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Ecological Adaptations in Douglas-fir Populations. II. Western Montana

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RESEARCH SUMMARY

Seedlings from 50 populations of Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) from Montana west of the Continental Divide were compared in nursery, laboratory, and shadehouse studies. Analyses of variance indicated significant differences among populations in six traits: bud burst, bud set, 3-year height, growth rate, cold injury, and flushing periods during the first or third growing season. Most traits were highly intercorrelated; thus, populations that expressed a high growth potential also set buds late, flushed twice, grew at a rapid rate, but were most severly injured by freezing. Consequently, adaptation of populations for numerous traits is viewed as a balance between selection of high growth potential in relatively mild environments and selection for cold hardiness in severe environments.

Multiple regression analyses related genetic differentation of populations to geographic and ecologic conditions of the seed source. The regression model that best fit the data described adaptive variation according to two physiographic zones, elevation within each zone, and latitude within zones. Patterns of adaptive differentiation were used to develop seed transfer guidelines for reforestation and tree improvement.

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INTRODUCTION

Genetic differentiation among populations of Douglas-fir (*Pseudotsuga menziesii*) is closely related to the environment. In the coastal variety (*Pseudotsuga menziesii* var. *menziesii*), genetic variation within a single drainage was clearly related to elevation and topographic setting (Campbell 1979; Campbell and Franklin 1981). For the Rocky Mountain variety (*Pseudotsuga menziesii* var. *glauca*), the growth potential and cold hardiness of populations depends on geographic origin: populations from northern Idaho tend to be faster growing and less hardy than those from western Montana which, in turn, are faster growing and less hardy than populations from southern Idaho (Rehfeldt 1979b). Within northern Idaho alone, differences among populations are closely related to the elevation, latitude, and longitude at the seed origin (Rehfeldt 1979a).

The main objective of the present study is to describe patterns of genetic variation among Douglas-fir populations from Montana west of the Continental Divide (fig. 1). The study excludes the extreme northwest portion of the area which presents patterns of environmental variation (Pfister and others 1977) and genetic differentiation (Rehfeldt 1979a,b) that are similar to those of northern Idaho. Patterns of variation will be used to: (1) develop guidelines for the transfer of seeds that should limit maladaptation in reforestation, and (2) delineate the breeding zones within which genetic gains from tree improvement will accrue.

Western Montana (fig. 1), a region of diverse montane environments, is separated from contiguous areas by the Continental Divide on the east and south, the Cabinet and Bitterroot Mountains on the west, and a political boundary to the north. Within this region, climatic, physiographic and ecologic conditions follow a well-described pattern from the west and northwest toward the Continental Divide (Pfister and others 1977). Remnants of a maritime climate in the northwest are gradually lost as the general climate becomes continental. The elevation of valley floors increases from about 2,000 ft to 4,000 ft (600 m to 1 200 m). Concomitant changes in the frequency of particular habitat types largely reflect a gradual decrease in species most common in moist environments. Finally, effects of topography are superimposed on general environmental trends to produce the extreme environmental heterogeneity that characterizes the region. And within this region, Douglas-fir occupies a range of sites from the relatively warm, near lower timberline, to relatively cold subalpine environments above 6,500 ft (2 000 m) elevation (Pfister and others 1977).

MATERIALS AND METHODS

To assess population differentiation, cones were collected from several squirrel caches in each of 50 populations from western Montana (fig. 1). Populations, selected to represent the ecological amplitude of the species within the region, differed in elevation by as much as 4,300 ft (1 300 m); and represented habitats (Pfister and others 1977) as dry and warm as the *Pseudotsuga menziesii/Agropyron spicatum,* as cool as the *Abies lasiocarpa/Vaccinium globulare,* or as moist as the *Thuja plicata/Clintonia uniflora* habitat types. In addition to populations from western Montana, some populations from adjacent geographic provinces (fig. 1) were included in separate studies of (1) growth potential and phenology, (2) cold hardiness, and (3) patterns of first-year shoot elongation. Data from all studies were used to assess patterns of geographic and ecologic variation.

