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A Comparison of Habitat Type and Elevation for Seed-Zone Classification of Douglas-fir in Western Oregon

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ABSTRACT. Habitat type (identified by plant indicators) and elevation were compared as alternative bases for stratifying forest land into breeding zones or seed zones for reforestation. The comparison was based on the assumption that the genetic variation in an indigenous population of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) reflects the adaptively important environmental variation in the area inhabited by the population. Relative values for habitat type and elevation were then estimated by the amount of genetic variation explained by each in classification and regression models. Elevations, habitat types and tree genotypes were sampled in a 6100-hectare watershed in the Cascade Range of western Oregon. Parent trees (190) were from 114 locations (sources) in the watershed. Genetic variation was estimated by the performance (in 15 traits) of 3-year-old seedling families (190) grown in a common garden. Neither elevation nor habitat type were completely satisfactory for classifying environments into zones, in that elevation explained only about 56 percent of the source-related genetic variation, habitat type only about 35 percent. *FOREST SCI.* 27:49-59.

ADDITIONAL KEY WORDS. *Pseudotsuga menziesii*, adaptation, genecology, plant indicators.

AN INITIAL PROBLEM in artificial forest regeneration is one of dividing a forest region into compartments of adaptively homogeneous environments for use as seed zones. Developing "breeding zones" for genetic tree improvement is a closely related task. In each case a classification based on environmental parameters would be ideal for both uses but is seldom possible. Forest regions, especially mountainous ones, are inadequately sampled by weather stations; and even when data are available, the operational factors in natural selection are imperfectly known.

An alternative method, pioneered by Eneroth (1926) and Langlet (1936), is to describe the source-related genetic variability in a species indigenous to the region and to use the resulting pattern as an indicator of environmental variability. By measuring source-related variability we measure population response to natural selection. By classifying this response, we insure that classification is being applied, indirectly, to the environmental complex that has been active in natural selection. We further assume that this complex is the one critical in seed transfer.

For seed transfer rules, the most useful descriptive model would be the one which explained most or all of the source-related variation by using easily measured predictors. Three general types of models have been proposed or used: (1) the classification model, e.g., by ecotype (Wright and Bull 1963), land productivity classes (Morgenstern 1972), elevational classes (Langlet 1945), or habitat types

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TABLE 1. Forest communities described by Dyrness and others (1974) and the number of trees and locations from which seed was collected within each community.

Community	Abbreviation	Number of trees	Locations
<i>Pseudotsuga menziesii</i> - <i>Tsuga heterophylla</i> / <i>Corylus cornuta</i>	Psme-Tshe/Coco	4	2
<i>Tsuga heterophylla</i> / <i>Castanopsis chrysophylla</i>	Tshe/Cach	3	2
<i>Tsuga heterophylla</i> / <i>Rhododendron macrophyllum</i> / <i>Gaultheria shallon</i>	Tshe/Rhma/Gash	21	13
<i>Tsuga heterophylla</i> / <i>Rhododendron macrophyllum</i> / <i>Berberis nervosa</i>	Tshe/Rhma/Bene	69	40
<i>Tsuga heterophylla</i> / <i>Polystichum munitum</i>	Tshe/Pomu	3	2
<i>Tsuga heterophylla</i> - <i>Abies amabilis</i> / <i>Rhododendron macrophyllum</i> / <i>Berberis nervosa</i>	Tshe/Abam/Rhma/Bene	9	6
<i>Tsuga heterophylla</i> - <i>Abies amabilis</i> / <i>Rhododendron macrophyllum</i> / <i>Linnaea borealis</i>	Tshe-Abam/Rhma/Libo	15	9
<i>Tsuga heterophylla</i> - <i>Abies amabilis</i> / <i>Linnaea borealis</i>	Tshe-Abam/Libo	24	13
<i>Abies amabilis</i> - <i>Tsuga mertensiana</i> / <i>Xerophyllum tenax</i>	Abam-Tsme/Xete	5	4
<i>Abies amabilis</i> / <i>Vaccinium membranaceum</i> / <i>Xerophyllum tenax</i>	Abam/Vame/Xete	12	6
<i>Abies amabilis</i> / <i>Rhododendron macrophyllum</i> - <i>Vaccinium alaskense</i> / <i>Cornus canadensis</i>	Abam/Rhma-Vaal/Coca	2	2
<i>Abies amabilis</i> / <i>Achlys triphylla</i>	Abam/Actr	2	2
<i>Abies amabilis</i> / <i>Tiarella unifoliata</i>	Abam/Tiun	21	13

