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1701

GENECOLOGY OF DOUGLAS-FIR IN A WATERSHED IN THE OREGON CASCADES[1]

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Abstract. To gain insight into genetic microstructure of subregional populations of coastal Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*), genetic variability in a population found on a 6100-ha, central Oregon watershed is described. Genotypic values of 193 parent trees located throughout the watershed were estimated from progeny grown in a common garden. Then, genetic variation was partitioned into components attributable to parent-tree location and to differences among trees within locations. Within-location variation appeared to be homogeneous in the watershed; between-location variation was related to topography, but the patterns of trait variation differed depending on the trait measured. Growth traits exhibited strong gradients with elevation, but the relationship varied depending on position within the watershed. Based on estimates of proportions of nonadapted seedlings in hypothetical transfers of seed from one part of the watershed to another, genetic differentiation within the watershed was surprisingly large. In one transfer of 3.5 km between north- and south-facing slopes at the same elevation, ≈80% of seedlings were estimated to be poorly adapted.

Although other possibilities exist, the topoclinal variation in traits probably results from selection as does the large within-location variation. Both kinds of variation are due to high selection intensities in the seedling stage, the former to selection by average environmental differences along gradients, the latter to microenvironmental heterogeneity. The combination of high within- and between-habitat variation is suited to a species which episodically colonizes an environment that is extremely heterogeneous in time and space.

Key words: adaptation; Douglas-fir; genetic differentiation; genetic variance; natural selection; provenance; seed source; seed transfer; topocline.

INTRODUCTION

The term "genecology" was applied by Turesson (1923) to the study of infraspecific genetic variation of plants in relation to environments. Classically, this relationship has been examined by seeking correlations between "plant type" and "habitat type." In experiments designed to eliminate conditioning effects, consistently found correlations are taken to indicate adaptive significance (Heslop-Harrison 1964). Thus, a central problem in genecology has been to partition genetic variance of populations in such a way that the part attributable to habitat type can be estimated and evaluated.

In this report, I describe two components of genetic variation in a Douglas-fir population found on a small representative drainage in the Cascade Range, Oregon, USA: one component is associated with location of parent trees; the other indicates variability among trees at a location. My working hypothesis was that genetic variation in coastal Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*) is directly related to the complex climatic gradients common to mountainous topography. If so, the genetic variation attributable to parent-tree location would best be described by a topocline. This hypothesis follows from the concept that for any area delimited in space and time, the range of environments can be represented by an average effect and deviations from the average. For plants within such an area, an analogous average genetic effect and deviations exist because adapted plant types occur in proportion to environments (Levins 1969). If there is a gradient change in environments in several adjacent locations, there should also be a gradient change in genotypes, forming a cline (Langlet 1936, Levins 1963). Further, genetic variation among plants within locations along the gradient can be expected to be proportional to the number of environments sampled at each location.

My specific objectives were: (1) to describe patterns of genetic variation among trees in the watershed and (2) to estimate the proportions of seedlings that would be nonadapted in transfers from one spot to another within the watershed. An answer to the first is valuable as an insight into the adaptive strategy of Douglas-fir. The second provides a quantitative assessment of the degree of differentiation along gradients. It is also a vital step in developing seed-transfer rules and breeding zones for artificial reforestation of Douglas-fir.

MATERIALS AND METHODS

The sampled Douglas-fir population is in the H. J. Andrews Experimental Forest. The Andrews constitutes the 6100-ha watershed of Lookout Creek, which is a part of the McKenzie River drainage on the west-

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TABLE 1. Description of traits.

Trait	Description	Units
1. Seed weight	Based on 60-seed average*	mg/seed
2. Germination rate	Cumulative on probit scale	probits/d
3. Days to 50% germination	Interpolated from probit graph	days
4. Cotyledon number	Based on 20-seed average*	cotyledons/seedling
5. Bud set in 1972	First visible terminal-bud scales	weeks after 11 August
6. Bud burst 1973	First green needles from terminal bud	half-weeks after 24 March
7. Bud burst 1973 variability	Variability in trait 6 among 16–20 seedling*	$\log_{10}$ (variance in trait 6)
8. Bud set 1973	First visible terminal-bud scales	weeks after 6 July
9. Bud burst 1974	First green needles from terminal bud	days after 22 December
10. Bud burst 1974 variability	Variability in trait 9 among 16–20 seedlings*	$\log_{10}$ (variance in trait 9)
11. Second flush	Proportion of 3-yr seedlings with lammas growth	arcsin (percentage)
12. Height	3-yr total	cm
13. Height variability	Variability in trait 12 among 16–20 seedlings*	$\log_{10}$ (variance in trait 12)
14. Diameter	3-yr stem, cotyledon height	mm
15. Dry weight	3-yr-top	g × 10
16. Survival percent	3-yr seedlings surviving drought treatment	arcsin (percentage)

* Base number represents the number of seed (seedlings) per plot in each to two replications.

ern slope of the Cascade Range in west-central Oregon. It is a study site of the U.S. International Biological Program (IBP) Coniferous Forest Biome and recently has been thoroughly described (Wiens and Nussbaum 1975, Zobel et al. 1976). Elevations within the watershed range from ≈500 to 1600 m. At low elevations the mean temperature is 23°C, and extremes range from −19° to 38°C. Annual precipitation averages 2300 mm at low elevations. Precipitation and snowfall increase with elevation; areas above 1000 m commonly have winter snowpacks of 1–3 m (Dyrness et al. 1974). Actual evapotranspiration is ≈538 mm, and potential evaporation exceeds available water by ≈84 mm because of the region's typically low precipitation during summer months (Rothacher et al. 1967).

Timber stands are mainly in the 450-yr age-class, dominated by Douglas-fir except at highest elevations. Seeds were collected in late September and October from 193 trees as one-, two-, and occasionally three-tree samples. The samples were well distributed in 115 locations (sources) over the watershed, except for a circular roadless area of ≈800 ha in the watershed's southeastern corner.

From each individual-tree collection, 60 seeds in each of two replications were stratified for 5 wk and germinated in peat. From each replication, 22 randomly selected germinated seeds were pricked into a row plot in a corresponding replication in a nursery seedbed at Corvallis, Oregon, 80 km northwest of the Andrews Experimental Forest. Spacing was 7.5 cm in rows by 9.5 cm between rows. Families resulting from each seed collection were randomly assigned to rows within replications. Seedlings which died soon after transplanting were replaced. Thirteen traits of the internal 16–19 seedlings in each plot were measured through the third growing season (Table 1). After terminal extension had ceased in the third growing season, plants were stressed by withholding water. Diameter and dry weights were recorded only for drought survivors.

Data analysis was designed to describe genetic variation in the watershed, and it consisted of several steps. First, the genetic variation for 16 traits among parent trees was estimated by mean nursery-bed performance of the 193 open-pollinated families. Then trait variation among trees was partitioned by analysis of variance into components attributable to source and to additive genetic variation among trees at a source. Because traits are commonly interrelated by genetic and environmental correlations, the genetic variation pattern of a particular trait in a population reflects in part its genetic correlation with other variables. Consequently, a second step used principal component (PC) analysis to summarize the total variation in all traits in fewer than the original 16 variables, by taking into account the correlation structure among variables. Prior to PC analysis, data were scaled to the experimental error for purposes explained later. In the final step, family means were related to parent-tree locations by multiple regression.

