Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) populations. III. Central Idaho

GERALD E. REHFELDT[1]

Intermountain Forest and Range Experiment Station, Forest Service, United States Department of Agriculture, Ogden, UT, U.S.A. 84401

Received November 10, 1982[2]
Accepted March 23, 1983

REHFELDT. G. E. 1983. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) populations. III. Central Idaho. Can. J. For. Res. **13**: 626–632.

Growth, phenology, and cold hardiness of seedlings from 74 populations of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) from central Idaho were compared in four contrasting environments. Analyses of 3-year-old seedlings revealed population differentiation for eight variables: bud burst, bud set, multiple flushing, height, deviation from regression of 3-year height on 2-year height, spring frost damage, fall frost damage, and winter injury. These analyses, as well as high intercorrelations among population means, suggested that adaptations result from a balance between selection for a high growth potential in mild environments and selection for cold hardiness in severe environments. Consequently, genetic variation among populations was closely related to the elevation, geography, and climate of the seed source.

REHFELDT. G. E. 1983. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) populations. III. Central Idaho. Can. J. For. Res. **13**: 626–632.

Sous des conditions différentes du milieu, on a comparé la croissance, la phénologie et la rusticité de semis provenant de 74 populations de douglas taxifolié (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) de l'Idaho central. L'analyse des semis de 3 ans a révélé des différences de population reliées à huit variables: l'éclatement des bourgeons, la disposition des bourgeons, le développement multiple des pousses, la hauteur, les déviations à la régression de la longueur de la 3^{e} année sur celle de la 2^{e} année, les dommages attribuables aux gels tardifs et hâtifs et les blessures d'origine hivernale. Ces analyses, autant que les fortes inter-corrélations entre les moyennes de populations, suggèrent que des adaptations résultent d'une balance entre une sélection portant sur un potentiel élevé de croissance en milieu doux et une sélection portant sur la rusticité en milieu rigoureux. La variation génétique entre les populations est donc en rapport direct avec l'élévation, la géographie et le climat d'où proviennent les semences.

[Traduit par le journal]

Introduction

Ecological adaptations differentiate Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) populations within the northern Rocky Mountains. In northern Idaho (Rehfeldt 1979) and western Montana (Rehfeldt 1982), differentiation is based on a network of traits that reflect adaptation to the cold. Populations from mild environments display a higher growth potential but lower hardiness than populations from severe environments. Genetic differentiation, therefore, is strongly related to environmental gradients. The present study considers adaptive differentiation of populations from central Idaho. Patterns of variation are used to develop seed transfer guidelines that are intended to limit maladaptation in reforestation.

The forests of central Idaho, the region located south of the Salmon River (Fig. 1), occupy diverse montane environments. Bordered on three sides by arid steppe vegetation, this geologically complex region is dominated physiographically by the massive Salmon River Mountains that reach 3300 m. To the west of these mountains, the valley floor near Boise occurs at about 825 m, but at Challis, on the east, valleys are positioned at about 1600 m. Remnants of a maritime climate to the northwest are rapidly lost as the climate becomes continental and arid to the east, south, and southeast (Ross and Savage 1967). These climatic trends are expressed in average frost-free periods which vary by as much as 100 days within a geographic interval as small as 80 km (Fig. 1). While precipitation generally declines from the northwest to the southeast, the amount is strongly influenced by orographic effects of the various major and minor mountain ranges. For instance, in the northwest, precipitation averages 100 cm; in central areas, annual precipitation may reach 160 cm; but on the steppe at Boise and Challis, precipitation averages less than 30 cm (Ross and Savage 1967). In addition to these general climatic trends, effects of topography are superimposed on climatic gradients to produce the extreme environmental heterogeneity that characterizes the region.

The distribution of plant communities varies con-

[1]Present address: Intermountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Moscow, ID, U.S.A. 83843.

[2]Revised manuscript received March 14, 1983.

