ing and outbreeding causing intra-provenance variation in all characters except germinative energy.

3. Trends in inter-provenance variation and selection pressures on many characters have been demonstrated by regression analyses but not by BONFERRONI t-tests. South to north trends are shown in seed weight, germinative capacity, hypocotyl length, and seedling height; and east-west trends in seed weight, cotyledon numbers and seedling height.
4. Germinative capacity and juvenile characters are significantly and positively correlated with seed weight. This confirms the earlier finding that in white spruce seed weight can be included among the criteria for selection of plus trees and superior provenances.
5. Provenances with high germinative energy also have high germinative capacity and fast juvenile growth.
6. The fifteen promising provenances are 8001, 8007, 8034, 8045, 8066, 8080, 8096, 8098, 8128, 8129, 8131, 8171, 8232, 8267 and 8270.

Acknowledgement

The help received from the Application Software and Quantitative Methods Branch of the Systems and Information Directorate, Environment Canada, Ottawa in conducting the statistical analyses is acknowledged. Acknowledgement is also made of the constructive review of the draft report by Dr. A. W. DOUGLAS, Director of the above branch and Dr. E. K. MORGENSTERN, Professor, Department of Forest Resources, University of New Brunswick, Fredericton, New Brunswick. The help received from Mr. T. M. MCDONOUGH, Newfoundland Department of Forest Resources and Lands and Mr. L. MAY, Canadian Forestry Service is also acknowledged.

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Mapped genetic variation of Douglas-fir to guide seed transfer in southwest Oregon

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(Received 7th May 1985)

Summary

A procedure is illustrated for using mapped genetic variation in indigenous species to develop provisional seed transfer rules and seed zones. Genotypic values for 13 traits of 135 parent trees from 80 locations furnished data for Douglas-fir in a region about 110 × 130 km in southwest Oregon. Genotypic values were estimated from open-pollinated progeny grown in two nursery beds. The data were reduced to manageable dimensions by principal component analysis. The genetic correlation matrix at the seed-source level was used as input for the analysis. Two principal components accounted for about 96 percent of the total family and seed-source variation in all traits. Factor scores derived from principal components exhibited strong gradients with location variables: elevation, latitude, distance from the ocean, slope, and sun exposure as affected by shade of adjacent mountains. Seed transfer rules and a procedure for calculating relative risk indicated that risks were largest when seed was transferred either east-west along the southern boundary or north-south along the western boundary of the region. These gradients in risk coincide with the steepest precipitation and temperature gradients within the region.

Advantages, disadvantages, and potential sources of error in the procedure are discussed. In spite of the limitations of genetic mapping, the conclusion is that for genetically heterogenous species in mountainous regions, genetic mapping is a prerequisite to directly estimating transfer effects by long-term tests.

Key words: Genetic variation, seed source, seed zones, provenance, Douglas-fir, *Pseudotsuga menziesii*, southwest Oregon.

Zusammenfassung

Es wird ein Verfahren beschrieben, um die bei einheimischen Arten bereits kartographisch festgehaltene genetische Variation zu benutzen und daraus vorläufige Saatgut-Transfer-Vorschriften und Saatguterntezonen zu ent-

wickeln. Genotypische Werte für 13 Merkmale von 135 Elternbäumen von 80 Standorten versorgten eine Region von 110 × 130 km in Südwestoregon mit Douglasien-Daten. Die genotypischen Werte wurden an der frei abgeblühten Nachkommenschaft in zwei Baumschulen beurteilt. Die Daten wurden mittels Hauptkomponenten-Analyse auf leicht zu handhabende Dimensionen reduziert. Die genetische Korrelationsmatrix wurde auf dem Herkunftsniveau als Input für die Analyse benutzt. Zwei Hauptkomponenten trugen zu 96% zu der gesamten Familien- und Herkunftsvariation aller Merkmale bei. Faktorengruppen, die sich von den Hauptkomponenten herleiteten, zeigten einen starken Gradienten mit den Herkunftsvariablen: Höhe über NN, geographische Breite, Entfernung vom Meer, Hangneigung und Sonnenexposition, wie durch Schatten, der durch an grenzende Berge verursacht wird. Samentransfer-Vorschriften und eine relative Risikoberechnung zeigten an, daß das Risiko am höchsten war, wenn das Saatgut entweder von Ost nach West entlang der Südgrenze oder von Nord nach Süd entlang der Westgrenze der Region transferiert wurde. Diese Risikogradienten treffen mit den steilsten Niederschlags- und Temperaturgradienten innerhalb der Region zusammen. Vor- und Nachteile sowie potentielle Fehlerquellen bei diesem Verfahren werden diskutiert. Trotz der Grenzen der genetischen Kartierung ist die Schlußfolgerung die, daß für genetisch heterogene Arten in Bergregionen, dieses eine Voraussetzung für die unmittelbare Beurteilung von Transfereffekten bei Langzeitversuchen ist.

Introduction

Since 1966, guidelines for transferring seed in Oregon have been taken from a seed-zone map prepared by the Western Forest Tree Seed Council (Anonymous 1966). The map ostensibly divides the State into regions of similar physiographic and climatic characteristics. Zone boundaries were established by consensus of several local committees comprised of forest and research officers familiar with the characteristics of local forests. The map has served to minimize potentially dangerous transfers of seed, but its scientific basis requires evaluation.

In 1966, there was little information within the region about patterns of genetic variation, vegetation, or soils. Information pertinent to meterological classification of forest environment was also lacking. It may never be forthcoming because meterological stations in Oregon are widely spaced and are better suited for gathering information for agriculture than for forestry.

Genetic-mapping principles have been used to guide seed transfer for many years in many regions. The procedure involves several steps: sampling indigenous trees within a circumscribed region, evaluating the genotypes of sampled trees, describing variation patterns, and quantifying risk in seed transfer. Langlet's early work (1945) recognized the use of genetic-variation maps to identify potentially risky transfers. Many studies (for example: Squillace 1966, Morgenstern and Roche 1969, Campbell and Sorensen 1978, Griffin 1978, Rehfeldt, 1981) have advocated limiting seed transfer by the mapping principle.

This paper describes patterns of genetic variation for seedlings of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in southwest Oregon and suggests a general procedure for using mapped geographic variation to develop provisional seed-transfer rules and seed zones. The procedure is based on the following assumptions, also implicit in many previous studies. These are:

(1) the region to be zone-mapped has been sampled sufficiently to determine the true patterns of variation in the region;

(2) some adaptive variations can be equated with the geographic origin of the parent tree (seed-source variation) and can be separated from other genetic and environmental variations;

(3) seed-source variation can be characterized by measurements of phenotipic traits in one or more common-garden environments;

(4) seed-source variation can be related to measurable regional attributes, such as latitude and elevation (location variables), and can be mapped in terms of these attributes;

(5) the map of adaptive genetic variation is a map of the environmental complex active in natural selection;

(6) a population of a given species is better adapted to its place of origin than is any other population;

(7) the relative risks in seed transfer indicated by seedling data apply to older trees; and

(8) seed transfer along any gradient of increasing risk imposes the same relative risk regardless of whether transfer is to milder or harsher conditions.

Corollaries of assumptions 5 and 6 relate directly to seed transfer; the greater the difference in genotypes between mapped points within the region, the greater the difference between environments at the corresponding points. Therefore, the greater the difference in genotypes at seed origin and plantation site, the greater the risk in seed transfer.

I describe patterns of genetic variation based on a sample of 135 parent Douglas-fir trees from 80 locations throughout southwest Oregon and use the date to devise provisional seed transfer rules. I then discuss results in relation to some of the above assumptions.