For each trait, components of variance (Snedecor and Cochran 1967:291) were calculated from the model:

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

where Y_{ijk} = the mean of 16–20 seedlings (depending on trait) for the *k*th replication of the *j*th family in the *i*th source. From this the proportions of total trait variance of a randomly selected family due to source or to tree within source are, respectively,

$$\frac{\hat{\sigma}_s^2}{\hat{\sigma}_s^2 + \hat{\sigma}_{t(s)}^2 + \hat{\sigma}_e^2} \text{ and } \frac{\hat{\sigma}_{t(s)}^2}{\hat{\sigma}_s^2 + \hat{\sigma}_{t(s)}^2 + \hat{\sigma}_e^2};$$

where $\hat{\sigma}_s^2$, $\hat{\sigma}_{t(s)}^2$, and $\hat{\sigma}_e^2$ are estimated components of variance for source, tree-within-source, and error, respectively: $\hat{\sigma}_s^2$ estimates the genetic variation among the 115 sources and is hereinafter called "source variance" (or "source variation" in some contexts); $\hat{\sigma}_{t(s)}^2$ estimates ≈⅓ of the additive genetic variation among trees within sources and is called "within-source variance."

Principal component analysis (Morrison 1967) summarizes the variation in a multivariate system by transforming one set of variables (and their respective included variates) into another set. This second set has a number of useful properties: (1) derived variables (and included variates) are independent; (2) total variation in derived variates is equal to total variation in original variates; (3) variates in each derived variable account for proportions of the total variation which can be estimated; and (4) usually most of the total variation in original variates can be described by a few derived variables.

Derived variables are principal components, and corresponding variances of derived variates for each principal component are eigenvalues. The set of coefficients of the equation used to calculate derived variates from original observations is the eigenvector; each principal component has a characteristic eigenvector.

Before PC's were calculated, an observation $Y_{ij\cdot}$ of the *i*th family, *j*th source, was scaled $Y_{ij\cdot}/\hat{\sigma}_{ex}$ for the *x*th trait where $\hat{\sigma}_{ex}$ was derived from the error component of variance ($\hat{\sigma}_{ex}^2$) as established in the nursery experiment. Because families were grown in replicated randomized blocks, family and environmental effects are uncorrelated, except for seed traits. Consequently, the relation between variances of scaled observations (σ_o^2) and family ($\sigma_s^2 + \sigma_{t(s)}^2$) and error ($\sigma_e^2$) variances is:

$$\sigma_o^2 = 1 + \frac{\sigma_s^2 + \sigma_{t(s)}^2}{\sigma_e^2}.$$

Thus, scaled observations are relatively more variable for traits which are genetically more variable or phenotypically less plastic; i.e., a trait's contribution to the total variability described by principal components is in proportion to the trait's capacity for response to natural selection.

From scaled observations, an SSCP (sums of squares and cross products) matrix for the 193 families was calculated from family means:

$$\mathbf{S}_{(m\times n)} = \mathbf{O}_{(m\times n)}\mathbf{O}'_{(n\times m)}$$

where $\mathbf{S}_{(m\times m)}$ is the SSCP matrix for the 15 traits (height variability was omitted for lack of genetic variation), $\mathbf{O}_{(m\times n)}$ is the observation matrix, and $\mathbf{O}'_{(n\times m)}$ is its transpose.

Eigenvalues and eigenvectors were calculated in the usual manner:

$$\mathbf{SV} = \mathbf{VL};$$

where **V** is an m × m matrix whose *i*th column is the eigenvector associated with the *i*th eigenvalue, and **L** is a diagonal matrix whose *i*th diagonal entry is the *i*th eigenvalue.

Transformed variates for each family were obtained from the principal components by:

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

where y_{in} = a transformed variate for the *i*th principal component (i = 1–15), the *n*th family (n = 1–193). A = an eigenvector having coefficients a_{ik}, the subscript *i* referring to the eigenvector of the *i*th principal component, the *k* referring to the vector element corresponding to the *k*th original variable (x_k; k = 1–15).

To describe the association of source variation with physiographic variation within the watershed, nursery performances of families were related to parent origin by multiple regression. For each trait and PC, equations were fitted, respectively, to family means and transformed variates by selecting predicting variables from a preliminary model. This model was designed to describe source variation in as few variables as possible. Consequently, I used variables based on position within the watershed rather than on the more meaningful parameters such as slope, aspect, slope position, etc. A model including all potential physiographic variables and their interactions would have been large indeed. The preliminary model, therefore, included 19 "independent" variables constituted as an expansion series of linear, quadratic, and cubic terms of three primary variables, elevation, and north and east departures from an arbitrary point 1.5 km southwest of the westernmost reach of the Experimental Forest. Such a series with two primary variables has the form:

$$Y = b_0 + b_1X_1 + b_2X_2 + b_3X_1^2 + b_4X_2^2 + b_5X_1X_2 + b_6X_1X_2^2 + b_7X_1^2X_2 + b_8X_1^3 + b_9X_2^3;$$

where X_1 and X_2 are, for example, elevation and east departure and b_i are coefficients calculated from the data. From this model, in a backward elimination procedure (Draper and Smith 1966:167), equations were selected in which all included variables contributed significantly ($P < .05$) in reducing sums of squares in the dependent variables.

Two steps were used to judge equation adequacy. First, lack of fit ("equation bias," Draper and Smith 1966:26) of data to the selected equation was tested by using, as "repeats," data from the two or more families collected at 60 of the 115 locations. Then, for bias-free equations, the proportions of variation accounted for by the regression equation (R^2) and the proportions of variation related to parent tree source (source variance) were compared directly by the function $R_i^2 = a + bX_i$, where X_i = the source component of variance as a proportion of total variance for the ith trait. If equations have successfully explained source variation, then $a = 0$, $b = 1$, indicating that the regression equations have adequately described the source-related component of family variation as measured in the experiment.

Coefficients in complex regression equations often cannot be interpreted directly. Consequently, to illustrate results I chose to present the graphic surfaces predicted by equations by a process similar to trend analysis (Harbaugh 1964). First, the selected equations were solved for appropriate elevations and north or east departures at the intersections of a grid (0.7-km squares) superimposed on the watershed map. Then isograms were visually interpolated on a map of the watershed, the resulting contour-like lines being separated by an arbitrary but constant value for each trait.

I used two methods for estimating proportions of nonadapted seedlings in transfers from one location to another. The first follows from the proposition that if there is an average difference in environment between two locations, the relative proportions (z) of "micro" environmental types (i) will vary between locations. Since by Levins' (1965) optimum strategy hyopthesis the proportions of adapted types change in a continuous way with changes in z_i, some proportions of types in the first location will not be adapted to the second location; the greater the average environmental difference between locations, the larger the proportion of nonadapted seedlings in transfers from one location to another.