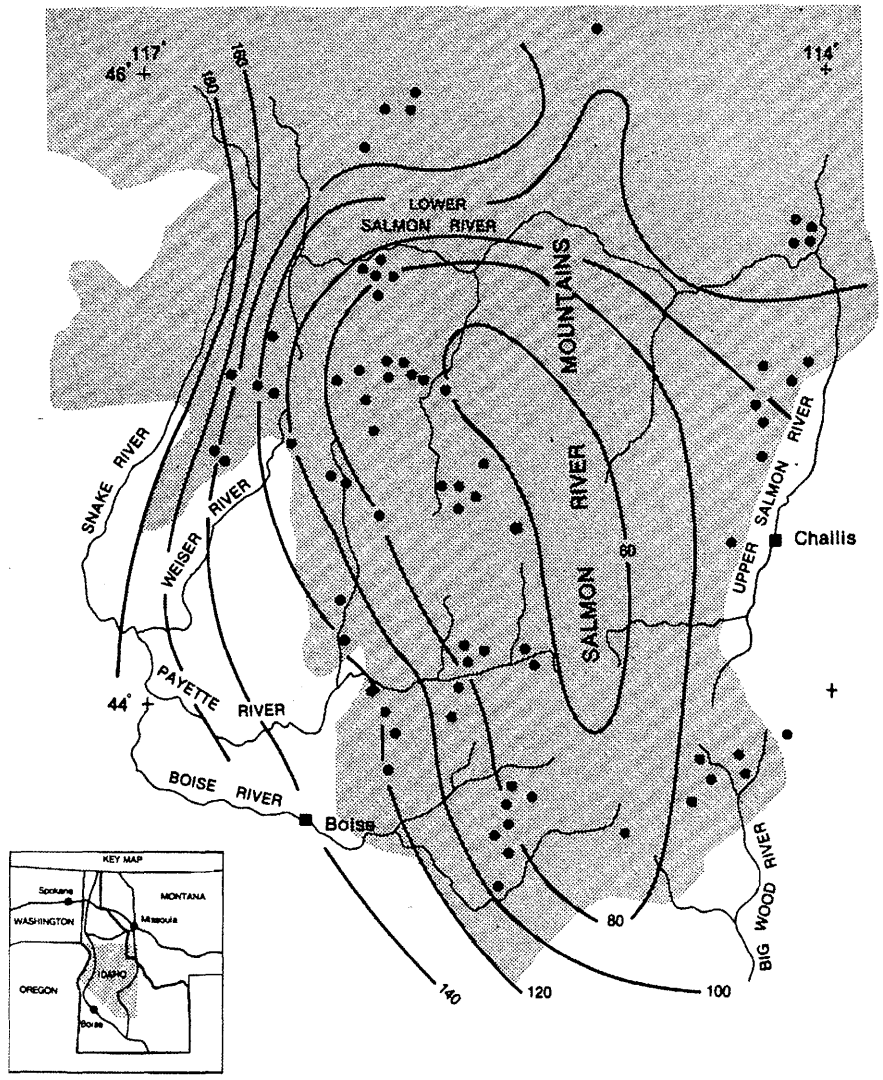

FIG. 1. Drainage map of central Idaho locating the populations (dots) under study within the general distribution of forested lands (shading). Contours estimate average frost-free periods (from Ross and Savage 1967).

comitantly with the climate; changes in the frequency of particular habitat types largely reflect a gradual decrease (from northwest to southeast) in species most common in warm, moist environments (Steele et al. 1982). Throughout the region, however, Douglas-fir displays a broad ecological amplitude. According to Steele et al. (1982), the species ranges from areas receiving a maritime climatic influence to those that receive a strong continental climate. In some areas, Douglas-fir occurs from lower timberline to upper timberline while occupying a range of environments from the warm and dry habitats that border the steppe to cold subalpine habitats. And, nearly everywhere, Douglas-fir is distributed across an altitudinal interval of about 1500 m.

Methods

To assess differentiation of populations, cones were collected from several squirrel caches in each of 74 populations (Fig. 1). Sixty-nine populations represented the geographic distribution and the ecological amplitude of the species in central Idaho. In addition, five populations from northern Idaho were included for assessing differentiation between populations of northern and central Idaho.

