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GENETIC VARIATION IN THE PONDEROSAE OF THE SOUTHWEST[1]

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Ninety-five seedling populations of southwestern ponderosa pine (*Pinus ponderosa* var. *scopulorum*) along with single populations of *Pinus engelmannii* and *Pinus arizonica* were compared in four environmentally disparate common gardens. Differentiation among ponderosa pine populations was detected for a diverse assortment of variables that included patterns of shoot elongation, measures of growth potential, winter and spring freezing damage, and leaf characteristics. Multiple regression models accounted for as much as 85% of the variance among populations and described complex clines that were dominated by elevational and latitudinal effects. Although *P. ponderosa, P. arizonica,* and *P. engelmannii* were readily differentiated, the performance of progenies from one population suggested introgression primarily involving *P. ponderosa* and *P. arizonica* but also implicating *P. engelmannii.*

Microevolutionary processes allow natural systems of genetic variability to be molded by environmental heterogeneity to produce populations genetically attuned to a local environment. As demonstrated repeatedly by the experimental approach of Clausen, Keck, and Hiesey (e.g., 1940), culturing plant populations in common gardens so frequently demonstrates geographic variation that adaptive differentiation of populations commonly is assumed (Mayr, 1970). Species, however, face environmental heterogeneity with diverse assortments of genetic variability. As a result, responses to natural selection are varied. In the Rocky Mountains, for example, clines in adaptive traits suggest differentiation among populations separated in altitude by 200 m in *Pseudotsuga menziesii* (Rehfeldt, 1989), 250 m in *Pinus contorta* (Rehfeldt, 1988), 350 m in *Pinus ponderosa* var. *ponderosa* (Rehfeldt, 1991), and 450 m in *Larix occidentalis* (Rehfeldt, 1982). But in *Pinus monticola,* clines cannot be demonstrated for either morphological traits (Rehfeldt, Hoff, and Steinhoff, 1984) or allozymes (Steinhoff, Joyce, and Fins, 1983). Yet in the mountains of northern Idaho, these species frequently cooccur (Daubenmire and Daubenmire, 1968) across as much as 1,000 m of elevation, an interval associated with a difference of about 90 frost-free days (Baker, 1944). Populations of these wind-pollinated sympatric conifers have responded much differently to selection along similar environmental gradients. An environment perceived as being coarse-grained to *Pseudotsuga menziesii* and *P. contorta* is apparently fine-grained to *P. monticola.*

To the widespread ponderosa pine (*P. ponderosa*), the grain of the spatially variable environment is unquestionably coarse. Geographic races are recognized within each of three varieties (Conkle and Critchfield, 1988). Genetic variation among populations within races is abundant for a variety of characters reflecting growth and survival in long-term field tests (Conkle, 1973; Read, 1983; Sheppard and McElderry, 1986; Van Haverbeke, 1986), growth and development in common gardens (Madsen and Blake, 1977; Read, 1980; Rehfeldt, 1990, 1991), tolerance to environmental stress (Read and Sprackling, 1981; Rehfeldt, 1986a, b), disease resistance (Hoff, 1988b, 1990, 1991), and allozymes (Mitton et al., 1977; Mitton, Sturgeon, and Davis, 1980; Linhart et al., 1981; Hamrick, Blanton, and Hamrick, 1989).

These disparate results document extensive population differentiation, much of which is interpretable as adaptation to heterogeneous environments. Nevertheless, to *P. p.* var. *ponderosa* of the Inland Northwest, the grain by which the environment is perceived apparently is much finer than for populations of *P. p.* var. *scopulorum* on the Colorado Plateau. Population differentiation is associated with habitats that differ by at least 35 frost-free days in the Northwest (Rehfeldt, 1991) but by only 22 frost-free days on the Colorado Plateau (Rehfeldt, 1990). In addition, genetic variation within populations tends to occur in patches (Linhart, 1989) and is pronounced for numerous traits reflecting growth (Conkle, 1973; Namkoong and Conkle, 1976; Rehfeldt, 1980), allozymes (Linhart et al., 1981), and adaptation to the biotic (Hoff, 1988a, b, 1991) and abiotic environment (Rehfeldt, 1992).