A calculation of this proportion is based on several assumptions (validity will be discussed later): (1) parents are survivors of at least 45 decades of natural selection—parental genotypes have been screened from many thousands of zygotes by the microenvironments at a location—the niche-variation hypothesis; (2) in the absence of definite information, the simplest assumption is that, because of screening, differences among adapted genotypes at a location closely reflect differences in environmental types—that is, genetic variation among trees at a location can be used to estimate directly variation in environmental elements that are active in natural selection; (3) thus, at a specific location, genotypes and environments have the same mean and variance; hence distributions correspond exactly assuming normal distribution; (4) when genotypes are transferred to new locations by seed or other means, new environments may have different means or variances depending on the transfer distance and the trait or traits used to measure genetic and environmental variations; (5) in transfers, the proportion of nonadapted seedlings is defined as the probability of a seedling finding itself in a microenvironment to which it is not adapted.

With estimates of within-source genetic variability and of mean differences between sources, this probability is easily calculated from properties of the normal distribution (a similar procedure has been used by Stern 1964, and Morgenstern and Roche 1969). For comparisons made later in this paper, source means for specific locations were calculated from regression equations. Within-source additive genetic variance was calculated as $3\hat{\sigma}_{t(s)}^2$. The multiplier 3 presupposes 0.33 as 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 of 7% production of seed by self-fertilization in Douglas-fir (Sorensen 1973).

The second method for estimating nonadapted proportions is based on the assumption that a transfer of seed from one location to another by natural or artificial means represents a change in the mean fitness of the transferred population. The genetic load associated with this change was calculated by O'Donald's (1967) equation:

$$L = \frac{\Delta\bar{X}(X_{max} - \bar{X})}{\sigma_A^2 + \Delta\bar{X}(X_{max} - \bar{X})};$$

where L = genetic load,
$\bar{X}$ = trait mean in the population being transferred (calculated by regression for the source location of the population being transferred),
X_{max} = trait mean after it has become stabilized by natural selection at the new location (estimated by the trait mean of the native population at the new location),
σ_A^2 = trait additive genetic variance.

Means and variances were estimated from family performance in the nursery experiment.

If fitness is the probability of survival, then the genetic load is the proportion of the deaths which arise from variation in fitness. Thus, genetic load measures the intensity of natural selection and also provides an estimate of proportions of nonadapted seedlings in seed transfers.

Proportions of nonadapted genotypes are mainly used here as indices of genetic differentiation, and indices are devised to provide an estimate of the "average" effect of seed transfer. Individuals are "nonadapted" only in the sense of not being likely to

TABLE 2. Composition of variation in traits. Columns 1, 2, and 3 are proportions of the total variance of a randomly selected family* due to experimental error, maternal parent within source, and source, respectively. Column 4 is the proportion of total variance due to families. Column 5 is the proportion of variance among families due to source.†

Trait	(1) $\hat{\sigma}_e^2/\hat{\sigma}_T^2$	(2) $\hat{\sigma}_{t(s)}^2/\hat{\sigma}_T^2$	(3) $\hat{\sigma}_s^2/\hat{\sigma}_T^2$	(4) $\dfrac{\hat{\sigma}_{t(s)}^2 + \hat{\sigma}_s^2}{\hat{\sigma}_T^2}$	(5) $\dfrac{\hat{\sigma}_s^2}{\hat{\sigma}_{t(s)}^2 + \hat{\sigma}_s^2}$
Seed weight	0.04	0.76	0.20	0.96	0.21
Germination rate	.69	.20	.11	.31	.36
Days to 50% germination	.60	.20	.20	.39	.50
Cotyledon number	.44	.45	.11	.56	.20
Bud set 1972	.31	.56	.12	.69	.18
Bud burst 1973	.40	.53	.07	.59	.11
Bud-burst 1973 variability	.89	0	.11	.11	1.00
Bud set 1973	.82	.14	.04	.17	.21
Bud burst 1974	.33	.57	.10	.67	.15
Bud-burst 1974 variability	.84	0	.16	.16	1.00
Second flush	.44	.28	.28	.55	.50
Height	.41	.19	.40	.58	.67
Height variability	1.00	0	0	0	N/A
Diameter	.68	.17	.15	.31	.46
Dry weight	.63	.13	.24	.38	.65
Survival	.66	.16	.18	.34	.54

* A family comprises the 30 to 40 seedlings grown from seeds of a single tree (wind pollinated).

† $\hat{\sigma}_e^2$ = component of variance for error. $\hat{\sigma}_{t(s)}^2$ = component of variance for effects due to maternal parent within sources. $\hat{\sigma}_s^2$ = component of variance for effects due to sources. $\hat{\sigma}_T^2 = \hat{\sigma}_e^2 + \hat{\sigma}_{t(s)}^2 + \hat{\sigma}_s^2$.

survive the 450 yr of climate and competition experienced by their parents. In fact, in any transfer some genotypes might reach higher adaptive peaks in the new environment, but we expect that many nonadapted types would be culled immediately by hostile microhabitats (Eiche 1966, Campbell 1974) and some by rare catastrophes (Silen 1964). Others, less maladapted but still poorly synchronized with seasonal cycle and weakened by accumulated minor climatic insults, would fail later by disease (Dietrichson 1968) or in competition with better adapted cohorts (Namkoong and Conkle 1976).

RESULTS

The 193 families differed significantly ($P < .05$) in all traits except 1973 bud-burst variability and height variability (Table 2, column 4). When variation among families was further partitioned into components due to source and to differences among trees within sources, the proportion due to source varied considerably, depending on the trait. For growth traits (height, diameter, dry weight) source variance averaged 59% of the total variance due to families; for seed traits (seed weight, germination rate and days to 50% germination, cotyledon number), 32%; and for developmental cycle traits (bud burst, bud set, and second flushing), 23% (Table 2, column 5).

Within-source variance apparently did not change with source location in the watershed, but the evidence is indirect. First, irrespective of trait, the deviations of individual families from the regression surface, which related family performance to elevation and watershed locations, were random. For within-source variance to differ from one part of the watershed to another, some patterning of deviations should be evident, particularly at locations where two or more parent trees were sampled. Second, within-family variability (i.e., bud-burst variability 1973, 1974, and height variability), which represents the normal genetic variability among individuals at a location as augmented by added variability due to gene flow, differed significantly among families only for bud-burst variability 1974. In this case, families differed because those bursting late, on the average, burst in a warm period, which restricted within-family variation compared with earlier families. Thus, neither analysis provided evidence for variation in within-source variance in the watershed. For subsequent calculations of proportions of nonadapted seedlings in seed transfers, I assumed that within-source variance is homogenous.

Apparently the relative magnitude of between-location and within-location components of genetic variation was little affected by environment in the test. The ratio of source variance to total family variance remained quite constant from year to year in traits measured in two succeeding years. For bud burst and bud-burst variability 1973 and 1974, comparisons were, respectively, 0.11 vs. 0.15 and 1.00 vs. 1.00 (Table 2, column 5). For bud set 1972 and 1973, the similarity in ratio (0.18 vs. 0.21) persisted despite a much larger proportion of error variation in 1973 measurements (0.82 vs. 0.31, Table 2, column 1).

The above analysis treats traits as being independent when, in fact, most are correlated to some extent. When the 15 traits were analyzed together, six principal components accounted for 90% of the total variation among traits (Table 3). Eigenvectors of addition-

TABLE 3. Principal components (PC) with trait loadings (l) and eigenvector coefficients (a), eigenvalues and eigenvalue total (next to last line) and proportions of total system variation explained by principal components (last line).