After growing for 5 months in plastic tubes (65 cm^3) in a shadehouse at Moscow, Idaho (46.5° latitude and 116.7° longitude), seedlings from each population were transplanted into four test environments (Table 1). Two environments were at Moscow (700 m elevation) where frost-free periods average 130 days. In one, the planting medium consisted of equal parts of peat and vermiculite, and in the second, the planting medium consisted of equal parts sand and the peat–

TABLE 1. Mean values according to test environment

Environment	Bud burst (date)	Bud set (%)	Two flushes (%)	Height (cm)	Height deviation[a]	Spring frost damage (%)	Fall frost damage (%)	Winter injury (%)
Moscow, peat, 700 m	April 25	93	56	15.2	0.11	25	—	—
Moscow, sand, 700 m	April 27	92	28	10.8	−0.16	10	—	—
Priest River, 670 m	April 29	98	59	16.5	0.16	30	—	—
Priest River, 1500 m	June 4	77	31	10.6	−0.08	—	6	9

[a]Deviation from regression of 3-year height on 2-year height; means are derived from the difference of logarithms and, therefore, are without units.

vermiculite mixture. The remaining environments were located on the Priest River Experimental Forest (48.5° latitude and 117° longitude). One was at 670 m elevation where frost-free periods average 90 days. A second was at 1500 m where growing seasons are extremely short, and snow commonly covers the site for 8 months, reaching a depth of about 3 m. Plantings at Priest River were in the residual soil from which rocks, roots, and competing vegetation had been removed before tilling. Ten seedlings from each population were planted in row plots in each of two blocks at Moscow and three blocks at Priest River. Rows were separated by 13 cm; 10 cm separated seedlings within rows.

Populations were compared according to the following variables obtained for each population in all replicates.

1. Bud burst	The day after April 1 by which 50% of the seedlings had burst terminal buds during the third growing season
2. Bud set	The proportion of seedlings that had set terminal buds by mid-August in the third growing season
3. Two flushes	The proportion of seedlings that flushed twice during the third growing season
4. Height	Average seedling height after 3 years
5. Height deviation	Deviation from regression of 3-year height on 2-year height; an index to the rate of growth from a constant height at age 2 that is, therefore, independent of previous genetic and environmental effects
6. Spring frost injury	The proportion of seedlings damaged by spring frosts at the start of the third growing season
7. Fall frost injury	The proportion of seedlings damaged by fall frosts at the conclusion of the third growing season
8. Winter injury	The proportion of seedlings that exhibited mechanical damage largely from snow accumulations during the second winter; injuries included broken branches, stems, and buds

Population differentiation was assessed from a model of random effects:

$$[1]\quad Y_{ijk} = \mu + p_i + e_j + r_{jk} + g_{ij} + d_{ijk}$$

where Y_{ijk} is the performance of population i in replicate k of environment j; μ is the overall mean; p_i is the effect of population i; e_j is the effect of environment j; r_{jk} is the effect of replicate k in environment j; g_{ij} is the interaction of population i in environment j; and d_{ijk} is the residual variation. To normalize distributions, proportions were transformed to arc sine $\sqrt{X}$, measurements were converted to logarithms, and bud burst was transformed to $\sqrt{X + \frac{1}{2}}$ (Steel and Torrie 1960).

A series of regression analyses was made to develop a model that depicted geographic patterns of genetic variation. For all regression analyses, variation among populations from central Idaho was related to geographic and ecologic criteria of the seed sources according to the general model:

$$[2]\quad Y_i = b_0 + b_1X_{i1} + b_2X_{i2} \ldots + b_nX_{in}$$

where Y_i is the mean performance of population i; b's are regression coefficients; and X's are various quantitative or qualitative independent variables. Qualitative variables were included in the model by fitting constants. Adequacy of a model was judged according to the goodness of fit (R^2), residual variance ($s_{y\cdot x}$), and geographic patterns displayed by residuals (Draper and Smith 1966). Since the primary objectives of the study pertain to central Idaho, three populations from northern Idaho were not included in regression analyses.

The series of regression analyses is summarized by four models which were developed sequentially.

Model I

Model I used elevation of the seed origin as an independent variable.

Model II

Model II used the residuals from model I as dependent variables and seven river drainages (North Fork and South Fork Payette River; Weiser River; Boise River; Big Wood River; and both the Lower and Upper portions of the Salmon River (Fig. 1)) as independent variables.

Model III

Model III used elevation as an independent variable within each of three geographic zones suggested by results of model II. These zones were (*i*) lower Salmon, including populations from the Weiser and North Fork Payette drainages; (*ii*) upper Salmon; and (*iii*) southern, including the South Fork Payette, Boise, and Big Wood drainages.