Materials and Methods

Sampling From Natural Populations

The sampled area is approximately square with west and east boundaries 64 and 192 km from the Pacific Ocean. The southern boundary is on the northern California border, and the northern boundary is along the 43° N parallel. The area lies within the Mixed-Conifer and Mixed-Evergreen Zone (Franklin and Dyrness 1973). Geology, soils, and topography are extremely variable. Data from meteorological stations indicate strong environmental gradients within the region. Annual precipitation, primarily rain except at highest elevations, grades west to east from about 160 to 50 cm, and from north to south along the western Cascade Range from about 100 to 50 cm. Precipitation falls mainly in winter; at Medford, in the southeast quarter of the region, only 3.6 cm are expected from June through August. Temperatures follow similar gradients. January mean minimum temperatures range from 2.5° C to − 5.0° C from west to east. July mean maximums range from 24.5° C to 31.0° C, northwest to southeast (Franklin and Dyrness 1973).

In 1976, cones were collected from 135 parent trees, from 2 trees separated by more than 133 m at each of 55 locations, and from 1 tree at the remaining 25 locations. The geographic origin of each parent tree was described by eight location variables: elevation, latitude, distance from ocean, vertical height of the major slope on which it was found, vertical distance from the bottom of the drainage, aspect, slope, and sun exposure. For determining sun exposure the vertical angle from tree to horizon was measured at 12.5° intervals of azimuth from east (90°) to west (270°). These data were plotted to provide a graph of the elevations of the horizon across the southern sky. From this graph and the graphed path of sun height throughout the day of April 3, the number of minutes of direct sun exposure at the parent-tree location was calculated.

For five of eight location variables, locations of parent trees almost evenly sampled the range of potential values. For the other three variables--sun exposure, vertical height of main slope and vertical distance from the drainage bottom--the values of samples tended to cluster around an average which, for the two vertical measures, occurred above the mode.

Common-Garden Procedures

For an evaluation of genotypes of parent trees, seeds were stratified for 30 days and germinated in petri dishes; seedlings were pricked into nursery beds when radicles were 1 to 10 mm long. Open-pollinated offspring from the parent tree were planted in two environments in nursery beds at Corvallis, Oregon. A family was represented by five-seedling row plots, allocated randomly in each of four replications in an environment. The environments of one of the nursery beds was modified to create differences between the beds in seasonal temperature cycle. In this "warm" bed, air and soil temperatures were increased to provide warm temperatures in early spring and late fall. Warm soil was produced by burying heating cables at 15-cm depth and spacing. A polyethylene tent was placed over the bed to create warm air by the greenhouse effect. Differences in temperature between heated and unheated beds depended on radiation and time of day and year but ranged between 0^0 C and 10^0 C in both soil and air.

Traits expressing timing of the seasonal vegetative cycle and growth potential were evaluated. Since traits in one environment or growing season might involve expression of some aspects of genotypes not experienced in the other environment or year, seedling responses were evaluated separately in the two environments and two growing seasons. For each trait, the genotypic value of a parent tree was estimated by the mean of 20 seedlings growing in one environment. Pertinent traits are described in *Table 1*. Standard deviations of trait values within plots were calculated and analyzed for all traits in *Table 1* except second flushing. Except for WSDHT, family standard deviations within plots did not vary among sources and are not listed in the table.

Table 1. — Description of traits.

Code: Nursery environment			
Cold[a]	Warm[b]	Trait	Unit
CBS77[c]	WBS77	Budset[d]	Weeks after 16 August 1977
CBB78	WBB78	Budburst[e]	1/2 week after 13 February 1978
CBS78	WBS78	Budset	Weeks after 7 April 1978
CHT	WHT	2-year height	cm
CDIA	WDIA	2-year diameter	mm
CFLU	WFLU	% 2-year seedlings with second flush	arcsin (%)
	WSDHT	Standard deviation of height within plot	cm

a/ Nursery bed uncovered and soil unheated.
b/ Nursery bed covered and soil heated in fall and winter.
c/ Trait code; the first letter is for "cold" bed, the remainder is trait identification such as bud set in 1977.
d/ Time when first terminal bud scales were visible.
e/ Time when first needles expanded from terminal bud.

Table 2. — Analysis of variances for each trait.

Source of variation	df	Expected mean squares[a]
Total	539	
Replications	3	
Sources	79	$\sigma_p^2 + 4\sigma_{f(s)}^2 + 6.743\sigma_s^2$
Families in sources	55	$\sigma_p^2 + 4\sigma_{f(s)}^2$
Error	402	σ_p^2

a/ σ_s^2 = variance of seed-source effects;
$\sigma_{f(s)}^2$ = variance of family within seed-source effects;
σ_p^2 = variance of plot effects.

Analysis

Analysis of genotypic values involved five steps:

(1) analyzing the variability to determine which traits varied significantly among families and to partition this genetic variation into source and within-source components;
(2) partitioning the genetic (source level) correlation matrix into its principal components;
(3) transforming genotypic values of individual traits for each parent into factor scores for the major principal components for each parent;
(4) determining which location variables were significantly related to factor scores; and
(5) mapping factor scores in terms of location variables.

For each trait (or combination of two traits), components of variance (or covariance) were calculated from the model,

$$Y_{ijk} = u + R_k + S_i + F_{ij} + e_{ijk};$$

where Y_{ijk} = mean of five seedlings for the kth replication (R) of the jth family (F) in the ith source (S); u is the overall experiment mean and e is experimental error consisting of the pooled interactions of both sources and families with replications. Analyses were conducted separately for each environment (program NESTAV--Oregon State University Computer Center, Corvallis, Oregon). To partition variance (or covariance) into components, mean squares in the analysis of variance were equated to their expectations and the resulting equations were solved *(Table 2)*. Covariances were calculated from components of variance of the sums of observations by the relationship given in Griffing (1956:489) or Kempthorne (1957:264).

Growth and vegetative-cycle traits may form a coadapted, highly correlated, multivariate system. In the second step, the matrix of genetic correlation coefficients describing correlated responses applicable to sources was used as input for principal component analysis (Morrison 1967). The analysis transforms the original set of variables into a new set. The new set includes all the variation in the original set; furthermore, one or two of the new variables, the principal components (PC's), often account for most of the variation in the original set. Use of a genetic correlation matrix ensures that all variables in the original set are scaled according to their genetic contributions to total measured phenotypic variation among sources.

Transformed factor scores for each family were obtained for each significant PC by the equation:

$$y_{in} = a_{i1}x_1 + a_{i2}x_2 + \ldots a_{ik}x_k;$$

where y_{in} = factor score for the ith PC
(i = 1—13), the nth family (n = 1—135),

and eigenvectors having coefficients a_{ik}, for the ith PC and kth original variable (x_k; k = 1—13).

Factor scores of parent trees for each of the significant principal components were fitted to location variables by multiple regression. The preliminary model included quadratic and interaction terms suggested from previous experience (Campbell and Sorensen 1978, Campbell 1979) for some variables in addition to linear terms for all variables. Because radiant energy is related to both aspect and slope, measurements of aspect and slope were combined by the sine-cosine-tangent transformation of Stage (1976). From the preliminary model, an equation in which all variables significantly reduced sums of squares in factor scores was selected by backward elimination (Draper and Smith 1966: 167). Lack of fit of data to the selected equation was tested by use of data from the two trees collected at 55 locations as "repeats" (Draper and Smith 1966:76).