Trait		PC-1	PC-2	PC-3	PC-4	PC-5	PC-6	Communality
Seed weight	l	0.99	0.03	0	−0.04	−0.03	0	0.98
	a	.98	.06	0	−.13	−.12	−.02	
Germination rate	l	−.09	−.13	−.10	.45	−.36	.31	.46
	a	−.02	−.07	−.06	.35	−.36	.34	
50% germination	l	0	.14	.10	−.49	.48	−.26	.57
	a	0	.08	.06	−.41	.51	−.30	
Cotyledon number	l	.45	−.02	.01	.22	.55	.47	.77
	a	.13	−.01	.01	.22	.69	.64	
Bud set 1972	l	−.17	−.72	.33	−.33	−.04	.05	.77
	a	−.06	−.56	.28	−.39	−.06	.08	
Bud burst 1973	l	.07	−.28	.78	−.05	.02	.01	.69
	a	.02	−.19	.59	−.05	.03	.02	
Bud-burst 1973 variability	l	.05	−.15	.24	−.09	.08	−.05	.10
	a	.01	−.07	.12	−.06	.07	−.05	
Bud set 1973	l	−.09	−.17	.23	−.03	−.13	.13	.12
	a	−.02	−.08	.12	−.02	−.12	.13	
Bud burst 1974	l	.09	.24	.80	.24	−.08	.02	.77
	a	.03	.18	.67	.27	−.12	.03	
Bud-burst 1974 variability	l	−.09	−.08	.29	−.13	−.01	.19	.15
	a	−.02	−.04	.15	−.09	−.01	.19	
Second flush	l	0	−.51	−.35	−.37	−.14	.30	.63
	a	0	−.33	−.25	−.36	−.17	.41	
Height	l	.27	−.74	−.12	.26	.06	−.12	.72
	a	.08	−.50	−.09	.25	.08	−.17	
Diameters	l	.30	−.49	−.02	.39	.17	−.20	.55
	a	.07	−.26	−.01	.31	.17	−.22	
Dry weight	l	.24	−.56	−.11	.36	.14	−.18	.56
	a	.06	−.31	−.07	.30	.15	−.21	
Survival	l	.21	−.49	−.09	.19	−.05	−.13	.35
	a	.05	−.26	−.05	.15	−.05	−.14	
Eigenvalue		26.80	5.22	4.34	2.35	1.44	1.21	45.75
Variation percent		58.6	11.4	9.5	5.1	3.1	2.6	90.3

al PC's individually explained virtually none of the remaining variation.

Before PC analysis, observations were scaled by a procedure designed to emphasize genetic relationships among traits. Had the procedure been entirely successful, characteristics of that part of the genotype which controlled expression of the traits I measured could have been approximately described by one or more vectors (Grafius and Kiesling 1958, Grafius 1963), e.g., principal components. Although not completely satisfactory, scaling apparently did minimize environmental effects. Trait communalities (the percentage of a trait's variance held in common with transformed variates of the six PC's) ranged from 0.10 to 0.98 (Table 3) and were largest for traits in which total variation was due to family differences rather than to experimental error. For example, the correlation between values in column 4, Table 2, and communality was $r = 0.94$. Thus, it is mainly the family or genetic variability which has been partitioned into six principal components; and by hypothesis, these represent six uncorrelated, underlying latent variables.

For most PC's latent variables apparently represent gene constellations acting through physiologic processes common to more than one trait. The exception is PC-1. As indicated by loadings (Table 3), which are the simple correlations of variables with transformed variates of the PC'S, PC-1 represents seed weight. Seed weight is not genetically correlated with other traits—small eigenvector coefficients in PC-1 for factors other than seed weight provide little scope for common metabolic pathways. Furthermore, a secondary PC analysis excluding seed weight affected the structure of other PC's hardly at all.

In the secondary analysis, eigenvector coefficients for PC's 1–5 were almost identical to those for PC's 2–6 in Table 3, excluding seed weight. Also, eigenvalues were only slightly different from values for PC's 2–6 in Table 3, accounting for 27.7, 21.8, 14.6,

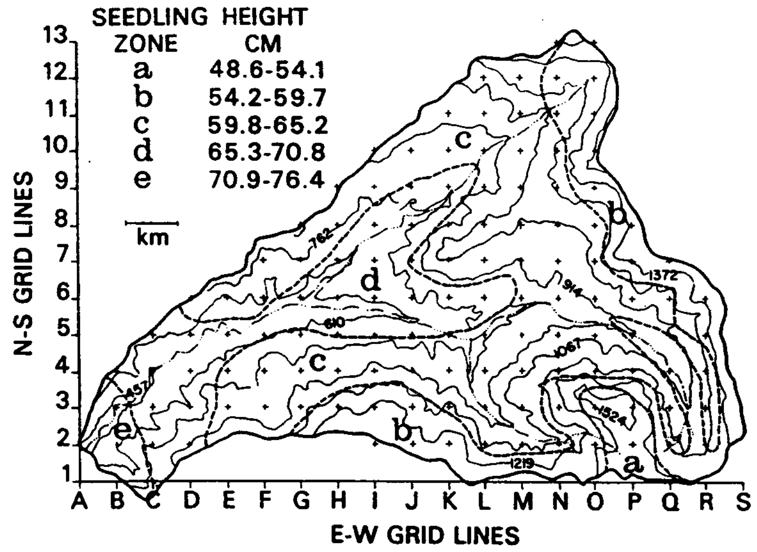

FIG. 1. Map of Lookout Creek drainage (H. J. Andrews Experimental Forest), showing watercourses (—· · ·), 152.4-m (500-ft) elevational contours, and zones for height classes of source variation in seedling families grown in a Corvallis nursery.

8.5, and 6.1% of total variation, respectively. Thus, PC-1 reflects seed weight almost exclusively. In the primary analysis, seed weight contributed heavily to total variation among traits because error variation for seed weight is small compared with family variation. Family variability in seed weight is accordingly expanded relative to other traits during the scaling procedure. Seed weight consequently contributes more to total variation.

Other PC's are not so easily named. However, general trait-constellations can be identified by examining loading and eigenvector coefficients in Table 3. For example, the larger the transformed variate representing PC-2, the earlier the annual vegetative phase is initiated and completed, the fewer the seedlings exhibiting lammas growth, the poorer the survival under drought stress, and the shorter and smaller the seedlings.

The larger the transformed variate in PC-3, the later the vegetative phase is initiated and completed. Growth in height, diameter, and dry weight are negligibly influenced.

The larger the transformed variate in PC-4, the sooner the earliest seeds germinate and the sooner 50% of seeds germinate; the larger the variate, the bigger the seedlings.

In PC-5, the larger the variate, the greater the number of cotyledons, the later the earliest seeds germinate and the later 50% of seeds germinate. Seedling diameters and dry weights are marginally increased with larger variates, whereas height is little influenced.

The variance in PC-6 is small (1.21). As in PC-5, this component represents mainly an amalgam of traits in seed germination and cotyledon number.

Regression equations relating family performance to elevation and topography were generally significant,

TABLE 4. Summary of multiple regression analyses of 14 individual traits.