as identified by plant indicators (Daubenmire 1976, Rehfeldt 1974); (2) the regression model using simple or complex clines (Schotte 1923, Squillace 1966, Roche 1969, Morgenstern and Roche 1969); or (3) the mixed regression-classification model by analyzing clines within some subdivisions of the population, such as regions (Hattemer and König 1975) or ecotypes (Nienstaedt 1975). Models may vary in utility depending on species and forest region.

In this paper we compare elevation and habitat type as contrasting bases for classifying seed zones. Elevation has a long history of such use in the Pacific Northwest (see Isaac 1949). Vegetation classification in the Pacific Northwest has only recently progressed (Dyrness and others 1974) to a stage where habitat type is a feasible alternative. We also examine the combination of elevation and habitat, since zones based on both predictors might be better than zones based on either alone. We report on several model types: (1) classification models for elevation and habitat type, analyzed separately, (2) an elevational clinal model, (3) an elevational clinal model including an index for habitat type, and (4) a classification model including both elevation and habitat type.

Comparisons were restricted to the coastal Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco] population within a 6100-hectare watershed in the central Oregon Cascade Range where vegetation of the watershed had been intensively studied and the population had been sampled for an earlier experiment. By sampling only one watershed the comparison of elevation and habitat was unencumbered by extraneous genetic effects associated with such factors as latitude or distance from the ocean.

TABLE 2. *Description of traits measured in nursery bed.*

Trait	Description	Unit
1. Seed weight	Based on 60-seed average ¹	mg/seed
2. Germination rate	Cumulative germination on probit scale	probits/day
3. Days to 50 percent germination	Interpolated from probit graph	days
4. Cotyledon number	Based on 20-seed average ¹	cotyledon/seedling
5. Budset in 1972	First visible terminal-bud scales	weeks after 11 Aug
6. Budburst 1973	First green needles from terminal bud	half-weeks after 24 March
7. Budburst 1973 variability	Variability in (6) among 16–19 seedlings ¹	log ₁₀ (variance in trait 6)
8. Budset 1973	First visible terminal-bud scales	weeks after 6 July
9. Budburst 1974	First green needles from terminal bud	half-weeks after 31 March
10. Budburst 1974 variability	Variability in (9) among 16–19 seedlings ¹	log ₁₀ (variance in trait 9)
11. Second flush	Proportion of 3-year seedlings with lammas growth	arcsin (percent)
12. Height	3-year total height	cm
13. Height variability	Variability in (12) among 16–19 seedlings	log ₁₀ (variance in trait 12)
14. Diameter	3-year stem diameters, cotyledon height	mm
15. Dry weight	3-year top-dry-weight	gm × 10
16. Survival	Proportion of 3-year seedlings surviving drought treatment	arcsin (percent)

¹ Base number represents the number of seed (seedlings) per plot in each of two replications.

PROCEDURES

Data for the comparisons came from a study reported previously (Campbell 1979), which provided genotypic values (as estimated by family means) for a sample of 190 parent-trees in 114 locations dispersed uniformly (i.e., roughly proportional to habitat types and elevations) in the H. J. Andrews Experimental Forest on the west slope of Oregon's Cascade Range. For each location, elevation above sea level and habitat type (using the classification of Dyrness and others 1974) were recorded (Table 1).

The Andrews Forest is an intensive study site for the U.S. International Biological Program's Coniferous Forest Biome Project and has been thoroughly described elsewhere (Zobel and others 1976). It includes the watershed of Lookout Creek in the west central Oregon Cascade Range and is approximately the shape of a right triangle with maximum north-south and east-west dimensions of 12 and 18 km, respectively. Elevations within the watershed range from 500 to 1,600 m.

