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Adaptive Variation in *Pinus ponderosa* from Intermountain Regions. II. Middle Columbia River System

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RESEARCH SUMMARY

Seedlings representing 138 populations of ponderosa pine from drainages of the middle Columbia River system were grown and compared in common environments. Field studies of 3-year-old trees on mesic and xeric test sites detected population differentiation for traits reflecting growth and development. Populations that expressed the greatest growth potential under mesic culture suffered the greatest reduction in height under xeric culture. Consequently, a different set of populations was performing the best on the two sites when 3-year height was expressed as the growth from a common height at age 2.

Greenhouse studies of the periodicity of shoot elongation revealed that populations of high growth potential achieved a large stature by means of a long duration, late cessation, rapid rate, and large amount of elongation.

Multiple regression models accounted for as much as 60 percent of the variance between populations and described adaptive landscapes in which populations from low elevation have a high growth potential while those from high elevations have a low growth potential. Geographic variation at a common elevation indicated that populations of high growth potential come from areas where the frost-free period is long and precipitation is relatively high. Thus, growth potential is directly related to the length of the growing season, which can be truncated by either frost or moisture stress.

Adaptive landscapes are used to construct guidelines for limiting seed transfer in artificial reforestation. In general, seed from a single source should not be transferred more than ±200 m in elevation.

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INTRODUCTION

Populations that occupy contrasting environments tend to differ genetically for numerous traits that convey environmental adaptation. In accordance, adaptive differentiation in the widespread ponderosa pine (*Pinus ponderosa*) is well documented (Wang 1977) and is related to the elevation and geographic origin of the seed. For just the Inland Northwest, populations from mild environments tend to have a high growth potential while populations from areas where growing seasons are short tend to have a low growth potential (Wang 1977; Madsen and Blake 1977; Rehfeldt 1979b, 1980, 1986).

Forest managers rely on geographic patterns of adaptive variation to estimate the distance that seeds can be transferred from their origin before maladaptation begins to limit the productivity of artificial regeneration. However, previous studies were of insufficient power and scope for providing managers with this information. Consequently, a series of studies was begun to determine the appropriate limits to seed transfer for the Intermountain Region. While the first study of this series concerned populations from central Idaho (results published in Forest Science, Rehfeldt 1986), the present involves populations from the middle Columbia River system of northeastern Washington, northern Idaho, and western Montana.

MATERIALS AND METHODS

Population differentiation was studied in seedlings from 138 populations that sampled the ecologic, geographic, and elevational distribution within which the species is of commercial importance in the Inland Northwest (fig. 1). Genetic diversity of each population was sampled in a manner to assure that seedling populations represented a large number of parental trees. Most populations were represented by an equal volume of wind-pollinated cones from 10 trees. Some, however, were represented by samples of cones collected from several squirrel caches. Genetic diversity was assured by selecting cones with a variety of morphologies, sizes, and colors. Seedlings were used in separate studies of (1) growth and development in the field and (2) the periodicity of shoot elongation in a greenhouse. The results from both were used to assess patterns of genetic variation.

Growth and Development

Seedlings were grown for 6 months in plastic containers (65 cm^3) in a shadehouse at Moscow, ID (lat. 48.5° N., long. 116.7° W.). In the fall, seedlings were planted at two sites at about 670 m elevation at the Priest River Experimental Forest, 190 km north of Moscow. Although both sites averaged 90 frost-free days, one was on sandy loam soil and was maintained under a mesic cultural regime. This site was tilled before planting, competing vegetation was controlled, and the planting was irrigated twice each summer during the course of the study. The second site, on glacial till, was maintained under xeric cultural conditions. Irrigation was provided early in the second growing season to ensure seedling establishment, but water supplemental to natural precipitation, which averages 81 cm, was withheld thereafter. This site was also tilled before planting, and competing vegetation, gophers, and white grubs were controlled. Nine seedlings, planted in row plots, represented each population in each of three blocks at each site. At the mesic site, 0.5 m separated rows and 0.3 m separated trees within rows. To allow conversion of the test to a demonstration plot, the corresponding spacings at the xeric site were wider than at the mesic site: 1 m and 0.5 m.

Population performance was described by five variables:

1. Height, the 3-year height (centimeters) of individual trees.
2. Leaf length, the length (centimeters) of a leaf from near the center of the 3-year shoot of an individual tree.
3. Adjusted height, 3-year height (centimeters) of individual trees adjusted by regression on 2-year height, a value that depicts the 3-year height expected if all trees had been the same height at age 2. Consequently, the value is relatively independent of early environmental effects (such as seed weight or transplanting shock) and genetic effects and is capable of reflecting the adaptive response of populations to a particular environment in a relatively short time.
4. Xeric height reduction, the amount (centimeters) by which the height of trees cultured under xeric conditions failed to reach the potential expressed under mesic conditions. The value was calculated as the difference between the xeric height of an individual tree and the mean mesic height of the population from which the individual originated.