The multiple regression equations were solved for factor scores at intersection points on a multidimensional grid of location values. The three main dimensions, which represented the location variables accounting for most of the variation among sources, were elevation, latitude, and distance from ocean. To form the grid, the range of elevations was divided into eight 150-m intervals. This provided nine slices (plane surfaces) through the region, one for each delimiting elevation. One side of each slice was divided into ten 11.1-km units of latitude and the other into ten 12.8-km units of distance from the ocean. Then factor scores were predicted for the location values at the intersections of lines connecting division points in the three dimensions. This provided a main grid consisting of nine 11 × 11 matrices of factor scores, one matrix for each slice. Vertical height of major slope, vertical distance from slope bottom, slope, and sun exposure accounted for smaller amounts of variation related to source. For these variables, predictions were limited to the two extreme values (e. g., greatest and least sun exposure). Values for these location variables were used with values from the main grid to predict factor scores for secondary matrices. Secondary matrices were useful for illustrating the maximum deviation expected from differences in the minor variables. Contour lines for factor scores were mapped in each matrix (program CONTUR-Oregon State University Computer Center, Corvallis, Oregon). Contour lines for factor scores were separated by intervals based on a seed-transfer risk index.

Estimating Transfer Risks

As a corollary of assumption 5, the mean genotypic value predicted for a location and the additive genetic variation among individuals at the location (σ_A^2) is assumed to also estimate the mean environment and the variation in space and time of the microenvironmental elements at the location (Campbell 1979). Equal genetic variances (σ_A^2), and therefore equal environmental variance, are also assumed at all locations.

When seedlings are planted in a new location, the mean of the plantation environments may differ from the mean of the environments of the seed parents. I assumed that the degree of mismatch between genotypes and microenvironmental elements indicates the relative risk in seed transfer. A mismatch index is estimated by the difference in frequency distributions of genotypes in native populations at the seed source and at the plantation site.

The mismatch index estimates the proportion of a curve of the genotypic lot at a seed origin which does not overlap the curve for a plantation site *(Figure 1)*. The corollary of assumption 5 states that for a given seed source micro-

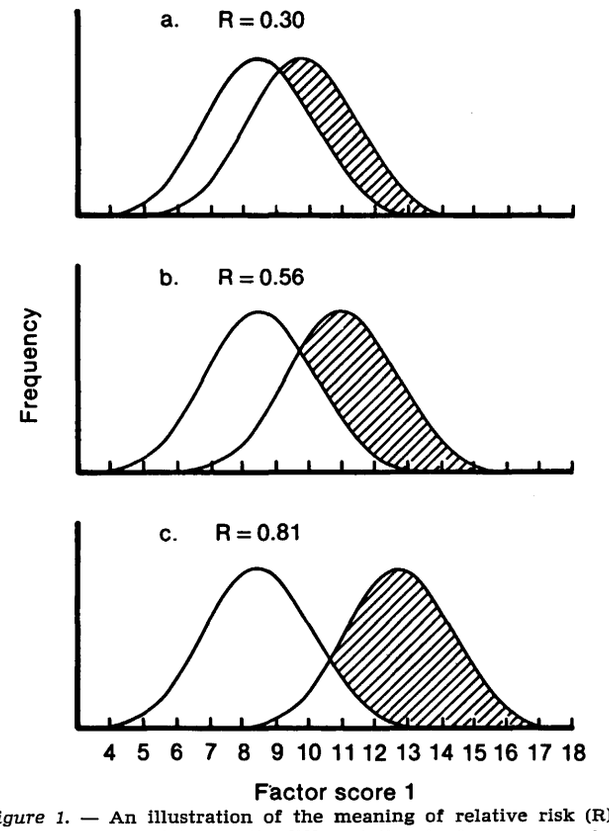

Figure 1. — An illustration of the meaning of relative risk (R). Each example depicts genetic differentation in factor scores for PC-1 between two hypothetical populations--at seed origin and at plantation site; a, b, and c give three degrees of relative risk in moving seed from origin to plantation. Risks are calculated as the proportion of the right-hand curve (cross-hatched area) not congruent with the curve on the left.

environmental and genotypic frequencies are described by the same curve. We can, therefore, take the curve representing the plantation site to represent the relative frequencies of available microenvironments into which a population of genotypes described by the curve for the seed source is being planted. The degree of noncongruence represents the frequency of genotypes not matching available environments. Noncongruence is estimated from the probability density functions of within-source genetic variability at the two sites. When the within-source genetic variability is equal for both sites, the proportion of overlap in the two curves can be calculated as:

$$V = 1\text{-}2\alpha$$

where $\alpha = P\ [0 < z < (x/2)/\sigma_A]$ = the area under the standard normal curve from 0 to z (e. g., *Table A3,* Snedecor and Cochran 1967:548) and $z = x/(2\sigma_A)$.

x = difference between mean factor scores at seed origin and plantation;

σ_A = standard deviation of the additive genetic variation of factor scores within sources;

z = standardized factor score.

The risk (R) in transfers between the two sites is: R = 1-V = 2α. To calculate x corresponding to a given R, first find z at which α = R/2. Then $z = (x/2)/\sigma_A$, and $x = 2z\sigma_A$.

Within-source genetic variance σ_A^2 was calculated as $3\sigma_{f(s)}^2$. The multiplier (3) assumes that 0.33 is the genetic correlation among offspring of open-pollinated parents; it reflects the greater likelihood of pollination by adjacent related trees (Squillace 1974) and an average 7-percent production of seed by self-fertilization (Sorensen 1973). The

Table 3. — Analyses of variance for traits and factor scores of principal components (PC-1 and PC-2).

Trait[a]	$\bar{X}$	Components of variance,[b] percent of total			
		Total			
		$\sigma_s^2 + \sigma_{f(s)}^2 + \sigma_p^2$	σ_s^2	$\sigma_{f(s)}^2$	σ_p^2
CBS77	5.32	1.392	42**[c]	19**	39
CBB78	13.20	1.213	27**	30**	44
CBS78	10.83	1.576	24**	22**	53
CHT	28.35	36.509	48**	10**	43
CDIA	5.56	1.080	36**	16**	48
CFLU	.97	.231	17**	0	83
WBS77	5.19	1.228	34**	27**	39
WBB78	7.64	1.358	34**	30**	36
WBS78	5.12	2.077	12**	28**	60
WHT	35.62	79.349	49**	12**	39
WDIA	7.41	1.543	43**	15**	42
WFLU	.45	.165	19**	8*	73
WSDHT	9.58	24.554	13*	10*	77
		$\sigma_s^2 + \sigma_{f(s)}^2$			
PC-1	11.24	3.987	78**	22	N[d]
PC-2	7.53	1.159	61**	39	N[d]

a/ See *Table 1* for Trait code and units of measurement.
b/ Symbols defined in *Table 2*.
c/ Significance in analyses of variance; ** = $P < 0.01$, * = $P < 0.05$.
d/ Plot effects were not calculated for factor scores.

family component of variance of factor scores ($\sigma_{f(s)}^2$) was estimated by analysis of variance of a one-way classification with two levels (sources and families within sources).

When a risk contour map is being built, the distance between contour lines depends on the risk (R) chosen as acceptable. After R has been decided, the x corresponding to the R is calculated and it serves as the interval between contour lines in the map of factor scores.

Results

Genetic Variability and Correlation

The vegetative cycle in the second growing season started (WBB78) and finished (WBS78) earlier in the warm environment than in the cooler environment; bud burst by 19 days and bud set by 40 days *(Table 3)*. Consequently, the time the terminal shoot grew was longer in the cooler environment (83 versus 62 days). But seedlings from the warm environment were 26 percent taller and 33 percent larger in diameter than those from the cooler environment. Fewer seedlings in the warm nursery bed produced second flush growth.