Growth and Phenology

Seedlings from 54 populations were grown for 1 year in plastic tubes (4 in^3, 65 cm^3) in a shadehouse at Moscow, Idaho. In autumn of the first growing season, seedlings were transplanted into six environments (table 1) on the Priest River Experimental Forest in northern Idaho (fig. 1). While two plantings were in a nursery, four were established on various forest sites. Although plantings on these four sites were made in the residual soil, rocks, roots, and competing vegetation had been removed before tilling. All plantings received natural precipitation. Twelve seedlings from each population were planted in row plots in each of two replicates in all environments. Rows were separated by 4 in (10 cm); 3 in (8 cm) separated seedlings within rows.

Growth potential and phenology of seedlings was assessed from the following scores and measurements obtained for each population in all replicates:

1. Bud burst: the day after April 1 by which 50 percent of the seedlings had burst terminal buds during the third growing season.
2. Bud set: the week by which 50 percent of the seedlings had set terminal buds during the third growing season.
3. Two flushes: the proportion of seedlings that flushed more than once during the third growing season.
4. Height: average seedling height after 3 years.
5. Growth rate: 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.

Population differentiation was assessed from the model of random effects:

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

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; g_{ij} is the interaction of population i in environment j; and d_{ijk} is the residual variation. While most analyses were made on the original variables, proportions were transformed to arcsin $\sqrt{X}$ and bud set was transformed to $\sqrt{X + ½}$. ■

Cold Hardiness

Tolerance to freezing was studied with 50 seedlings from each of 58 populations that had been growing for 2 years in plastic containers (9 in^3; 150 cm^3) in a shadehouse at Moscow, Idaho. In general accordance with procedures outlined by Levitt (1972), freezing tests were made to assess hardiness of each population in mid-September when first autumnal frosts can be expected. This single date was chosen because northern Idaho populations expressed greatest differentiation in cold hardiness after bud set but prior to the first frost of autumn and because previous tests indicated that the ranking of populations according to hardiness did not change in subsequent sampling dates (Rehfeldt 1979d).

Terminal shoots from each of the 58 populations were cut and arranged into 5 sets of 10 shoots (3 in; 8 cm long). Each set was moistened, packaged in a plastic bag, and stored overnight at 37° F (3° C). The following morning, plastic bags were suspended in a freezing chamber equipped with two fans for providing circulation. One set of shoots from each population was frozen at the rate of 9° F (5° C)/h to one of five test temperatures between 7° F and 0° F (−14° C and −18° C). While within the plastic bags, shoots were removed from the freezer when remote temperature sensors indicated that internal air temperatures had reached desired levels, were thawed for 24 h at 37° F (3° C), and were placed on a shaded greenhouse bench. After 2 days, the presence or absence of injury to each shoot was scored by discoloration of leaves. For each population, the number of seedlings exhibiting leaf injury was recorded for each test temperature.

Differentiation of populations was assessed by an analysis of variance of random effects on the percentage of shoots of each population exhibiting injury at each test temperature:

$$Y_{ij} = \mu + p_i + t_j + g_{ij} + e$$

where Y_{ij} is the percentage of twigs injured from population i at temperature j; μ is the overall mean; p_i is the effect of population i; t_j is the effect of temperature j; g_{ij} *is the interaction of population* i at temperature j; and e is the theoretical variance of an observation in a binomial distribution (Steele and Torrie 1960). Percentages were transformed to arcsin $\sqrt{X}$ before analyses were made.

Patterns of First-Year Growth

Douglas-fir seedlings exhibit contrasting patterns of growth during the first growing season (Rehfeldt 1979c). For essentially all seedlings from western Montana. a terminal bud is set about 1 month after germination. But, only a portion of these seedlings burst bud and resume growth in late July or August. To test for differences among Montana populations in patterns of first-year elongation, 30 to 40 seedlings from 50 populations were grown in plastic containers (4 in^3; 65 cm^3) in each of four replicates. The proportion of seedlings that exhibited a single growth period was recorded for each population in all replicates. Proportions were transformed (arcsin $\sqrt{X}$) before statistical analyses that followed a model identical to that used for freezing tolerance.