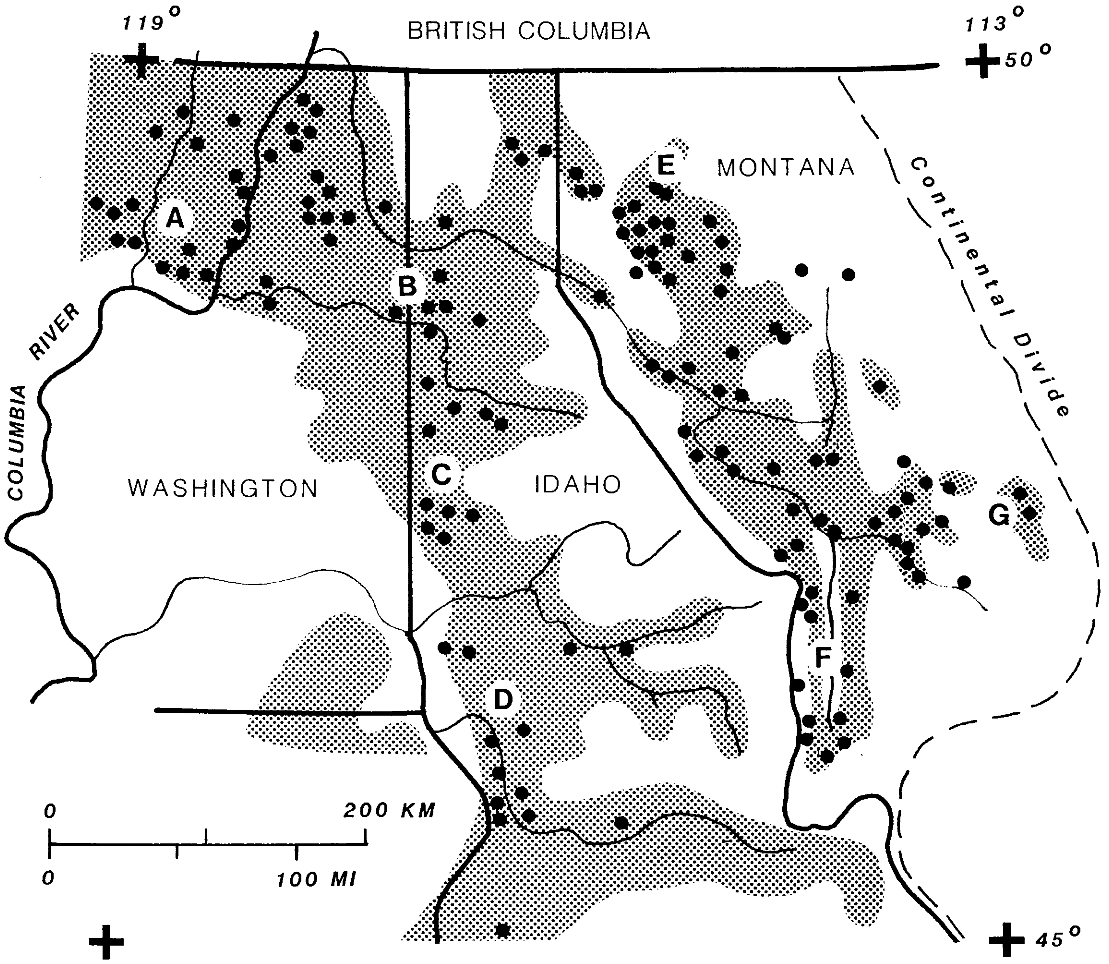

Figure 1—Geographic distribution of ponderosa pine (shading) within the major drainages of the middle Columbia River system and location of sampled populations. Letters A to G locate the elevational clines presented in figure 2.

5. Drought mortality, the proportion of trees within each plot that died from drought under xeric conditions.

Analyses of variance were performed on each variable according to a model in which the effects of populations, planting sites, and blocks within sites were considered as random variates. A harmonic mean of 7.31 reflected the number of seedlings in each block.

Periodicity of Shoot Elongation

Seedlings from 98 of the populations were grown for 2 years in plastic containers (740 cm^3) in a shadehouse at Moscow. Each population was represented by nine seedlings in each of three blocks. In mid-March of the second growing season, seedlings were moved into a greenhouse before shoot elongation had begun. Greenhouses were maintained under natural photoperiods and light intensities. Temperatures were held at about 24±3 °C during the day and were allowed to cool to a minimum 13 °C at night. All seedlings were measured three times each week until elongation was well under way. Thereafter, measurements were made twice each week until elongation of the preformed shoot had ceased.

As described by Rehfeldt and Wykoff (1981), shoot elongation of individual trees was expressed by a modified logistic function with a hyperbolic time term:

$$Y = [1 + be^{(-rX + c/X)}]^{-1}$$

where Y is the proportion of total increment attained by day X; b, r, and c are regression coefficients; and e is the base for natural logarithms.