TABLE 2. Results of analyses of variance presented as intraclass correlations. σ^2_E, σ^2_P and σ^2_{PE} = variance components for effects of environments, populations, and their interaction; σ^2_W = component for error; σ^2_T = total variance = sum of all components; σ^2_{PH} = phenotypic variance = $\sigma^2_P + \sigma^2_{PE} + \sigma^2_W$

Variable	σ^2_E/σ^2_T	σ^2_P/σ^2_{PH}	$\sigma^2_{PE}/\sigma^2_{PH}$	σ^2_W/σ^2_{PH}	Error mean square
Bud burst	0.98**	0.36**	0.11**	0.54	2.337
Bud set	0.31**	0.34**	+0.00	0.61	0.035
Two flushes	0.34**	0.32**	0.03	0.65	0.038
Height	0.38**	0.80**	0.07**	0.13	0.011
Height deviation	0.64**	−0.00	0.10**	0.90	0.009
Spring frost injury	0.28**	0.16**	0.07**	0.76	0.031
Fall frost injury	—	0.44**	—	0.56	0.010
Winter injury	—	0.29**	—	0.72	0.014

**Significance of associated F value at the 1% level of probability.

Model IV

Model IV involved a stepwise program (Barr et al. 1979) for maximizing R^2, the goodness of fit. To facilitate interpretation of geographic patterns of variation, dependent variables for model IV involved residuals from the elevational regression of model I. Independent variables included latitude, longitude, northwest departure, and southeast departure. The last two variables were created by rotating the grid of latitude and longitude by 45°. These four quantitative variables were also considered within each of the three geograhic zones. Thus, 16 independent variables were used in stepwise analyses.

Results

Test environments greatly influenced the growth and development of seedlings (Table 1). Bud burst occurred approximately 1 month later at 1500 m than at low elevations. Consequently, only seedlings growing at low elevations were susceptible to frost damage in early May. Bud set was also delayed at 1500 m. In fact, 23% of the seedlings growing at high elevations had not set buds in mid-August when nearly all seedlings at low elevations had already set buds. Consequently, at 1500 m, injuries accrued from fall frosts as well as from mechanical effects of the snow depth. The height of trees growing in either the sandy substrate or at high elevation was only two-thirds that of trees at the most favorable sites. This difference developed partially as a result of negative height deviations and partially from a relatively low proportion of trees that flushed twice in severe environments.

While main effects of test environments dominated analyses of variance (Table 2), effects of populations were also strong for all variables except height deviation. Approximately one-third of the phenotypic variance of most traits was determined by the main effects of populations. Indeed, populations accounted for 80% of the phenotypic variance in 3-year height. These strong effects are illustrated by mean differences among populations that amount to nearly 6 days in bud burst, 47% in seedlings that had set buds by mid-August, 71% in the number of seedlings that flushed twice, 18 cm in 3-year height, 40% for spring frost damage, 44% in fall frost damage, and 36% for winter injuries.

A lack of significant differences among populations for height deviation suggests that 3-year height, on a logarithmic scale, was predictable nearly exactly from height at age 2 ($R^2 = 0.77$). (For no differences to be detected in height deviation on a logarithmic scale means, however, that actual (centimetres) differences at age 2 continued to increase through the third growing season.) An evaluation of differentiation within each test environment revealed, however, significant main effects of populations ($\sigma^2_P/\sigma^2_{PH} = 0.16$) for only the environment at high elevation. Because of this, subsequent analyses involving height deviation used only those data from the site at 1500 m.

Interactions of populations and environments were statistically significant for only four variables. These effects, however, accounted for negligible proportions of the phenotypic variance (Table 2). Thus, mean values, averaged for all test environments, are suited for assessing adaptive differentiation along the environmental gradient.