Genotypic values of sample trees in the watershed's primarily 450-year-old Douglas-fir stand were estimated by growing seedlings from open-pollinated seed collections in a nursery bed in Corvallis. The family resulting from each collection was randomly assigned to rows within two replications. Twelve traits of the internal 16 to 20 seedlings in each plot were measured through the third growing season (Table 2).

Trait means per plot for each trait were analyzed by analysis of variance in a

TABLE 3. Model of analyses showing expected mean squares for genetic differences among zones (habitat or elevation) and within zones.

Source variation	d.f. ¹	Parameters estimated by mean squares
Zones	12 (5)	$\sigma^2 + 2\sigma_F^2 + 3.42\sigma_L^2 + 25.76\sigma_Z^2$ (2) (4.07) (60.17)
Locations within zones	101 (108)	$\sigma^2 + 2\sigma_F^2 + 3.32\sigma_L^2$ (2) (3.29)
Families in locations	76 (76)	$\sigma^2 + 2\sigma_F^2$ (2)
Error	190	σ^2

where: σ_Z^2 = variance of zone effects

σ_L^2 = variance of effects due to locations within zones

σ_F^2 = variance of effects due to trees within locations

σ^2 = variance of plot effects (replications within families in locations in zones)

¹ Degrees of freedom and coefficients (in parentheses) are for zones based on six elevational classes of 175-m width; others are for habitat types (Table 1).

classification model for effects due to habitat (or elevational zone), locations within habitat (or within elevational zone), and trees within locations. The hierarchies in elevation and habitat models were identical, but degrees of freedom in analyses were different (Table 3) because parent-tree locations were classified in fewer elevational zones than there were habitat types. Elevational bands narrower than about 175 m have not been used for seed zones in the Pacific Northwest and, consequently, were not used for our analysis.

Components of variance for each effect for each trait were then estimated by equating mean squares to expectations (Table 3). The sum of the variances attributable to habitat ($\hat{\sigma}_Z^2$) and to location within habitat ($\hat{\sigma}_L^2$) represents the total source-related genetic variability (i.e., $\hat{\sigma}_Z^2 + \hat{\sigma}_L^2$). The remaining variance includes the average variation among means of families from a location ($\hat{\sigma}_F^2$) and variation among replications plus interaction of families with replications ($\hat{\sigma}^2$). The ratio of habitat variance to source-related variance ($\hat{\sigma}_Z^2/(\hat{\sigma}_Z^2 + \hat{\sigma}_L^2)$) is an estimate of the proportion of source-related variation due to habitat (Kempthorne 1957, p. 243). It is therefore a measure of the populational component of genetic variance associated with differences in habitat type.

By dividing the Experimental Forest into elevational bands of different widths, the same hierarchical analysis (and component analysis) was made for each of three different elevational classifications: six zones of 175-m width, three zones of 350-m width, and two zones of 525-m width. For a classification model including both elevation and habitat, the analysis using six elevational zones was partitioned further into habitat types within elevational zones (habitats in zones, 19 d.f.; locations in habitats, 89 d.f.).

Finally, for each trait, elevational clines were described by fitting family means to parent-tree elevation by multiple regression. Predicting variables were selected from the following preliminary model:

$$Y = \beta_0 + \beta_1 X_1 + \beta_{11} X_1^2 + \beta_{111} X_1^3$$

where

Y = mean family response as determined in the nursery,

X_1 = parent-tree elevation (m),

β_i = coefficients estimated from the data.

From this model, a stepwise procedure (Draper and Smith 1966, p. 171) selected an equation in which all included predicting variables (X_i) contributed significantly ($P < 0.05$) to reducing sums of squares in the response variable (Y).

For comparing the simple habitat and clinal models with one incorporating their combined effects, an identical stepwise procedure was used to select an equation for describing the combined effects. The expanded preliminary model was

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_{11} X_1^2 + \beta_{22} X_2^2 + \beta_{12} X_1 X_2 + \beta_{112} X_1^2 X_2 + \beta_{122} X_1 X_2^2 + \beta_{1122} X_1^2 X_2^2$$

where

Y and X_1 are as above,

X_2 = X -axis coordinate of the vegetative ordination of Dyrness and others (1974),

β_i = coefficients estimated from the data.

