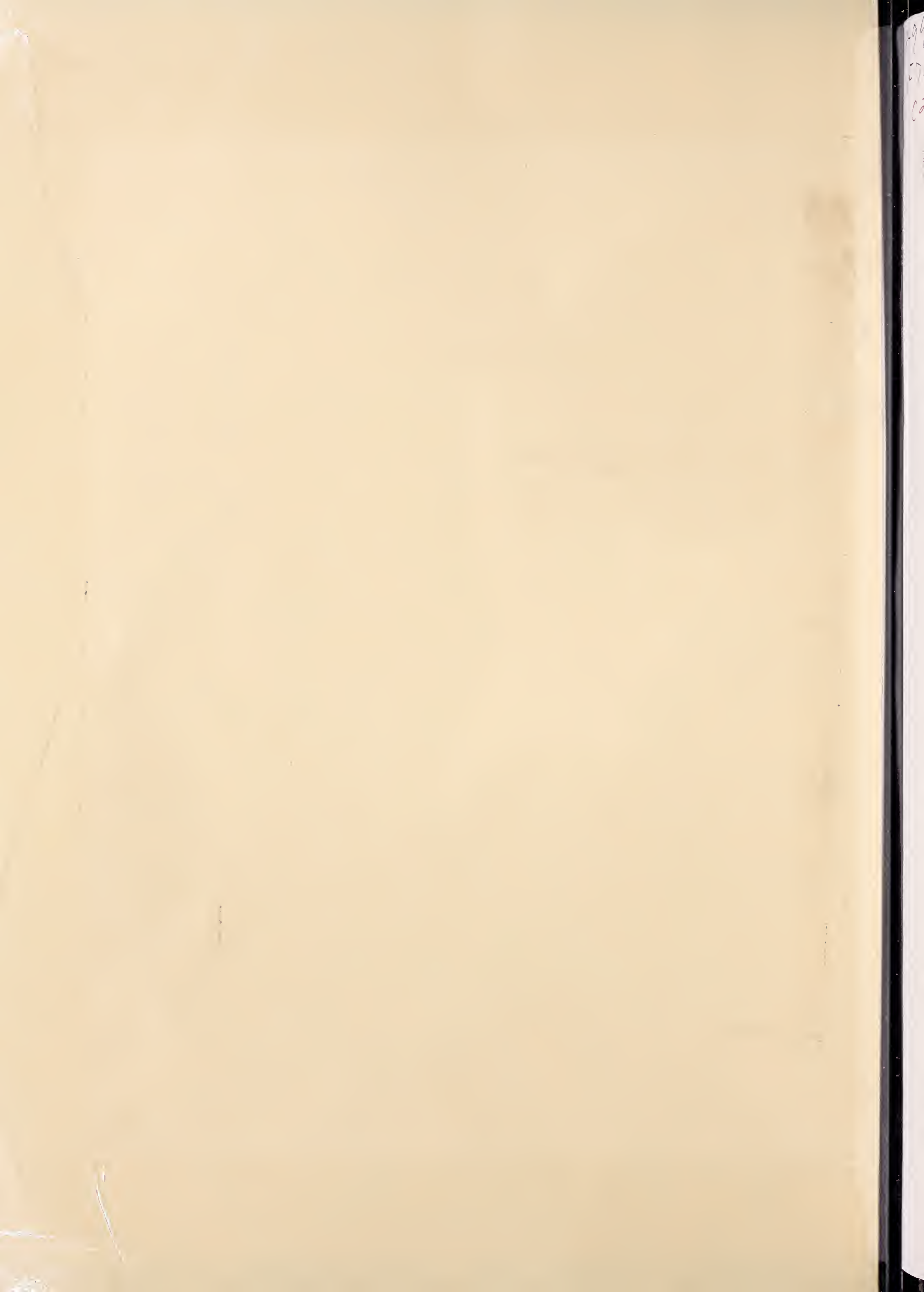
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Genetic Variation and Seed Zones of Douglas-Fir in the Siskiyou National Forest

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Abstract

Provisional seed zones and breeding zones were developed for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the Siskiyou National Forest in southwestern Oregon. Zones were based on maps of genetic variation patterns obtained by evaluating genotypes of trees from 260 locations in the region. Genotypes controlling growth vigor and growth rhythm were assessed in a common garden. Within the Forest, three breeding blocks were recommended, with different numbers of elevational bands in each block: from 0 to 610 meters, from 611 to 838 meters, and then a series of bands 152 meters wide at higher elevations.

Keywords: *Pseudotsuga menziesii,* geographic genetic variation, adaptation, ecological genetics, genecology.

Summary

This paper reports new seed-transfer zones (or breeding blocks) based on genetic variation patterns for Douglas-fir in the western Klamath Mountains in southwestern Oregon. Seedling progenies of 316 trees from 260 locations were grown as families in common gardens to evaluate genotypes of parents. Two principal components of genetic expression (growth vigor and growth rhythm) described the adaptive differences among families. Among families, 80 percent of variance in scores of the first principal component (PC1-scores) was contributed by variance associated with parent origin. In scores of the second principal component (PC2-scores), the corresponding contribution was 58 percent. Variance among families within origins accounted for remaining variation. Variation in PC1-scores closely reflected gradient trends in precipitaion and temperature within the Forest. The same gradients accounted for little of the variation in PC2-scores, which were more closely associated with elevational effects as secondarily influenced by other topographic and physiographic variables. Results from this study closely agreed with results from previous investigations of geographic genetic variation of Douglas-fir in adjacent regions just to the east and south.

Introduction

This paper reports a study of geographic genetic variation of Douglas-fir in the Siskiyou National Forest in southwestern Oregon. The revealed patterns of variation are then used to propose alternatives to the present breeding blocks for guiding seed transfer and tree-breeding decisions.

The Forest comprises an area extending about 80 kilometers north to south and 50 to 65 kilometers west to east, in which the Kalmiopsis Wilderness Area occupies about 260 square kilometers in the south-central portion. The Forest is wholly included within the northern Klamath Mountains, a deeply dissected peneplain now consisting of rugged mountains and narrow canyons with 600 to 1500 meters of relief (Baldwin 1964). Several short coastal streams and two major rivers (the Rogue and the Illinois, a tributary) drain the Forest. In most of the Forest, annual precipitation exceeds 2540 millimeters, but on the eastern slopes of the main range, it drops to 1270 millimeters within a west-to-east distance of about 20 kilometers (Froelich and others 1982). Within the same distance, dry-season precipitation (May through September) drops from 450 to 100 millimeters (McNabb and others 1982). A rather steep temperature gradient also exists west to east across the Forest. January mean minimum temperatures decrease from about 5 to -2.5 °C, and July mean maximum temperatures increase from about 20 to 27 °C (Franklin and Dyrness 1973). Consequently, the annual temperature amplitude almost doubles within the width of the Forest (Sorensen 1983).

The study area sustains vegetation of two major types. The western third of the Siskiyou Forest, securely within the wet, mild influence of the Pacific Ocean, supports flora diagnostic of the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973). Most of the remaining two-thirds is in the Mixed Evergreen Zone. In both vegetation types, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is a dominant tree species, associated with other conifers, *Tsuga heterophylla* (Rab.) Sarg. and *Thuja plicata* (Donn ex D. Don) in the western third and *Pinus ponderosa* Dougl. ex Laws., *P. lambertiana* Dougl., and *Libocedrus decurrens* Torr. in the eastern two-thirds. Present also and often dominant in the Mixed Evergreen zone is *Lithocarpus densiflorus* (Hook. & Arn.) Rehd. and a variety of other hardwoods.

Because of the range in elevations and the diversity in climate and vegetation within the region, the Forest has been partitioned into six breeding blocks, each including 460-meter and 305-meter elevational bands. This translates into 22 units that must be considered in breeding plans. There is uncertainty whether this number is justified by adaptational or other constraints, and larger blocks would greatly decrease the costs of breeding and increase the benefits.

An infallible basis for decisions regarding breeding or seed-transfer zones unfortunately requires rotation-age evaluation trials. Genetic architecture studies provide less satisfactory but more attainable information, namely the patterns of genetic variation associated with geography. With the assumption that these patterns reflect natural selection by local environments, the region can be blocked into provisional zones. The objective of this study was to describe genetic variation in the native stands of Douglas-fir in the Siskiyou National Forest.

Procedures

Procedures employed in the study included collecting open-pollination seed from individual sample trees, growing the seed in common gardens to evaluate family performance, using principal component analysis of a genetic correlation matrix to provide genotypic values for the parent trees, and relating the values to parent origin in regression and classification models. Details in some of these steps are omitted here because the procedures have been reported previously (Campbell 1986, 1991; Campbell and others 1989; Sorensen 1992).

Seeds from 316 parent trees, well distributed in 260 locations within the Forest but not within the Wilderness Area, provided the sample of genotypes for the study (fig. 1). Measured at each location were elevation, latitude, departure, slope, aspect, sun exposure, vertical distances from slope top and bottom, and direction of the river drainage below the point of origin. Also available were soil and watershed maps, used to classify each location.

