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GENETIC DIFFERENTIATION AMONG POPULATIONS OF PINUS PONDEROSA FROM THE UPPER COLORADO RIVER BASIN

G. E. REHFELDT

Forestry Sciences Laboratory, Intermountain Research Station, USDA Forest Service, Moscow, Idaho 83843

Genetic variation among 62 populations of ponderosa pine was studied by comparing seedlings from all populations according to (1) growth and development of 4-yr-old seedlings in three disparate common gardens and (2) patterns of shoot elongation of 2-yr-old seedlings in a greenhouse. Genetic variation was detected among populations for 19 of the variables, most of which were intercorrelated. Two principal components accounted for 60% of the total interpopulation variance. Multiple regression analyses were used to relate genetic variation in 19 variables and two principal components to the elevation and geographic origin of the seed. The regression models produced values of R^2 as large as .78 and accounted for more than 40% of the variance among populations for 14 of the variables, including both the first and second principal components. These models described genetic variation as occurring along a relatively steep elevational cline and along both primary and secondary geographic clines of relatively gentle slope. All clines paralleled patterns of environmental variation, particularly the length of the frost-free season and patterns of precipitation. Because genetic variation occurs along three clines simultaneously, genetic differentiation can be described as rampant. Nevertheless, similar genotypes tend to recur in similar environments.

Introduction

Seventy-five years of provenance testing (WEIDMAN 1939; SQUILLACE and SILEN 1961; WELLS 1964; STEINHOFF 1970) has demonstrated pronounced racial differentiation in ponderosa pine (*Pinus ponderosa*). Two varieties have long been recognized: var. *ponderosa* to the west and var. *scopulorum* to the east, and, within each variety, northern and southern races have been delineated (CONKLE and CRITCHFIELD 1988). Stimulated by the species' importance to Western forestry, studies of genetic variation within races are revealing the ecological genetics of populations from the Sierra Nevada (CALLAHAM and LIDDICOET 1961; CONKLE 1973; NAMKOONG and CONKLE 1976), eastern slopes of the Rocky Mountains (READ 1980, 1983; VAN HAVERBEKE 1986), and Inland Northwest (MADSEN and BLAKE 1977; REHFELDT 1986*a*, 1986*b*). Within each diverse region, genetic differences among populations not only have been detected but also have been related to the elevation and geographic location of the seed source.

This study assesses genetic variation among populations in Utah and adjacent portions of Arizona and Colorado (fig. 1), a region within which genetic variation in ponderosa pine has not been systematically studied but, nevertheless, a region within which CONKLE and CRITCHFIELD (1988) separate the southwestern race from the Rocky Mountain race of var. *scopulorum*. The results of this study not only will contribute to an understanding of microevolution and racial variation within the species' southwestern distribution but also are directly applicable to developing the seed transfer guidelines that are intended to limit poor adaptation in artificial reforestation.

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Address for correspondence and reprints: G. E. REHFELDT, Forestry Sciences Laboratory, 1221 South Main Street, Moscow, Idaho 83843.

Physiography, climate, and ecology

Most of the region of study (fig. 1) is within the Colorado Plateau, a physiographic province (FENNEMAN 1931) with the distinguishing features of flat tablelands, numerous plateaus and mountain ranges, and deeply incised canyons. Also included are the areas contiguous to the Colorado Plateau that support ponderosa pine: (1) the Uinta Range in central Utah, the southernmost range of the Central Rocky Mountain Province, (2) the San Juan Mountains in southwest Colorado, the most westerly range in the Southern Rocky Mountain Province, and (3) the Tushar Mountains, the most easterly range in the Basin and Range Province.

The climate of the region is arid in all areas except at the highest elevations. Although the total amount of precipitation at a given elevation remains relatively constant across the region, the pattern of precipitation varies greatly (BAKER 1944; JEPPSON et al. 1968; U.S. DEPARTMENT OF COMMERCE 1968). Typical of Rocky Mountain physiographic provinces, precipitation in the Uinta and San Juan Mountains occurs mostly in the winter and spring. But toward the southwest, however, spring tends to be dry while summer precipitation, brought on by thunderstorms off the Gulf of Mexico, gradually dominates the yearly pattern. Frost-free periods in valleys as low as 1,200 m may be as long as 150 d (U.S. DEPARTMENT OF COMMERCE 1968) but decrease by about 80 d for each elevational increase of 1,000 m (BAKER 1944).

In this region, ponderosa pine occurs at elevations between 1,800 and 2,800 m (JOHNSON 1970).

FIG. 1.—Shading indicates the distribution (LITTLE 1971) of ponderosa pine in the upper Colorado Basin. Sampled populations were from three geographic zones: ▲ = populations from north (Z1); ● = southwest (Z2); ○ = southeast (Z3).

According to this elevational distribution, the environmental gradients (BAKER 1944), and the distribution of recurring plant associations (YOUNGBLOOD and MAUK 1985), ponderosa pine tends to inhabit lands that are high enough to receive at least 40 cm of annual precipitation but are low enough to supply a frost-free period of at least 60 d. With less precipitation, *Juniperus* spp. woodlands occur, and with shorter growing seasons, *Abies concolor* and *Pseudotsuga menziesii* become common (YOUNGBLOOD and MAUK 1985).

Material and methods

Genetic variation was studied by growing seedlings from natural populations in common environments, an approach championed by CLAUSEN et al. (1940). Ten cones were collected from each of 10 trees in 62 natural populations (fig. 1). Although no collections were made from the lowest limits of the species distribution where ponderosa pine occurs as scattered individuals in the *Juniperus* spp. woodlands, these populations otherwise sampled the geographic distribution and ecological diversity of the species within the region of study. Seedlings from these populations were used in separate studies of growth and development of 4-yr-old trees in three field environments and of the pattern of shoot elongation of 2-yr-old trees in a greenhouse.