For each plant community (Table 1), a value for X_2 (the xeric index) was obtained by averaging x -coordinate values obtained by Dyrness and others (1974) from two-dimensional gradient analyses of 300 reference plots within or near the H. J. Andrews Experimental Forest. Gradient analyses for plots from high- and low-elevation zones involved different sets of vegetative descriptors and might not measure identical moisture gradients. In our analysis, however, we used X_2 values derived from both zones because: 1) Dyrness and others (1974) hypothesized that x -axes measured in the two zones covered similar moisture gradients, and 2) x -values from the two gradient analyses have been shown to be strongly correlated with maximum summer moisture stress in reference plots (r^2 's ranged from 0.79 to 0.95 depending on year and zone; Zobel and others 1976). We did not use y -axis gradient values as a variable in the model. The y dimension has been hypothesized by Dyrness and others (1974) to reflect population response to temperature; it therefore may measure the same complex temperature gradient that elevation is commonly assumed to measure.

After an equation had been selected from above models for each trait, the equation was tested for lack of fit to the data (Draper and Smith 1966, p. 63). The two or more trees sampled at some locations were repeat observations of genotypic value at a location and mean squares for trees within locations could thus be used as an estimate of "pure error" for testing lack of fit. Significant lack of fit indicated that genotypic values of some trees deviated significantly from the cline as described by the regression equation. When this occurred, source-related variation was not completely accounted for by the equation, usually because not all pertinent descriptive variables had been included in the model.

RESULTS

Averaged over all traits except seed weight, 6.2 percent of total variation among plot means was associated with habitat type in our sample (Table 4, col. 2(i)). Seed weight was excluded because it may be unduly influenced by nongenetic maternal effects. A further 8.7 percent of variation was connected with location of parent trees within habitat type (col. 3(i)). Thus about 14.9 percent of variation could be attributed to parent-tree location within the watershed. The remainder represented genetic variation among trees within a location (23.1 percent, col. 4(i)) and error (62.0 percent, col. 5(i)).

Thirty-five percent of the genetic variation that was associated with parent-tree location was also associated with habitat type (Table 4, col. 1(i)), when averaged

TABLE 4. Partitioning of variation in plot means by genetic categories when families are classified according to origin: (i) habitat type—13 zones, (ii) 175-m elevational bands—6 zones, (iii) 350-m elevational bands—3 zones.

Trait and (origin class)	Zone related ¹ variation among sources (1)	Zone ² (2)	Location ² within zone (3)	Trees within ³ location within zones (4)	Error ⁴ (5)
a. Seed weight					
(i)	19.5	4.8	14.7	76.6**	3.9
(ii)	22.4	4.4	19.1	77.0**	3.9
(iii)	0.0	0.0	19.1	77.0**	3.7
b. Germination rate					
(i)	0.0	0.0	11.7	14.4*	74.0
(ii)	33.1	3.9**	7.9	14.6*	73.6
(iii)	14.7	1.7*	9.9	14.6*	73.8
c. Germination date					
(i)	9.1	1.5	15.0	0.1	83.0
(ii)	0.0	0.0	16.8*	1.7	81.6
(iii)	0.0	0.0	16.3*	1.7	82.1
d. Cotyledon number					
(i)	21.9	2.5	8.9	44.7**	43.8
(ii)	73.4	9.4**	3.4	43.9**	43.3
(iii)	44.5	5.7**	7.1	43.9**	43.3
e. Budset in 1972					
(i)	100.0	14.8**	0.0	49.7**	35.5
(ii)	100.0	19.4**	0.0	47.9**	32.7
(iii)	100.0	23.3**	0.0	45.9**	31.3
f. Budburst in 1973					
(i)	0.0	0.0	4.3	47.4**	48.3
(ii)	100.0	3.1*	0.0	48.0**	48.9
(iii)	100.0	3.4**	0.0	47.8**	48.8
g. Budset in 1973					
(i)	0.0	0.0	3.3	9.4	87.4
(ii)	0.0	0.0	3.4	9.4	87.3
(iii)	0.0	0.0	2.9	9.4	87.7
h. Budburst in 1974					
(i)	70.5	4.3	1.8	50.7**	43.2
(ii)	98.5	6.6*	0.1	50.4**	42.9
(iii)	100.0	8.7**	0.0	49.3**	42.0
i. Second flush					
(i)	16.5	4.0	20.2**	19.7**	56.1
(ii)	27.9	6.9**	17.8*	19.8**	55.5
(iii)	30.1	7.7**	17.9*	19.6**	54.8
j. Height					
(i)	61.4	19.0**	11.9*	15.3**	53.8
(ii)	63.4	19.9**	11.8*	15.1**	53.5
(iii)	62.9	21.2**	12.5*	14.6**	51.7

TABLE 4. Continued.