Seeds were sown in nursery beds in Corvallis, Oregon, in 1984 (bed 1), 1985 (bed 2), and 1986 (bed 3). In beds 1 and 2, the planting design consisted of 315 five-seedling family plots in each of four replications (total=20 seedlings/family) at 7- by 7-centimeter spacing. In bed 3, the design was four-seedling family plots in each of two replications (8 seedlings/family) at 8.5 centimeters between rows by 11.7 centimeters within rows. Seedlings were established by planting three stratified (60 days) seeds per planting spot in April with random thinning to the crop seedling in August.
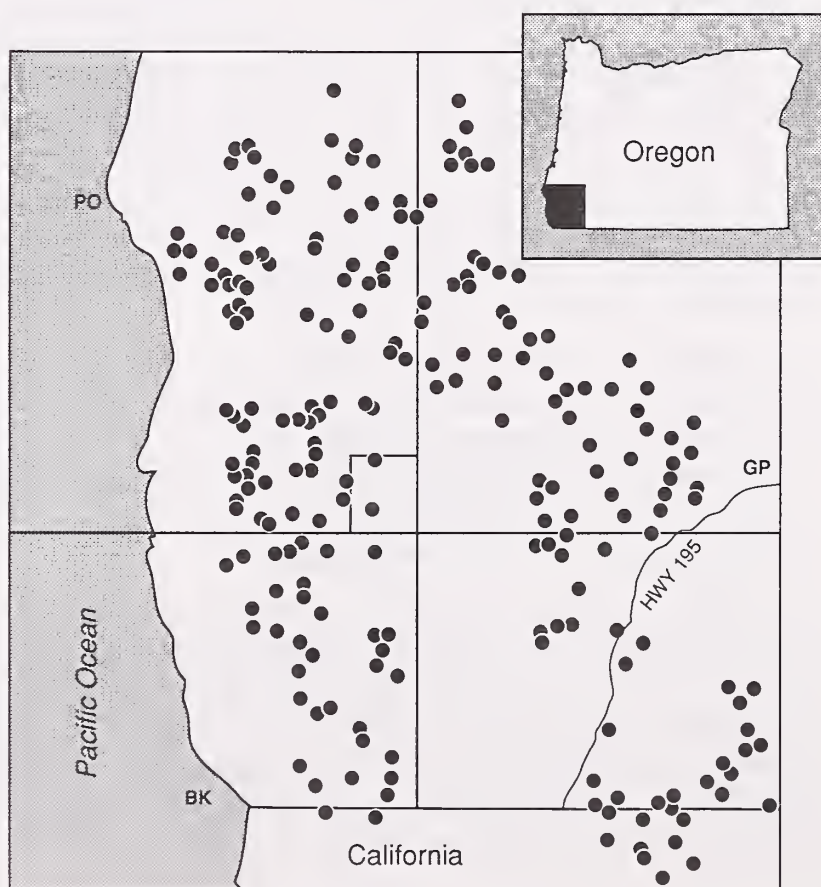

Figure 1—Parent-tree locations. The central square is given to indicate scale and represents a township (10 by 10 kilometers). Three cities are indicated: PO=Port Orford, BK=Brookings, and GP=Grants Pass.

Seedlings were grown for 3 years, and in each bed, 10 traits were measured: bud-set dates in years 1, 2, and 3; bud-burst dates in years 2 and 3; total heights in years 1, 2, and 3; and diameters in years 2 and 3. From these measurements, three additional secondary traits were constructed: growing and dormant season lengths, and first-year height as a percentage of third-year height. Of the resulting 39 traits (13 in each bed), 13 were chosen for final analyses by methods explained below. Two other traits, seed weight and frost damage, were measured but were subsequently not a factor in estimates of parental genotypes. The frost damage occurred in three fall frost events that, in total, visually injured leaders in about 25 percent of first-year seedlings in bed 1.

We analyzed data by procedures used in similar experiments with Douglas-fir (Campbell 1986, 1991). The analysis involved six steps: (1) analyzing variance and covariance of data for each trait in each bed by the model,

$$Y_{ijkl} = u + R_l + S_k + F(S)_j + P_l + e_{ijkl} ,$$

where u is the experimental mean, y_{ijkl} is the performance of the ith seedling in the jth family $[f(s)_j]$ from the kth location (s_k) in the lth replication (r_l), p_l is the plot error, and e_{ijkl} the within-plot error; (2) estimating additive components of variance and covariance for the traits and trait combinations; (3) estimating genetic correlations among traits at the location level; (4) reducing the dimensions in the data by a principal-components analysis of the genetic correlation matrix; (5) calculating factor scores for each parent tree from coefficients produced in the principal components analysis; and (6) describing patterns of geographic genetic variation by using regression or classification models.

Data were analyzed by the VARCOMP-Type I (SAS 1987) procedure to provide statistical tests and components of variance for location (parental origin) and family-within-location effects. Components of covariance also were obtained at the location level of variation. Variance and covariance components were then used to calculate genetic correlation coefficients among the 39 traits. The resulting matrix of correlation coefficients included loosely patterned subsets of coefficients that estimated very high intercorrelations among traits. To reduce intercorrelation in the matrix, a representative trait was chosen from each of the subsets, usually because family heritabilities suggested more precision in the estimates of family means for that trait than for other traits within the subset.

From the resulting 13-trait matrix of genetic correlations, a principal component analysis extracted most of the information about the genetic variation among sources as two principal components. The eigenvectors describing these components were then used to calculate two factor scores (PC1-scores and PC2-scores) for each family. These factor scores, taken together, represent the common-garden estimate of the genotypic value of a parent tree.

Two general procedures were used to describe the association of parent-tree factor scores with geographic origin of the parents. Physiographic models selected by multiple regression (backward elimination) were constructed to describe relations with latitude, elevation, and other geographic or topographic variables. Analysis of variance was used to select classification models for categorizing scores according to their representation in breeding blocks, watersheds, elevational bands, and soils (Meyer and Amaranthus 1979). These models often included nesting; for example, elevational bands nested within watersheds or soils within watersheds within elevational bands. Watersheds also were combined into larger blocks, and elevational bands then were

nested within the watershed blocks. In physiographic and in classification models, lack of fit to the model was tested by a "pure error" representing the pooled variation among the two trees sampled at 56 of the locations. Lack of fit in regression represents the variation among source deviations from the regression plane; it estimates the genetic variation at locations that is not described by the regression equation and is beyond that accounted for by variation among trees at a location. In the classification model, lack of fit estimates the variation among locations within a category. If the model includes nesting, lack of fit pertains to the lowest level; in a model of soils nested in elevational bands, for example, lack of fit describes the mean variation among locations within a soil type within an elevational band.

By making an assumption that the indigenous mixture of additive genotypes in a stand reflects adaptation to the stand environment, relative risks can be calculated in seed transfers (Campbell 1986). The regression model makes it clear that two sorts of risk may exist in any transfer guided by a model. The first is predictable and is described by the change in mixtures from point to point along the regression surface. The second is an unpredictable risk incurred by lack of fit to the model. The same two kinds of risk exist in transfers guided by classification models, but usually only the latter is of interest; commonly, transfers are made within classification units (seed zones, etc.) but not between them. Calculation of risk associated with lack of fit in classification models provides a scale for judging heterogeneity of source-related genetic variation within the classification unit. If heterogeneity is large, the unit may be judged too large for a seed zone or breeding block.

Seed-transfer risks due to lack of fit are easily calculated assuming that lack-of-fit deviations are normally distributed. First, an average difference is calculated between genotypes (factor scores) at source and planting sites given an infinite number of randomly assigned transfers (Sorensen 1992). From the half-normal distribution (Patel and Read 1982, p. 34), this value is:

$$N_d = \sigma_{x_1 - x_2}\sqrt{1/\pi}$$
$$= \sqrt{2}\,\sigma_{1of}\,\sqrt{2}\,\sqrt{1/\pi}$$
$$= 2\,\sigma_{1of}\sqrt{1/\pi},$$

where N_d is the average difference between factor scores at seed origin and planting site in random moves,

x_1 is the mean factor score (PC1 or PC2) at seed origin,

x_2 is the mean factor score at planting site,

σ_{1of} is the square root of the component of variance for lack of fit, and

π is pi (3.1416).

When the difference between mean factor scores at seed origin and plantation site (N_d) has been calculated, risk can be calculated as in Campbell (1986, p. 88).

Results

Statistical trends common to all 39 traits measured in the study were reflected in the 13 traits chosen to describe geographic variation patterns. That is, most traits showed highly significant variation among locations (σ^2_s) or among families within locations ($\sigma^2_{f(s)}$), or both (table 1). Of variation among seedlings in the experiment (averaged over the 13 traits), within-plot variation accounted for 71 percent, plots for 11 percent, family within locations for 6 percent, and locations for 13 percent. For the record, statistics of frost damage (1FST1) and seed weight (SDWT) also are given in table 1, though these traits were not used in further analyses because data were available only for plot means. About two-thirds of family variation in 1FST1 was contributed by locations and in SDWT by families within locations (table 1).