GROWTH AND DEVELOPMENT

Seedlings were grown for 6 mo in plastic containers (65 cm^3) in a shadehouse at Moscow, Idaho (lat. 48.5 N, long. 116.7 W, elevation 790 m) and were planted in the autumn at three sites in the Priest River Experimental Forest, 190 km north of Moscow. All sites were at 670 m elevation where frost-free periods average about 90 d, annual precipitation averages 85 cm, and only 11% of the total precipitation occurs between July 1 and October 1 (FINKLIN 1983).

A randomized complete block design was used at each site with each population represented by 10 trees planted in row plots in each of three blocks. The sites, however, were managed under cultural regimes that were optimal, harsh, and severe for tree growth. The optimal regime was on a sandy loam soil and was irrigated twice each summer. Here the trees were spaced at 1 m between rows and 0.3 m within rows. The other test sites were on glacial till. The harsh regime was irrigated once

during August of the first two growing seasons but thereafter received only natural precipitation. Here also, the trees were spaced at 1 m between rows and 0.3 m within rows. For the severe regime, the glacial till received only natural precipitation (about 75 cm), and the effects of the gravelly substrate and low precipitation on growth and development were accentuated by a close spacing of trees: 0.3 m between rows and 0.15 m within rows. For all cultural regimes, soils were tilled before planting, competing vegetation was controlled, and sites were fenced.

Growth and development were described by the following 14 variables. Except where noted, variables were measured on individual trees.

UNDER OPTIMUM CULTURE

1. Growth potential: 4-yr height in centimeters, an expression of the innate capability to produce carbohydrate and assimilate wood in the absence of biotic and abiotic effects that mask the genotype.
2. Leaf length: the length of a leaf in millimeters from near the center of the 4-yr shoot.
3. Relative growth rate: the deviation from regression of 4-yr height on 2-yr height, a value that is relatively independent of early genetic and environmental effects and thereby can reflect adaptation to a particular environment in a relatively short time.
4. Late growth: the amount of the 4-yr preformed shoot that elongated after May 27, an index to the duration of shoot elongation.

UNDER HARSH CULTURE

5. Decrease in height: the amount by which the height of trees grown under harsh culture failed to reach the potential expressed under optimum culture. As the difference between the height of an individual tree in the harsh environment and the mean growth potential (variable 1) of the population from which that individual originated, this variable directly expresses interactions between populations and environments.
6. Relative growth rate: see variable 3.
7. Decrease in leaf length: the amount by which leaf lengths under harsh culture failed to reach the potential expressed under optimum culture and calculated similarly to variable 5.
8. Winter injury: the proportion of trees in each plot that suffered death of terminal shoots or buds during either the second or third winters.
9. Spring frost injury: the proportion of trees in each plot on which developing leaves were injured by a spring frost at the beginning of the fourth growing season. Injury was defined as death to more than 1 cm of the emerging leaves.

UNDER SEVERE CULTURE

10. Decrease in height: see variable 5.
11. Relative growth rate: see variable 3.
12. Decrease in leaf length: see variable 7.
13. Winter injury: see variable 8.
14. Mortality: the proportion of trees in each plot that died during the course of the studies.

Analyses of variance were performed on each variable according to the following model:

$$Y_{ijk} = \mu + P_i + B_j + E_{ij} + W_{ijk},$$

where Y_{ijk} is an observation on seedling k in block j from population i; μ is the mean; P_i and B_j are the effects of populations and blocks, respectively; E is the experimental error, the interaction of blocks with populations; and W_{ijk} is the sampling error. Under the assumption that blocks and populations are random variates, the experimental error becomes the variance appropriate for testing differences among populations. The sampling error, of course, did not exist for the four variables that were measured as plot means.

PATTERN OF SHOOT ELONGATION

Nine seedlings from each population, arranged in row plots in each of three randomized complete blocks, were grown in plastic containers (740 cm^3) for 6 mo in a shadehouse at Moscow. The seedlings were transferred to an unheated greenhouse for the winter months, and in early March of the second growing season, they were exposed to a daytime temperature of about 25 C, which was allowed to cool to a minimum of 13 C at night. All seedlings were measured three times each week until elongation was well under way. Thereafter, each tree was measured twice each week until elongation of the preformed bud was complete.

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 of natural logarithms.

Regression statistics allowed calculation of six variables that described the pattern of shoot elongation of individual seedlings in the greenhouse environment: (1) initiation of activity—the day by which 2 mm of growth had occurred; (2) start of elongation—the day on which 8 mm of growth had occurred; (3) cessation of elongation—the day on which all but 2 mm of growth had occurred; (4) duration of elongation—the number of days between the start and cessation; (5) rate of elongation—elongation in millimeters per day during the period of most rapid elongation, defined as the period between which 20% and 80% of the shoot had elongation; and (6) total elongation in millimeters. Analyses of variance were performed on each variable according to the model described previously.

PATTERNS OF GENETIC VARIATION

Patterns of genetic variation were assessed by means of stepwise multiple regression models for maximizing R^2 (SAS INSTITUTE 1982). Dependent variables included the population means for all of the original variables for which genetic variation was detected by the analyses of variance. In addition, a principal component analysis was employed to aid interpretation. Such analyses explain the variance-covariance structure by means of linear combinations of the original variables and thereby reduce the number of dimensions about which variation is being expressed (JOHNSON and WICHERN 1982). Population means for those components that accounted for more than 10% of the variance in the original variables were also used as dependent variables in the stepwise analyses. Because all variables were not measured on each tree, principal components had to be calculated (SAS INSTITUTE 1982) from the correlation matrix of population means. This meant that an error variance could not be calculated to express the probability that an observed difference was real.

The objective of the regression analyses was to describe patterns of variation in relation to the elevation and geographic location of each population rather than to test the effects of individual environmental variables on genetic differentiation. This objective was adopted because weather stations in the region of study not only are few but also are generally located on the valley floor. Environmental gradients such as those published by the U.S. DEPARTMENT OF COMMERCE (1968) illustrate general patterns but are highly extrapolated and are unable to accurately describe environmental conditions at specific locations.