Similarities among variables for analyses of variance are reflected in the intercorrelations among population means (Table 3). With the possible exception of bud burst, the variables formed an intercorrelated network. Populations with a high innate growth potential were tall, had a high proportion of seedlings that flushed twice, and tended to set buds late. These populations, however, displayed the most damage from spring frosts, fall frosts, and snow accumulations. Conversely, populations of low growth potential were also cold hardy. Thus, in the severe environment at 1500 m, populations with a high innate growth potential expressed low rates of growth from a constant height at

TABLE 3. Simple correlation coefficients relating population mean values

Variable	Bud set	Two flushes	Height	Height deviation[a]	Spring frost injury	Fall frost injury	Winter injury
Bud burst	−0.21	0.37**	0.40**	−0.16	0.43**	0.23*	0.21
Bud set		−0.85**	−0.87**	0.45**	−0.68**	−0.59**	−0.65**
Two flushes			0.88**	−0.39**	0.66**	0.62**	0.62**
Height				−0.51**	0.79**	0.66**	0.71**
Height deviation[a]					−0.50**	−0.30**	−0.49**
Spring frost injury						0.44**	0.50**
Fall frost injury							0.60**

[a]Deviation from regression of 3-year height on 2-year height for seedlings growing only at 1500 m.
*Significance at the 5% level.
**Significance at the 1% level.

age 2, a result that accounts for negative correlations between height deviation and variables reflecting growth potential. This means that a future assessment of performance doubtlessly will yield genotype by environment interactions: the ranking of populations for such variables as height will change along the environmental gradient.

Patterns of adaptive variation were assessed from a series of regression models that began by relating population performance to the elevation of the seed source. Model I was significant for all variables (Table 4); elevation accounted for as much as 72% of the variance among population means (Fig. 2). Then, as a preliminary assessment of geographic pattens of variation, model II related deviations from the first model to seven major river drainages. Even though model II was significant for only two variables (Table 4), regression coefficients which, for constant terms, represent deviations from the mean, showed that the seven drainages could be arranged into three geographic zones: lower Salmon, upper Salmon, and southern.

Model III addressed the possibility that the relation between performance and elevation of the seed source varied according to geographic zone. This model, however, accounted for no significant variance that was additional to the variance already attributable to model I. Thus, regression coefficients did not differ significantly among geographic zones. Regression coefficients from model I show that, on the average, populations differing in elevation by 1000 m also differ by 1.6 days in bud burst; 15% in the proportion of seedlings that set buds by mid-August; 29% in the proportion of seedlings that flush twice; 7 cm (53% of the mean) in 3-year height; and as expressed as a percentage of mean injury, 16, 21, and 10% in seedlings injured from spring frosts, fall frosts, and snow accumulations, respectively. Somewhat incidentally, similar relationships exist for performance and elevation of the seed source for populations from northern Idaho as for populations from central Idaho (Fig. 2).

In model IV, a stepwise program for maximizing R^2 was used to assess patterns of geographic variation. Since this model used deviations from model I as independent variables, results of model IV accounted for variance additional to that accounted by elevation alone. Even though 16 geographic variables were available, R^2 was maximized and standard errors minimized with seven or fewer independent variables included in the model. All regressions were statistically significant except that for height deviation (Table 4). Geographic patterns of variation, as predicted from model IV, are presented in Fig. 3 by contours of relatively equal performance. As discussed subsequently, contour intervals (Fig. 3) have been scaled to a value of $1/2\ lsd$ (0.2), the least significant difference (Steel and Torrie 1960) among populations at the 80% level of probability. Patterns of variation are not shown for two variables: those for bud set were identical to those of two flushes, and those for height deviation were not significant.

Because elevation and geographic variables may have been correlated, the joint determination of performance by elevation and geography was assessed by a single regression which included all the independent variables represented in models I and IV. Joint determination ranged from 20% for height deviation to 87% for 3-year height (Table 4). These values, however, were nearly identical to those calculated separately from the results of models I and IV. For example, model I accounted for 72% of the variance in 3-year height; of the remaining variance, 47% was attributable to model IV; an estimated joint determination of 85% differs from the actual (model V) by only 2%. The correspondence in the estimated and actual values for joint determination of all variables illustrates independence of elevation and geography.

In contrast to most other variables, population means for height deviation at high elevation were weakly related ($R^2 = 0.09$) to the elevation of the seed source

and showed no significant relationships with geographic variables. These results arose because contrasting conditions produced low growth rates at 1500 m. On the one hand, populations from cold environments (above 2000 m) tended to grow slowly in all environments. On the other, populations from mild environments suffered injuries from the cold at 1500 m. In both cases, 3-year height was less than that expected on the basis of 2-year height. Consequently, population means for height deviation were only weakly correlated with elevation and geographic variables.