Regression statistics allowed calculation of the following variables for describing the periodicity of shoot elongation of individual seedlings: (1) initiation of elongation: the day on which 2 mm of growth had occurred; (2) cessation of elongation: the day on which all but 2 mm of growth had occurred; (3) duration of elongation: the number of days between initiation and cessation; (4) rate of elongation: elongation (millimeters) per day during the period of maximum elongation; and (5) total elongation (millimeters).

Population differentiation was assessed according to an analysis of variance in which the effects of populations and blocks were considered to be random. A harmonic mean of 8.83 reflected the number of seedlings from each population in each block.

Patterns of Genetic Variation

Multiple regression models were used to relate genetic variation between populations to the elevation and geographic location of the seed source. Independent variables included elevation, latitude, longitude, northwest departure, southwest departure, and their squares. Squared values were used to accommodate the possibility of nonlinear patterns of variation. Northwest and southwest departures were derived by rotating the grid of latitude and longitude by 45°. Elevation was considered without geographic interaction because preliminary analyses suggested that the relationship between performance and elevation was similar throughout the region of study. Thus, 10 independent variables were included in a stepwise regression for maximizing R^2 (SAS 1982) according to the general model:

$$Y_i = \beta_0 + \sum_j \beta_1 X_{ij} + \sum_j \beta_2 X_{ij}^2$$

where Y_i is the performance of population i; X_{ij} is independent variable j for population i; and β_0, β_1, and β_2 are regression coefficients, $j = 1 \ldots 5$.

Adequacy of a model was judged according to the goodness of fit (R^2), residual variance ($s_{y \cdot x}$), patterns displayed by residuals (Draper and Smith 1981), and the degree by which results were biologically plausible.

RESULTS

The analyses detected differences between populations for numerous traits involving (1) growth and development and (2) the periodicity of shoot elongation. Genetic variation in these traits was related to the elevation and geographic origin of the seed.

Growth and Development

Planting sites had a tremendous effect on the growth and development of seedlings. Under mesic cultural conditions, the average 3-year-old tree was 46 cm tall with leaves 14 cm long, but under xeric conditions, the average tree was only 23 cm tall with leaves 7 cm long. Thus, xeric culture reduced the growth potential expressed under optimal growing conditions by an average of 23 cm. Values of adjusted height show that if trees on both sites had been the same height at age 2, those growing under the mesic regime would still have been 11 cm taller at age 3 than trees on the dry site even though 3-year height accounted for 69 percent of the variance in 2-year height.

Because of these differences associated with cultural conditions, main effects of test sites accounted for most (68 to 85 percent) of the variance for those variables measured on both sites and, therefore, dominate analyses of variance (table 1). Nevertheless, differences between populations were detected for all variables measured on both sites even though the main effects of populations accounted for less than 5 percent of the total variance (table 1).

The significant interactions (table 1) for height and adjusted height indicate that the differences between populations on one site were not the same as the differences between the same populations on the other site. Because these interactions accounted for nearly a third as much variance as the main effects of populations, subsequent analyses involving population means will consider height and adjusted height from each site as separate variables. By contrast, the lack of a significant interaction for leaf length shows that the relative performance of populations was similar at each site even though leaves were much shorter under xeric conditions.

Populations also differed significantly in the reduction in height attributable to xeric culture. The absolute amount of reduction ranged from 28 cm (56 percent) for one population to 14 cm (43 percent) for another. But populations did not differ in mortality under xeric conditions because drought mortality reached only 16 percent and was confined to essentially one block.

Periodicity of Shoot Elongation

Shoot elongation of individual seedlings was completed between 31 and 53 days after being placed in the greenhouse. This means that 11 to 17 observations were

Table 1—Results of analyses of variance of growth and development in field environments presented as intraclass correlations, the ratio of a variance component to the sum of all components

	Variable				
Source of variance	**3-year height**	**Adjusted height[1]**	**Leaf length**	**Xeric height reduction[2]**	**Drought mortality**
Sites	0.850**	0.689**	0.850**	—	—
Blocks in site	.000	.002**	.008**	0.006**	0.977**
Populations	.028**	.021**	.004**	.317**	.012
Sites × populations	.010**	.009**	.002	—	—
Experimental error	.007**	.047**	.020**	.103**	.010
Within plots	.106	.232	.116	.574	—
Error mean square[3]	107.433	72.969	5.824	3.119	.027

**Statistical significance of the F-value at the 1 percent level of probability.

[1] 3-year height adjusted by regression on 2-year height.

[2] Difference between xeric height and the growth potential expressed by mesic height.

[3] Absolute value of the interaction mean square that was used to test for differences between populations.