Analyses indicated significant genetic variability in all traits except those measuring the variability among seedlings within plots (within families). Although within-plot standard deviation was analyzed for five traits in two environments, it varied significantly among sources only for height in the warm environment *(Table 3)*. Averaged for 13 traits, seed-source variation (σ_s^2) comprised 64 percent of the source and family variation ($\sigma_s^2 + \sigma_{f(s)}^2$). In turn, source and family variation accounted for 48 percent of the total variation among plots.

The genetic correlations among traits varied, depending on whether they were calculated from seed source on family components of variance and covariance *(Table 4)*. The correlations based on source components were generally larger. For the 15 combinations among six traits common to the two environments, source correlations were about 54 percent larger than were family correlations *(Table 4)*. Within each of the two environments, correlations between seed-source traits were also larger, averaging 0.95 for sources and 0.52 for families. Approximate standard errors of correlation coefficients (Becker 1964) varied among traits depending on the size of the coefficient and trait heritabilities. Standard errors, however, were smaller than 0.03 for source correlations larger than 0.90 and smaller than 0.10 for family correlations larger than 0.50.

Relationships between traits differed qualitatively among sources compared with families. Comparisons among seed sources showed that early bud set in the first growing

Table 4. — Matrix of genetic correlation coefficients; above diagonal, for seed-sources, below diagonal, for families.

	CBS77	CBB78	CBS78	CHT	CDIA	CFLU	WBS77	WBB78	WBS78	WHT	WDIA	WFLU	WSDHT
CBS77		-.210	.719	.887	.843	.972	.976	-.423	.715	.941	.943	.950	1.069
CBB78	.593		.524	-.208	-.281	-.009	-.076	.947	.597	-.201	-.273	-.293	-.137
CBS78	.556	.517		.671	.545	.615	.710	.173	.858	.686	.665	.831	.830
CHT	.957	.653	.672		1.001	.870	.811	-.404	.725	.960	.973	1.066	.962
CDIA	.462	.100	.380	.792		.772	.821	-.458	.719	.934	1.003	.904	.879
CFLU	.000	.000	.000	.000	.158		.966	-.316	.563	.748	.633	.933	1.082
WBS77	.711	.363	.383	.459	.225	.095		-.330	.856	.910	.939	1.015	.977
WBB78	.445	.672	.328	.177	.011	.188	.460		.457	-.408	-.380	-.248	-.360
WBS78	.399	.424	.552	.263	.111	.241	.522	.605		.681	.803	.789	.841
WHT	.328	.168	.191	.448	.392	.257	.626	.159	.577		.935	.994	.973
WDIA	.306	.232	.096	.487	.561	.233	.365	.041	.141	.830		.922	.398
WFLU	.257	.065	.121	.052	.132	.191	.628	-.069	.455	.950	.557		.466
WSDHT	.114	.132	.200	.176	.127	.110	.444	.171	.289	.630	.8521		.125

season (CBS77 and WBS77) was associated with late bud burst (CBB78 and WBB78) the next spring ($\bar{r} = -(0.210 + 0.330)/2 = -0.27$, *Table 4*). But, comparisons among families showed early bud set was followed by early bud burst ($\bar{r} = 0.53$). The smallest of the source and family correlations had a standard error of < 0.15, the largest had a standard error < 0.10. Seed sources with early bud burst had average seedlings that were larger in both height and diameter. But families with earlier bud burst usually produced smaller seedlings.

Principal Components

The correlation matrix for seed source was used as input for the principal component (PC) analysis because variation among seed sources more clearly pertained to adaptive variation important in seed transfer. The first two principal components were statistically significant ($P \leq 0.001$), and together they explained 96 percent of the seed-source variation in all traits. The variance in factor scores (eigenvalue = 9.77) derived from PC-1 was more than three times the variance (eigenvalue = 2.69) in factor scores for PC-2 *(Table 5)*. Trait communalities (the percentage of a trait's variance held in common with the factor scores for the two PC's) indicated that the two PC's accounted for most of the variation in all traits. Because of errors in estimates, some genetic correlation coefficients were larger than 1 *(Table 4)*. This contributed to the overlarge communalities and eigenvalues in *Table 5*.

General effects can be identified by examining loading and eigenvector coefficients in *Table 5*. Principal componet 1 expresses mainly growth vigor whereas PC-2 expresses aspects of growth timing not correlated with seedling size. This "naming" of PC's is not definitive but only to provide a feeling for the complex relationships involved. The smaller the factor score for PC-1, the earlier the bud set and the smaller the seedling. Also, the smaller the factor score, the fewer the seedlings that second flush and the less the variation in height among seedlings within families. The smaller the factor scores for PC-2, the earlier the bud burst and bud set.

Principal components 1 and 2 consolidate the parts of the correlated genetic system connected with parent-tree origin. Factor scores derived from the PC's measure two independent expressions of the genotype, both hypothetically important in seed-source adaptation. But trees within sources, as well as sources, vary in the two expressions. In factor scores derived from PC-1, 78 percent of variation was associated with seed sources and 22 percent with families. In factor scores from PC-2, corresponding values were 61 percent and 39 percent *(Table 3)*.

Table 5. — Principal components (PC) with seed-source trait loadings, eigenvector coefficients and eigenvalues.

	PC-1[a/]		PC-2[b/]		
Trait	Loading	Coefficient	Loading	Coefficient	Communality
CBS77	.983	.010	-.084	-.034	.973
CBB78	-.123	-.004	1.008	.375	1.031
CBS78	.759	.082	.542	.200	.870
CHT	.974	.099	-.100	-.040	.959
CDIA	.928	.093	-.171	-.066	.890
CFLU	.896	.092	-.006	-.004	.803
WBS77	.971	.100	.037	.011	.944
WBB78	-.324	-.025	.933	.348	.976
WBS78	.790	.087	.660	.244	1.060
WHT	.958	.097	-.100	-.040	.928
WDIA	.947	.096	-.096	-.038	.906
WFLU	1.026	.105	-.023	-.011	1.053
WSOHT	1.031	.106	.011	.002	1.065

a/ Eigenvalue, 9.770; % variation, 75.2.
b/ Eigenvalue, 2.685; % variation, 20.7.

Mapped Genetic Variation

Regression equations relating factor scores to variables describing parent-tree origin were complex, a condition consistent with the intricate environmental gradients in the region. The regression equation for PC-1 accounted for 68 percent of the sums of squares ($R^2 = 0.68$) in factor scores. Regression coefficients of the environmental variables were highly significant *(Table 6)* and had small standard errors--consistently about 25 percent the size of coefficients. Some seed-source variation remained unexplained. In analysis of variance, seed-source variation accounted for 78 percent of total genetic variation *(Table 3)* but regression explained only 68 percent *(Table 6)*. The difference, 10 percentage points, represents seed-source variation that may or may not be associated with variables not considered in the environmental model. Residuals did not reveal any weaknesses in the model, and lack of fit was not statistically significant at $P \leq 0.05$ *(Table 6)*.

Genetic variation in PC-1 was most strongly associated with distance (D) from the ocean (standardized partial regression coefficient, $D = -42.16$, *Table 6)*. Latitude influenced the association with distance from the ocean ($LD = 39.44$). The average association of genetic variation with elevation was less than with distance ($E = 33.5$), but the association was modified considerably by latitude ($EL = -34.90$) and slightly by distance ($ED = 5.13$, $DE^2 = -2.76$).

The regression equation for PC-2 accounted for 48 percent of the total genetic variation *(Table 6)*. Standard errors of regression coefficients averaged 26 percent of the size of regression coefficients. Since seed-source variation made up 61 percent of the genetic variation in analysis of variance *(Table 3)*, the regression equation apparently did not describe all the seed-source variation; however, lack of fit to the model was not statistically significant *(Table 6)*. Genetic variation in PC-2 was mainly associated with distance from the ocean modified by elevation ($ED = -8.72$, $ED^2 = 4.46$, *Table 6)* and with elevation ($E = 4.33$).