	Germination rate	50% germination	Cotyledon number	Bud set 1972	Bud burst 1973	Bud burst 1973 var.	Bud set 1973	Bud burst 1974	Bud burst 1974 var.	Second flush	Height	Diameter	Dry weight	Survival
Regression coefficients‡	(8)	(10)	(8)	(3)	(5)	(6)	(8)	(11)	(2)	(10)	(11)	(5)	(11)	(6)
Sig. $P < .05$	3	0	0	1	1	3	1	4	2	7	1	1	6	1
Sig. $P < .01$	5	10	8	2	4	3	7	7	0	3	10	4	5	5
Regression equation§	**	**	**	**	*	**	*	**	*	**	**	**	**	**
P of lack of fit ‖	.16	.10	.34	.75	.36	.10	.47	.90	.01**	.02*	.07	.26	.15	.12
Residual df	185	183	185	190	188	187	185	182	191	183	182	188	182	186
Standard error	.21	1.20	.28	1.1	.86	.13	.18	.67	.14	.17	4.3	.52	2.2	.18
R^2	.07	.15	.13	.22	.06	.09	.08	.18	.02	.19	.42	.18	.30	.17

† Traits described in Table 1.

‡ Number of coefficients in regression equation and summary of significance.

§ Significance of regression equation; *, ** significant at 5 and 1%, respectively.

‖ Probability of lack of fit (Draper and Smith 1966) in equation.

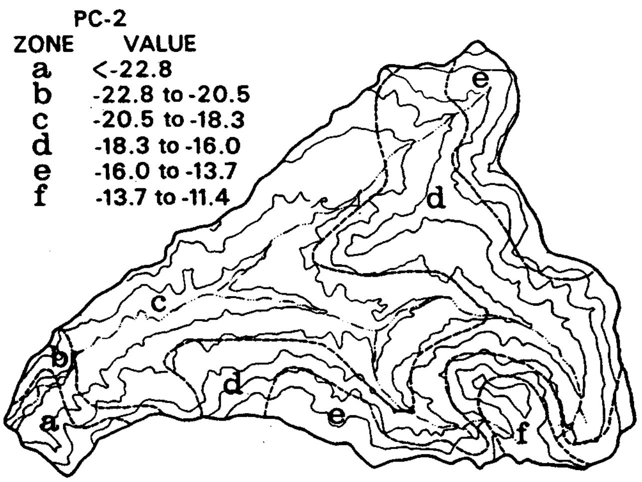

FIG. 2. Lookout Creek drainage, showing zones for source variation in principal component 2; the higher the value (e.g., zones e, f), the earlier the annual vegetative phase is initiated and completed, the fewer the seedlings exhibiting lammas growth, the poorer the survival under drought stress, and the shorter and smaller the seedlings.

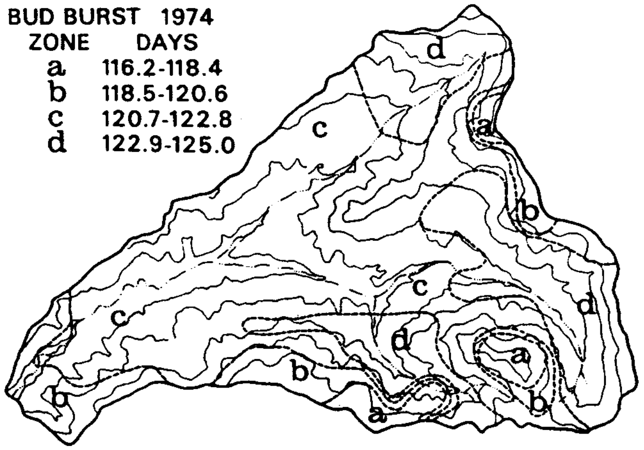

FIG. 3. Lookout Creek drainage, showing zones for source variation in bud burst as estimated by 1974 family averages (number of days from December 22 to bud burst) in Corvallis nursery beds.

and except for 1974 bud-burst variability and second flushing, lack-of-fit tests were nonsignificant (Table 4). Also, equations explained almost all of the experimentally determined source variation. This can be seen by comparing R^2's (Table 4) and individual trait source variances (X) as proportions of total variance (Table 2, column 3) after omitting equations for seed weight and for traits exhibiting lack of fit. R^2's and source variances were highly correlated ($r = 0.90$) and related by $R^2 = 0.021(\pm0.027) + 0.981(\pm0.154)X$. Thus, the hypothesis that R^2's are a direct expression of the measured source variation cannot be rejected.

Family responses were not simple functions of parent elevation or topographic location. Selected regression equations were complex and included from 2 to 11 statistically significant regression coefficients (Tables 4 and 5). All except one included significant coefficients for interaction, indicating that the association of family performance with parent tree elevation also depended on the parent's north-south or east-west location within the watershed.

For some traits, particularly those related to vegetative growth, source variation appeared to be mainly associated with elevation. For these traits, isograms in trend maps conformed nicely to elevational contour lines, particularly on north- and west-facing slopes. This is illustrated in Fig. 1 for seedling height; maps for diameter, dry weight, bud-set date, and second flushing showed similar patterns.

PC-2 is the principal component which most nearly reflects growth factors (Table 3). Higher values of transformed variates in PC-2 (i.e., families with earlier beginning and end of vegetative elongation in Corvallis nursery beds, with lower proportions of seedlings exhibiting lammas growth and with smaller seedlings) were found in families from higher elevations (Fig. 2). Values decreased on the average as elevation decreased. As expected from patterns discovered in individual growth traits, isograms and elevation contours were more congruent on north-facing slopes.

Responses in other traits were less obviously asso-

TABLE 5. Summary of multiple regression analyses of transformed variates from principal components.

	Principal components					
	PC-1	PC-2	PC-3	PC-4	PC-5	PC-6
Regression coefficients ‖	(9)	(11)	(8)	(5)	(6)	(8)
Sig. $P < .05$	0	0	2	1	5	2
Sig. $P < .01$	9	11	6	4	1	6
Regression equation†	**	**	*	**	*	*
P lack of fit‡	.16	.18	.44	.10	.35	.34
Residual df	184	182	185	188	187	185
Standard error	5.0	1.6	2.0	1.5	1.2	1.1
R^2	.12	.51	.08	.12	.06	.08

‖ Number of coefficients in regression equation and summary of significance.
† Significance of regression equation; *, ** significant at 5 and 1%, respectively.
‡ Probability of lack of fit in equation.

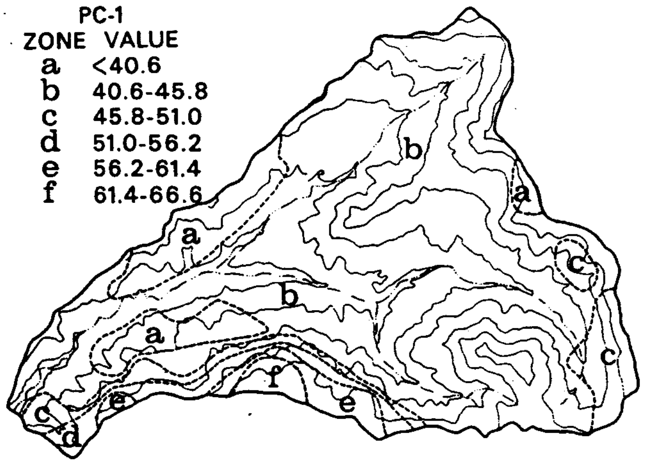

FIG. 4. Lookout Creek drainage, showing zones for source variation in principal component 1. Larger values indicate heavier seeds.