Patterns of Variation

Data from the separate studies were used to assess differentiation in relation to geographic and ecologic criteria of the seed sources according to the general model:

$$Y_i = b_0 + b_1 X_{i1} + b_2 X_{i2} \ldots + b_n X_{in}$$

where Y_i is the mean performance of population i; b's are regression coefficients; and X's are various independent variables (table 2). Qualitative independent variables were included in the model by fitting constants, values of zero or one (Draper and Smith 1966). Of the independent variables, habitat types included five major series on which Douglas-fir is common (Pfister and others 1977); Idaho departure is distance from the State line; and northwest departure is an imaginary grid distance from northwest to southwest through western Montana.

Table 1.—Trait means according to environment

Environment	Bud burst	Bud set	Two flushes	Height	Growth rate[1]
	Days	*Weeks*	*Percent*	cm	cm
Nursery shade, 730 m	33.4	2.9	24.5	18.6	10.8
Nursery sun, 730 m	31.7	5.5	54.8	17.2	7.9
Reservoir, 790 m	31.4	5.4	51.6	15.4	4.3
M-2 Road, 1 100 m	35.8	5.7	38.3	11.6	−7.8
North Ridge west, 1 520 m	60.8	9.4	44.3	12.6	−4.9
North Ridge east, 1 580 m	66.3	11.9	61.1	10.6	−10.4

[1] Deviation from regression of 3-year height on 2-year height.