Except for aspect, the other location variables--slope percent, height of main slope, and sun exposure--contributed slightly, but significantly, to the explanation of variation in PC's *(Table 6)*. Genetic variation in the two PC's was not associated with aspect *(Table 6)*.

The complex patterning of genetic variation within the region made straightforward topographic mapping impossible. For example, if factor scores indicating seed-source variation in PC-1 were mapped on a mountain, the factor score at a point on the mountain would depend mainly on elevation, latitude, and distance from the ocean with minor adjustments for the size of the mountain and shading of the point by surrounding mountains. The illustration of genetic variation on a topographic map would require maps of variation for every mountain and valley. Furthermore, since the two PC's and resulting factor scores represent uncorrelated expressions of the genotype, separate maps would be necessary for each PC.

My approach was to make a series of two-dimensional grids of latitude and distance from the ocean. Each grid in the series incorporated factor scores predicted for appro-

Table 6. — Regression analyses of factor scores from principal components.

Principal component 1				Principal component 2			
Variable[a/]	Partial coefficient	Significance P < ...	Standard coefficient	Variable[a/]	Partial coefficient	Significance P < ...	Standard coefficient
E	.5470E-01	.002	33.53	E	.3888E-02	.000	4.33
LD	.8847E-01	.000	39.44	ED^2	.2973E-06	.000	4.46
VE^2	.6821E-10	.000	0.46	EDT	.2662E-04	.001	1.44
DE^2	-.6983E-08	.000	-2.76	ET	-.1832E-02	.001	-1.48
ED	.7302E-04	.000	5.13	DV	.6842E-04	.000	2.83
PV^2	-.5741E-09	.000	-.37	ED	-.6814E-04	.000	-8.72
EL	-.1358E-02	.002	-34.90	DVP	-.1032E-06	.000	-3.07
D	-3.9728	.000	-42.16	DP	.6881E-04	.000	1.13
DP	.5719E-04	.027	.51	CONST	2.5275	.004	
CONST	21.4381	.000					

Probability of lack of fit for PC-1 is 0.055; $R^2 = 0.68$.
Probability of lack of fit for PC-2 is 0.090; $R^2 = 0.48$.
a/ Where E = elevation in feet (0.3047 m),
L = latitude in degrees,
D = distance from the ocean in miles (1.609 km),
P = sun exposure in minutes exposed to direct sun on April 3,
V = vertical height of the major slope in feet (0.3047 m),
T = slope in degrees/45,
CONST = constant.

priate latitudes and distances from the ocean, but also for a representative combination of the other significant variables: elevation, sun exposure, vertical height of the main slope, and slope percent. Factor scores were predicted for intersecting points on each grid. Then, isolines connecting equal values of factor scores were mapped, one set of lines for PC-1 and one for PC-2.

The clines, which run perpendicularly to the isolines, describe average genotypic values at points along the gradients. There may be considerable variation among genotypes (within-source variation) at any point on the cline. The magnitude of the within-source variation does not appear to vary appreciably from source to source in this experiment, although the evidence is indirect. If the genetic variation among trees is greater at one location than at another, the difference should be reflected in the variation among individuals within families (2/3 of the within-source additive variation is found within families). In the analysis of several growth and phenological traits in this and a previous experiment (Campbell 1979), significant variation among sources in within-plot standard deviations rarely occurred. When it did occur, variation among sources was small. For the calculation of seed-transfer risk, within-source genetic variability was therefore assumed to be similar at all locations.

Seed Transfer Risks

For each PC, major and minor isolines were mapped *(Figure 2)*. For PC-1, the distance between a major and minor line was 1.26 factor-score units. Major lines were separated by 2.51 units. For PC-2, corresponding values were 0.89 and 1.79. These distances represent arbitrarily selected amounts of risk in seed transfer. Seed transferred from any origin on a PC-1 major line, for example, to a plantation site on an adjacent PC-1 minor line represents a relative risk of 0.30 in respect to the part of the genotype indexed by PC-1 *(Figure 1a)*. From the corollary of assumption 5, this implies that 30 percent of seedlings will be poorly preadapted to available microhabitats. The 30 percent is relative to the likelihood of a genotype matching a microhabitat in its native environment--even in the native environment not all genotypes are adapted to available microhabitats. Because plantation environment may be changed from the natural environment, however, the risk value must be considered mainly as an indicator of relative risk. A move to the nearest adjacent PC-1 major line increases the risk to 0.56 *(Figure 1b)*.

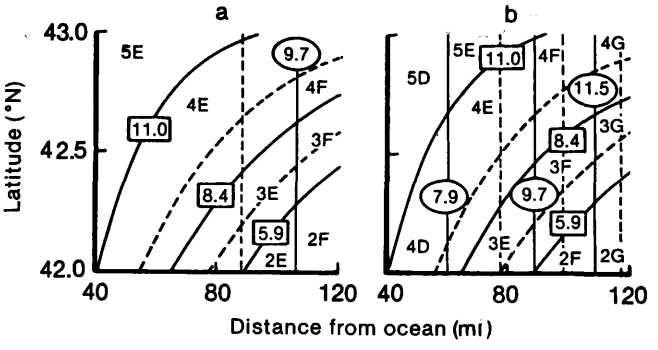

Figure 2. — Provisional seed-transfer zones for southwest Oregon in an area 40 to 120 miles (64 to 192 km; mile = 1.61 km) from the ocean by 42° to 43° N latitude. Zones (3F, 4F, 4E, etc.) are circumscribed by major isolines (solid) and subdivided by minor isolines (dashed). Major isolines are labeled with factor scores for PC-1 (rectangles) and PC-2 (ovals). Zones in both a and b illustrate boundaries appropriate for areas with elevation = 609 m, sun exposure = 550 minutes on April 3, and vertical height of the main slope of mountains = 762 m. Zones in a are specific for areas with no slope (degrees/45 = 0). Zones in b are for steep slopes (degrees/45 = 0.8). The differences in boundaries in a and b are caused by the placement of isolines for PC-2. This placement reflects the association of genetic variation in PC-2 with slope. PC-1 did not vary with slope; a map of isolines for PC-1 is therefore the same for a flat or a steep slope.

Principal components 1 and 2 represent different and independent aspects of the genotypes. A seedling moved might risk poor adaptation for PC-1, PC-2, both, or neither. The total risk (CR) in seed transfer takes into account the proportions (Pro) of seedlings poorly adapted in PC-1 or PC-2 or both:

$$CR = Pro\ (1) + Pro\ (2) - [Pro\ (1) \times Pro\ (2)].$$

Therefore, the risk in transferring seed from a place where major lines for PC-1 and PC-2 cross, for example, to a place where minor lines cross is 0.51 [0.30 + 0.30 — (0.30 × 0.30)]. Transfer between places where major lines cross increases the risk to 0.81 *(Figure 1c).*

Seed Zones and Transfer Rules

Risk information is useful for defining seed zones *(Figure 2).* Zones characterized as 4D, 4E, 4F, etc., represent the area bordered by major isolines. The 4 represents a segment within the range of predicted factor scores for PC-1, from 8.4 to 11.0. The E represents a segment, 9.7 to 11.5, within the range of factor scores for PC-2. The maximum predicted risk within a zone (0.81) would be in movement between opposite corners of a zone. Risks for all other seed transfers within the zone would be smaller. In *Figure 2,* each zone includes four subzones, each bordered by two major and two minor lines. Maximum predicted risk within subzones would be 0.51.