Describing patterns of variation, therefore, required independent variables that could serve as surrogates for the complex three-dimensional environmental gradients that likely operate in natural selection. Geographic variables were derived from the four coordinates: latitude (LT), longitude (LN), northwest departure (NW), and southwest departure (SW). The latter two were calculated as the products of LT with LN and LN with LT^{-1}, respectively, defined a grid, therefore, in which LT and LN had been rotated by about 45°, and were included to accommodate the possibility that geographic patterns might be oblique to LT or LN. These four geographic variables plus their squares also were nested within three geographic zones that account for the natural grouping of the sampled populations (fig. 1): northern (Z1) with nine populations, southwestern (Z2) with 28, and southeastern (Z3) with 25. Nested variables were defined such that LT in zone 1 (LT1), for instance, equaled LT if population i was in zone 1; otherwise, LT1 = 0. Likewise, the three geographic zones were included among the independent variables as constants: if, for example, population i was in zone 1, then Z1 = 1, but otherwise Z1 = 0. Elevation (EL) was included among the independent variables by its first and second powers and thus provided for the possibility that elevational clines were nonlinear.

These procedures produced 37 independent variables that were available for describing patterns of variation. Of these, however, 35 were either transformed or nested effects of LT or LN. Consequently, only a portion (< 20) of the independent variables could be used in a particular regression model without producing a variance-covariance matrix that was singular when inverted. Among the models tested, the best models were judged as those that (1) were statistically significant, (2) displayed residuals with no elevational or geographic patterns, and (3) produced the lowest residual variance when the Mallows statistic first equaled the number of included variables (DRAPER and SMITH 1981). The Mallows statistic assured that a model was the least biased of all other models capable of being developed from a particular group of independent variables.

Results

Statistically significant differences were detected among populations for nearly all variables regardless of whether they described growth and development in disparate field environments or patterns of shoot elongation in the greenhouse. Genetic variation also was related to the elevation and geographic location of the seed source.

GROWTH AND DEVELOPMENT

Test environment had a pronounced effect on growth and development (table 1). Under optimal conditions, the average tree was 53 cm tall after 4 yr, but under the harsh and severe regimes, this average height was reduced by 16 and 20 cm, respectively. Differential severity of the environment also was expressed in the length of leaves that averaged 13 cm under optimum culture but only 9 cm under harsh and severe culture. In addition, one-third of the trees at the harsh site suffered winter injuries; nearly 50% were injured at the severe site; but no trees were injured under optimal conditions. Mortality was nearly zero under optimal conditions, was low at the harsh site, but was 45% at the severe site.

Mean differences among populations were both large and statistically significant for all variables except the winter injuries suffered under harsh conditions (table 1). Population differentiation was particularly pronounced for growth potential, late growth, spring frost injury, and the decrease in height due to harsh and severe culture.

TABLE 1

POPULATION MEANS, RANGE OF MEAN DIFFERENCES AMONG POPULATIONS, AND RESULTS OF ANALYSES OF VARIANCE FOR 20 VARIABLES

VARIABLE	UNITS	MEAN	RANGE	SOURCE OF VARIANCE			
				Blocks[a]	Populations[a]	Experimental error[a]	Sampling error[b]
Growth and development:							
Optimum culture:							
Growth potential	mm	526	83	.05**	.52**	.28**	898.50
Leaf length	mm	133	47	.27**	.35**	.26**	28.02
Relative growth rate	mm	−0	182	.05**	.33**	.43**	747.37
Late growth	mm	67	89	.03**	.57**	.18**	108.23
Harsh culture:							
Decrease in height	mm	158	183	.13**	.47**	.19**	616.74
Relative growth rate	mm	−1	100	.08**	.16**	.33**	457.79
Decrease in leaf length	mm	38	28	.15**	.29**	.04	40.43
Winter injury	%	33	50	.00	.09	.91	.0279[c]
Spring frost injury	%	28	81	.02*	.49**	.48	.0278[c]
Severe culture:							
Decrease in height	mm	196	200	.01	.55**	.14**	860.25
Relative growth	mm	−5	109	.04*	.22**	.20**	686.73
Decrease in leaf length	mm	43	47	.02*	.34**	.15**	77.40
Winter injury	%	49	66	.19**	.21**	.60	.0312[c]
Mortality	%	45	63	.19**	.20**	.61	.0322[c]
Patterns of shoot elongation:							
Initiation	d	3.5	3.3	.07**	.23**	.11	.7290
Start	d	8.9	4.3	.04*	.31**	.30**	.6286
Cessation	d	33.8	12.0	.00	.63**	.27**	1.4018
Duration	d	30.3	12.0	.01	.58**	.11**	4.5938
Rate	mm/d	3.3	3.0	.10**	.31**	.34**	.1559
Elongation	mm	68	66	.05**	.39**	.37**	70.64

[a] Intraclass correlations, the ratio of the variance component for the indicated effects to the sum of all components.
[b] Mean square based on harmonic means of trees within plots of 9.64 for optimum culture, 7.93 for severe culture, 4.36 for harsh culture, and 4.09 for studies of the pattern of shoot elongation.
[c] Experimental error.
* Statistical significance of the F-value at the 5% level.
** Statistical significance of the F-value at the 1% level.

PATTERNS OF SHOOT ELONGATION

Shoot elongation of individual trees was completed between 27 and 55 d after the greenhouse was warmed. Consequently, between seven and 16 observations were available for the logistic regressions that described the shoot growth of individual trees nearly perfectly: values of R^2 ranged from .91 to essentially 1.0, averaging .98.

The regression statistics showed that elongation began almost immediately after trees were exposed to warm temperatures. The average tree had initiated shoot activity (elongated 2 mm) in only 3.5 d and by day 9 had produced 8 mm of new shoot. On the average, shoot elongation was completed after 34 d, having lasted for about 30 d and having developed at a rate of 3.3 mm per day during the period of most rapid shoot growth. Total elongation averaged 68 mm.