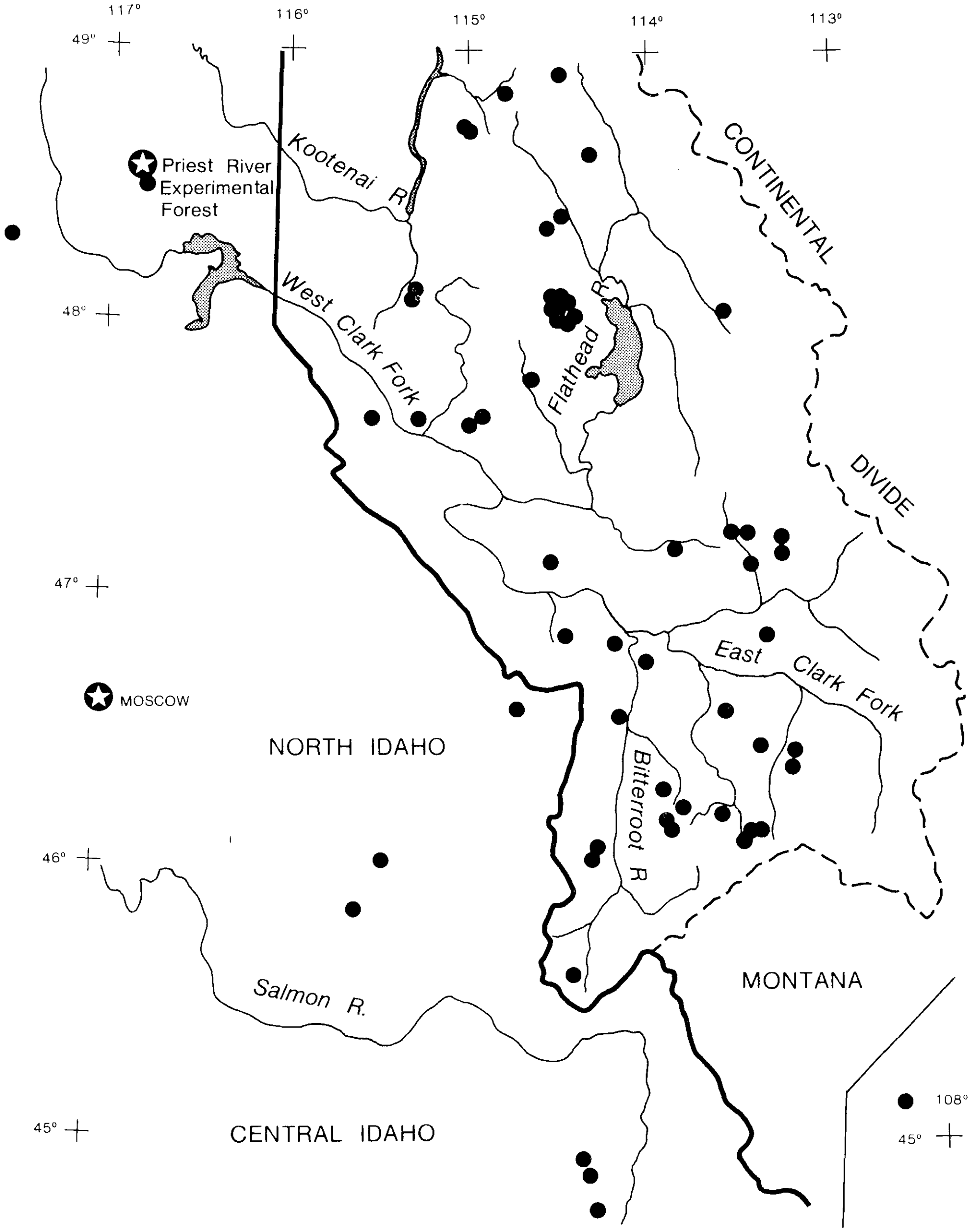

Figure 1.—Major drainages of western Montana and adjacent regions showing location of populations.

For all regression models, residuals from regression were examined visually in relation to observed and predicted values to assess homogeniety of error variances and the fit of data to regression models (Draper and Smith 1966). Thus, seven regression models were fitted to the data (table 2). Adequacy of a model was judged according to the goodness of fit (R^2), residual variance ($s_{y \cdot x}$), and geographic or ecologic patterns displayed by residuals.

RESULTS

Six environments exerted considerable influence on the growth and phenology of seedlings (tables 1 and 3). Most of this influence was directly related to elevation. As compared to seedlings growing in the nursery at low elevation, seedlings growing at high elevations on North Ridge burst bud about 4 weeks later, set buds about 6 weeks later, grew at a slower rate (negative deviation from regression), and, consequently, were about 3 in (7.5 cm) smaller. Only the proportion of seedlings that flushed twice seemed to be independent of elevation, but perhaps not independent of shade. The two environments with the lowest proportion of seedlings that flushed twice included the nursery that received 50 percent shade and M-2 Road that received afternoon shade.

Table 2.—Independent variables included in various models for relating population differentiation to geographic and ecologic conditions of the seed source

Independent variable	Variables included in model: 1	2	3	4	5	6	7
Latitude	x						
Longitude	x						
Habitat types	x						
Elevation	x	x	x		x		
Northwest departure		x					
Idaho departure		x					
Three major drainages			x	x			
Elevation within drainages				x			
East and west physiographic zones					x	x	x
Elevation within zones						x	x
Northwest departure in zones					x	x	
Latitude in zones							x

Populations differed greatly in phenology and growth potential (table 3). In the average environment, populations from western Montana differed by as much as 6 days in bud burst, 6.2 weeks in bud set, 53 percent in seedlings that flushed twice, 2.7 in (7 cm) in height, and 1.2 in (3 cm) in growth rate (third-year growth from a constant height at age 2). In addition, populations performed essentially the same in all environments. Interactions of genotype and environment were detected for only bud burst and height. While accounting for little variance, these interactions, like those detected for north Idaho populations (Rehfeldt 1979a), resulted from mean differences not associated with changes in the ranking of populations.

Laboratory studies of freezing tolerance revealed significant differences among 58 populations (table 4A). Even though test temperatures spanned only 9° F (5° C), percentage of injury to all twigs ranged from 19 percent at 7° F (−14° C) to 75 percent at 0° F (−18° C). Across this range of temperatures, mean injury to populations from western Montana ranged from 16 to 69 percent.

Shadehouse studies of the pattern of first-year elongation revealed significant differences among populations in the proportion of seedlings that exhibited a single growth period (table 4B). Mean values for Montana populations ranged from 24 to 74 percent.

Table 4.—Analyses of variance for freezing injury (A) and one period of growth (B)

Source of variance	Degrees of freedom	Mean square
A. Freezing injury		
Temperatures	4	6.2206**
Populations	57	.1280**
Temperature x Population	228	.0424
Sampling error[1]	—	.0250
B. One period of growth		
Replication	3	0.0478**
Populations	49	.0499**
Replication x Population	147	.0155
Sampling error[1]	—	.0148

[1] Theoretical variance of a binomial distribution.