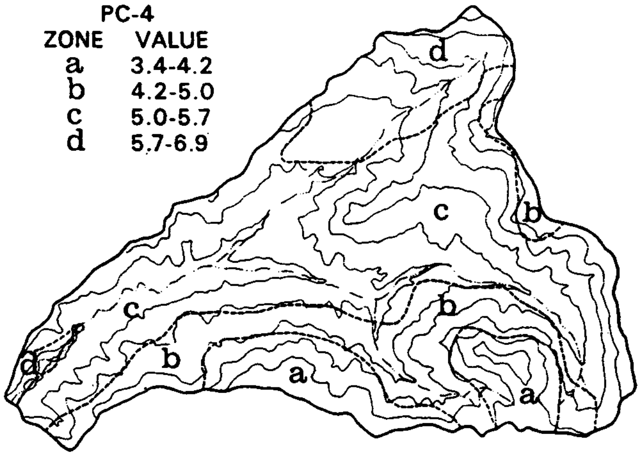

FIG. 5. Lookout Creek drainage, showing zones for source variation in principal component 4; the larger the value, the faster the seeds germinate, and the larger the seedlings tend to be.

ciated with elevation. Zones (i.e., the areas between adjacent isograms) for families with early bud burst (zone b, Fig. 3) were found at both high and low elevations. The zone (d, Fig. 3) for latest bud burst in Corvallis nursery beds extended over a 609-m elevational range in three distinct parts of the watershed.

The first principal component (PC-1), representing mainly seed weight, graded steeply from higher values on a north-facing slope at high elevations (e and f, Fig. 4) to low values for most of the remaining watershed. Zones e and f include some distinctive and extensive areas of seepage and springs.

Larger values for PC-4 (families having seed with faster germination rate and larger seedlings) were associated with slopes generally facing south (zones c and d, Fig. 5). Highest values on south-facing slopes were found at both highest and lowest elevations (d, Fig. 5). On north-facing slopes, highest values (zone b) were at lowest elevations.

In terms of genetic differentiation, isograms in above figures are not separated by equivalent distances. Consider, for example, a hypothetical transfer of native genotypes between extreme parts of zone c; i.e., between the b–c and the c–d isograms that delimit the c-zone. For height (Fig. 1), the resulting proportion of nonadapted genotypes is estimated by the probability method to be 0.69. Corresponding estimates for PC-2 (Fig. 2), PC-4 (Fig. 5), and 1974 bud burst (Fig. 3) were 0.33, 0.24, and 0.39, respectively. Estimates by the genetic load method agreed in relative value but were consistently higher.

Even for traits in which source variation was closely associated with elevation, clines associated with elevation gradients were steeper on some slopes than on others. For example, estimated proportions of nonadapted seedlings in a hypothetical transfer of 300+ m along north- and south-facing slopes were, respectively, 0.54 and 0.29 (Table 6, comparisons 1 and 3). Thus, in this particular comparison the rate of differentiation with elevation was 60% greater on the north slope (0.0015 p units/m on N-slope compared with 0.0009 p units/m on S-slope). Estimates are based on genetic diversity in PC-2, but a qualitatively similar conclusion is reached for PC-4, which is uncorrelated with PC-2 (Table 6, comparisons 2 and 4).

Differences in predicted performances of families from locations at identical elevations were sometimes large; family heights at grid intersections D2, G8, and P5 (Fig. 1) which represent points on a northwest-facing slope, a ridge top and a V-valley bottom, all at 914 m were 66.7, 64.1, and 57.9 cm. Between D2 and P5 the difference (8.8 cm) is almost one-third the range between extremes predicted for families in the watershed.

For PC-2, genetic differentiation among these same points is somewhat less; predicted variates were, respectively, −22.9, −18.6, and −16.9, the difference (6) between D2 and P5 being 44% of the range predicted for watershed families. In hypothetical transfers between D2 and P5, the proportion of nonadapted seedlings based on PC-2 is 0.73 (Table 6, comparison 6), substantially lower than the value (0.89, Table 6, comparison 5) based on seedling height. The discrepancy results because height variation is imperfectly described by PC-2, i.e., the correlation of height with transformed variates in PC-2 is −0.74 (Table 3, loading). Comparable differences between estimated proportions in transfers between D5 and G8 are even greater (Table 6, comparisons 7 and 8).

An even more striking case of differentiation is predicted between grid points B2 and E6, both at 609 m, only 3.55 km apart on northwest- and southeast-facing slopes on either side of Lookout Creek. Proportions of nonadapted seedlings were estimated at 0.74 and 0.81, depending on whether they are based on PC-2 or seedling height (Table 6, comparisons 11 and 12).

TABLE 6. Estimated proportions of nonadapted genotypes in transfers between locations in the watershed.

		Hypothetical transfer				Predicted non-adapted genotypes	
				Distance			
Comparison	Principal component or trait	Description	Coordinates from Fig. 1	Horizontal (km)	Elevation (m)	Method*	Proportion
1	PC-2	High (1280 m) and low (914 m) elevation, N-slope	J2 and J4	1.42	366	*P* *L*	.54 .69
2	PC-4	High (1280 m) and low (914 m) elevation, N-slope	J2 and J4	1.42	366	*P* *L*	.29 .35
3	PC-2	High (1249 m) and low (945 m) elevation, S-slope	N7 and N10	2.13	314	*P* *L*	.29 .36
4	PC-4	High (1249 m) and low (945 m) elevation, S-slope	N7 and N10	2.13	314	*P* *L*	.02 0
5	Seedling height	V-valley bottom and high north slope, both 914 m	P5 and D2	8.78	0	*P* *L*	.89 .91
6	PC-2	V-valley bottom and high north slope, both 914 m	P5 and D2	8.78	0	*P* *L*	.73 .83
7	Seedling height	V-valley bottom and ridge top, both 914	P5 and G8	6.73	0	*P* *L*	.74 .84
8	PC-2	V-valley bottom and ridge top, both 914 m	P5 and G8	6.73	0	*P* *L*	.25 .29
9	Height	Ridge top and high north slope, both at 914 m	D2 and G8	4.76	0	*P* *L*	.37 .47
10	PC-2	Ridge top and high north slope, both at 914 m	D2 and G8	4.76	0	*P* *L*	.58 .72
11	Height	Northwest- and southwest-facing slopes, both at 609 m	B2 and E6	3.55	0	*P* *L*	.81 .87
12	PC-2	Northwest- and southwest-facing slopes, both at 609 m	B2 and E6	3.55	0	*P* *L*	.74 .84

* *P* = calculated as probability that a seed (seedling) will encounter an environment to which it is not adapted by optimum strategy; *L* = genetic load as in O'Donald (1967).

DISCUSSION

Population microstructure in coastal Douglas-fir apparently is hierarchical. For any one trait, genetic variability among trees can be separated into an effect due to tree location and an effect due to variability among trees at a location. Microstructure is then described by the relative contributions of within- and between-source variations and their respective patterns.