The curved lines that delimit two of the four boundaries of zones in *Figure 2* reflect the gradient in PC-1 that runs perpendicular to the lines, generally from northwest to southeast corners of the region, apparently in response to gradients in precipitation. Seedlings from sources along this gradient decrease in size and set buds earlier. Fewer seedlings from southeastern sources produce lammas shoots. The gradient is steep at low elevations but almost disappears at high elevations. But seedlings from most high elevation sources are smaller than those from middle elevations.

The vertical lines that delimit the other two boundaries of the zones in *Figure 2* reflect an east-west gradient in PC-2. This may correspond to the influence of the average temperature on early spring frost which has selected parent trees for timing of bud burst. The gradient in PC-2 depended strongly on slope percent, sun exposure, and size of mountains as measured by the height of slope.

Figures 2 through *5* provide a sample of potential zone maps derived from seed-transfer equations. The grids on which isolines were drawn were chosen from a more complete set of grids to provide comparisons of the influence of some location variables when other location variables were held constant. Effect of extremes in slope percent can be seen by comparing *Figures 2a* and *2b;* the effect of elevation by comparing *Figures 3a* and *3b;* the effect of sun exposure by comparing *Figures 4a* and *4b;* and the effect of height of the main slope by comparing *Figures 5a* and *5b.*

Some zones appear to extend over an extreme range of elevation; for example, 4E, which crosses 758 m (2,500 feet) of elevation. Zone 4E, from areas on flat ground at low elevation that are heavily shaded by surrounding mountains *(Figure 2a;* sun exposure = 550 minutes, slope = 0, elevation = 609 m), appears to be suitable for plantations on unshaded steep slopes at much higher elevation *(Figure 3b;* sun exposure = 750 minutes, slope = 0.8, elevation = 1371 m). Some of the zones indicated in *Figures 2* through *5* are applicable to only a small part of the actual topography. This may partly explain the appearance given that some zones (e.g., 4F and 4G) are appropriate to both

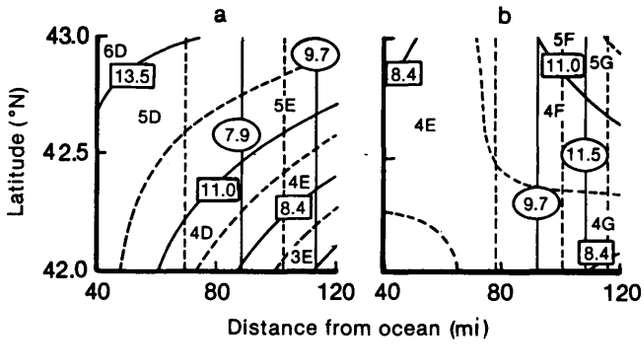

Figure 3. — Provisional zones for areas with sun exposure = 750 minutes, vertical height of main slope of mountains = 152 m, and steep slopes (degrees/45 = 0.8). Zones in a are specific for a low elevation = 609 m. Zones in b are for a high elevation = 1371 m. (See caption of *Figure 2* for definitions of symbols.)

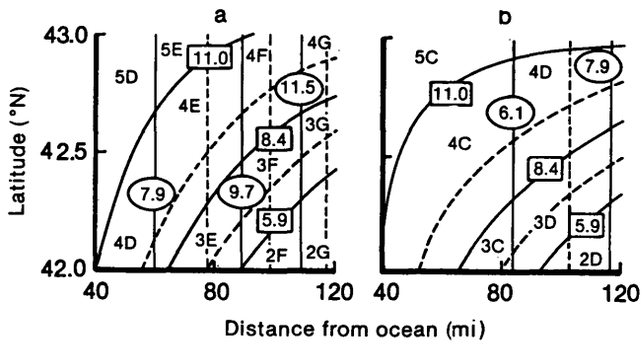

Figure 4. — Provisional zones for areas with elevation = 609 m, vertical height of main slope of mountains = 762 m, and steep slopes (degrees/45 = 0.8). Zones in a are for areas with sun exposure of 750 minutes. (See caption of *Figure 2* for definitions of symbols.)

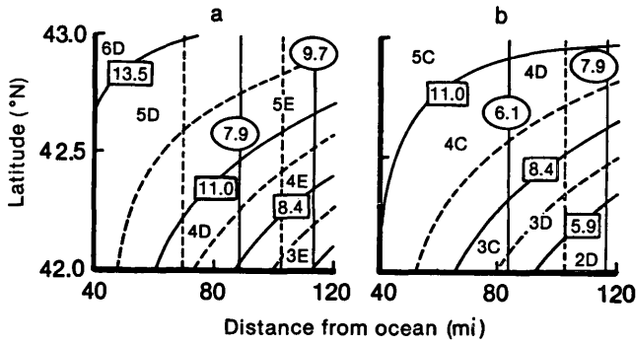

Figure 5. — Provisional zones for areas with elevation = 609 m, sun exposure = 750 minutes, and steep slopes (degrees/45 = 0.8). Zones in a are for mountains with main slopes of height = 152 m. Zones in b are for mountains with main slopes of height = 762 m. (See caption of *Figure 2* for definitions of symbols.)

high elevations *(Figure 3b)* and low elevations *(Figure 4a).* Along the eastern edge of the region, only the deep valley floors are at or below 610 m (2,000 feet). In the northwestern quarter of the region, only the tips of the tallest mountains extend above 1372 m (4,500 feet).

Seed-transfer zones, especially those based only on geography and elevation, are administratively efficient but may oversimplify the seed-transfer problem in southwest Oregon. As information accrues, zones are likely to become more complex *(Figures 2* through *5).* It may be more practical and informative to calculate directly the relative risk

Table 7. — Risk indexes (proportions of seedlings poorly preadapted in seed transfer) based on differences in predicted factor scores at seed origin and plantation site.

Difference in factor score for PC-1	Difference in factor score for PC-2			
	0.5	1.0	2.0	3.0
.5	.27	.41	.66	.83
1.0	.37	.49	.71	.85
2.0	.55	.64	.79	.89
3.0	.70	.76	.86	.93
4.0	.82	.85	.91	.96
5.0	.90	.92	.95	.98

in any projected seed transfer. This can easily be done by use of the regression coefficients in *Table 6* to compute factor scores. It involves solving two equations *(Table 6)*, each twice. First, calculate the factor score for PC-1 for values of location variables measured at seed origin, then for values measured at the plantation site. Second, compute factor scores for PC-2 at seed origin and plantation site. Third, calculate the difference in factor scores between seed origin and plantation site for each PC. Finally, enter *Table 7* with these differences to estimate relative risk in seed transfer within the region sampled.

Discussion

Evaluating the use of a genetic map to guide seed transfer requires consideration of two criteria. How well does the experiment fulfill the assumptions on which the mapping procedure is based? Is there a better alternative?

Sampling Natural Populations

Whether or not sampling has been adequate depends mainly on the amount and pattern of environmental and genetic variation in the region.

In southwest Oregon, aspect and other features of topography strongly influence vegetation composition and distribution, indicating substantial environmental heterogeneity (Franklin and Dyrness 1973). Since environment exists as a continuum, seed-source variation in southwest Oregon tends to be patterned in gradients (Hermann and Lavender 1968, White 1981). The genetic gradients shown in this experiment followed trends reported for other parts of the Pacific Northwest. Steep E-W gradients exist farther north at high elevations in western Oregon and Washington (Campbell and Sorensen 1978), south in northern California (Griffin 1978), and west in the Coast Ranges (Sorensen 1983). In the latter two reports, the steepest E-W gradients coincided with the mountain ridge closest to the coastline, regions west of the area sampled by this experiment.