**Statistical significance at the 0.01 level of probability.

Table 3.—Mean squares from analyses of variance for population performance in nursery environments

Source of variation	Degrees of freedom	Bud burst	Bud set	Two flushes	Height	Growth rate[1]
Environments	5	27,290.59**	38.400**	1.9907**	1097.39**	84.64**
Reps/environment	6	10.22**	1.079**	0.2538**	23.25**	21.33**
Populations	53	20.54**	1.499**	.3116**	95.51**	6.43**
Pops. x environment	265	1.78	0.312*	.0433	5.36**	1.53
Residual	318	1.92	.247	.0447	2.07	1.57

[1] Deviation from regression of 3-year height on 2-year height.

**Significant at the 0.01 level of probability.

*Significant at the 0.05 level of probability.

Variation in growth, phenology, cold hardiness, and first-year flushing of western Montana populations formed an intercorrelated network of traits to which only bud burst was unrelated (table 5). This network, like that for northern Idaho populations (Rehfeldt 1979a), seems keyed to adaptation to the cold. Populations that set buds early were also characterized by a low proportion of seedlings that flushed twice, a low growth rate, a short height, but a high tolerance to freezing.

Because of strong intercorrelations, results of the series of regression analyses (table 6) showed similar patterns for all traits. In general, the sequence of regression models shows an increase in values of R^2 and a decrease in residual variances. Regression model 1 (table 2) indicated that (1) genetic variation was related to elevation; (2) geographic patterns of variation followed a grid that was oblique to latitude and longitude; and (3) habitat types were related to neither dependent nor independent variables. A lack of association between habitat types and genetic variation in western Montana corresponds with results for Douglas-fir populations from northern Idaho (Rehfeldt 1979a) and for *Pinus ponderosa* from southern Idaho (Rehfeldt 1980).

Residuals from model 2 suggested that geographic patterns of variation were discontinuous at 40 to 60 mi (60 to 100 km) from the Idaho state line, a boundary that roughly follows the crests of the Cabinet and Bitterroot Mountains. Populations from the Bitterroot and west Clark Fork drainages differed from eastern populations representing similar latitudes and elevations. This discontinuous pattern of variation was incorporated in models 3 to 6, which represent sequential steps toward the model that best represented the data. Regression model 7 generally produced the highest fit and lowest residual variance. But also, residuals displayed no obvious geographic or ecologic patterns.

In model 7, genetic variation is described according to six independent variables: two physiographic zones, elevation within each zone, and latitude within zones. The western physiographic zone includes the Bitterroot and west Clark Fork drainages; the eastern zone is composed of the Flathead and east Clark Fork drainages (fig. 1). Results of multiple regression analyses are presented graphically for each variable (fig. 2). These graphs were generated by predicting population performance (*Y*) from multiple regression equations. Because of high

Table 5.—Matrix of simple correlation coefficients among population means

	BS	TWF	H	GR	OP	FZ
Bud burst (BB)	−0.13	−0.22	0.12	−0.02	0.21	−0.05
Bud set (BS)		.91**	.72**	.49**	−.45**	.49**
Two flushes (TWF)			.61**	.54**	−.44**	.40**
Height (H)				.25	−.26	.45**
Growth rate (GR)					−.42**	.28**
One period (OP)						−.31*
Freezing injury (FZ)						—

*Statistical significance at the 0.05 level of probability.
**Statistical significance at the 0.01 level of probability.

Table 6.—Results of several multiple regression models (table 2) for relating genetic variation to geographic and ecologic conditions of the seed source

Regression model	Bud burst		Bud set		Two flushes		Height		Growth rate		One period		Cold hardiness	
	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	$s_{y \cdot x}$	R^2	$s_{y \cdot x}$	R^2	$s_{y \cdot x}$
1	0.26**	1.021	0.30	0.2435	0.32**	0.1044	0.60**	1.138	0.11	0.5500	0.12	0.0980	0.23**	0.1199
2	.30**	.991	.38**	.2299	.38**	.1003	.61**	1.127	.10	.5534	.13	.0975	.31**	.1148
3	.23	1.039	.42**	.2225	.45**	.0939	.58**	1.167	.10	.5534	.12	.0982	.31**	.1145
4	.31**	1.011	.48**	.2146	.50**	.0916	.59**	1.177	.27*	.5095	.17	.0975	.37**	.1121
5	.28**	1.011	.46**	.2166	.49**	.0917	.68**	1.031	.18	.5355	.13	.0984	.34**	.1130
6	.32**	1.005	.49**	.2126	.51**	.0909	.70**	1.006	.21	.5300	.18	.0970	.35**	.1136
7	.32**	1.003	.52**	.2071	.52**	.0900	.72**	.978	.23*	.5245	.19	.0964	.35**	.1131