Within-source variation is tentatively described as being homogeneous within the watershed; i.e., genetic variation among trees in locations did not differ among locations. Although evidence on this point was indirect and fragmentary, any deviations from homogeneity are not likely to have been large. In contrast, virtually all of source variation could be accounted for by parent-tree location. The patterns in the watershed suggest a three-dimensional cline, in which trait values are a function of elevation and N–S or E–W location, the function varying somewhat for each trait.

Such patterns could conceivably have any one of several bases—seed preconditioning (maternal effects), genetic drift, migration from founder populations, or selection—but only the latter seems to explain the results reasonably. The influence of seed weight, the major source of maternal effects, was discounted by its lack of association with other traits in any eigenvector. Rowe (1964) proposed other conditioning effects, but none are likely to produce differences of the magnitude found in the experiment.

For any appreciable differentiation to occur as a result of drift, gene flow must be negligible (Endler 1973), which is probably not the case in Douglas-fir. Gene flow is not easily measured, but an impression of its magnitude can be gained by estimating Wright's

(1943) neighborhood size. Using Wright's (1952) equations, following Gregory's (1945) turbulence hypothesis, pollen dispersal and seed dispersal distances for Douglas-fir were calculated from several data sources: pollen dispersal from single trees (Wright 1952, Silen 1962) and seed dispersal from five stand edges (Isaac 1930, Dick 1955). In every case, 90% of pollen, or seed, fell within three times tree height, but dispersal distances were larger and more varied for seed, which is winged and falls slowly in still air (0.87 ± 0.12 m/s; Tusco 1963).

Neighborhood size depends on density of breeding units as well as on dispersal distance. Stand density in Douglas-fir is related to site productivity and tree age (McArdle 1949), and all living trees are not necessarily breeding trees. Based on an estimated 74 breeding trees/ha in 450-yr-old Douglas-fir, neighborhood sizes (Falconer 1960:78) averaged 147 (range 30–263) and 1169 individuals (range 294–2703) from pollen and seed data, respectively. Particularly for pollen, average dispersal distances probably provide minimum estimates of gene flow. For Douglas-fir, high levels of background pollen and upslope or downslope transport of 100–300 m have been reported (Silen 1962, Ebell and Schmidt 1964). Thus, the effective breeding population probably is greater than 1000 and gene flow among adjacent sources should have been sufficient to preclude source differentiation in the absence of selection.

Of the alternatives to selection as a basis for clines, migration is the most likely. A strong cline could result from migration between formerly isolated stands—for example, after a catastrophic fire, a common precursor to regeneration in Douglas-fir. Candidates for founder populations within the watershed are most probable at high and low elevations, at the ends of the steepest clines in the watershed. High- and low-elevation populations are strongly differentiated—for most of the traits measured, there is little coincidence between estimated genotypic values of individuals in the two populations.

This last item makes it unlikely that clines shown here are caused by migration. Because the hypothetical founder populations are greatly different, migrating gametes or zygotes from each would contribute genetic variability not found in the other. Variability of intermediate populations would be expanded accordingly. This apparently has not happened—within-source variation could not be shown to change within the watershed. Thus, either migration has had a minor role in cline formation or selection has reduced within-population variability at intermediate locations. If selection has occurred, it is expected to foster clines, since environmental parameters such as temperature or precipitation do not vary discretely, but continuously (along gradients). Therefore, selection remains the likely cause for population differentiation.

Source differences were of types that could reasonably be expected to arise from selection—e.g., quick-starting, short vegetative periods for higher elevation sources on the cline to fit the shorter growing periods vs. tall, vigorous seedlings from lower elevation sources to fit the competition stresses expected there. Most of the source variation was related to elevation probably as a result of the general relationship between temperature and elevation (−0.42 C/100 m, Baker 1944). Even the large differences among some sources at identical elevations (comparisons 5–12, Table 6) may reflect temperature climate. Differences in temperature at any given elevation within the watershed can be quite large; for example, unexplained variations in mean July daytime temperature of seven stands, all at ≈500 m, have been reported to be about two-thirds the range between stands separated by 1000 m (Zobel et al. 1976). For some comparisons, there are discernible potential reasons for temperature differences, such as cold-air drainage and delayed spring snowmelt in a V-valley bottom (map corrdinate P5, Fig. 1). Delayed snowmelt at higher elevations on north-facing slopes compared to south-facing slopes may account for the steeper gradients of differentiation on north-facing slopes (comparisons 1 and 3, Table 6). On the other hand, gradients in source differences are not noticeably steeper at higher elevations (Figs. 1–5), which they should be if selection is severely temperature conditioned. Zobel et al. (1976) reported steeper temperature gradients (higher lapse rates) at higher elevations in the watershed.

Insight into whether or not selection pressures are adequate to account for differentiation in the face of abundant gene flow can be gained by estimating the number of seedlings required to replace a parent. On north-facing slopes, near the timber edge, a stand can regenerate in 5 yr; but additional seedlings augment the stand for another 10 yr (Isaac 1943). On southwest slopes at stand edge, seedlings from natural seedfall may not fully occupy a site for 20 yr. At greater distances from seed source, complete regeneration may take more than a century. At timber edge, the new stand results from an estimated seedfall of 328 000 seeds$\cdot$ha$^{-1}\cdot$yr^{-1} (Isaac 1943). If we assume 74 breeding trees/ha, each tree occupies 135 m^2. In 5 yr, 22 162 seeds fall in this area on the average. From Gashwiler (1967), 31% of seeds survive to start germinating, and 76% of sprouting seeds reach seedling stage. This leaves 5221 seedlings. Some, possibly more than half, may die by chance, victims of falling debris, etc.; this reduces the number succumbing to natural selection. Still, even under a most conservative position—that randomness is the major component in mortality, that stand regeneration takes only 5 yr, and that selection is inoperative before the seedling stage—a parent tree is probably selected from 2000+ seedlings. The resulting selection intensity should be sufficient to account for source variation.

Natural selection intensities may account for within-source variation as well, if the within-location environment is heterogeneous and coarse grained (Levins 1963)—an environment whose differences are large compared with a plant's tolerance. Heterogeneity is determined by the number of environmental components affecting individuals and by their spatial and temporal arrangements; grain is indicated by the severity of effects and the proportion of the life span affected. Douglas-fir seedlings are culled by a multiplicity of factors such as heat injury at the soil-air interface, drought, frost, and predators (Isaac 1938). Culling severity is influenced by microclimate—major factors being shade (Geiger 1957, Heatly 1967), soil color (Isaac 1938), soil organic matter (Hermann 1963), and surface roughness (Spurr 1957, Eiche 1966). Depending as these factors do on such chance factors as seeding-in of brush species, patterns of debris and fire, and micro- and macrotopography, the spatial component of environmental heterogeneity is large indeed.

The temporal component may be even larger. In a sample of dates of last spring killing frost (−2.2°C) obtained from 36 weather stations in western Washington and Oregon, year-to-year variation accounted for 43% of total variation. The corresponding proportion for first fall killing frost was 45%. Since sampled weather stations spanned coastal and alpine environments and 6° of latitude, between-location differences were emphasized and yearly fluctuations probably contribute even more to total variation within the watershed.