Gradients with elevation were generally less steep than with distance from the ocean and were influenced by distance from the ocean and latitude. In the area between my sample and the coast, Sorensen (1983) finds a similar dependency between distances from the ocean, E-W aspect, and elevation. Strong interactions, including some with latitude, caused Griffin (1978) to consider elevation alone inadequate as an environmental index in northern California. Sorensen finds no trends with elevation at his most inland sample points.

Because of the complexity of environmental and genetic variation in southwest Oregon, the experiment should have included samples from more locations. Sampling was designed for 120 locations, but various problems reduced the actual number to 80 seed sources; however, these were well distributed within the region. Collections sampled extreme environments in the region. Collections also were stratified to reduce correlations between location variables, such as the correlation between latitude and elevation. These features of the sampling design helped to decrease standard errors of regression coefficients and to minimize problems associated with collinearity. Collecting from a relatively small number of source locations is adequate only if a few location variables are known to fully characterize the environmental complex active in natural selection. If too few locations are sampled in a heterogeneous region, seed-source variation may be inadequately sampled and mapped.

Estimating Genetic Variation in the Common Garden

Another assumption in using mapped genetic variation is that genotypic values can be adequately characterized in common-garden experiments. Such experiments must have precision to distinguish small differences among families and sources. That objective was attained in this experiment; but the more traits and environments involved in the experiment, the more completely the genotype is evaluated. Important parts of the genotype remain undescribed if independent adaptive traits are not measured.

Genotypes are poorly characterized if values are not determined over a range of test environments. The gradients of geographic variation associated with mapping attributes may be variable (Hermann and Lavender 1968, Morgenstern 1976, Campbell and Sorensen 1978, White 1981) or even opposite (Falkenhagen 1979) when evaluated in different test environments. Aspects of the genotype selected by nature to guard against rare adverse climatic events may be particularly elusive. Such events have been emphasized by Griffin and Ching (1977) as being potential major causes of genetic differentiation in Douglas-fir of northern California.

Test environments in this experiment were chosen to differentiate genotypes by fostering source × environment interactions in traits of the vegetative cycle (Campbell and Sorensen 1978). The nursery did not duplicate field environments. The nursery environments provided less frost and drought stress than is common in southwest Oregon. But traits correlated with frost and drought resistance were measured. Most of the variation in resistance of coastal Douglas-fir to frost in the fall can be associated with the date of bud set (Campbell and Sorensen 1973, Griffin and Ching 1977), and resistance to spring frost is closely associated with date of bud burst (Larsen 1976, Christophe and Birot 1979). Griffin and Ching (1977) found that discrimination among sources was better at low and moderate moisture stress, indicating better evaluation of genotypes at low levels of drought. Source differentiation has been reported as being greater in greenhouse and growth room trials than in nurseries (Hermann and Lavender 1968, White 1981). Mild test environments may be better than severe environments for estimating genotypic values of seedlings.

Analysis and Mapping of Genetic and Environmental Variation

Most failures in choosing models for describing genetic and environmental variation lead to underestimating variation among seed sources and risk in seed transfer.

A polynomial model was used in this experiment because several topographic and geographic variables are required

to index environments. Multicollinearity is unavoidable in polynomial models in multiple regression analysis. Multicollinearity makes it difficult to assess the relative importance of environmental variables. It also increases standard errors of regression coefficients; some significant coefficients may be omitted from the regression equation causing "lack of fit" and poor descriptions of variation in seed sources. If, however, the purpose of analysis is to make inferences about the dependent variable, multicollinearity is usually not a problem provided inferences are made within the range of samples (NETER and WASSERMAN 1974).

An alternative to the polynomial model is not apparent. Even if genetic variation could be attributed entirely to two climatic variables (for example, growing season length and precipitation), mapping climatic variation in mountainous regions is as uncertain as mapping genetic variation. To map climatic variation would require complex equations and more weather data than are commonly available.

The genetic mapping done here is provisional; it should be verified and added to by other experiments. In this experiment, the microgeographic variables--such as sun exposure, slope, and slope length--accounted for small percentages of variation. Their inclusion in the equations influenced zone boundaries *(Figures 2* through *5);* however adding other microgeographic variables would explain successively smaller proportions of variation, and each variable would magnify the complexity of equations and zone maps. Adding environmental variables increases the required number of tree samples and expands the common-garden experiment. Another major index of environment is needed to substitute for microgeographic variables in explaining remaining seed-source variation. Soil type is one promising possibility because soil types evolve (JENNY 1941) in response to many of the factors that affect survival in long-lived plants.

FALKENHAGEN (1982) objects to using common-garden tests for devising provisional seed-transfer rules. His main objection originates in a misconception. Because regression coefficients are calculated in the mapping procedure, he assumes that transfer rules are based on predicting the change in phenotypes when seedlings are moved from seed origin to planting site. But the mapping procedure does not predict phenotypes at plantation site. Instead, genotypic values (as determined in the common garden) are estimated for values of location variables by the principle that multiple regression gives the most probable value of one of the variates for given values of other variates regardless of causal relations (WRIGHT 1921). The regression equation describes the differences in average genotypic value associated with differences in location. Assumptions about adaptation and genotypes are then required to ascribe relative risks to seed transfer between locations.

Seed Transfer Risk Evaluation

Three assumptions in the genetic mapping procedure relate to assigning risks. The first includes three parts: (1) variation in genotypic value results from natural selection; (2) the environment presumably is the impelling force in natural selection; a map of genetic variation is therefore also a map of variation in those factors that have contributed to selection pressure; and (3) the greater the differences in environments and genotypes at two locations, the greater the risk in moving seedlings from one to the other. Variation in genotypic values of Douglas-fir can theoretically result from several causes other than selection. Often, however, the main patterns of variation seem to be best explained as resulting from selection (CAMPBELL 1979). This inference is strengthened if patterns repeat from mountain to mountain (e. g., with elevation or sun exposure or slope) and also closely follow other climatic trends in the region as they do in this study. The first two parts of the assumption are implied in most studies of geographic variation in which results are used to suggest seed-transfer guidelines (LANGLET 1945, REHFELDT 1981). The third seems reasonable given the validity of the first two.

The second assumption--that the relative risk indicated by seedling studies applies to older trees--raises the question of whether seedling measurements give an adequate evaluation of the growth potential of genotypes in later stages. Perennial growth depends on production and accumulation of material, its allocation to tissues, the timing of allocation, and the synchronization of these functions with the seasonal climatic cycle.

The common garden evaluates differences in growth timing and growth potential among seedlings. Phenology events that contribute to growth timing and duration (e. g., bud burst) seem to be quite consistent from younger to older ages (MORRIS *et al.* 1957), but seedling growth by itself often is not closely correlated with mature growth (PERRY 1976). This may be because duration of growth and growth rate at older ages both contribute to the "explanation" of total seasonal height and diameter (WORRALL 1973). Generally at mild sites, longer duration of growth and total growth are positively correlated. At one mild site, duration of seedling growth and total growth at an older age were positively correlated; the correlations were stronger as the older plants increased in age and were always much stronger than the correlations of seedling height with height at the older ages (CANNELL *et al.* 1981). On harsher sites, the correlation was lower (CANNELL *et al.* 1981), or was lacking, or was even negative (HAGNER 1970). This relationship has been interpreted (DIETRICHSON 1964, HAGNER 1970) as indicating that effects of growth timing and synchronization accumulate over seasons. At a mild site, the full growth potential provided by a long duration of growth and high growth rate can be realized. At a harsh site, an inherently long vegetative period may be detrimental and effects may show up as growth limitation in later ages. Various examples have been reported for the effects of poor synchronization: decreased height growth (DIETRICHSON 1968, ERIKSSON 1972), inadequate lignification (DIETRICHSON 1964), needle and twig damage (HOLZER 1969), immediate or delayed mortality caused by freezing of buds or cambium (EICHE 1966, STEFANSSON and SINKO 1967), and increased susceptibility to disease (DIETRICHSON 1969).