Table 2—Results of analyses of variance for the periodicity of shoot elongation presented as intraclass correlations, the ratio of a variance component to the sum of all components

Source of variance	Variable				
	Elongation	Initiation	Cessation	Duration	Rate
Replications	0.04**	0.03**	0.01**	0.01**	0.07**
Populations	.20**	.02**	.34**	.17**	.15**
Interaction	.05**	.09**	.16**	.03**	.06**
Within plots	.71	.86	.49	.79	.71
Error mean square[1]	766.931	4.811	18.109	22.553	1.428

**Significance of the F-value at the 1 percent level of probability.

[1] Absolute value of the interaction mean square that was used to test for differences between populations.

Table 3—Results of stepwise regressions for relating genetic variation to the elevation and geographic origin of the seed

Variable	Number of independent variables	R^2	Residual mean square
Growth and development			
3-year mesic height	5	0.52**	10.09
3-year xeric height	6	.31**	4.55
Adjusted mesic height	6	.17**	2.14
Adjusted xeric height	6	.13**	1.91
Leaf length	5	.10**	.20
Xeric height reduction	8	.40**	6.20
Periodicity of shoot elongation			
Elongation	5	.49**	86.98
Initiation	5	.09	.24
Cessation	6	.59**	1.74
Duration	5	.58**	1.89
Rate	6	.43**	.14

**Statistically significant at the 1 percent level.

available for the logistic regression that described shoot elongation of individual trees nearly perfectly. Values of R^2 ranged from 0.90 to essentially 1.0, averaging 0.99.

Analyses of variance not only detected significant differences between populations for all variables (table 2) but also attributed substantial variance to the effects of populations for all variables except the initiation of shoot elongation. These effects were reflected in mean differences between populations as large as 9 days in cessation, 10 days in duration, 2.8 mm per day in rate, 73 mm total elongation, but only 2.3 days in initiation. Although these differences seem small, culturing plants under optimal conditions allows shoot development to proceed rapidly, and developmental events are condensed into a short time interval. Under natural conditions development occurs over a long period and differences in the periodicity of shoot elongation become relatively large.

Patterns of Genetic Variation

By accounting for as much as 60 percent of the variance between populations, regression models were statistically significant for all variables except the initiation of shoot elongation (table 3) and drought mortality, two variables for which population differentiation was not pronounced (tables 1 and 2). Thus, genetic differences between populations follow systematic patterns that can be related to the elevation and geographic origin of the seed. These patterns can be presented as (1) elevational clines for several geographic localities (fig. 2), (2) geographic clines at a constant elevation (fig. 3), or (3) geographic clines at the base elevation, the lowest elevation at which the species occurs in a given locality (fig. 4).

These results, however, were based on five to eight independent variables and, therefore, are susceptible to overfitting, a condition that occurs when models are fit to single samples rather than to general trends described by all samples (Draper and Smith 1981). Consequently, in this paper, population differentiation is interpreted according to the least significant difference (Steel and Torrie 1960) at the 80 percent level of probability—*lsd*(0.2). A relatively low level of probability is used to guard against accepting no differences between populations when differences actually exist. Thus, in figure 2, populations separated by an elevational interval sufficient to subtend a mean difference equal to *lsd*(0.2) are judged to be statistically different at

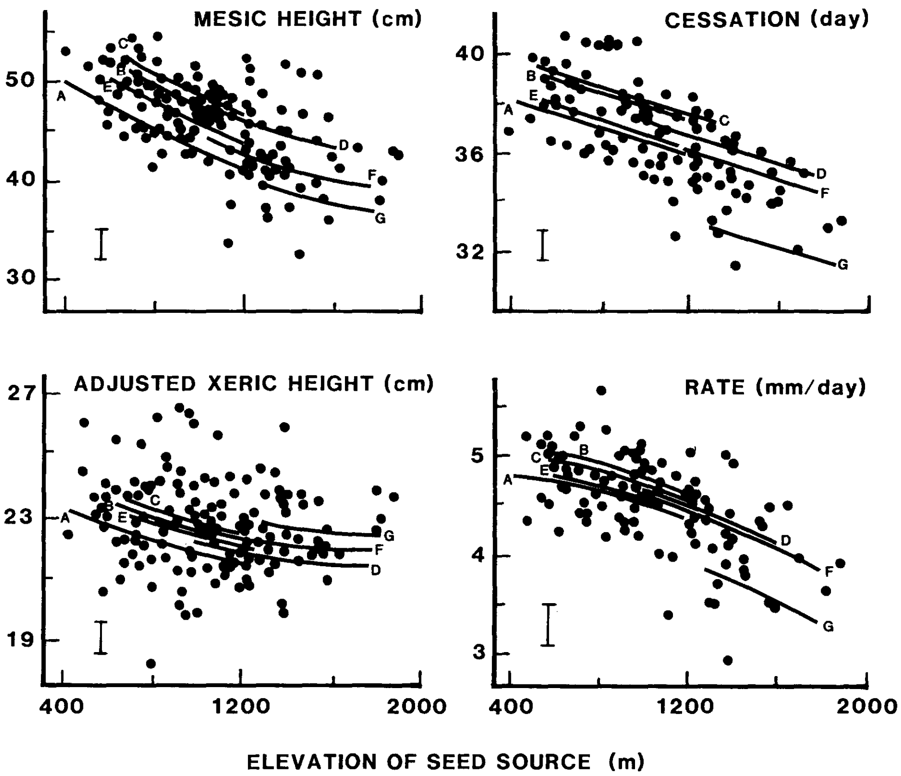

Figure 2—Elevational clines for four variables at seven geographic locations keyed to figure 1. Brackets quantify lsd (0.2).