*Statistical significance at the 0.05 level of probability.
**Statistical significance at the 0.01 level of probability.

intercorrelations among dependent variables, similar results of regression models (fig. 2) were expected for bud set, two flushes, height, growth rate, and freezing injury. But the same model was also effective for bud burst largely because of strong effects of latitude and elevation within the western zone. Similarly, elevation within the western zone was the only independent variable significantly associated with the proportion of seedlings that displayed one growth period. Consequently, results of the multiple regression for the latter variable are presented even though the entire model was not significant.

The regression models generally depict: (1) decreasing growth potential and increasing hardiness of populations in association with increasing elevation of the seed origin; (2) greater growth potential but lesser hardiness of populations in the western zone than in the eastern zone; (3) effects of elevation on genetic differentiation that are generally stronger in the western zone than in the eastern zone; and (4) effects of latitude in the west that are the reverse of those in the east. Thus, at a constant elevation, hardiness of populations increases while growth potential decreases northward through the western zone and then southward through the eastern zone. Thereby, genetic differentiation in populations from different physiographic zones is greater in the southern portion of western Montana that in the northern portion.

Finally, since nursery and laboratory studies included a few populations from geographic regions adjacent to western Montana, geographic variation can be assessed further. As noted previously (Wright and others 1971; Rehfeldt 1979b), populations from northern Idaho express greater growth potential but lesser hardiness than western Montana populations from comparable elevations (table 7). In addition, populations from the severe environments of central Montana and central Idaho express an extremely low growth potential but high hardiness.

DISCUSSION

By illustrating strong geographic and ecologic patterns in genetic differentiation, the present results further exemplify intense physiological attunement of Douglas-fir populations to their environment. Adaptation of populations is readily interpreted as a balance between selection of high growth potential in mild environments and selection for cold hardiness in severe environments. Montana populations, like those from northern Idaho, were readily differentiated by a network of intercorrelated traits: populations of high growth potential were tall, set buds late, grew at a rapid rate, expressed pronounced tendencies for multiple flushing, but suffered the most injury from freezing. Accordingly, as compared to populations from western Montana, those from northern Idaho expressed adaptations to a milder climate; and those from southern Idaho and central Montana expressed adaptations to a more severe climate.

In addition, patterns of genetic variation depicted by multiple regression models seem uniquely suited to the climate and physiography of western Montana. A western physiographic zone contained populations of higher