Trait and (origin class)	Zone related ¹ variation among sources (1)	Zone ² (2)	Location ² within zone (3)	Trees within ³ location within zones (4)	Error ⁴ (5)
k. Diameter					
(i)	49.4	8.3**	8.5	11.1	72.1
(ii)	54.4	9.2**	7.7	11.6*	71.5
(iii)	58.7	10.8**	7.6	11.4*	70.2
l. Dry weight					
(i)	56.8	13.8**	10.5*	10.3	65.4
(ii)	62.3	15.4**	9.3	10.2	65.1
(iii)	66.8	18.1**	9.0	9.9	63.0
m. Survival					
(i)	39.6	5.7*	8.7	4.3	81.4
(ii)	60.5	8.9**	5.8	5.0	80.3
(iii)	47.1	7.2**	8.1	5.0	80.3
Average—excluding seed weight					
(i)	35.4	6.2	8.7	23.1	62.0
(ii)	56.1	8.6	7.0	23.1	61.4
(iii)	52.1	9.0	7.6	22.7	60.8

¹ Estimated as $100 \hat{\sigma}_Z^2 / (\hat{\sigma}_Z^2 + \hat{\sigma}_T^2)$. Symbols as in Table 3.

² Partitioned effects of parent tree locations: Zone effects = $100 \hat{\sigma}_Z^2 / \hat{\sigma}_T^2$ where $\hat{\sigma}_T^2 = \hat{\sigma}_Z^2 + \hat{\sigma}_L^2 + \hat{\sigma}_F^2 + \hat{\sigma}^2$. Within-zone effects = $100 \hat{\sigma}_L^2 / \hat{\sigma}_T^2$.

³ Estimated as $100 \hat{\sigma}_F^2 / \hat{\sigma}_T^2$.

⁴ Estimated as $100 \hat{\sigma}^2 / \hat{\sigma}_T^2$.

*** *F*-ratios significant at $P < 0.05$ and $P < 0.01$, respectively.

over 12 traits. This habitat-related variation, as a percentage of source-related variation, differed greatly among traits, averaging 10 percent for seed traits (lines b–d, Table 4), 37 percent for developmental cycle traits (lines e–i), and 56 percent for growth traits (lines j–l).

When family means were classified into six elevational zones of 175 m, genetic variation among zones was larger than variation within zones ($P < 0.05$) for 10 of 13 traits. In similar analyses of habitat type, only 5 of the 13 comparisons were significant (Table 4, col. 2). Averaged over all traits except seed weight, variation among elevational zones accounted for 56.1 percent of the source-related genetic variation, as compared to the 35.4 percent accounted for by habitat type (Table 4, col. 1). Thus, classification of the population by elevation explained more of the source-related genetic variability than did classification by habitat type, by 20.7 percentage points with 95-percent confidence limits of 1.4 to 39.9. Classification by elevation explained more of the total experimental variation, also, by 2.4 percentage points (8.6–6.2; Table 4, col. 2) with 95-percent confidence limits 1.0 to 3.8. The ordering of families by three elevational classes rather than six produced approximately the same results (Table 4, col. 1(iii) and 2(iii)).

When analyzed by regression, variability among seedling families was signifi-

TABLE 5. Relation of family performance (Y) to parent-tree elevation (X).