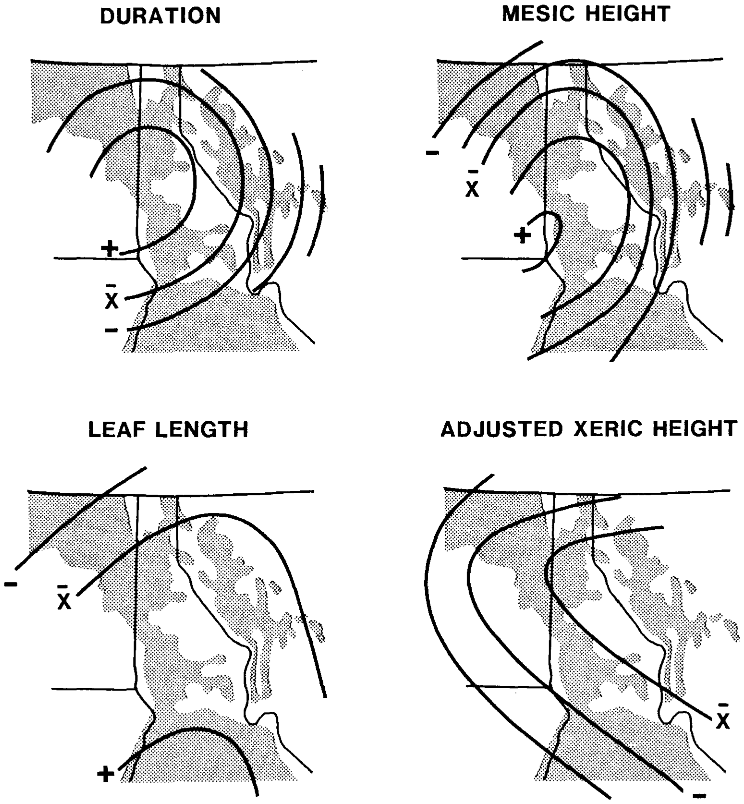

Figure 3—Geographic patterns of variation for four variables described by isopleths (contour lines) of equal performance at the mean elevation (1,075 m). The interval between isopleths equals ½[lsd (0.2)]. Isopleths represent positive or negative deviations from the mean value (x̄) of all populations.

Figure 4—Geographic patterns of variation for mesic height presented as isopleths of equal performance for base elevations, the lowest elevation at which ponderosa pine occurs in a given area. The interval between isopleths equals ½[lsd(0.2)]. Isopleths represent positive or negative deviations from the mean ($\bar{x}$) of all base populations.

about the 80 percent level of probability. In figures 3 and 4, the distance between isopleths (contour lines) is scaled to ½[*lsd*(0.2)]. This means that populations separated by a distance equivalent to two isopleths are assumed to differ with a probability of about 0.2.

The relationship between the elevation of the seed source and population performance is presented in figure 2 for four variables that span the range of responses for all variables. Not shown are the elevational clines for adjusted mesic height and xeric height reduction, which nearly duplicated that for mesic height. Clines for the cessation and amount of shoot elongation were similar to that of the duration of elongation, and clines for adjusted xeric height, leaf length, and the initiation of shoot elongation failed to depict differentiation in excess of *lsd*(0.2).

These elevational clines indicate that growth potential decreases as elevation of the seed source increases. In contrast to populations from high elevations, those from low elevations tend to be tall, they exhibit a late cessation, long duration, and rapid rate of elongation, and under xeric culture, their growth is reduced the most.

The elevational interval associated with a mean difference between populations that equals *lsd*(0.2) is approximately 440 m for the linear cline involving cessation of shoot elongation (fig. 2). Although the interval for the nonlinear clines would change as elevation changes (fig. 2), population differentiation at the mean elevation (1,075 m) can be detected across about 400 m for both mesic height and adjusted xeric height, but about 450 m for rate of elongation.

Geographic patterns of variation at the mean elevation are illustrated in figure 3 for the four variables that represent the range of patterns. Patterns for all variables not presented follow those for the duration of shoot elongation and mesic height. Thus, when comparing populations from the same elevation, populations from west central areas display the largest values of traits reflecting growth potential. From this area, growth potential declines in all directions.