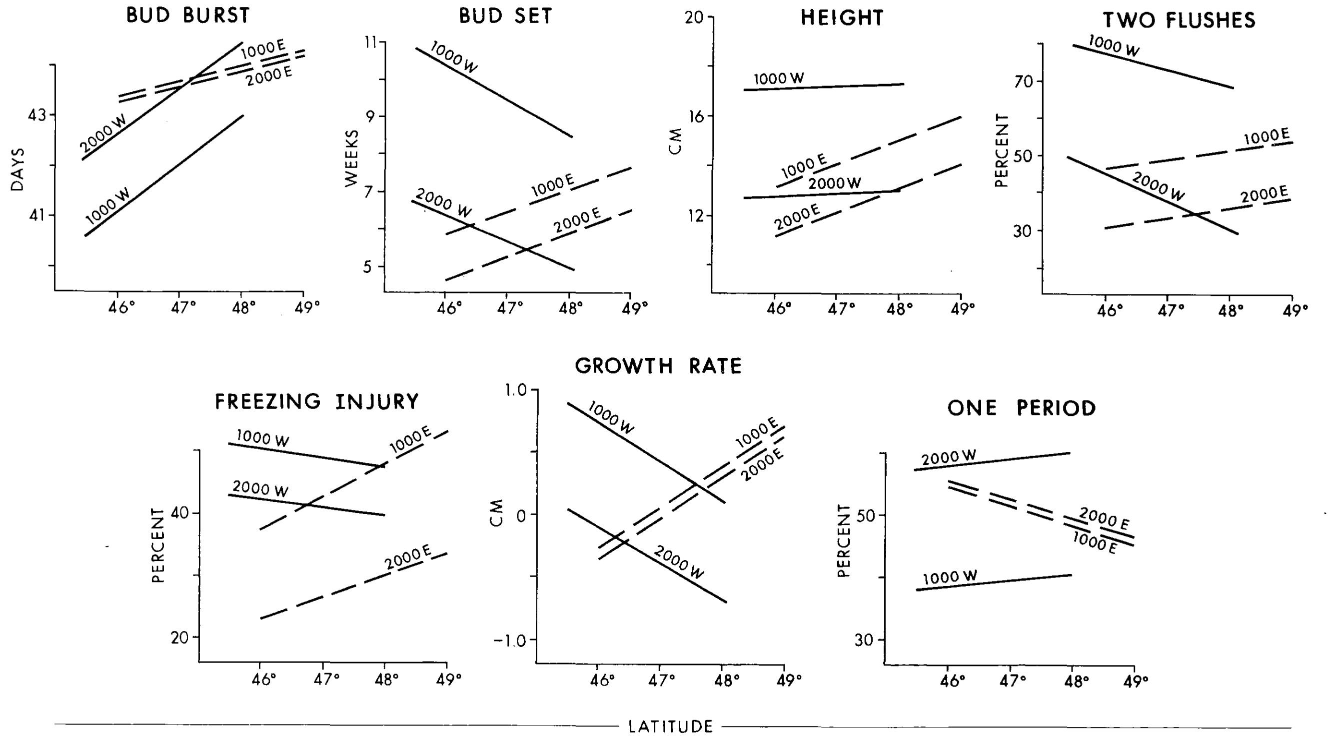

Figure 2.—Results of multiple regression model 7 (table 2) depicting the predicted performance (ordinate) in relation to the latitude (abscissa), geographic zone (E = eastern, W = western), and the elevation (1 000 m or 2 000 m) of the seed source.

Table 7.—Average deviation in performance of populations from peripheral areas from the predicted performance of western Montana populations at comparable elevations

Geographic area	Sample populations	Bud burst	Bud set	Two flushes	Height	Growth rate	One period	Freezing injury
	Number	*Days*	*Weeks*	*Percent*	*cm*	*cm*	*Percent*	*Percent*
Northern Idaho	3	−0.6	1.9	6.3	5.6	0.51	—	4.6
Central Idaho	3	−2.2	−1.5	−17.0	−2.6	−.34	5.2	−11.0
Central Montana	1	−2.0	−.8	−10.4	−3.5	−.52	11.9	−15.0

growth potential and lesser hardiness than populations from similar elevations and latitudes in an eastern zone. The boundary between eastern and western zones generally follows the crest of the Sapphire Mountains, which separate the Bitterroot Drainage from the eastern Clark Fork, and includes the Jocko Range and the Cabinet Mountains, which separate the Flathead Drainage from the western Clark Fork (fig. 1). Moreover, a climate with considerable maritime influence in the west and northwest becomes decidedly more continental as the Continental Divide is approached; this climatic pattern is reflected in the distribution of plant communities (Pfister and others 1977; Arno 1979). Consequently, it is appropriate for Douglas-fir populations from the western zone to express adaptations to a milder climate than populations from the eastern zone.

For genetic variation to be related to elevation of the seed source is not surprising: growing seasons generally decrease with increasing altitude; an intercorrelated network of traits is keyed to adaptations to the cold; and for both Oregon (Campbell and Sorensen 1978; Campbell 1979) and northern Idaho (Rehfeldt 1979a) populations, genetic variation has been related to elevation. However, the strength of the relationship between differentiation and elevation depended on the physiographic zone. For instance, in the western zone, 3-year height of populations decreased by about 26 percent over an elevational difference among seed sources of 3,280 ft (1 000 m). The corresponding decrease for the eastern zone amounted to about 14 percent while that for the northern Idaho populations was about 28 percent (Rehfeldt 1979a). Thus, in areas where climatic gradients in altitude should be the steepest, the strongest associations between differentiation and elevation were apparent. Near the Continental Divide, the difference in environmental severity between high and low elevations, judged by the distribution of habitat types (Pfister and others 1976), is the least, and clinal gradients are relatively flat.