Differences among populations were statistically significant and pronounced for all of these variables (table 1). The differences are illustrated in figure 2 by the growth curves of seven populations

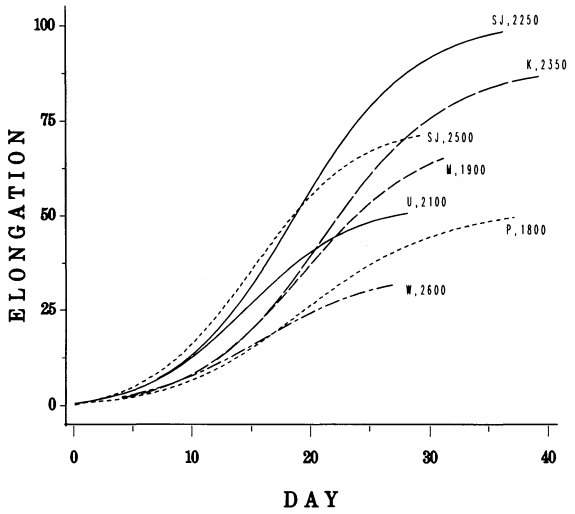

FIG. 2.—Patterns of shoot elongation (mm) for seven populations at the indicated elevations (m) and geographic location for which K = Kaibab Plateau, P = Paunsaugunt Plateau, M = Markagunt Plateau, W = Wasatch Plateau, U = Uinta Mountains, and SJ = San Juan Mountains.

that encompassed the range of patterns. The curves were generated from the mean of values predicted by the logistic model for individual trees and aptly illustrate tremendous genetic variation among populations in both the pattern and amount of shoot elongation.

Patterns of genetic variation

Stepwise regressions were made for 21 dependent variables, the 19 original variables for which differences were detected (table 1) and the first two principal components. These two principal components were the only components that individually accounted for more than 10% of the interpopulation variance. Together the two accounted for 60% of the total variance. Eigenvectors (table 2) show that the first principal component, which accounted for 42% of the variance, was composed primarily of those variables associated with growth potential, including the cessation of shoot elongation. The second component, accounting for 18% of the variance, seemed to be reflecting (1) the effects of the severe environment and (2) the beginning of shoot elongation.

Of the numerous combinations of the 37 independent variables that could be included in a single stepwise regression model, the 17 listed in table 3 not only were nonsingular but also produced error variances that were as low as those of any other group of independent variables tested. Using these 17 independent variables in the stepwise program produced models that were statistically significant for all of the dependent variables except the decrease in leaf length attributable to harsh culture. Values of R^2 were as high as .78, averaged .45, and were less than .4 for only seven variables. (The regression coefficients are available from the author.)

These regression models, however, included an average of five and as many as 11 independent variables (table 3). The models, therefore, were subject to both overfitting and overparameterizing (Draper and Smith 1981), even though the level of significance of the individual coefficients was generally high (table 3). (Note that individual coefficients failing significance at the 5% level were those whose effect acted in combination with other variables, e.g., nonlinear effects or geographic constants.) Because of this, two precautions were taken to guard against accepting fallacious results. First, models that accounted for less than 40% of the variance among populations were ignored. This left 14 variables for interpreting patterns of variation; these 14 are referenced subsequently as the key variables. Second, patterns of differentiation are interpreted in reference to the least significant differences (LSD) (Steel and Torrie 1960) that were calculated from the experimental error of the analysis of variance. The 80% confidence level (LSD .2) is used to guard against the error of accepting no differences when differences actually exist. Because values of LSD could not be calculated for the principal components, the patterns expressed by these variables are interpreted in reference to a multiple of $s_{\bar{x}}$ that scaled differentiation in each principal component to that described by values of LSD for those variables of largest eigenvector (table 2). For the first principal component, $5s_{\bar{x}}$ seemed appropriate; for the second, $8s_{\bar{x}}$.

The best-fitting regression models described genetic variation as occurring along elevational (fig. 3) and geographic clines (fig. 4). Rates of differentiation along either cline can be evaluated according to multiples of $s_{\bar{x}}$ or LSD .2, which are quantified by vertical brackets in figure 3 and represent twice the distance between isopleths in figure 4. Populations are expected to differ with a probability of about .8 if they are separated by (1) two isopleths (fig. 4) or (2) an elevational interval that subtends a mean difference equal to the vertical brackets in figure 3.

Elevational clines, presented in figure 3 with five geographic intercepts, were detected for all key variables except for the relative growth rate under severe culture. The clines for the first and second

TABLE 2

Eigenvectors and eigenvalues for the two principal components that accounted for more than 10% of the variance among populations in the 19 variables for which population differentiation was detected

Variable	First component	Second component
Growth and development:		
Optimum culture:		
Growth potential	.34	.08
Leaf length	.28	.13
Relative growth rate	.31	−.04
Late growth	.33	.03
Harsh culture:		
Decrease in height	.26	.16
Relative growth rate	.21	−.20
Decrease in leaf length	−.01	−.01
Spring frost injury	−.26	−.13
Severe culture:		
Decrease in height	.25	.27
Relative growth rate	.18	−.30
Decrease in leaf length	.09	.19
Winter injury	−.08	.35
Mortality	−.08	.33
Periodicity of shoot elongation:		
Initiation	.02	.42
Start	.04	.42
Cessation	.29	.05
Duration	.29	−.04
Rate	.23	−.24
Elongation	.27	−.19
Eigenvalue	7.89	3.42
Percent variance	42	18

TABLE 3

RESULTS OF MULTIPLE REGRESSION ANALYSES—INDEPENDENT VARIABLES INCLUDED IN A MODEL ARE INDICATED BY THE LEVEL OF SIGNIFICANCE OF THE REGRESSION COEFFICIENT