Discussion

Results of the present study, like earlier work in this series, describe population differentiation in Douglas-fir for an intercorrelated network of traits. This network, founded on negative relationships between variables reflecting growth potential and those reflecting cold hardiness, seems keyed on cold adaptation. And because of strong intercorrelations among traits within the network, patterns of population differentiation were closely related to the altitude and geographic origin of the seed source.

Patterns of genetic variation, moreover, closely reflect environmental patterns. As elevation increases, the length of the frost-free period decreases. Consequently, elevation of the seed source was negatively associated with the growth potential of populations but was positively associated with cold hardiness. In addition, geographic patterns of variation that were independent of elevation relegated the lowest growth potential and greatest hardiness to populations from the rugged east-central region, the headwaters of central Idaho's major drainages. From this area, hardiness of populations decreases and growth potential increases in all directions. These clines, however, are steepest toward the north and northeast where the climate is mildest and populations are of highest growth potential and lowest hardiness. Correspondence between patterns of genetic variation (Fig. 3) and frost-free periods (Fig. 1) are unmistakable for all variables except bud burst. Patterns of variation for bud burst, like those for many forest trees, were weakly related to latitude.

These results have direct implications to forest management. To limit maladaptation in planted trees, seed transfer guidelines must reflect adaptive variation. One estimate of an appropriate limit to seed transfer involves the minimum geographic or elevational interval over which differentiation can be detected (Rehfeldt 1979). This interval is estimated by the ratio $lsd\,(0.2)/b$, where b is a regression coefficient and $lsd\,(0.2)$ is derived from the analysis of variance as the least significant difference among population means at the 80% level of probability. (A rather low level of probability is used to

TABLE 4. Results of regression analyses for assessing patterns of genetic differentiation

Variable	Model I[a]		Model II[b]		Model III[c]		Model IV[d]		Joint determination of models I and IV[e]	
	R^2	$s_{y\cdot x}$	R^2	$s_{y\cdot x}$	R^2	$s_{y\cdot x}$	R^2	$s_{y\cdot x}$	R^2	$s_{y\cdot x}$
Bud burst	0.14**	0.1249	0.13	0.1211	0.19**	0.1235	0.20*	0.1164	0.33**	0.1166
Bud set	0.60**	0.0856	0.09	0.0845	0.61**	0.0851	0.37**	0.0715	0.75**	0.0708
Two flushes	0.65**	0.0870	0.05	0.0880	0.66**	0.0866	0.26**	0.0791	0.76**	0.0762
Height	0.72**	0.1212	0.23**	0.1108	0.76**	0.1126	0.47**	0.0930	0.87**	0.0874
Height deviation[f]	0.09**	0.0562	0.02	0.0571	0.09**	0.0561	0.13	0.0565	0.20*	0.0566
Spring frost injury	0.41**	0.0824	0.21**	0.0759	0.42**	0.0754	0.41**	0.0667	0.65**	0.0671
Fall frost injury	0.27**	0.0675	0.15**	0.0645	0.29**	0.0677	0.28**	0.0606	0.48**	0.0602
Winter injury	0.41**	0.0726	0.02	0.0746	0.42**	0.0731	0.19*	0.0686	0.53**	0.0688

[a]Independent variable = elevation of the seed origin.
[b]Independent variables = seven river drainages; dependent variables = residuals from model I.
[c]Independent variables = elevation within three geograhic zones.
[d]Stepwise assessment of 19 geographic variables on deviations from model I.
[e]Independent variables of models I and IV.
[f]Deviation from regression of 3-year height on 2-year height for trees growing at 1500 m.
*Statistically significant at the 5% level.
**Statistically significant at the 1% level.

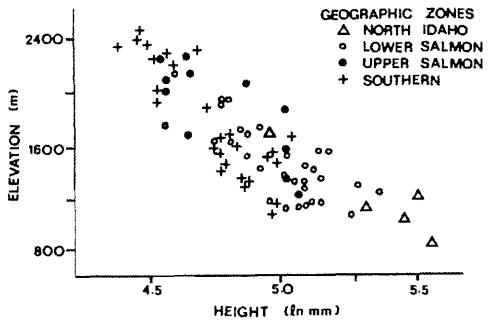

FIG. 2. Relationship between mean height of populations from four geographic zones and the elevation of the seed source.