Table 1—Analysis of variance for traits and factor scores of principal components

Trait code[a]	$\overline{x}$	Total variance	Components of variance as percentage of total variance			
			σ^2_s	$\sigma^2_{f(s)}$	σ^2_p	σ^2_w
1FST1	25.60	244.5727	32.6***	14.9***	52.4	
1BB2	47.73	.2300	3.8*	6.5***	7.2***	82.6
1BS2	58.39	1.5674	13.0***	4.4***	8.5***	74.2
1HT2	46.12	113.3808	8.1***	4.8***	14.8***	72.3
1DIA2	50.09	177.9163	9.0***	2.6*	13.4***	75.0
2BS2	57.27	3.9796	16.0***	3.8**	16.0***	64.1
2DSL	19.34	2.2274	22.6***	4.8***	10.7***	61.8
2HT2	32.85	4.7499	12.7***	5.8***	15.5***	66.0
2DIA2	38.09	5.0413	9.3***	3.1*	23.5***	64.1
3BS1	27.15	1.8130	18.7***	8.1***	2.0 NS	71.2
3BB3	84.37	.4427	12.7***	11.1***	8.3***	67.9
3HT3	91.78	553.2743	19.0***	9.4***	4.2**	67.4
3DIA3	9.56	8.1226	13.3***	5.9***	5.0**	75.8
3PHT1	16.94	19.6359	14.3***	.6 NS	10.0**	75.1
SDWT	13.70	4.2990	34.3***	62.7***	3.0	
FS-1	0	36.8669	79.6***	20.4		
FS-2	0	12.2651	57.5***	42.5		

* = 0.10>(P%=0)>0.05, ** = 0.05>(%=0)>0.01, *** = P(%=0)<0.01; NS = nonsignificant.

[a] Trait codes: First numeral refers to nursery bed number; FST is percentage of seedlings frosted per plot, BB, BS, HT, and DIA are, respectively, bud-burst date, bud-set date, height, and diameter; DSL is dormant-season length calculated as BB2-BS1; PH1 is 1st-year height as a percentage of 3d-year height. SDWT is mean seed weight in micrograms of seed per plot. FS=1 and FS=2 are mean family factor scores of the first and second principal components, respectively. Bud burst and bud set are measured in days+10 starting January 1 of the year of planting. Height is measured in centimeters. Diameter is measured in various units: 1DIA2 in millimeter × 10, 2DIA2 in (log n millimeter) × 10, 3DIA3 in millimeter.

Table 2—Structural relations (x 100) in the variability among seedlings[a]

Trait[b]	$\sigma_s/\bar{x}$	$\sigma_A/\bar{x}$	$\sigma_s^2/(\sigma_s^2+3\sigma_{f(s)}^2)$	$2\sigma_{f(s)}^2/\sigma_w^2$	$\sigma_p/\bar{x}$	$\sigma_u/\bar{x}$	h^2
1BB2	0.9	2.0	16.3	15.6	1.2	4.2	20
1BS2	2.1	2.1	49.9	11.8	1.7	4.9	15
1HT2	6.5	8.8	36.0	13.3	8.9	19.6	16
1DIA2	8.0	7.4	53.3	7.0	9.7	23.1	9
2BS2	3.8	3.2	58.8	11.7	3.8	7.7	13
2DSL	3.6	2.9	61.1	15.6	2.5	6.1	19
2HT2	2.4	2.8	42.4	17.5	2.6	5.4	20
2DIA2	1.8	1.8	49.7	9.8	2.9	4.7	10
3BS1	2.1	2.4	43.5	22.7	0.7	4.2	30
3BB3	2.0	3.3	27.5	32.7	1.7	4.8	38
3HT3	11.2	13.6	40.2	27.9	5.3	21.0	35
3DIA3	10.9	12.6	42.9	15.6	6.6	25.9	21
3PHT1	9.9	21	88.3	1.7	4.3	11.7	2

[a] Illustrated by coefficients of variation for locations ($100\sigma_s/\bar{x}$), additive genetic variation ($100\sigma_A/\bar{x}$), plot variation ($100\sigma_p/\bar{x}$), within-plot variation ($100\sigma_w/\bar{x}$), heritability (h2) at the individual seedling level ($\sigma_A^2/(\sigma_w^2+\sigma_p^2+\sigma_{f(s)}^2)$), where $\sigma_{f(s)}^2$ is the variance of families within locations and additive genetic variance is $3\sigma_{f(s)}^2$.

[b] Trait codes and measurement units as in table 1.

Based on 13 traits of 316 families sampled in 260 locations, variation among locations contributed about half (47 percent) of the estimated genetic variation in Douglas-fir (table 2, col. 4). Traits deviated only slightly from this ratio, with two notable exceptions: Families within locations accounted for most of the genetic variation in budburst date (table 2, 1BB2 and 3BB3), and locations accounted for most of the variation in the percentage contribution of first-year height to third-year height (table 2, 3PHT1).

The matrix of genetic correlations among the 13 traits (table 3) reflects the remaining genetic variances and covariances after subtraction of error and those genetic effects specific to trees within locations. Genetic correlation coefficients in table 3 thus summarize the genetic attributes associated with geography; this matrix was used as data for the principal component analysis. All subsequent references to variation in factor scores, whether among locations or within locations, therefore apply to factor scores calculated from the analysis of correlations at the location level.

Table 3 also includes estimates of correlations between location means for all trait combinations. The coefficients are usually somewhat smaller than for corresponding genetic correlations. Families from locations producing seedlings that grew vigorously (larger heights and diameters) tended to suffer more frost damage. And most-frosted families generally burst and set buds later and had shorter dormant-season lengths than did families from the average location in the study. In contrast, families from locations with heaviest seeds tended to have earlier bud-burst and bud-set dates and a longer dormant season length. These trends were not strong. Apparently reflecting this web of rather weak correlations, families from locations suffering the most frost damage tended also to have the smaller seed weights ($r=-0.13$, $p<0.05$).

Table 3—*Above diagonal*: genetic correlations based on source-level components (d.f.=259); *below diagonal*: correlations among source means (d.f.=258)

Trait code[a]	1BB2	1BS2	1HT2	1DIA2	2BS2	2DSL	2HT2	2DIA2	3BS1	3BB3	3HT3	3DIA3	3PHT1
1BB2	1.00	0.56	0.02	-0.02	0.40	-0.41	0.44	0.25	0.75	0.50	0.43	0.34	-0.22
1BS2	.38	1.00	-.04	.04	.83	-.85	.60	.33	.98	.71	.64	.59	-.53
1HT2	-.02	-.15	1.00	.94	.22	-.32	.60	.52	.03	-.60	.85	.87	-.61
1DIA2	-.03	-.13	.81	1.00	.37	-.39	.66	.66	.17	-.65	.88	.99	-.62
2BS2	.26	.66	.12	.16	1.00	-.91	.81	.53	.93	.43	.95	.92	-.66
2DSL	-.14	-.58	-.25	-.28	-.67	1.00	-.97	-.73	-.97	-.35	-.85	-.76	.71
2HT2	.08	.34	.49	.50	.46	-.64	1.00	.75	.81	-.14	.93	.84	-.81
2DIA2	-.00	.12	.41	.51	.17	-.46	.77	1.00	.64	-.19	.71	.74	-.58
3BS1	.28	.67	.02	.10	.72	-.76	.51	.30	1.00	.56	.67	.61	-.58
3BB3	.54	.43	-.22	-.24	.21	-.10	-.04	-.12	.24	1.00	-.06	-.25	.15
3HT3	.00	.33	.57	.58	.54	-.63	.73	.57	.56	-.16	1.00	.96	-.80
3DIA3	-.01	.23	.53	.60	.44	-.52	.64	.57	.48	-.15	.92	1.00	-.62
3PHT1	.02	-.27	-.40	-.40	-.43	.56	-.47	-.35	-.38	.25	-.68	-.54	1.00
1FST1	.27	.58	.04	.15	.66	-.66	.53	.37	.71	.14	.60	.53	-.41
SDWT	-.13	-.27	.19	.31	-.26	.25	.09	.34	-.30	-.15	.07	.19	.17

[a] Trait codes as in table 1.