Douglas-fir is commonly considered a long-lived species, but more than half of the individuals in any population die before 3 yr. For example, an approximate life table, calculated from mortality data in Isaac (1943), McArdle (1949), and Gashwiler (1967), projects an average life expectancy of 400–500 d, if a maximum life span is assumed to be 500 yr. Year-to-year weather fluctuations cause culling by different spatial factors in different years (Isaac 1938). This leads to differential mortality and, presumably, to genetic differentiation (Mulcahy 1975) among seedling-year cohorts.

The conclusion is that genotypes surviving the seedling stage have been severely screened by an extremely heterogeneous within-location environment. With reference to seedlings, the environment is coarse grained; microenvironments are different enough to favor distinctive adaptive plant types. Seedlings in adjacent spots may be culled by quite different selecting agents. Also, at a single spot, environmental factors, especially frost events in spring and fall, are likely to vary as much from year to year as do average environments over large distances. As surviving seedlings age and grow, the environmental grain becomes finer; but because selection occurs principally in seedling and sapling stages, within-source variation is taken to reflect mainly early culling. Included are the effects of poor seedling adaptation on the subsequent placement of tree crowns in the developing stand (Namkoong and Conkle 1976).

Findings in this study are not unexpected in terms of general trends in past reports, or in their relation to environmental variation in the watershed. Genetic variation in many wide-ranging tree species is clinally related to major habitat factors (Langlet 1936, Nienstaedt and Olson 1961, Sweet 1965, Eiche 1966, Dietrichson 1969, Roche 1969). Within-location variation is apparently always associated with this clinal variation (Squillace 1966, Morgenstern 1969, Hagner 1970, Lester 1970). Numerous studies have connected genetic variation to subregional habitat factors; for example, in transects through small parts of forest regions (Irgens-Moller 1957, Sorensen 1967, Conkle 1973), or even along individual mountain slopes (Hermann and Lavender 1968, Holzer 1969, Fryer and Ledig 1972).

Although trends were expected, the complicated ordering of source variation within the watershed, and the degree of genetic differentiation, were not. Because source variation was almost completely explained by regression, it can be deduced that the source-related component of genetic variability among trees is not patchy or random but well ordered in complex clines within the watershed. In the absence of other likely causal factors, I have proposed that these topoclines reflect adaptation to gradient changes in environmental factors. In terms of differentiation of subpopulations along clines, the gradients were often surprisingly steep. For example, the trend established on a north-facing slope (comparison 1, Table 6) indicates that none of the seedlings of a subpopulation would be adapted to locations ≈670 m higher or lower on the same slope. On steep slopes, the airline difference between such subpopulations may be only 3 or 4 km. On a south-facing slope, the same degree of differentiation is expected to occur in ≈1100 m of elevation over an airline distance of 4 or 5 km. Differentiation can be almost as great over a similar distance at one elevation; for example, in the western part of the watershed, 70–80% of seedlings were expected to be nonadapted in a move of only ≈4 km (comparison 12, Table 6).

For estimating proportions of poorly adapted seedlings, I used additive genetic variation within location to estimate variation among microenvironments at a location (Stern 1964, Morgenstern and Roche 1969). Additive genetic variation may underestimate environmental variation (Levins 1964, 1965) and, if so, differentiation is not as great as I have suggested. There is, however, some evidence to indicate that the discrepancy is not large. From seedling to adult, within-population genetic variances in tree species have been estimated to be reduced from two to five times (Langner and Stern 1964, Hamrick 1976), presumably in response to stabilizing selection by culling of extreme types. This indicates tight screening of the genotypic set by the environmental set. In effect, the environmental set appears to mold the genotypic set (Hancock and Wilson 1976). Consequently, when selection culls from many genotypes, genotypes probably reflect, rather closely, the environments in which they find themselves.

Close adaptation in this relatively mild part of the Douglas-fir region may explain Rehfeldt's (1974) inability to find topographic clines in Rocky Mountain Douglas-fir. In the harsher Rocky Mountain environments, subpopulations could be expected to be even more tightly adapted to habitat (Campbell 1974). Therefore, Rehfeldt's sampling scheme based on a classification model, ordinarily a powerful experimental design, may not include enough categories to yield a pattern. That is, sampling may have been textured too coarsely to model the results of selection by a finely textured culling environment.

The life history of Douglas-fir and the underlying genetic system appear to be admirably suited to Douglas-fir's common mode of reproduction, the episodic colonizing of an extremely heterogeneous environment. Douglas-fir produces seed crops of varying size sporadically throughout its life. Only a few of these crops, often those either early or late in the life of the parent, have any chance of producing viable offspring. This condition favors iteroparity (repeated seed-bearing at several ages. See Harper 1967, Murphy 1968, Schaffer 1974) and iteroparity supplies seed in large numbers for repeated experiments in matching reproductive efforts to opportunities.

The genetic system of Douglas-fir, mainly outbreeding (Sorensen 1973), allows maximum repatterning of the gene pool in each reproductive effort. This, along with iteroparity, helps to ensure that some proportion of genotypes will encounter appropriate habitats. Habitats of Douglas-fir consist of a mosaic of specific microenvironments and, especially for seedlings, the number of microenvironmental "types" in a mosaic comprising even a small area and period of time may be large (Harper 1977). If microenvironments are to be occupied efficiently by a species, some genetic differentiation may be needed—phenotypic plasticity is usually insufficient to preadapt individuals to all local environments due to limitations in physiological processes. According to theory (Allard 1965, Levins 1969), the genetic variation in a population should correspond more or less to the variation in microenvironmental "types" that can be distinguished by genetic materials in the population. Douglas-fir's ample genetic variation, and a large seed supply, provide an opportunity for the chance fitting of genotypes with microenvironments to which they are optimally preadapted.

The genetic system of a species is part of the life history tactic of the species. Such a tactic has been defined (Stearns 1976) as the set of coadapted traits designed by natural selection to solve an ecological problem, i.e., the optimal allocation of resources among reproduction, maintenance, and growth (Gadgil and Bossert 1970). Thus, the manner in which a set of traits is coadapted may change along a clinal gradient because the allocation of resources may be different along the gradient. In this experiment, the patterns of source-related variation within the watershed differed considerably among traits. Apparently selection pressures along the gradients have acted differently on the various traits (similar results have been found in other coniferous species; Hamrick and Libby 1972). The probable process is one of balancing parts of the phenotype so that the total phenotype is designed by natural selection to solve problems of survival and reproduction which are different in different parts of the watershed. Coadapted constellations of traits have been hypothesized to be underlain, in turn, by coadapted sets of genes which control the relevant metabolic processes (Giesel 1974). In Douglas-fir there may be considerable autonomy of constellations or gene sets; the principal component analysis indicated that source-related variation contributed more strongly to PC's 2 and 4 than to other PC's in which family differences mainly reflected within-source variation.

The genetic variation described in this experiment reflects an adaptive response to environmental heterogeneity within the context of an iteroparious life strategy. The maintenance of within-source variation is apparently an important part of the response; within-source variance generally made up a large part of family differences (Table 2). Variation among sources is also important; source variance made up about 20% of family variance. Source variance, however, was probably underestimated since, in this experiment, genotypic values of families were estimated in only a single environment. Source-related variation depends on the test environment as well as on the trait (Campbell and Sorensen 1978); any single test environment exposes only part of the population's genetic variation and presumably only part of its differentiation.

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