The size and condition of the older tree therefore appears to be a function of inherent growth potential as modified by events related to growth timing. Because timing varies among individuals (HAGNER 1970), these modifications may partly account for poor correlation of growth measurements in seedlings and mature trees. For this reason, nursery tests which measure timing as well as growth rate may be better predictors of seed source variation in later growth stages than are short-term field tests that measure only cumulative growth. In field tests, fluctuations in climate can provide quite different responses to synchronization in successive measurement periods (CAMPBELL 1974). This could influence short-term growth assessments. Nursery trials can evaluate timing and growth differences among genotypes more precisely than field tests do because

tests can be measured in environments chosen to express timing differences. The disadvantage in using nursery evaluation is that some seedling traits may be adaptively important only in the seedling stage. One example is: Needle characteristics conferring resistance to drought were concluded to be present only in the seedling stage; field tests indicated that the differences in drought hardiness that occurred during the first 2 years were the most critical for survival (VAN BUIJTENEN *et al.* 1976).

The third assumption — that transfer of a given distance along a gradient imposes an equivalent degree of risk regardless of direction — extends from the idea that differentiation in Douglas-fir follows gradients between mild and harsh environments; populations from mild environments display a higher growth potential but lower hardiness than populations from harsh environments (REHFELDT 1983). In southwest Oregon the growing season is limited by cold on some flat landforms and at high elevations, and by drought at low elevations with high sun exposure. Transfer from harsh to mild sites entails a risk of losing productivity because the transferred source does not have growth potential equivalent to the native source. Transfer from mild to harsh sites creates the risk of catastrophic damage leading to lower productivity.

It should be emphasized, however, that risks indicated by genetic mapping are relative to one another and cannot be extrapolated directly to losses in productivity. Seedlings poorly adapted to the natural situation may be less poorly adapted to the plantation (NAMKOONG 1969). To assign productivity values to risk assessments will require long-term tests.

Conclusions

If variation among families has been underestimated or location variables have been incorrectly included in the regression equation, relative risks in seed transfer may be overestimated. But most failures to meet the assumptions underlying the procedure lead to underestimates of seed-source variation: in sampling, which is usually limited by financial or other restrictions to too few or poorly located sources; in evaluation of genotypes, which may omit important traits; or in description of variation by regression, which may miss important environmental variables. Therefore, relative risks are more likely to be underestimated than overestimated.

In mountainous regions lacking the financial resources for intensive climatic mapping or for long-term seed-source trials, use of seed-transfer guides from genetic variation patterns is an alternative to use of subjectively delimited zones. Guides are designed to incorporate all the available quantitative information about differences among families, seed sources, and plantations. Adequately constructed and reasonably used, such rules would minimize risks associated with seed transfer.

Seed-transfer rules also provide a provisional model to be tested by long-term seed-source trials. The effect of seed transfer on harvest value cannot be estimated except by field tests carried to rotation age. Rules can provide a framework for locating long-term tests within an environmental grid and for extrapolating long-term effects within the region sampled by the tests. Without such a framework, long-term tests to develop transfer rules will have sampling problems equal to those involved in genetic mapping. Parsimony in sampling seed sources or test sites limits the ability to extrapolate growth effects to commercial sites and seriously compromises the value of the long-term test. Given the cost of long-term field experiments, it is doubtful whether enough test sites to adequately sample the Pacific Northwest can ever be afforded. A genetic map is a reasonable prerequisite for long-term trials.

Acknowledgements

I thank Mr. W. WESSEL, Mr. D. VAN DEN BERG, and Dr. R. STEVENS of the Bureau of Land Management, U. S. Department of the Interior, for managing the seed collections for a complicated sampling design; to Drs. M. T. CONKLE, M. A. K. KHALIL, E. K. MORGENSTERN, and G. REHFELDT for their helpful comments in review; and Mr. A. SUGANO for computer applications.

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Within-population variation in frost damage in Pinus contorta Dougl. seedlings after simulated autumn or late-winter conditions

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(Received 10th May 1985)

Summary

Single-tree progenies from a few populations of *Pinus contorta* were cultivated in a climate chamber and tested with respect to frost tolerance. The plants were exposed to -10^0 C for three hours during the hardening period, simulating autumn conditions. Single-tree progenies and population samples were exposed to two, six, or twelve large diurnal temperature fluctuations, -10^0—$+20^0$ C, simulating conditions inducing dehardening during late winter.

Significant differences in frost damage were found between populations as well as between single-tree progenies from one of the populations after freezing during autumn conditions. The family repeatabilities for frost damage exceeded 0.50 in two of the three populations studied.

Damage to plants increased with increasing number of simulated late-winter temperature fluctuations. This was the case both for the roots and the upper parts of the plants. No significant within-population variation in frost damage following exposure to simulated late-winter conditions was obtained. The simulating technique used is laborious and will not be further developed. There was a non-significant, positive relationship between frost damage induced in single-tree progenies by simulated autumn and late-winter conditions.

Key words: Pinus contorta, climate chamber, frost damage, within-population variation.

Zusammenfassung

Einzelbaum-Nachkommenschaften einiger Populationen von *Pinus contorta* wurden in einer Klimakammer angezogen und auf ihre Frosttoleranz hin getestet. Die Pflanzen wurden während der Aushärtungsperiode für 3 Stunden einer Temperatur von -10^0 C ausgesetzt, d. h. es wurden die Bedingungen im Herbst simuliert. Weiterhin wurden Einzelbaum-Nachkommenschaften und solche aus den Populationen 2, 6 oder 12 großen täglichen Temperaturschwankungen von -10^0 bis $+20^0$ C ausgesetzt, um die Bedingungen der Enthärtungsperiode im späten Winter zu induzieren. Sowohl zwischen Populationen als auch zwischen den Einzelbaum-Nachkommenschaften einer der Populationen wurden signifikante Unterschiede bei den Frostschäden gefunden, nachdem die Herbst-Frostbedingungen eingetreten waren. In zwei der drei untersuchten Populationen war der Wiederholbarkeits-Koeffizient für die Frostschäden auf der Familienbasis größer als 0,50. Die Schäden an den Pflanzen nahmen mit zunehmender Anzahl der simulierten Spätwinter-Temperaturschwankungen zu. Dies war der Fall sowohl bei den Wurzeln als auch bei den oberirdischen Pflanzenteilen. Es wurden jedoch keine signifikanten Unterschiede bei den Frostschäden innerhalb der Populationen erzielt, nachdem die Pflanzen den späten Winter-Bedingungen ausgesetzt worden waren. Die angewendete Simuliertechnik ist mühselig und soll nicht weiterentwickelt werden. Es gab eine nicht signifikante, positive Beziehung zwischen den Frostschäden, induziert durch simulierte Herbst- und Spätwinter-Bedingungen.

1 Introduction

For the three conifer species — *Picea abies, Pinus sylvestris, Pinus contorta* — planted in northerly Sweden hardiness is of decisive importance for the success of stand establishment.

In his comprehensive studies of plant survival in *Pinus sylvestris* populations, transferred altitudinally and/or latitudinally, Eiche (1966) unequivocally showed that the plant death originated from injuries occurring during late winter or early spring. He followed the plant death by annual inspection of all the 20 trials distributed over a latitudinal range of 61—68° and related his observations to the

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