The large genetic correlations in table 3 suggest control of the traits by a few gene complexes, which can be indexed by creating one or more new variables, each correlated with some aspects of the old variables. To do this, variation and covariation reflected in the genetic correlation matrix were partitioned by a principal component analysis. The first two principal components explained about 88 percent of the variation in all traits. The first principal component appeared to be an expression of vigor associated with shorter dormant-season length caused mainly by late bud set (table 4). Thus, a large factor score calculated for the first principal component (PC1-score) indicated a family with above average height and diameter, an average bud-burst date, later than average bud-set date, and a long growing season. The second principal component was more strongly associated with bud-burst timing. Larger factor scores (PC2-scores) indicated families with later bud-burst dates. Larger PC2-scores also were associated with smaller 2- or 3-year seedlings, especially in bed 1, which had been frosted at the end of the first growing season. Factor scores for lower ranked principal components tended to be comparatively more strongly affected by single traits. An example is given in table 4, in which eigenvector coefficients show that PC3-scores would reflect mainly 1BB2. Other examples not shown indicate strong affects of 2DIA2 on PC4-scores and 3PHT1 on PC5-scores. In these examples, however, the principal components accounted for minor percentages of total trait variation and therefore were not considered further.

Seven models relating the association of factor scores with origin of parents are reported here. One is a regression model and six are classification models. Three of the classification models involved only one category, such as soils, or breeding blocks, for example; the other three incorporated nesting, as soils within watersheds, or soils within watersheds within breeding blocks.

Table 4—Eigenvector coefficients and eigenvalues of principal components (PC1, PC2, PC3), and the percentage of trait variation accounted for by the principal components

Trait[a]	Eigenvector of PC1	Eigenvector of PC2	Eigenvector of PC3
1BB2	0.17	0.27	0.85
1BS2	.26	.34	-.13
1HT2	.21	-.40	.20
1DIA2	.24	-.40	.08
2BS2	.32	.17	-.25
2DSL	-.33	-.15	.23
2HT2	.34	-.04	-.02
2DIA2	.27	-.11	.03
3BS1	.30	.31	.05
3BB3	.02	.53	-.02
3HT3	.35	-.10	.06
3DIA3	.33	-.16	.09
3PHT1	-.28	.09	.27
Eigenvalue	8.03	3.40	.70
Percent of variation	62	26	5

[a] Trait codes and measurement units as in table 1.

Regression of factor scores on geographic (latitude, longitude, elevation) and topographic variables (aspect, slope, and so forth) accounted for only part of the variation (sums of squares), 66 percent for PC1-scores and 38 percent for PC2-scores (table 5). Type II sums of squares suggest that geographic variables, particularly elevation, explained most of the variation in PC1-scores. Geographic variables and variables measuring specific associations of topography with geography (interactions) accounted for the major part of explained variation in PC2-scores (table 5, type II sums of squares). The remaining unexplained variation in either set of scores could not be attributed entirely to variation caused by sampling two trees at some locations; significant lack of fit existed for each principal component (table 5).

Families with the highest growth potentials and longest growing seasons (larger PC1-scores) came from the southwestern part of the Forest at lower elevations (fig. 2). Growth potential became less and dormant seasons longer in families from higher elevations and farther east and north. An exception occurred at highest elevations, where PC1-scores were smaller close to the coast as well as farther east on the lee side of the main Klamath Mountains. Slope influenced the strong association of scores with elevation. The slope-related differences in score were largest at highest and lowest elevations (fig. 3). On flatter slopes, the scores decreased very rapidly with increasing elevation especially in southernmost parts of the Forest (fig. 3).

Table 5—Regression analyses of factor scores from principal components

	Principal component 1[a]				Principal component 2[b]		
Variable[c]	Partial coefficient	Significance $P(b=0\ s)<...$	Type II sum of squares	Variable[c]	Partial coefficient	Significance $P(b=0)<...$	Type II sum of squares
Q	0.9888	0.006	105	LA	-8279.8515	0.004	65
W	-1.6648	.003	124	LO	592.8200	.008	55
EL2	-48.2700	.000	494	N	-.0771	.004	63
LOEL	81.6642	.000	622	Q	-.6990	.009	53
ELSI	.0330	.009	95	LA2	821.0733	.006	60
LA2EL2	1.6568	.000	353	EL2	40.7400	.000	112
LA2TA2	-.0064	.002	131	SI2	-.2087	.025	39
LO2EL2	.5129	.000	635	LALO	123.1789	.001	52
LA2EL	-6.3189	.000	467	LOTA	1.2117	.004	65
LO2EL	-11.0936	.000	705	LOCO	.0122	.046	31
LO2TA	.1665	.000	319	ELTA	-19.0138	.001	83
EL2TA	.3962	.000	290	LO2EL2	2.2335	.000	120
LAELTA	.7167	.000	209	EL2SI2	.0052	.042	32
LOELTA	-1.2190	.000	361	LA2TA	-.2285	.003	68
				LOEL2	-19.0396	.000	115
				LOSI2	.0625	.007	56
				ELSI2	-.0313	.012	50
				LAELTA	4.0392	.001	83
				TASICO	-.0026	.018	43
CONST	-2.0332	.290	15	CONST	20833.8389	.003	69

[a] Probability of lack of fit for PC1 is 0.0013; $R^2 = 0.66$.

[b] Probability of lack of fit for PC2 is 0.0133; $R^2 = 0.38$.

[c] EL=elevation in meters ($\times$ 0.000305), LA=distance south to north in kilometers ($\times$ 0.001) taken from Geological Survey maps (Oregon [topographic], Coos Bay [1973] and Medford [1976]), LO=distance west to east in kilometers ($\times$ 0.01) from above maps, SI and CO=sine and cosine of aspect in radians ($\times$ 10), TA=slope percent ($\times$ 0.1), Q=vertical distance of parent origin above the drainage bottom ($\times$ 0.00305), N=sine (of radians) of direction of flow in drainage below the parent tree ($\times$ 10), W=southwest exposure=the sum ($\times$ 0.01) of 6 verticle angles to the horizon taken at 22-1/2 degree intervals from 108° to 293° azimuth, and CONST=intercept.
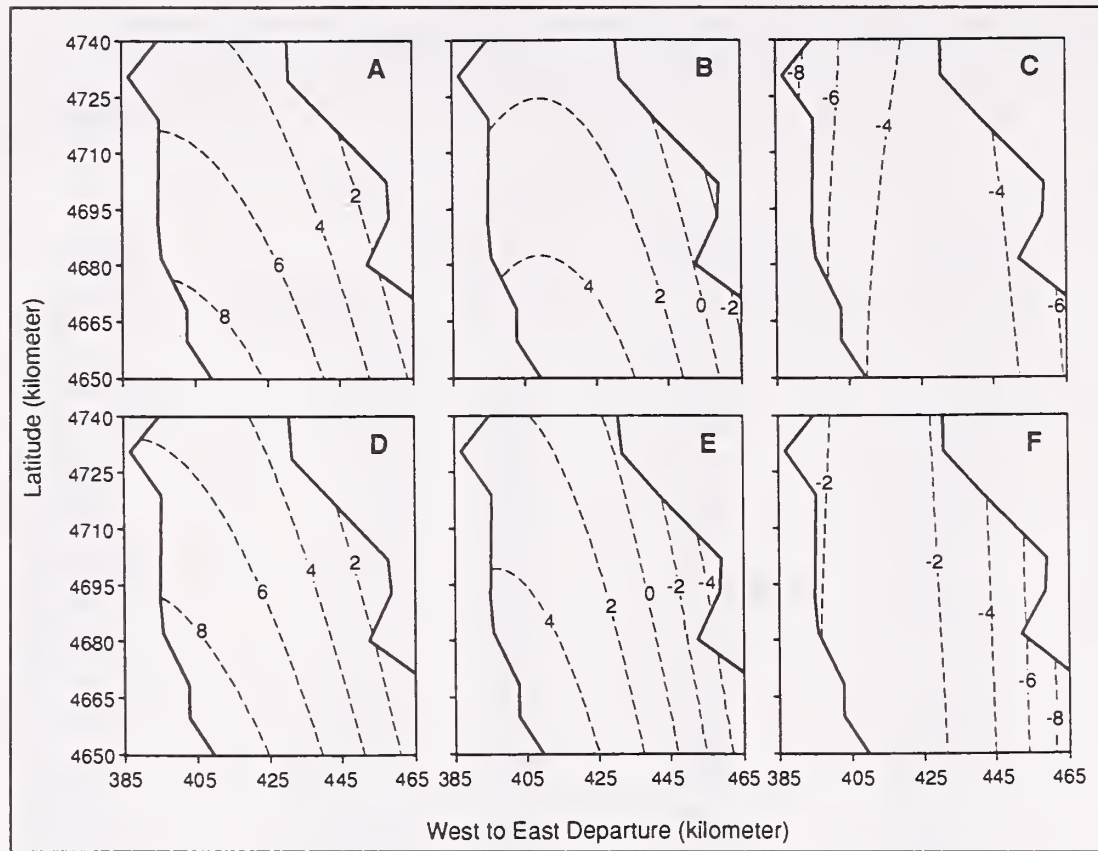
Figure 2—Isolines of predicted factor scores for the first principal component. Latitude as used here is an index of true latitude and is expressed in distance from the baseline given in the Geological Survey Maps (Oregon [topographic]), Coos Bay (1973) and Medford (1976). Departure distances are taken from the same maps. Internal boundaries in the diagrams represent limits of samples: (A) Elevation 457 meters, slope 20 percent. (B) Elevation 762 meters, slope 20 percent. (C) Elevation 1066 meters, slope 20 percent. (D) Elevation 457 meters, slope 60 percent. (E) Elevation 762 meters, slope 60 percent. (F) Elevation 1066 meters, slope 60 percent.
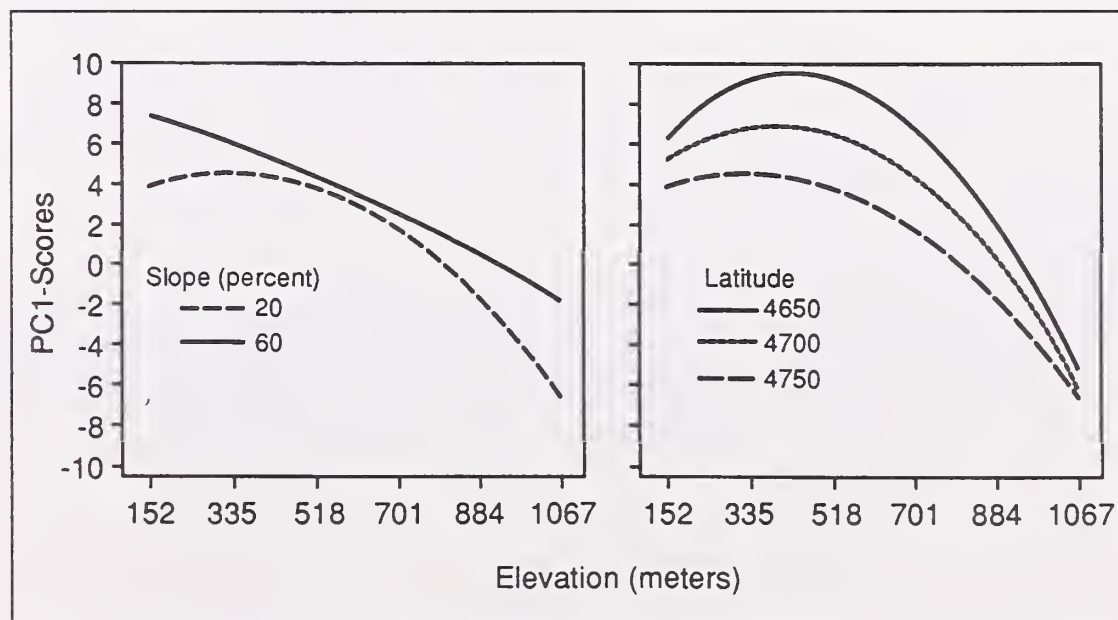
Figure 3—Factor scores of the first principal component (PC1-scores) as they were described by elevation, latitude, and slope. Latitude as used here is an index of true latitude and is expressed in distance (kilometers) from the baseline given in the Geological Survey maps (Oregon [topographic]), Coos Bay (1973) and Medford (1976).