Trait	Regression equation form	d.f.	F for regression	F for "lack of fit"	Percentage of sums squares explained by—	
					Regression on elevation	Habitat type
Seed weight	$Y = b_0 - b_1X + b_2X^2 - b_3X^3$	3;186	2.9*	1.4	4.5	10.6
Germination rate	$Y = b_0 - b_1X + b_2X^2$	2;187	5.5**	2.4**	5.5	4.0
Mean germination date	None significant	—	—	—	0	5.5
Cotyledon number	$Y = b_0 - b_1X + b_2X^2 - b_3X^3$	3;186	2.9*	1.8**	4.4	7.3
Budset 1972	$Y = b_0 - b_1X^2$	1;188	47.8**	1.2	20.3	17.5
Budburst 1973	$Y = b_0 + b_1X^2 - b_2X^3$	3;186	2.9	1.6*	3.0	2.4
Budset 1973	None significant	—	—	—	0	3.0
Budburst 1974	$Y = b_0 + b_1X$	1;188	19.9**	1.4*	9.6	8.4
Second flush	$Y = b_0 - b_1X$	1;188	21.8**	2.5**	10.4	8.5
Height	$Y = b_0 - b_1X^2$	1;188	65.1**	2.2**	25.7	20.2
Diameter	$Y = b_0 - b_1X$	1;188	29.5**	2.4**	13.6	10.8
Dry weight	$Y = b_0 - b_1X$	1;188	52.0**	2.3**	21.7	15.5
Survival	$Y = b_0 - b_1X$	1;188	25.1**	2.6**	11.8	8.5
Average—excluding seed weight					10.5	9.3

* Significant at probability $P < 0.05$.** Significant at probability $P < 0.01$.

cantly related to elevation for 10 of the 13 traits (Table 5). In general, family mean for height, diameter, and dry weight decreased linearly with elevation of parent origin. For seed traits and developmental cycle traits, equations indicated several types of nonlinear clines with elevation.

Equations derived by regression analyses of the provisional models which included the xeric index were identical to those selected from models involving elevation alone. Thus genetic variability among families was not associated with the part of the environmental complex measured by the xeric index after correlations of habitat type with elevation were discounted. Other indexes of habitat type probably would not have served any better. In an analysis of variance to check this possibility, elevational zones were partitioned into habitat types within zones. In this analysis, habitat type accounted for source-related variation in only three traits, seed weight (2.0, 6.7, and 11.9 percent for elevational zone, habitats in zones, and locations in habitats, respectively), germination date (0, 6.7, and 12.2 percent) and diameter (8.1, 3.4, and 6.2 percent). In all other traits, the estimated component of variance for habitats within elevational zones was zero. Therefore, for most traits, the variability among families that could not be accounted for by elevation also could not be accounted for by habitat type, whether analyzed by regression or analysis of variance.

DISCUSSION

Daubenmire (1976) has proposed that natural vegetation, in its composition and other attributes, integrates all of the environmental factors important to plants. Furthermore, he proposes that vegetal indicators are superior to human judg-

ments due to the difficulty of quantitatively relating aspects of climate, topography, and soils. Vegetation or "habitat type" is, therefore, considered the best indicator of environmental conditions. Consequently, it seems reasonable to expect that the adaptive genetic variability in Douglas-fir should be more closely associated with habitat type than with any other single descriptive variable. Instead, in this study a classification of tree locations by elevation explained substantially more of the source-related variation than did habitat type. Furthermore, the elevational regression models, which included a xeric index for habitat based on community gradient analysis, were no better than those for elevation alone. Apparently, in our sample and for the traits we measured, the environmental diversity relevant to adaption in Douglas-fir is more closely associated with elevation than with habitat type.

There are several possible reasons why habitat types were not more successful in explaining genetic variation in Douglas-fir. First, the field sampling was concentrated on a few, very widespread habitat types (Table 1)—Tshe/Rhma/Bene, Tshe-Abam/Rhma/Libo, Tshe-Abam/Libo, Tshe/Rhma/Gash, and Tshe-Abam/Rhma/Bene. These habitat types are indicative of relatively moderate environmental conditions and cover broad elevational spans which are, of course, temperature and moisture gradients. Very few samples were obtained from habitat types indicative of extreme environmental conditions, such as very dry, wet, or cold and snowy sites; the hottest and driest forested habitat, *Pseudotsuga menziesii*/*Holodiscus discolor* (Dyrness and others 1974) was not sampled at all. We could have sampled specifically by habitat types or along the major moisture, temperature, and snowpack gradients so as to include a greater number of extreme sites. This type of sampling, as opposed to our proportional sample of the entire landscape, might have resulted in habitat types accounting for a higher percentage of the Douglas-fir genetic variability encountered.