Patterns for adjusted xeric height and leaf length deviate from the general. Figure 3 shows that if all populations had been the same height at age 2, those from the dry lands to the east would have been tallest (largest adjusted xeric height) at age 3 on the xeric site. Geographic clines for leaf length indicate that southern populations have the longest leaves while those from the northwest have the shortest.

Because geography and elevation are not independent of each other, genetic variation between populations at the base elevation (fig. 4), the lowest elevation at which ponderosa pine occurs in a given locality, is arranged along much steeper clines than variation at a constant elevation (fig. 3). As judged by the number of and distance between isopleths, geographic clines at the base elevation are nearly twice as steep as those for a constant elevation. Figure 4 shows that populations of the highest growth potential should come from among base populations from the west central region. From this area, growth potential of base populations decreases regardless of whether elevation is decreasing toward the northwest or increasing toward the south or east. The average distance between differentiated populations occurs on a relatively small scale (54 km) across the landscape.

Similarities in patterns of variation between the variables (figs. 2 and 3) result from intercorrelations, some of which are extremely strong (table 4). Populations that were tall under mesic conditions exhibited other characters associated with a high growth potential: a late cessation, long duration, fast rate, and large amount of shoot elongation. Although these same populations tended to be the tallest under xeric culture (table 4), they suffered the greatest xeric height reduction in that the growth potential expressed under mesic culture was reduced the most by xeric culture.

DISCUSSION

Results have demonstrated genetic differentiation between populations for a variety of loosely intercorrelated traits. These intercorrelations, such as those in *Pseudotsuga menziesii* (Rehfeldt 1983b), *Pinus contorta* (Rehfeldt 1983a), and *P. ponderosa* from central Idaho (Rehfeldt 1986), involve traits that are part of an annual sequence of developmental events. This sequence begins with dehardening in the spring, includes shoot elongation, leaf expansion, bud development, and lignification, and concludes with cold acclimation. The components are intercorrelated because the entire sequence must fit into a growing season of finite length. Thus, populations that inhabit environments where growing seasons are short cease developmental events early and are, therefore, short, even when grown under optimal conditions.

For ponderosa pine, a species that commonly occurs in habitats that border the prairie, the growing season may

Table 4—Simple correlations among population means. Underlined coefficients failed to reach statistical significance at the 5 percent level.

Variable	Code	H3-X	AH-M	AH-X	LL	RED	DD	EL	IN	CES	DUR	RATE
Growth and development												
3-year mesic height	H3-M	0.74	0.56	0.31	0.30	0.84	0.02	0.76	−0.14	0.68	0.68	0.74
3-year xeric height	H3-X		.28	.69	.35	.25	−.18	.64	−.14	.48	.50	.64
Adjusted mesic height	AH-M			.19	−.02	.57	.04	.31	−.02	.30	.29	.29
Adjusted xeric height	AH-X				.22	−.11	−.29	.24	−.01	.17	.16	.24
Leaf length	LL					.15	−.18	.21	−.18	.08	.12	.23
Xeric height reduction	RED						.18	.55	−.08	.56	.56	.53
Drought mortality	DD							−.07	.07	.03	.01	−.06
Periodicity of shoot elongation												
Elongation	EL								−.37	.82	.87	.98
Initiation	IN									−.06	−.29	−.37
Cessation	CES										.97	.72
Duration	DUR											.78
Rate	RATE											

be limited by drought or frost or both. The species inhabits environments that differ by over 60 days in frost-free period and by 60 cm in precipitation (fig. 5). That populations have become differentially adapted to environmental differences of this magnitude is an expected result of natural selection.

Adaptive differentiation can be expressed by significant interactions involving populations and environments. However, the interactions that were evident for 3-year height and adjusted height arose for different reasons. On the one hand, the interaction for 3-year height represents a scale effect rather than an adaptive response. As evidenced by strong simple correlations (table 4), populations retained similar rankings in each environment, but the absolute difference in height of any two populations was greater under mesic than under xeric conditions.

On the other hand, the interaction for adjusted height reflects differential adaptation. Under mesic culture, populations of greatest growth potential would still have been tallest at age 3 even if all trees had been the same height at age 2. Thus, the superiority of these populations has increased between ages 2 and 3. But under xeric conditions, populations from dry eastern areas grew the most from a common height at age 2. This suggests that if xeric culture were to be maintained, these eastern populations would eventually become tallest on this particular site.