Variation in bud-burst dates, as indexed mainly by PC2-scores, showed few clear trends with geography. Families with later bud burst (larger PC2-scores) tended to come from the southwestern part of the Forest (fig. 4). In figure 4, most of the geographic variation appears to exist on the flatter slopes within the region, but other representations describing the trends in PC2-scores associated with other combinations of geographic variables (not shown) suggest more variation among scores at higher slopes. Scores also differed with aspect. Bud bursting was generally earlier from families originating on north or south slopes than for those from east or west slopes (fig. 5). This trend was not consistent, however. Scores differed only slightly with aspect among high-elevation sources in western parts of the Forest (fig. 5).
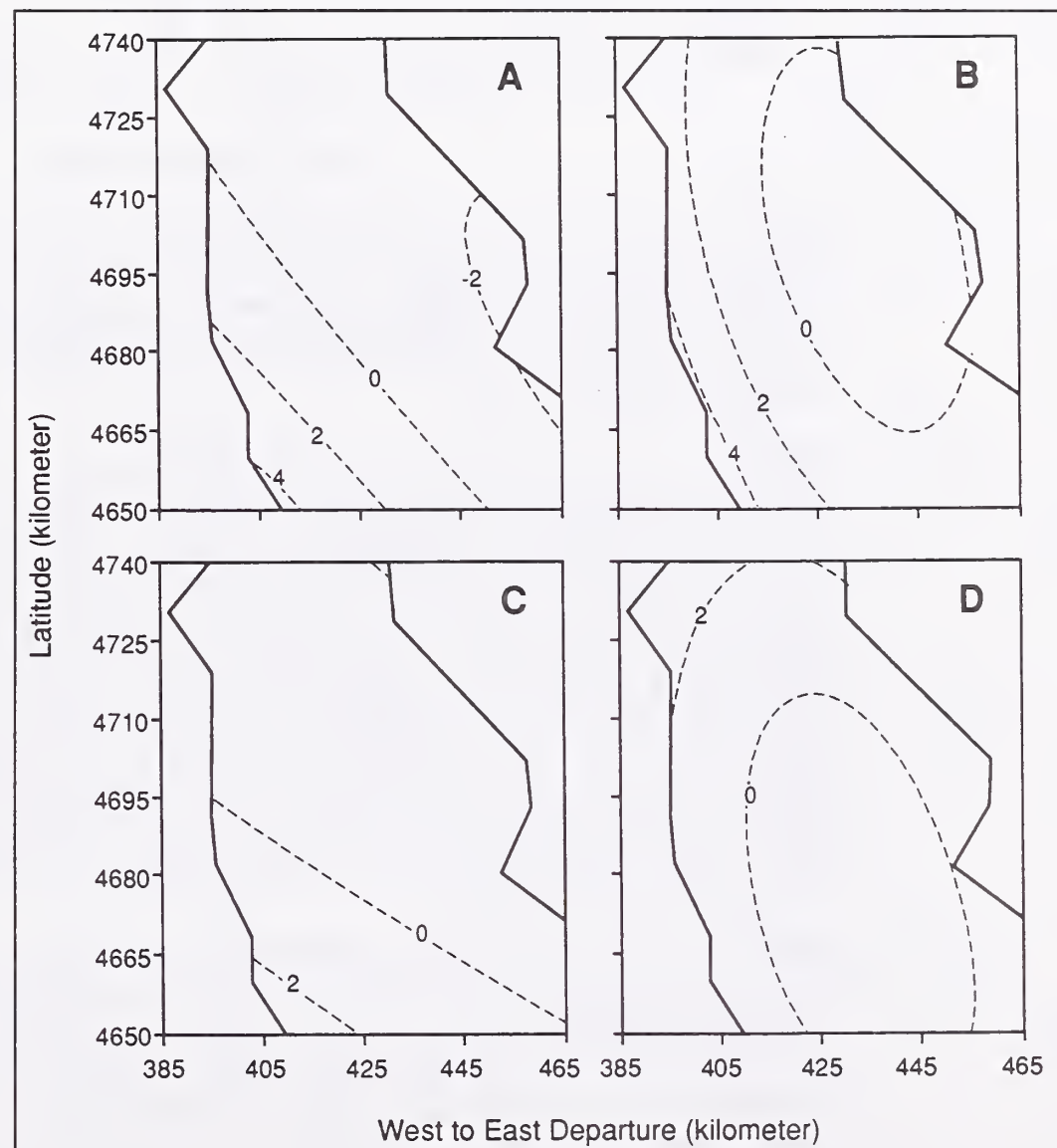