VARIABLE	R^2	RESIDUAL MEAN SQUARE	INDEPENDENT VARIABLES																
			E	E^2	Z1	Z3	LT	NW	LN	LN^2	SW^2	LN1	LT2	SW2	$(NW2)^2$	LN3	NW3	$(NW3)^2$	$(LT2)^2$
Growth and development:																			
Optimum culture:																			
Growth potential	.67**	1,423	...	.01	...	...	...	.04	...	...	...	.01	...	.03	.01	...	.01	...	...
Leaf length	.78**	27	.08	.04	...	...	.02	.01	...	.01	...	.01	.01	.01	...	.01	.01	...	...
Relative growth rate	.47**	1,196	...	.01	...	...	...	.01	...	...	...	...	.01	...	.01	...	...	...	...
Late growth	.66**	158	.32	.16	...	...	...	.01	...	...	...	...	...	...	...	...	...	...	...
Harsh culture:																			
Decrease in height	.30**	1,285	...	.04	.06	...	.01	...	...	...	...	...	.01	.01	...	...	...	...	...
Relative growth rate	.59**	221	.01	.01	.01	.01	.01	.01	...	...	...	.01	.01	.01	.01	.01	...	...	...
Decrease in leaf length	.02	37.2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Spring frost injury	.69**	.012	...	.01	...	...	...	...	...	...	...	.01	.01	...	.01	...	...	...	...
Severe culture:																			
Decrease in height	.35**	1,426	...	.01	...	.07	.01	...	...	.01	...	...	...	...	...	...	.08	...	...
Relative growth rate	.53**	329	...	...	...	.01	...	.01	.01	.01	.03	.01	.01	...	...	.01	.01	...	...
Decrease in leaf length	.29**	69	.01	...	.01	...	.01	.01	.01	...	.03	...	...	.04	...	...	...	...	...
Winter injury	.10**	.019	...	...	...	...	...	.01	...	...	...	...	...	...	...	...	...	...	...
Mortality	.08*	.020	...	...	...	...	...	.02	...	...	...	...	...	...	...	...	...	...	...
Patterns of shoot elongation:																			
Initiation	.38**	.399	...	.01	.03	...	...	...	.01	.01	.01	.10	.01	...	...	...	.01	...	...
Start	.52**	.529	.01	...	...	...	.01	.01	.01	.01	.03	.01	.01	...	...	.01	.01	...	...
Cessation	.51**	4.66	...	.01	...	...	...	.01	...	...	...	...	.02	...	.02	...	...	...	...
Duration	.41**	5.32	...	.01	...	...	...	.01	...	...	...	...	...	...	...	...	...	...	...
Rate	.43**	.192	...	.06	.01	.01	...	.01	...	...	...	...	.01	.01	.02	...	...	...	...
Elongation	.40**	108	...	.01	.07	...	...	.01	...	...	...	...	...	...	...	...	...	...	...
Principal components:																			
First	.74**	2.23	...	.01	...	...	...	.01	...	...	...	...	.01	.01	.02	...	...	...	...
Second	.47**	2.45	.01	...	...	...	...	...	.07	.08	.01	.01	...	...	...	...	...	.01	.01

* Statistical significance at the 5% level.

** Statistical significance at the 1% level.

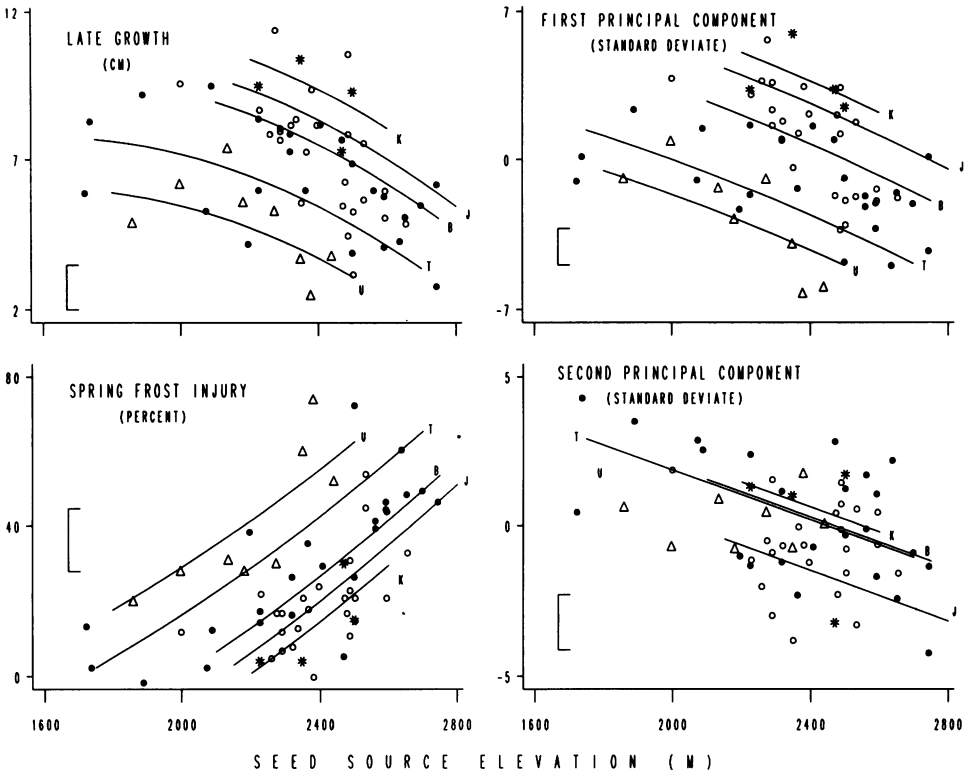

FIG. 3.—Elevational clines for four variables at five geographic localities, overlaid on the observed values which are coded for geographic zone: △ = northern (Z1) populations, ● = southwestern (Z2) populations, ○ = southeastern (Z3) populations. Clines represent populations from the Kaibab Plateau (*K*), the San Juan Mountains (*J*), the Boulder Mountains (*B*), the Tushar Mountains (*T*), and the Uinta Mountains (*U*) (see fig. 1). Brackets quantify LSD .2 for late growth and spring frost injury, $5s_{\bar{x}}$ for the first principal component, and $8s_{\bar{x}}$ for the second principal component.