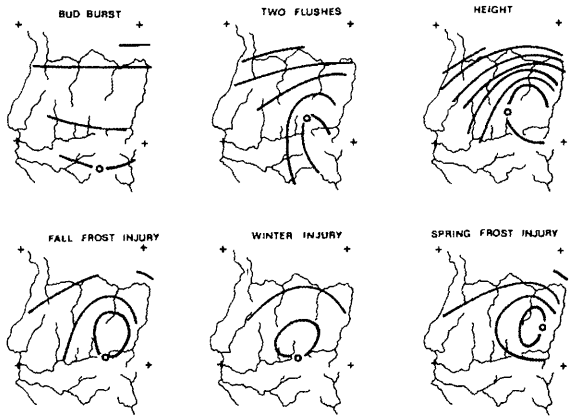

FIG. 3. Geographic patterns of variation independent of elevation. Contour lines of relatively equal performance are scaled to a value of *lsd* (0.2). The zero contour depicts the lowest mean performance.

avoid the error of accepting no differences when differences actually exist.) Elevational intervals associated with *lsd* (0.2) include 1000 m for fall frost injury, 600 m for winter injury, 400 m for bud set, and about 200 m for height. To accept the smallest interval requires the transfer of seed from a given source to be limited to ±100 m. Geographic patterns of variation were illustrated (Fig. 3) by contours scaled to a value of 1/2[*lsd* (0.2)]. Thus, lateral transfers of seed should be limited to ±1 contour from a given source. Again, to accept the most limiting of these patterns is to base geographic transfers of seed on patterns illustrated for 3-year height.

Practical application of these guidelines may involve either the construction of discrete seed zones or the implementation of floating guidelines. Discrete zones should be limited to two geographic contours and 200 m elevation. Floating guidelines rely on the relationship between geographic and altitudinal patterns of adaptive differentiation. One geographic band represents an equal amount of population differentiation as 100 m elevation. Thus, a given population is similar genetically to a population located at 100 m lower elevation within the adjacent band on the southeast (Fig. 3). Consequently, when transferring seed from northwest to southeast, the appropriate elevational interval should be lowered by 100 m for each geographic contour crossed.

Populations of Douglas-fir, whether from central Idaho, northern Idaho (Rehfeldt 1979), western Montana (Rehfeldt 1982), or western Oregon (Campbell 1979), are closely attuned physiologically to their environment. Adaptive variation among populations is closely related to geographic, physiographic, and climatic variables. In the Rocky Mountains, physiological specializations result from a balance between selection for cold hardiness in severe environments and growth potential in mild environments. Specialization, however, has not led to the depletion of genetic variance within populations. While differentiation of populations provides adaptation to spatial environmental heterogeneity, genetic variance within populations provides adaptation to temporal heterogeneity. Adaptation to spatial heterogeneity by means of specialization is balanced by temporal environmental variances (Rehfeldt 1983).

BARR, A. J., J. H. GOODNIGHT, and J. P. SALL. 1979. SAS user's guide, SAS Institute Inc., Raleigh, NC.

CAMPBELL, R. K. 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. Ecology, **60**: 1036–1050.

DRAPER, N. R., and H. SMITH. 1966. Applied regression analysis. John Wiley and Sons, Inc., New York.

REHFELDT, G. E. 1979. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) populations. I. North Idaho and northeast Washington. Heredity, **43**: 383–397.

——— 1982. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) populations. II. Western Montana. U.S. For. Serv. Res. Pap. INT-295.

——— 1983. Genetic variability within Douglas-fir populations: implications for tree improvement. Silvae Genet. In press.

ROSS, S. H., and C. N. SAVAGE. 1967. Idaho earth science. Idaho Bureau of Mines, Moscow, ID.

STEEL, R. G. D., and J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York.

STEELE, R., R. D. PFISTER, R. A. RYKER, and J. A. KITTAMS. 1982. Forest habitat types of central Idaho. U.S. For. Serv. Gen. Tech. Rep. INT-144.