Figure 4—Isolines of predicted factor scores for the second principal component. Latitude as used here is an index of true latitude and is expressed in distance from the baseline given in Geological Survey maps (Oregon [topographic]), Coos Bay (1973) and Medford (1976). Departure distance are taken from the same maps. Internal boundaries in the diagrams represent limits of samples. (A) Elevation 457 meters, slope 20 percent. (B) Elevation 1066 meters, slope 20 percent. (C) Elevation 457 meters, slope 60 percent. (D) Elevation 1066 meters, slope 60 percent.
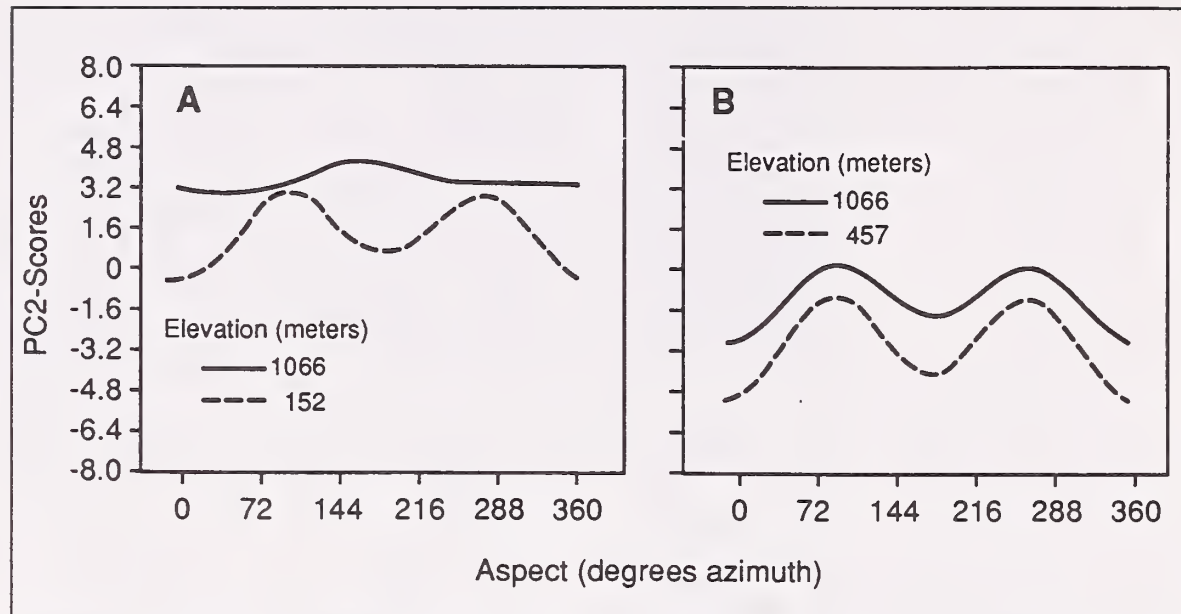
Figure 5—Factor scores of the second principal component (PC2-scores) as they are affected by aspect and elevation for: (**A**) departure = 400 kilometers and latitude = 4700 kilometers, and (**B**) departure = 445 kilometers and latitude = 4700 kilometers Latitude as used here is an index of true latitude and is expressed in distance (kilometers) from the baseline given in the Geological Survey maps (Oregon [topographic]), Coos Bay (1973) and Medford (1976). Departure distances are taken from the same maps.

Tables 6 and 7 summarize results from regression and classification models. To explore the characteristics of geographic genetic variation in the Siskiyou National Forest and to judge utility of models for seed zoning, it is useful to compare the models on three bases: (1) the amount of geographic genetic variation accounted for by the model, (2) lack of fit to the model, and (3) the number of partitioning units encompassed in the model. Note that the regression model predicts changes in genotype (that is, factor scores) along gradients and not between classification units. In regression models, lack of fit therefore measures the genetic variation remaining among locations after accounting for regression gradients and for the sampling variation encountered among trees within locations. In classification models, it reflects the average variation among locations within classification units after accounting for variation among trees within locations.

The three simple classification models, by watersheds, by soils, or by elevational bands, each explained about 50 percent of the geographic variation in factor scores of the first principal component (table 6, PC1-scores). This similar amount, however, is obtained by dividing the region into widely different numbers of units: 75 soil types, 31 watersheds, or 7 elevational bands. The percentage of variance in PC1-scores associated with lack of fit was largest in the soils model (48 percent) and smallest in the elevational-bands model (30 percent). Of the complex classification models, model 6, which nested soils within elevational bands within the figure 6 blocking of watersheds (nine blocks), accounted for 93 percent of the geographic variation in PC1-scores. Only about 8 percent of the total variance in scores was associated with a statistically nonsignificant lack of fit (table 6). This was achieved, however, only by blocking the

Table 6—The analyses of the geographical distribution of factor scores (PC1) of the 1st principal component by regression and classification models

Model	Breeding blocks	Elevation bands	Soils	Physiographic parameters	Lack of fit	Families in locations	R^2	Percent of geographic variation explained
1. Physiographic:								
D.f.[a]				14	245	.56		
M.S.				560.05***	15.48**	7.75		
Percent variance				NA	NA	NA	.658	67
2. 230-m elevational bands:								
D.f.		6			253	56		
M.S.		941.81***			23.05***	7.75		
Variance component		21.67			12.63	7.75		
Percent variance		52			30	18	.474	49
3. Watersheds:								
D.f.		30			229	56		
M.S.		185.62***			25.83***	7.75		
Variance component		15.85			15.01	7.75		
Percent variance		41			39	20	.467	48
4. Soils:								
D.f.			74		185	56		
M.S.			82.09***		29.23***	7.75		
Variance component			12.19		18.26	7.75		
Percent variance			32		48	20	.510	53
5. Present breeding blocks:								
D.f.	5	16			238	56		
M.S.	826.64**	148.62***			20.88***	7.75		
Variance component	13.19	9.50			10.88	7.75		
Percent variance	32	23			26	19	.546	57
6. Figure 6 blocking of watersheds:								
D.f.	8	35	151		65	56		
M.S.	602.59***	87.28***	18.84*		11.70[NS]	7.75		
Variance component	14.31	10.28	4.49		3.35	7.75		
Percent variance	36	26	11		8	19	.899	93

Table 6—The analyses of the geographical distribution of factor scores (PC1) of the 1st principal component by regression and classification models (continued)

Model	Breeding blocks	Elevation bands	Soils	Physiographic parameters	Lack of fit	Families in locations	R^2	Percent of geographic variation explained
7. Figure 7 blocking of watersheds:								
D.f.	2	14			243	56	.610	63
M.S.	1997.51**	234.06***			17.33***	7.75		
Variance component	16.70	13.30			7.95	7.75		
Percent variance	37	29			17	16		

** = 0.01>P>0.001, *** = P<0.001, NA = nonsignificant.

[a]D.f. = degrees of freedom, M.S. = mean squares, percent variance = percent of variance among families (first 6 columns); among locations (last column).

Forest into 195 units. In comparison, the present breeding blocks and elevational bands (table 6, model 5, 22 units) used by the Siskiyou National Forest, explained 57 percent of the geographic variation in PC1 with 3.25 times the amount of lack-of-fit. Model 7, which nests elevational bands within the figure 7 blocking of watersheds (three blocks) required 17 classification units and accounted for 63 percent of the geographic variation. Lack-of-fit in this model was only twice as large as in model 6.

Geographic variation patterns in factor scores of the second principal component (PC2-scores) were considerably different from those of the first principal component. Of simple models, soils and watersheds explained roughly the same amount of variation in PC2-scores, about 30-35 percent (table 7). The variance among scores attributable to lack-of-fit was about two to four times larger than the variance connected to classification units, and larger for soils than for watersheds. Elevational bands accounted for only a statistically nonsignificant 2 percent of variance (table 7). Of complex models, model 6 again explained more of the geographic variance than other classification models (36 percent) and showed the least lack of fit. Model 6 comprised elevational bands nested within the watershed blocking shown in figure 6.

Table 7—The analyses of factor scores (PC2) of the 2d principal component by regression and classification models

Model	Breeding blocks	Elevation bands	Soils	Physiographic parameters	Lack of fit	Families in locations	R^2	Percent of geographic variation explained
1. Physiographic:								
D.f.[a]				19	240	56		
M.S.				72.36***	8.321*	5.04		
Percent variance							0.376	41
2. 230-m elevational bands:								
D.f.		6			253	56		
M.S.		24.25[NS]			12.75***	5.04		
Variance component		0.25			6.37	5.04		
Percent variance		2			55	43	0	0
3. Watersheds:								
D.f.	30				229	56		
M.S.	33.89***				10.28***	5.04		
Variance component	2.32				4.36	5.04	.278	30
Percent variance	20				37	56		
4. Soils								
D.f.			74		185	56		
M.S.			17.27*		11.23***	5.04		
Variance component			1.27		5.33	5.04		
Percent variance			11		46	43	.349	38
5. Present breeding blocks:								
D.f.	5	16			238	56		
M.S.	138.79**	24.07**			9.63**	5.04		
Variance components	2.26	1.06			3.80	5.04		
Percent variance	19	9			31	41	.295	32
6. Figure 6 blocking of watersheds:								
D.f.	8	35			216	56		
M.S.	81.44*	19.32**			9.45**	5.04		
Variance components	1.71	1.35			2.47	5.04		
Percent variance	14	11			21	42	.363	39

Table 7—The analyses of factor scores (PC2) of the 2d principal component by regression and classification models (continued)

Model	Breeding blocks	Elevation bands	Soils	Physiographic parameters	Lack of fit	Families in locations	R^2	Percent of geographic variation explained
7. Figure 7 blocking of watersheds:								
D.f.	2	14			243	56		
M.S.	243.54**	32.51***			10.00**	5.04		
Variance components	2.02	1.35			4.11	5.04		
Percent variance	16	11			33	40	.258	28

** = 0.01>P>0.001, *** = P<0.001, NA = nonsignificant.
[a]D.f. = degrees of freedom, M.S. = mean squares, percent variance = percent of variance among families (first 6 columns); among locations (last column).