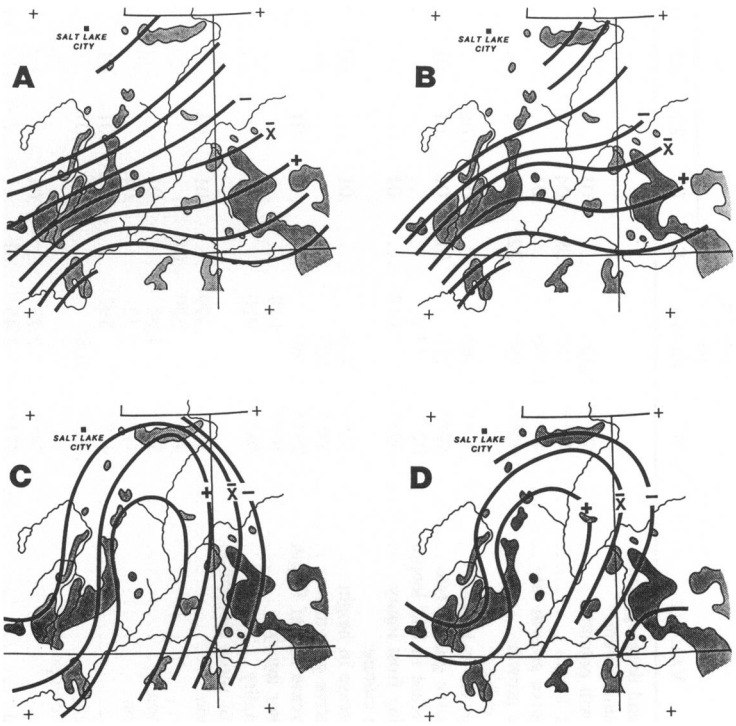

FIG. 4.—Geographic patterns of genetic variation predicted by regression models for an elevation of 2,350 m for four variables: *A* = the first principal component, *B* = growth potential, *C* = the second principal component, and *D* = the start of elongation. Shading shows the distribution of ponderosa pine (LITTLE 1971). Contour intervals are scaled to one-half LSD .2 for growth potential and the start of shoot elongation, $5s_{\bar{x}}$ for the first principal component, and $8s_{\bar{x}}$ for the second principal component.

principal components (fig. 3) assimilate the results; as the elevation of the seed source increased, the value of each principal component sharply decreased. This means, therefore, that as the elevation of the seed source increased (1) both growth potential and the duration of shoot elongation decreased, (2) shoot growth commenced faster, and (3) the effects of the severe environment became less pronounced. The slope of the elevational cline, however, varied considerably for the individual variables. For the relative growth rate under harsh culture, the elevational cline failed to depict differentiation that exceeded LSD .2, even though the regression itself was statistically significant. But for others, elevational clines were relatively steep, and populations separated by as little as 250 m were judged to be genetically different (80% level of probability).

A geographic component to genetic variation is illustrated in figure 3 by the regression lines with different intercepts. This component is detailed in figure 4 where predicted values for an elevation of 2,350 m are represented by isopleths. Only two general patterns were evident: (1) a primary pattern, illustrated by the first principal component and growth potential, that was displayed with only minor variations by 10 of the 14 key variables and by 13 of the 20 original variables, and (2) a secondary pattern, illustrated by the second principal component and the start of elongation, that recurred with minor variations for four of the key variables.

According to the primary pattern, when elevation is held constant, geographic variation appears as a gentle cline running diagonally across the region. Populations from the Kaibab Plateau and the Uinta Mountains occupy opposite ends of the cline; the former have the highest growth potential while the latter have the lowest. On the average, populations from the same elevation that are separated by about 80 miles (two isopleths) are expected to differ (80% level) genetically.

The secondary geographic pattern suggests that populations from areas adjacent to the San Rafael Desert (including the Kaibab Plateau) suffered the most under severe conditions and exhibited the slowest early rates of shoot growth. To the west, north, and east, populations from the same elevation commenced shoot growth more rapidly and suffered less under severe conditions (fig. 2).

Concomitant variation along elevational and geographic clines means that similar genotypes tend to recur at different elevations in separated localities, presumably in association with the recurrence of similar environments. For instance, a similar growth potential (principal component 1) can be expected between a population from the Uinta Mountains and a population 700 m higher in the Boulder Mountains and about 1,000 m higher in the San Juan Mountains (fig. 3). However, superimposing the clines of the second principal component on those of the first greatly complicates assessing patterns of recurrence. To illustrate such complex patterns, the regression equations were used to predict values of both principal components for the elevations at which the species occurs within individual mountain ranges and plateaus (fig. 1). In figure 5, ellipses outline the range of values predicted for the two principal components at each locality. The ellipses are elongated diagonally across the figure in association with elevation; for a particular locality, low elevations occur in the upper right portion of an ellipse, and high elevations in the lower left. Even though two ellipses may be coincident, however, similar genotypes quite likely recur at different elevations in the two localities (also fig. 3). The brackets in the lower right corner of figure 5 quantify $5s_{\bar{x}}$ and $8s_{\bar{x}}$ and thereby roughly indicate the amount of differentiation associated with the 80% confidence level. Each set of predicted coordinants thus is assumed to lie at the center of a rectangle the size of which is described by the brackets.