Other possible explanations for the failure of habitat types have to do with genetic variability in the indicator species. First, the environmental complex which influenced adaptation in Douglas-fir may not be identical to the complex which influenced distributions of the indicator species. Second, members of an indicator species at one sample location may differ genetically from members at another location. Consequently, the same community in two different areas could indicate two somewhat different environments.

Although direct evidence is lacking, the second hypothesis seems particularly reasonable. Daubenmire (1976) cautioned that the same species in different geographic areas is usually represented by different ecotypes, which by their nature have different indicator significance. It is likely that source-related genetic variation in some indicator species may be even larger than in Douglas-fir due to patchiness in distribution and consequent restrictions in gene flow. Thus, population differentiation can occur within much smaller regions than is connoted by Daubenmire's phrase, "different geographic areas." It is also likely that differentiation of indicator species will be clinal as well as ecotypic—in the H. J. Andrews, it may have paralleled differentiation in Douglas-fir, that is, partially along elevational gradients. If so, the niche inhabited by a community at its highest elevation may be quite different environmentally from the niche at lower elevations. This may be particularly true in the widespread habitats where our sampling was concentrated. Elevational ranges were 396 to 807 m in Tshe/Rhma/Gash, 457 to 932 m in Tshe/Rhma/Bene, and 807 to 1,219 m in Tshe-Abam/Libo; environmental measurements clearly indicate major variability within these habitat types over this elevational range (Zobel and others 1976).

It is unlikely that any of the models we tried are completely satisfactory for classifying environments into breeding zones or seed-transfer zones within the watershed. If source-related genetic variation can be equated, at least partially,

with environmental variation within the Experimental Forest, much of the environmental variability has remained unexplained. Even in the best case, classification by elevation into six zones, an estimated 44 percent of the source-related genetic variation was associated with differences among locations within zones. These differences cannot be attributed to chance grouping of genetically variable trees. Previous work within the watershed indicated that virtually all of the source-related variation in many traits was patterned in three-dimensional gradients according to elevation and N-S and E-W coordinates of parent trees (Campbell 1979). Such complex patterns could not be explained except as resulting from natural selection. Therefore, the variation among locations within zones described herein apparently represents adaptation to environmental diversity not associated with elevation. The diversity so measured is hypothesized to be in terms of environmental factors which have contributed to natural selection. Consequently, elevational bands, even as narrow as 175 m, may not be adequate as seed zones, because seedlings resulting from seed transfer between some locations within zones may be poorly adapted to the new site.

Classification of source-related variation probably would not have been improved by using narrower elevational zones. Elevation used as a continuous variable in regression accounted for only slightly more of the total sums of squares than did habitat type in the classification model (Table 5). Also, for 8 of the 10 traits in which an elevational cline was demonstrated, the responses of trees from some locations did not fit the general elevational trend (significant lack of fit, Table 5). These deviations are analogous to variation among locations within elevational zones and indicate unclassified environmental heterogeneity. Classification was not improved by including habitat type in conjunction with elevational zone either in the regression or classification models.

Habitat type may be a more satisfactory tool for classifying environments in a large region. Judging from data presented by Rehfeldt (1974), habitat type and elevation were about equally effective for classifying source-related genetic variation in Rocky Mountain Douglas-fir (about 50 percent in either case), in an area encompassing eastern Washington, northern Idaho, and northwestern Montana. Habitat types may also be more useful in locales where the landscape is composed of a mosaic of several, sharply contrasting environments or habitat types rather than a few, environmentally moderate habitat types. In such landscapes, gradients will probably be abrupt rather than extended and gradual, and contrasts between adjacent habitat types sharp.

In conclusion, in landscapes where broad, environmentally moderate habitat types dominate, better indices to genetic variability appear necessary. Elevation was a superior alternative in our study area; but it, too, was inadequate for indexing Douglas-fir variability.

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