Table 8—Relative seed-transfer risks indicated by models for describing genetic variation patterns of Douglas-fir in the Siskiyou National Forest

Model	No. of units	Risk associated with lack of fit		
		PC1-risk	PC2-risk	Combined risk
1. Physiographic	NA	0.232	0.188	0.376
2. Elevational bands (230 m)	7	.322	.286	.516
3. Watersheds	31	.350	.238	.504
4. Soils	75	.383	.262	.545
5. Present breeding blocks	22	.300	.225	.458
6. Figure 6 blocking of watersheds	195	.096	.181	.259
7. Figure 7 blocking of watersheds	17	.259	.232	.430

30 (10) 32 (14) 82 (1)

33 (15)

31 (15)

23 (8)

20 (7)

83 (6)

22 (13)

21 (5) 8 (18) 26 (12)

7 (9) 9 (8)

19 (10)

11 (18)

6 (3) 10 (1) 18 (10)

5 (17) 3 (2) 13 (7)

12 (10)

4 (39)

90 (3) 14 (6) 16 (6) 17 (28)

1 (5) Oregon

California 15 (9)

Pacific Ocean
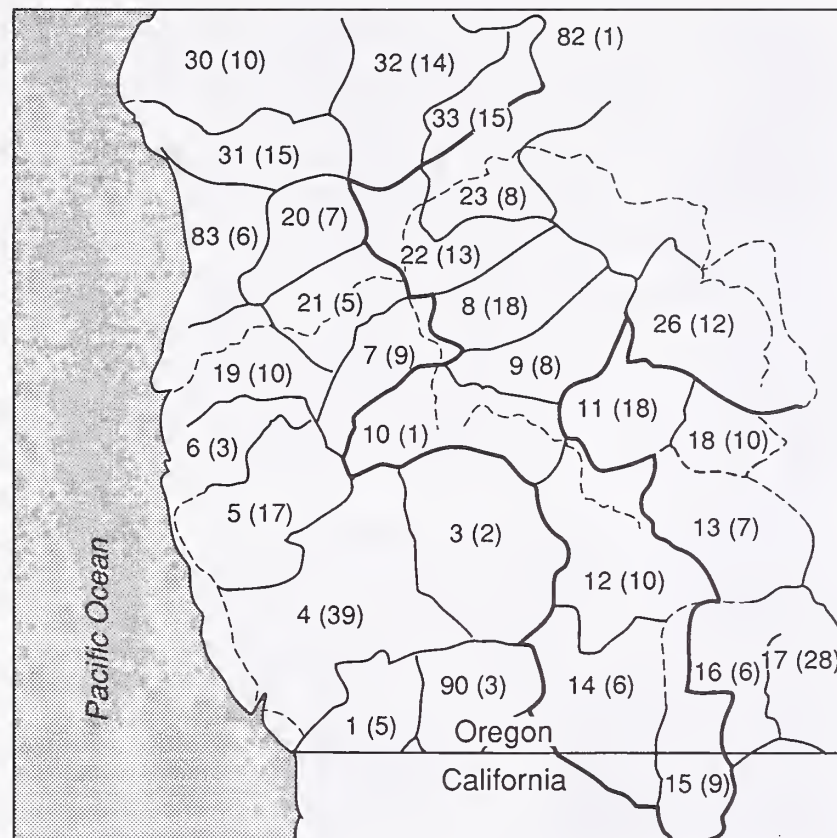
Figure 6—The blocking of watersheds into the nine breeding blocks (bold outlines) as used in model 6 (tables 6, 7, and 8). Watersheds are labeled with Siskiyou National Forest identifiers and the number of sample parents (in parentheses) found in each watershed. Watersheds 3 and 10 are almost entirely within the Kalmiopsis Wilderness Area.

For purposes of blocking the Forest into seed zones or breeding units, we examined many classification models. Results from only six have been described here (tables 6 and 7). Choosing among models required decisions on tradeoffs; adaptational risks had to be balanced against the number of units needed to categorize genetic variation. The models differed considerably in both risk and number, as can be seen in the examples given in table 8. The relative risk in model 6, for example, was half the size of the risk for model 2. Model 6 achieved this by blocking the Forest into 28 times more units than were used in model 2. Model 7, which we recommend in comparison with the presently used one (model 5), seemed to be the best compromise of the many combinations of watershed blocking and elevational bands we tried. It indicated that three breeding blocks may be sufficient, made up of the watershed grouping shown in figure 7. This compares with the six present breeding blocks. Model 7 provided lower relative adaptive risks than model 5 and with 25 percent fewer units than the 22 in present breeding blocks. The model suggested that elevational bands of variable width may be more appropriate than bands of uniform width. Specifically, it called for a band from 0 to 610 meters, then one from 611 to 838 meters, and then a series of bands 152 meters wide. Elevational bands in present breeding blocks start with a lower band of 457 meters and remaining upper bands 305 meters wide.

Discussion

This and a previous study (Campbell 1986) provide a record of genetic variation patterns of Douglas-fir in southwestern Oregon. The purpose of these studies was to devise provisional seed-transfer guidelines or delineate breeding blocks. The basis for so doing is an assumption that natural selection has caused trends in geographic genetic variation and that it is possible to develop models to adequately describe the trends.
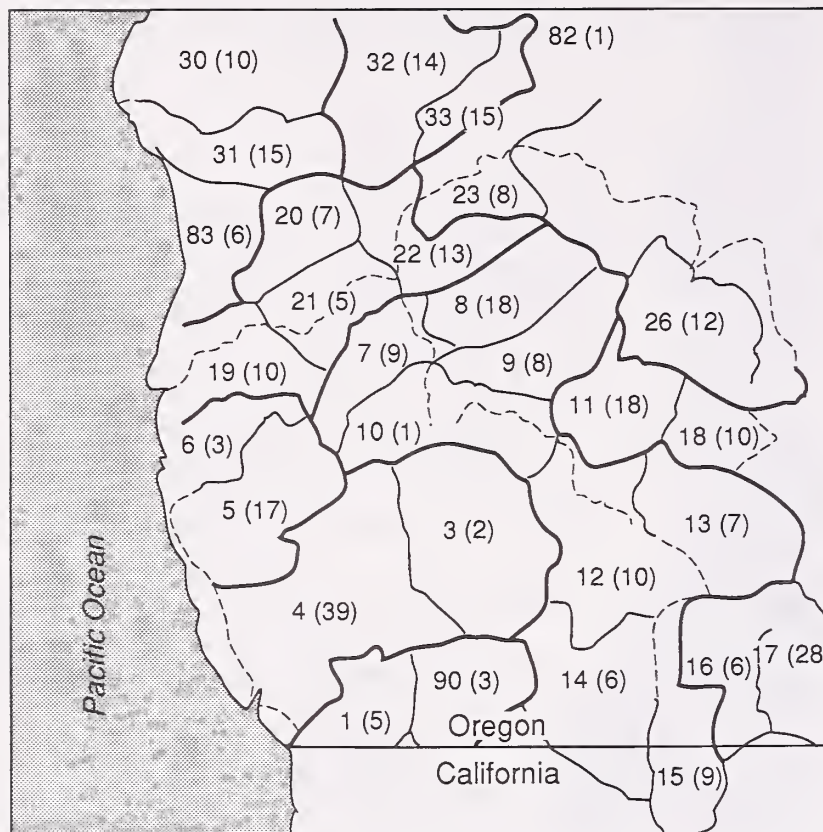
Figure 7—The blocking of watersheds into the three recommended breeding blocks (bold outlines) as used in model 7 (tables 6, 7, and 8). Watersheds are labeled with Siskiyou National Forest identifiers and the number of sample parents (in parentheses) found in each watershed. Watersheds 3 and 10 are almost entirely within the Kalmiopsis Wilderness Area.

This study focused on the western two-fifths of southwestern Oregon and the other study (Campbell 1986) on the remainder. The entire sampled region extends from near the Pacific Ocean to the crest of the Cascade Range and from the California border (lat. 42° N.) to almost 43° N. latitude. It is a mountainous basin drained mainly by the Rogue River. The more massive ranges in southwestern Oregon make up its western, southern, and eastern edges. These mountains and the storms generated by the Pacific Ocean govern the extremely diverse climates within the region. Mean annual temperatures decrease with increasing elevation and distance from the coast, and temperature amplitudes increase with distance from the coast (Sorensen 1983). Climate in western Oregon is generally mediterranean and therefore moisture limiting because of the dry summers; vegetation and site productivity closely reflect variation in annual precipitation (Franklin and Dyrness 1973). Rain shadow is a local factor figuring prominently in the distribution of precipitation in the region (Froehlich and others 1982). Snow and rain arrive in storms from the Pacific, and amounts of precipitation are affected by prominent ridges and mountains. The higher the mountains, the more effectively they scrub moisture from the clouds; highest annual precipitations are found on highest mountains and lowest precipitations in adjacent interior valleys to the east and north east (Froelich and others 1982). The effects of rain shadows

apparently accumulate in the passage of clouds through a mountain range or ranges. At equivalent elevations, precipitation decreases steadily from near the ocean to the Cascades. The very steep gradients of the southern edge of the basin become less steep on the northern edge (Froehlich and others 1982), because mountains to the west are smaller in the north. The driest parts of the region are therefore at lowest elevations at the southeastern edge of the basin.