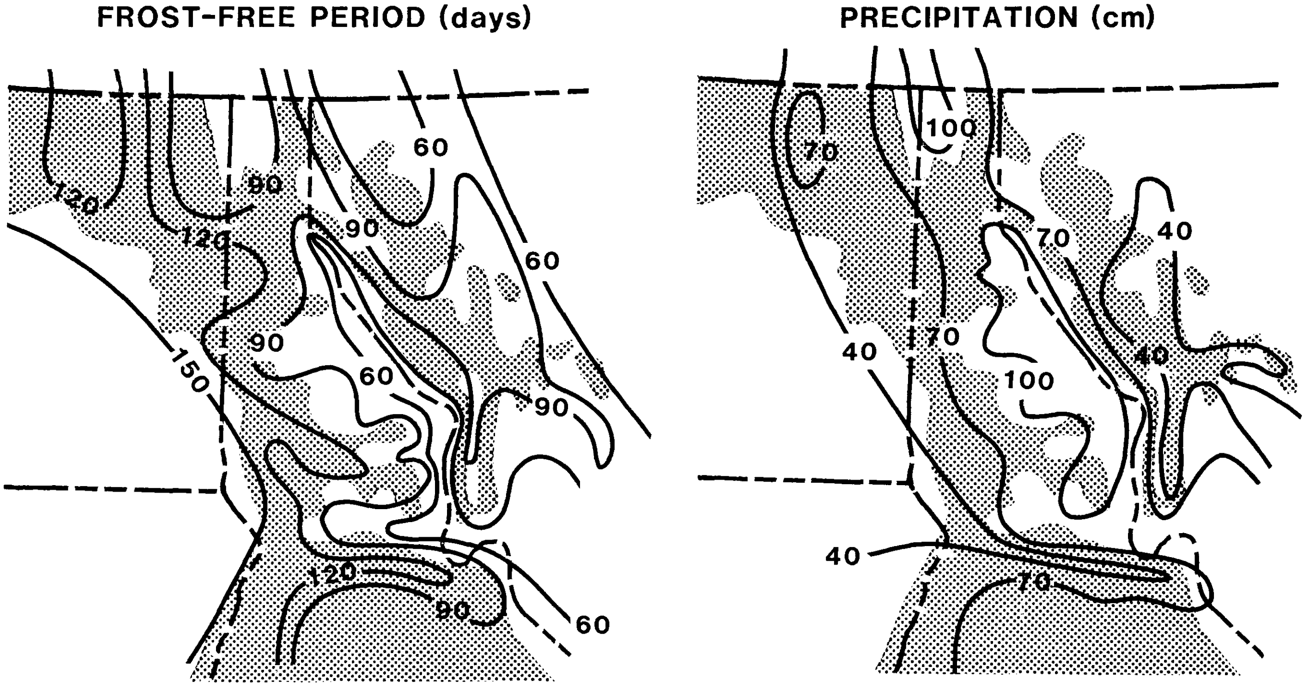

Figure 5—Regional environmental patterns of variation (enlarged from U.S. Department of Commerce 1968).

Regression models described population differentiation according to the elevation and geographic location of the seed source. As elevation increases, the length of the frost-free period rapidly decreases. Baker (1944) has shown that the frost-free period in the Inland Northwest varies by about 80 days across an elevational interval of 1,000 m. Consequently, populations from low elevation generally exhibit a high growth potential associated with a long duration and late cessation of elongation. Populations from high elevation express a low growth potential largely because developmental events must be completed within a short frost-free period. These general trends are remarkably similar to those described by the height of 2-year-old trees growing in nursery beds (Madsen and Blake 1977) and also are similar to the patterns exhibited by populations from central Idaho (Rehfeldt 1986). For both central Idaho and the Inland Northwest, an elevational interval of about 400 m is sufficient for detecting (80 percent level of probability) population differentiation.

Geographic patterns of genetic variation at either a constant or the base of elevation (figs. 3 and 4) were pronounced, consistent, and uniform. Moreover, these patterns roughly correspond to geographic patterns in precipitation and in the frost-free period (fig. 5). Populations of highest growth potential tend to occur in the west-central region where frost-free periods are long and precipitation is relatively high. From this area, growth potential of populations decreases in all directions in a pattern that is similar to that of the frost-free period. Toward the northwest, however, the rapid decline in growth potential is associated with only a small decline in the frost-free period but with a huge reduction in precipitation. Thus, the northwestern populations, which may originate from the lowest elevations (400 m), display a low growth potential. In addition, the eastern populations that exhibited the lowest growth potentials come from areas characterized by both low precipitation and a short frost-free period.

The elevational cline is much steeper than the geographic. In figure 3, the distance between any two isopleths represents half the distance required to detect (80 percent level of probability) genetic differentiation at a constant elevation. Because differentiation can be detected between populations separated by about 400 m in elevation, the distance between geographic isopleths represents the amount of genetic variation that occurs across 200 m of elevation at a single locality. Thus, the total amount of geographic variation that occurs within the region at a constant elevation can also occur across 1,000 m at a single locality.

Regardless, adaptive differentiation occurs along two interdependent clines. This means that populations of similar adaptive norms recur at different elevations across the landscape. As shown in figure 2, populations with a relatively long duration of shoot elongation, 38 days, occur at about 700 m at locality A (fig. 1), 750 m at E, 1,000 m at D, and 1,300 m at both A and B. Thus, similar genotypes are distributed across the landscape in a pattern that is oblique to elevation.