For instance, for the populations tested, those from the Kaibab Plateau seem to be unique genetically; genotypes associated with values of 6 for the first principal component and 2 for the second are expected only on the Kaibab Plateau (at an elevation of about 2,300 m) (fig. 5). Likewise, genetic differentiation between populations from the southern face of the Uinta Mountains and those on the north face seems pronounced. Ponderosa pine occurs on the north face only in the eastern portion of the mountain range (near Flaming Gorge), and these populations seem more similar genetically to populations from the southern plateaus than to those on the south face. In addition, genotypes capable of producing values of -5 for the first principal component and 1 for the second are expected to occur only on the Wasatch Plateau and the south face of the Uinta Mountains, while those associated with values of -1 and 3 for the first two components, respectively, are expected only in the San Juan Mountains. By contrast, genotypes capable of producing values of zero for both principal components are expected to recur in 11 of the localities: near 1,900 m on the north face of the Uinta Mountains; 2,300 m in the Markagunt Plateau, the Pine Valley Mountains, and the LaSal Mountains; near 2,400 m in the San Juan Mountains and on the Aquarius, Paunsaugunt, and Uncomphagre plateaus; near 2,500 m in the Abajo and Boulder mountains; and near 2,700 m on the Kaibab Plateau. Even though similar genotypes tend to recur across the landscape, differentiation along two gentle geographic clines and one relatively steep elevational cline nevertheless produces complex patterns of genetic variation.

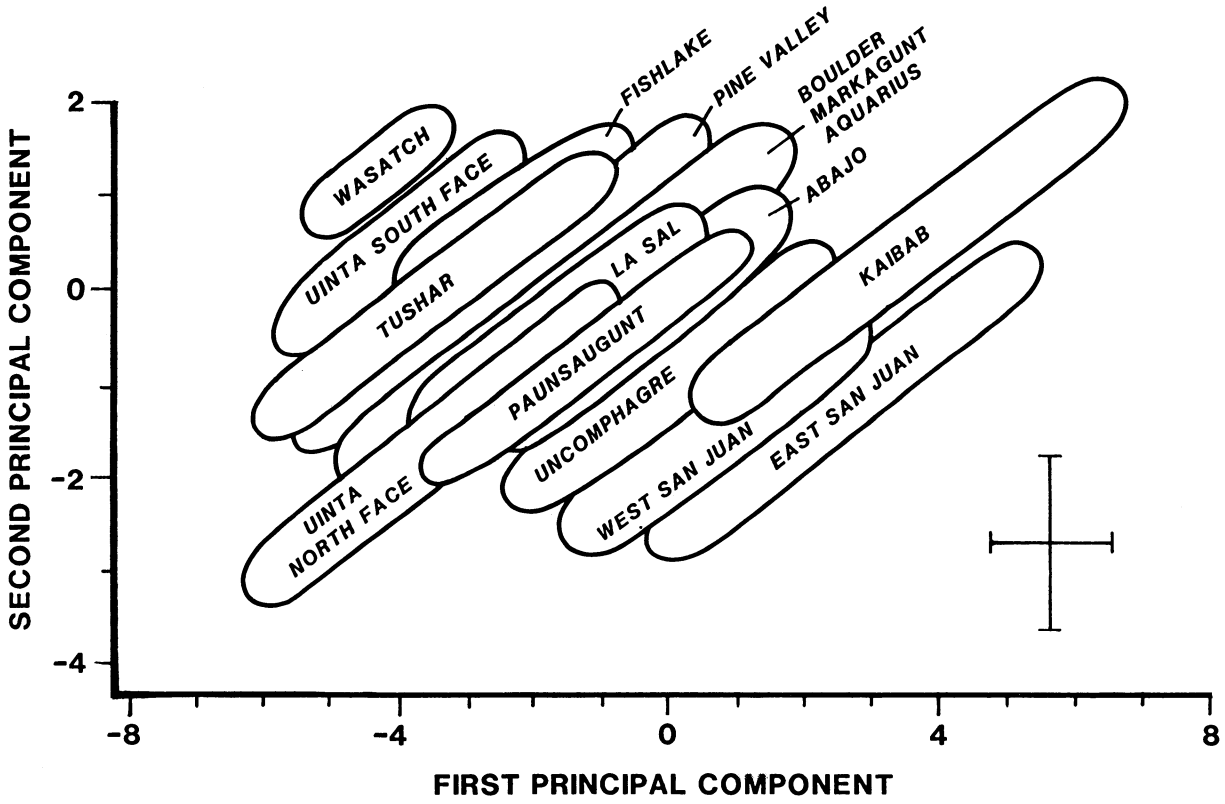

FIG. 5.—Ellipses outline the distribution of values of the first and second principal components predicted by regression models for 16 geographic localities. Values were predicted for only the range of elevations at which ponderosa pine occurs in each locality. Localities are keyed to the physiographic regions of figure 1. Brackets quantify $5s_{\bar{x}}$ for the first principal component and $8s_{\bar{x}}$ for the second.

Discussion

When grown under a variety of environmental regimes, seedling populations of ponderosa pine from the upper Colorado Basin exhibited genetic differences for 19 of the 20 traits analyzed. Genetic variation among populations was related to the elevation and geographic location of the seed source. Patterns of genetic variation were pronounced for some traits but tended to be consistent and relatively uniform for all traits. Elevational clines were the most prominent, but primary and secondary geographic clines also were evident. Because systematic patterns undoubtedly develop from selection along environmental gradients, natural selection has apparently molded a system of loosely intercorrelated, coherent traits (*sensu* CLAUSEN and HIESEY 1960) to convey adaptation of populations to specific segments of the environmental mosaic.

Genetic variation in traits associated with the first principal component has direct microevolutionary interpretation. The elevational cline describes rates of genetic differentiation in association with the elevation of the seed source. As elevation increases, temperature regimes and, consequently, the length of frost-free periods decrease. Seedlings from populations distributed along elevational gradients display adaptations to growing seasons of different length. When compared in a common environment, populations from low elevations express a high growth potential, grow for a long period, and become large; populations adapted to short growing seasons cease elongation early in the summer and tend to be small. In the upper Colorado River Basin, an elevational interval of 1,000 m tends to be associated with a change of about 80 frost-free d (BAKER 1944). Because populations separated by about 250 m tend to differ genetically (fig. 3), genetic differentiation is associated with an environmental change of about 20 frost-free d. Similar elevational clines typify adaptive variation in ponderosa pine from the Sierra Nevada (CALLAHAM and LIDDICOET 1961; CONKLE 1973) and from the Inland Northwest (MADSEN and BLAKE 1977; REHFELDT 1986*a*, 1986*b*) as well as for most northern Rocky Mountain conifers (REHFELDT 1984).