Various minor gradients that affect moisture and temperature also exist; for example, with aspect, slope, soil depths, and parent materials. And mountains influence storm-wind forces, which are higher nearer the coast and at higher elevations. These major and minor environmental gradients are reflected in diverse site productivities and growing season lengths, which must be accommodated by the Douglas-fir native to the region.

The two studies provided independent assessments of the genetic architectures of Douglas-fir populations in a climatically diverse region. The assessments were remarkably similar in most aspects. In the two studies, parent origin (location) accounted for 78 and 80 percent of variances in family means in PC1-scores and 58 and 61 percent of variances in PC2-scores. Variances among families within locations made up the remainders. For PC1-scores, the gradients of genotypes across the landscape were consistent from study to study. Each study showed the same strong association with elevation and the major precipitation trends in the region. Growth potential, as indicated by PC1-scores, generally decreased from low elevation to high and from west to east. Thus, genotypes with higher growth potentials originated in mesic locations at lower elevations and nearer the coast. But the growth-potential gradients also reflected the contrasting latitudinal precipitation trends that exist at lower elevations in the region (Froehlich and others 1982, McNabb and others 1982). Precipitation amounts (and growth potentials) decreased from south to north on the western edge of the region (this study) and from north to south in the eastern third (previous study). At highest elevations, PC1-scores at the very western boundary were lower than farther east (fig. 2), but this may represent adaptation to the higher wind forces expected at high elevations near the ocean. Sorensen (1983), in fact, found the same trend in genetic differentiation between west and east sides of a ridge paralleling the coast.

Superficially, trends in PC2-scores were not totally consistent in the two studies. In comparing landscape distributions of PC2-scores, however, it must be kept in mind that the scores in the two studies did not measure identical aspects of the genotype. In the previous study, scores reflected primarily variation in bud burst. In the present one, an aspect of growth vigor also was represented, specifically the growth of seedlings in bed 1, which had suffered severe frosts at the end of the first growing season. Nevertheless, PC2-scores in both studies indicated a major gradient with distance from the ocean. The trend was modified by elevation and slope. Generally scores were lower, and budbursts therefore earlier, in families from locations with shorter growing seasons; where growing season lengths are severely limited by drought or cold, early flushing is apparently an advantage (Campbell and Sorensen 1978, Campbell and Sugano 1979). In southwestern Oregon, drought and cold both restrict growing-season lengths to varying degrees and often at different elevations or in different parts of the region. In the eastern part, drought apparently was more effective than cold in hastening bud-burst; low-elevation families burst buds earlier than higher elevation families. But in the western part, the effects of drought and cold appeared

to be more evenly balanced. Elevation by itself became relatively less important as a predictor of score and slope, and aspect relatively more important. Over the whole region, trends of PC2-scores with elevation reflected local effects as indexed by interactions of elevation with distance from the ocean, latitude, aspect, and slope.

Not only did the two southwestern Oregon studies yield similar results, but the discovered trends also conformed with results reported for Douglas-fir in the Coast Ranges in northern California (Griffin 1978, Griffin and Ching 1977). Each of the three studies indicated large amounts of genetic variation associated with local stands as compared to variation within stands. Each showed strong trends tieing genotypes with high growth potential to environments that could support vigorous growth, such as are expected near the coast and at lower elevations. Each suggested strong gradients of geographic genetic variation with distance from the ocean, modified strongly by elevation and less strongly by latitude.

Basic to the development of provisional seed zones is an assumption that genetic variation exists among locations as a consequence of natural selection. Gradient trends in variation among locations may have several origins: random association of genes in small populations (genetic drift), gene migration from founder populations, maternal effects (seed preconditioning), and natural selection. When genetic gradients closely correspond with environmental gradients, natural selection seems a most likely alternative. When, in addition, the genotypes found along the gradient express just those phenotypes that might be expected as a consequence of adaptation, the likelihood is even stronger. Finally, trends in genotypes that are consistent from mountain to mountain in rugged terrain are especially indicative of natural selection (Campbell and others 1989). These three conditions existed in both studies. It seems reasonable, therefore, to assume that trends described by the physiographic model fairly represent genetic gradients due mainly to natural selection.

In this study, a substantial part of the location-related variation could not be described by most models. In the previous study, lack of fit was not significant in the physiographic model, whereas in this study it was. The difference occurred both for PC1, where the two physiographic models explained almost identical proportions of variation, and for PC2, where they did not. In this study, we sampled more than three times as many locations as in the previous one. Undoubtedly this provided more opportunity for sampling unique demes, thus increasing possibility of lack of fit. Also, compared with the previous study, the subregion sampled in this study may be more environmentally complex, because it crosses a major mountain range and the previous one did not. Rain-shadow effects may be more strongly localized here than farther east. Sorensen (1983), for example, found considerable genetic differentiation between west and east sides of ridges within the region. Furthermore, the differentiation was greater on the ridge closest to the coast than on an interior ridge. Our models, even the physiographic one, may not have included variables capable of indexing important localized environments. Other reasons exist, too, but none can be accepted as a conclusive answer.

Classification models also were not completely satisfactory in either study. Models classifying by major features of the landscape—watersheds and elevational bands in this study, and soils and seed zones in the previous study (Campbell 1991)—all had large lack of fit. In this study, the best models still left unexplained about 25 percent of location-related variance in PC1-scores (table 6) and about 45 percent in

PC2-scores (table 7). In this study, we found nonsignificant lack of fit (PC1-scores) in only one of several models examined. In model 6 (table 6), soils were nested within elevational bands within nine watershed blocks. The model required 195 units to classify variation at 260 locations. The model was one of a number examined, and the soils category was significant at a low level of probability. The model's predictive value is therefore questionable. Nevertheless, the model does indicate that genetic variation is highly structured in the Forest, that like genotypes are concentrated in small areas.

We have not been able to provide a comprehensive model of the genetic architecture of Douglas-fir in the Siskiyou National Forest. Indeed, this may be a difficult task in any region as heterogenous as the Forest. In the physiographic model, we included the variables commonly used for describing landscape-related genetic variation and a number of other variables rarely used for that purpose. We examined many terms for interactions and for fitting nonlinear relations. In the classification models, we used detailed soil maps. We also used watersheds as a category; in the deeply dissected peneplain encompassed in the Forest, gene migration seemed less likely across steep ridgelines than within the basin of a watershed. Population discontinuities might therefore occur at ridgelines. Only one complex classification model sufficed, with reservations, for categorizing the variation in PC1-scores among locations. None of the above expedients enabled us to describe genetic variation in PC2-scores. Furthermore, any model satisfactory for PC1-scores probably would have been inadequate for PC2-scores. For example, when PC2-scores were analyzed by the model best able to describe PC1-scores (table 6, model 6), the category of soils nested within elevational bands was not statistically significant. The remaining model, which included only statistically significant terms, had highly significant lack of fit (table 7, model 6).

The model we recommend as the basis for breeding blocks and seed zones had significant lack of fit. Lack of fit represents the geographic variation within blocks or zones that is not accounted for by the model. Our calculations of risk in seed transfers assume that all geographic variation results from natural selection and thus reflects adaptation to local environment. If this is true, then a certain amount of risk is expected in seed transfers within seed zones. If, furthermore, all the assumptions underlying risk evaluations are also true, risks within recommended seed zones may be larger than is desirable. A previous study (Campbell and Sugano 1987) indicated that within-block risk values of about 0.25 would ensure an acceptable representation of local genotypes in any transferred seed lot. The risk in the recommended model is 0.43 (table 8). A risk calculated from lack of fit, however, is not as firmly based as one calculated for a transfer along a known and relevant environmental gradient. Geographic variation discovered as lack of fit may or may not represent variation resulting from natural selection. We assumed, without evidence, that one-third to one-half of the lack-of-fit variance reflected geographic variation from genetic drift, historical accident, or other random source of variation. The risk in the recommended model then falls within boundaries suggested previously in other situations (Campbell and Sugano 1987).

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Provisional seed zones and breeding zones were developed for Douglas-fir (*Pseudotsuga menziesii (Mirb.)* Franco) in the Siskiyou National Forest in southwestern Oregon. Zones were based on maps of genetic variation patterns obtained by evaluating genotypes of trees from 260 locations in the region. Genotypes controlling growth vigor and growth rhythm were assessed in a common garden. Within the Forest, three breeding blocks were recommended, with different numbers of elevational bands in each block: from 0 to 610 meters, from 611 to 838 meters, and then a series of bands 152 meters wide at higher elevations.

Keywords: *Pseudotsuga menziesii,* geographic genetic variation, adaptation, ecological genetics, genecology.