Because patterns of genetic variation are systematically related to environmental variation, one logically accepts the patterns as reflecting adaptive differentiation. As such, the patterns have direct application to artificial reforestation. To maximize productivity, planted trees must be adapted to the planting site. Adaptation is secured by limiting the distance that seeds are transferred from their origin. Consequently, limits to seed transfer must reflect geographic and elevational patterns of variation.

One estimate of an appropriate limit to seed transfer is the smallest geographic or elevational interval across which differentiation is detected (Rehfeldt 1979a). Differentiation along the steepest elevational clines (fig. 2) suggests that a seed zone for ponderosa pine should encompass not more than 400 m of elevation. This means that seed from a single source should not be transferred more than ±200 m. In addition, the geographic clines of figure 3 describe seed zones that should not encompass more than two geographic bands between isopleths. Approximately three geographic zones would be suitable for the region, and seeds from a single source should not be transferred a distance equivalent to more than ±1 band.

Although seed zoning is an administratively simple procedure for limiting seed transfer, the procedure tends to be inflexible, inefficient, and uneconomical. This is because seed zones compartmentalize continuous genetic variation and fail to take advantage of the recurrence of similar genotypes at different elevations in geographically separated localities.

By contrast, floating transfer guidelines are based on the recurrence of similar environments in a pattern that is oblique to elevation. According to floating guidelines, seed can be transferred across isopleths (fig. 3), but each time seed is transferred across a geographic interval equaling the interval between isopleths, the elevations at which the seed is to be used should be adjusted. When transferring across isopleths of high to low value, the interval should be adjusted downward by 200 m. When transferring from lower to higher value, the interval should be adjusted upward by 200 m.

For example, assume that seed originates from 1,000 m on the isopleth representing the mean of all populations (fig. 3). This seed should be used between 800 and 1,200 m in lands adjacent to the isopleth. In transferring the seed across one isopleth of larger value, the seed should be used between 1,000 and 1,400 m. Transfers of two contours should be used between 1,200 and 1,600 m. And in transferring the seed across an isopleth of lesser value, the seed should be used between 600 and 1,000 m. In this way, seed from a single source or seed orchard can serve a much broader geographic area than under the concept of discrete seed zones.

These recommendations for limiting seed transfer evolved from statistical models based on the performance of young trees under controlled conditions. The models need practical verification. On the one hand, the environmental events responsible for the systematic patterns may occur so infrequently that managers might risk transferring fast-growing populations into severe environments in an attempt to increase productivity. Indeed, genetic differentiation may have been detected at levels associated with productive differences so small as to be immaterial. On the other hand, small adaptive differences observed at young ages may portend large differences in the future. Regardless, verification can come only from planting programs that not only incorporate these guidelines but also maintain precise records on the exact location from which planted trees originated. Productivity of such plantings will test the applicability of these guidelines.

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Seedling populations were grown and compared in common environments. Statistical analyses detected genetic differences between populations for numerous traits reflecting growth potential and periodicity of shoot elongation. Multiple regression models described an adaptive landscape in which populations from low elevations have a high growth potential while those from high elevations have a low growth potential. Patterns of genetic variation reflect adaptation to a growing season of variable length. Adaptive landscapes are used to construct guidelines for limiting seed transfer in artificial reforestation. In general, seed from a single source should not be transferred more than ±200 m in elevation.

KEYWORDS: microevolution, genetic differentiation, seed zones, seed transfer

INTERMOUNTAIN RESEARCH STATION

The Intermountain Research Station provides scientific knowledge and technology to improve management, protection, and use of the forests and rangelands of the Intermountain West. Research is designed to meet the needs of National Forest managers, Federal and State agencies, industry, academic institutions, public and private organizations, and individuals. Results of research are made available through publications, symposia, workshops, training sessions, and personal contacts.

The Intermountain Research Station territory includes Montana, Idaho, Utah, Nevada, and western Wyoming. Eighty-five percent of the lands in the Station area, about 231 million acres, are classified as forest or rangeland. They include grasslands, deserts, shrublands, alpine areas, and forests. They provide fiber for forest industries, minerals and fossil fuels for energy and industrial development, water for domestic and industrial consumption, forage for livestock and wildlife, and recreation opportunities for millions of visitors.

Several Station units conduct research in additional western States, or have missions that are national or international in scope.

Station laboratories are located in:

Boise, Idaho

Bozeman, Montana (in cooperation with Montana State University)

Logan, Utah (in cooperation with Utah State University)

Missoula, Montana (in cooperation with the University of Montana)

Moscow, Idaho (in cooperation with the University of Idaho)

Ogden, Utah

Provo, Utah (in cooperation with Brigham Young University)

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