The Southwest is a region in which the genetic structure of ponderosa pine (*P. p.* var. *scopulorum*) populations is poorly understood. While rangewide provenance tests unanimously attest to genetic differentiation of southwestern populations from those to the north (Squillace and Silen, 1962; Hanover, 1963; Wells, 1964; Read, 1980), patterns of variation among southwestern populations are obscure. This paper reports common garden studies and presents models that describe genetic variation. While differentiation can be either random or systematic, it is the systematic patterns that invariably correspond to environmental gradients and, therefore, most likely result from natural selection. Because systematic patterns are predictable, functional models can be applied to topics ranging from artificial reforestation to gene conservation.

Two factors complicate studies of genetic variation in southwestern ponderosa pine. First, Conkle and Critchfield (1988) separate the Rocky Mountain race from the southwestern race of *P. p.* var. *scopulorum* in southern Utah and southeastern Colorado. The abruptness of the transition between races, however, is largely unknown. Secondly, in southeastern Arizona and southwestern New

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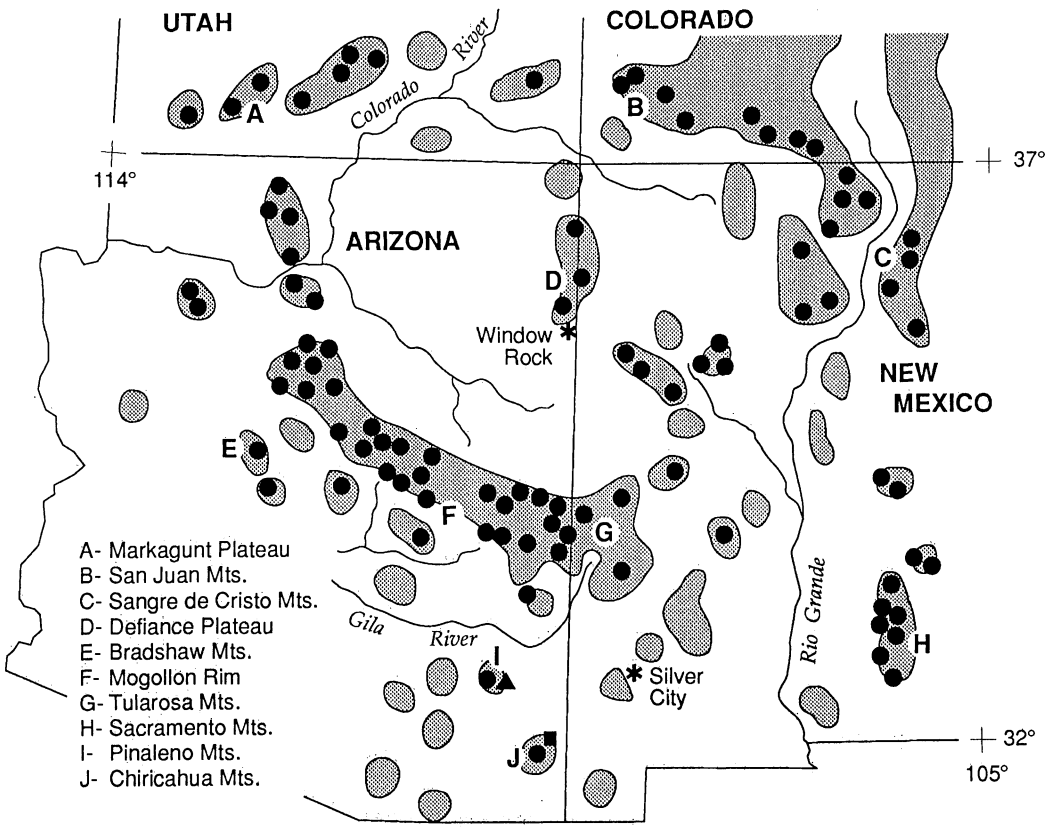

Fig. 1. Map of the region of study showing the distribution of ponderosa pine (shading, from Little, 1971) and populations sampled. Letters key geographic localities referenced in the text. Circle = ponderosa pine; triangle = Arizona pine; square = Apache pine.