In the Northern Hemisphere, populations of woody plants from southern latitudes generally show higher growth rates and lesser hardiness than populations from northern latitudes. Thus, differentiation among Douglas-fir populations in northern Idaho (Rehfeldt 1979a) and in Montana's western physiographic zone followed the expected trend even though the latitudinal interval was small (3.5 degrees). However, patterns of population differentiation in the eastern physiographic zone followed a contrasting pattern: northern populations were of the highest growth potential and lowest hardiness. Again, patterns of latitudinal differentiation in the eastern zone are readily interpreted by climatic patterns imposed by the unique physiognomy of the region: not only does a maritime climatic influence decrease from the northwest toward the southwest, but also, elevation of valley floors increases greatly toward the southeast. Consequently, much of the region drained by the eastern Clark Fork represents an ecotone between the relatively moist environment to the west and north and the severely cold and dry habitats to the east. Thus, it is appropriate for (1) northern populations of the eastern zone to be of higher growth potential and lower hardiness than southern populations, and (2) for genetic differentiation among populations from different zones to be greater in the southern portion of western Montana than in the northern.

Regression models accounted for only a portion of the variance among populations. However, a perfect fit of regression models to data cannot be expected even if all relevant independent variables could be assessed. High levels of genetic variability exist within populations regardless of geographic origin (Campbell 1979, Rehfeldt 1979b). Natural sampling errors coupled with selection pressures that vary in time and space can account for random patterns of differentiation within single drainages (Rehfeldt 1974). Moreover, experimental errors, including sampling errors, can account for additional extraneous variance. Perhaps it is surprising that regression models accounted for as much as 72 percent of the variance among populations.

Patterns of adaptive differentiation of forest trees determine the distance of seed transfer in reforestation for which maladaptation of planted trees is minimal. As proposed previously (Rehfeldt 1979a), $lsd(0.2)/b$ [where $lsd(0.2)$ = least significant difference among populations at the 80 percent level of probability, as estimated from analyses of variance, and b = regression coefficients from multiple regression models] estimates a geographic or elevational interval associated with differences among populations that are significant with a probability of about 80 percent. These intervals (table 8) imply that seed zones for reforestation or tree improvement should be limited to about one degree latitude and 920 ft (280 m) elevation in the Bitterroot and western Clark Fork drainages; and by about 1.5 degrees latitude and 2,100 ft (650 m) elevation in the Flathead and eastern Clark Fork drainages. Or, as general guidelines, the transfer of seed from a single source should be within ± 460 ft (140 m) elevation and ± 30 miles (50 km) north or south in the western physiographic zone, and within ± 1,050 ft (325 m) and ± 45 miles (75 km) in the eastern zone.

Table 8.—Geographic and elevational distances associated with mean differences among seed sources that correspond to a significance level of 80 percent

	Western zone			Eastern zone		
Trait	**Elevation**	**Latitude**		**Elevation**	**Latitude**	
	Meters	*Degrees*	*km*	*Meters*	*Degrees*	*km*
Bud burst	474	0.8	94	2 567	2.5	296
Bud set	422	1.9	222	1 195	2.3	266
Two flushes	359	1.5	171	708	3.8	448
Height	278	11.4	1 337	656	1.3	149
Growth rate	782	2.0	234	6 578	2.0	229
One period	586	11.5	1 350	9 928	3.5	414
Freezing injury	1 924	7.4	866	1 001	3.9	460

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Populations of Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) from Montana west of the Continental Divide were compared in common environments. Differentiation was observed for six variables reflecting growth potential, phenology and cold hardiness. Adaptation of populations for numerous traits is viewed as a balance between selection of high growth potential in relatively mild environments and selection for cold hardiness in severe environments. Adaptive variation is described according to two physiographic zones, elevation within each zone, and latitude within zones.

KEYWORDS: Douglas-fir, ecological genetics, growth potential, cold hardiness, phenology, tree improvement

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