The primary geographic cline that runs generally from northwest to southeast across the region also seems to associate traits influencing growth potential with geographic gradients in the frost-free period. BAKER (1944) shows that the frost-free period at an elevation of 2,500 m is 70 d shorter in the

Uinta Mountains than on the Kaibab Plateau and 60 d shorter in the Uinta Mountains than in the San Juan Mountains. Rates of differentiation along the elevational cline (20 frost-free d ≅ LSD .2) suggest that populations inhabiting environments that differ by 70 frost-free d also should differ by 3.5 units of LSD .2. Consequently, if geographic patterns also have developed from gradients in the frost-free period, seven isopleths, scaled to one-half LSD .2, should separate Uinta populations from Kaibab populations at the same elevation. Similarly, one isopleth should separate Kaibab populations from those at the same elevation in the San Juan Mountains. In figures 4*a* and 4*b*, populations from the Uinta Mountain, Kaibab Plateau, and San Juan Mountains indeed are separated by the number of isopleths expected under the supposition that the primary geographic cline also reflects adaptation to a variable frost-free period.

Patterns of variation for traits associated with the second principal component described a secondary geographic cline: early shoot elongation was the slowest for populations from low elevations in lands on the periphery of the San Rafael Desert (figs. 3 and 4). These same populations suffered the most winter injuries and mortality at the severe environment at Priest River. As either elevation or distance from this desert increased, winter injury and mortality to populations decreased while early shoot development became more rapid.

This secondary pattern of geographic variation is similar to patterns for a rather large number of environmental variables: total snowfall, frequency of precipitation in March, April, May, June, and December, and heating degree-days from May through September (U.S. DEPARTMENT OF COMMERCE 1968). However, the patterns of precipitation most credibly account for the observed results. In the lands surrounding the San Rafael Desert, summer precipitation dominates the annual pattern while winter and spring months are commonly dry (JEPPSON et al. 1968). Shoot growth of populations from these lands develops leisurely perhaps because of limited spring moisture supplies that are typically supplemented by precipitation during the growing season. At Priest River, summer droughts are typical, and the growth and development of these same populations undoubtedly were poorly synchronized with the climate, a condition contributing to the winter injury and mortality in the severe environment. As the geographic distance from the San Rafael Desert increases, summer droughts gradually dominate annual patterns of precipitation. And as elevation increases, total precipitation increases, thereby ameliorating the effects of spring droughts in a climate dominated by summer precipitation. Populations from either high elevations or geographic localities experiencing summer droughts had faster early shoot elongation while suffering fewer winter injuries and less mortality at Priest River.

Regardless of the possible explanations, elevational and geographic clines apparently have developed in response to the environmental transitions that occur within the region of study. The clines involve two sets of traits that describe steep clines and rampant differentiation. Yet similar genotypes recur in separated geographic localities in patterns suggesting that the genetic constitution of single populations is not unique. However, genetic variation in ponderosa pine has been detected for a variety of traits that could not be considered in this study: hail damage (READ and SPRACKLING 1981), freezing injury (REHFELDT 1986*a*), snow breakage (REHFELDT and COX 1975), tracheid length (ECHOLS 1973), and resistance to insects (HOFF 1988*a*) and diseases (HOFF 1988*b*). If genetic variation in such traits is both independent of growth potential and distributed along additional principal components, the observed patterns would be further fractionized. This eventuality would mean that the recurrence of similar genotypes would be more limited than that implied in figure 5.

Nevertheless, genetic differentiation among populations is pronounced, and much of the differentiation seems to have developed from selection in heterogeneous environments. The response to selection, moreover, undoubtedly has been abetted by the discontinuous distribution of ponderosa pine in the upper Colorado River Basin (fig. 1). In fact, the distribution is somewhat more fractionated than suggested by fig. 1; in most of the areas not sampled, ponderosa pine occurs as rare individuals or groups in a sea of pinyon and juniper. Such distributions limit panmixia and thereby promote selective differentiation.

While these results contribute to an understanding of the microevolution of ponderosa pine in the upper Colorado River Basin, they neither confirm nor refute the taxonomic subdivisions of *Pinus ponderosa* var. *scopulorum* proposed by CONKLE and CRITCHFIELD (1988). These authors imply that the Rocky Mountain race dominates all of this region except the Kaibab Plateau and San Juan Mountains, both of which support the southwestern race. Geographic patterns of variation (fig. 4) tend to support this interpretation for populations on the Kaibab Plateau but question it with regard to the San Juan Mountains. Future studies dealing with population differentiation in Arizona and New Mexico should better address racial differentiation.

Nevertheless, once documented, patterns of adaptive variation have direct practical application to forest management. To maximize productivity of artificial reforestation, planted trees must be adapted to the planting site. Adaptation is secured by limiting the distance that seeds from natural populations are transferred from their origin. Con-

sequently, limits to seed transfer must reflect geographic and elevational patterns of variation. One estimate (REHFELDT 1979) of an appropriate limit to seed transfer involves the geographic or elevational interval across which differentiation equals LSD .2. In accordance, differentiation along the steepest of the elevational clines suggests that seed transfer should be limited to ±125 m of the elevation of the seed source. Geographic limits to seed transfer also should recognize both the primary and secondary geographic clines. Because the intervals between isopleths (fig. 4) were scaled to one-half LSD .2, seeds from a given source should not be transferred a geographic distance greater than ±1 isopleth along either geographic cline.

An alternative approach to limiting seed transfer recognizes that the amount of genetic differentiation associated with one isopleth is equivalent to that which occurs across 125 m of elevation. Thus, transfers across isopleths of high value to those of low value are similar to transfers from low elevation to high elevation at a single locality. This relationship can be used to construct floating transfer guidelines (REHFELDT 1988) that allow greater versatility in designing reforestation programs.

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