Mexico, ponderosa pine co-occurs with two other pines, Arizona pine (*P. arizonica*) and Apache pine (*P. engelmannii*), the three of which are interfertile (Conkle and Critchfield, 1988) members of the Ponderosae subsection of the Diploxylon subgenus of *Pinus* (Little and Critchfield, 1969). Until recently, in fact, Arizona pine was considered to be a variety of ponderosa pine (cf., Perry, 1991). Studies of phenotypic variation in terpenes and in cone and leaf morphologies have prompted the conclusion that natural hybridization among these species is common (Peloquin, 1971, 1984). The extent of introgression, however, is unknown. While concentrating on genetic variation in the southwestern race of *P. p.* var. *scopulorum,* this report assumes secondary objectives of contributing to an understanding of the interrelationships among the southwestern Ponderosae.

MATERIALS AND METHODS

Population differentiation was studied by comparing the growth and development of seedlings from 97 populations in field and greenhouse tests. Each population was represented by a bulked sample of eight to ten wind-pollinated cones from each of ten trees. To decrease the possibilities of co-ancestry, sampled trees were at least 30 m apart and were separated by the crowns of at least two intervening trees. Although no collections were made from the lowest limits of the species' distribution where ponderosa pine occurs as scattered individuals in woodlands dominated by *Pinus edulis* or *Juniperus* spp., these populations otherwise sampled the ecologic, geographic, and elevational distribution of the species in the Southwest (Fig. 1). In this paper, populations reference groups of adaptively similar, interbreeding individuals. The localities of Fig. 1 are physiographic provinces that may contain numerous populations.

The 97 populations included single populations of Arizona and Apache pines (Fig. 1). After the experimentation was under way, it became obvious that a population (Barfoot) in the Chiricahua Mountains (locality J, Fig. 1) was either introgressed or contained a mixture of ponderosa and Arizona pines. As a result, the working hypothesis was adopted that Barfoot was a mixture of noninterbreeding species. Under this assumption, eliminating all seedlings from Barfoot with the leaf characteristics of Arizona pine (four or five narrow leaves/fascicle) from the Pinaleno Mountains (Fig. 1) allowed Barfoot to be considered as a population of ponderosa pine.

Field tests—Seedlings from each population were grown in plastic containers (65 cm^3) in a shadehouse in Moscow, Idaho (latitude 46.7° N, longitude 117° W), and first-year seedlings were planted in common gardens near Priest River, Idaho; Window Rock, Arizona; and Silver City, New Mexico. Priest River is 190 km north of Moscow; Window Rock and Silver City are shown in Fig. 1. The Priest River and Window Rock tests were planted in the fall, while the Silver City test was planted the following spring. At all sites, ten seedlings from each population were planted in row plots within each of four randomized

TABLE 1. *Physical characteristics, mean performance, and general climate at the field test sites*

Characteristic	Test site		
	Priest River	Silver City	Window Rock
Latitude (°N)	48.5	32.8	35.9
Elevation (m)	750	1,900	2,400
Frost-free period (d)	90	210	110
Dry season	Summer	Winter–Spring	Winter–Spring
Survival (%)	99.5	97.6	89.8
4-yr height (cm)	80.8	57.1	26.1

complete blocks. Rows were separated by 0.6 m, while 0.3 m separated seedlings within rows. All sites were tilled and fenced before planting and were irrigated and weeded periodically for three growing seasons after planting. Testing was completed after the trees reached age 4.

Because environmental effects at these planting sites differentially affected the growth and development of trees (Table 1), a different set and number of variables was necessary for describing growth and development at each site (Table 2). Field tests thus contributed a diverse array of 17 variables that included morphometric traits, spring and winter freezing damage, leaf morphology, and survival. Of these variables, note that the deviations from regression account for the autocorrelation of the annual shoot growth of trees and are, thereby, relatively independent of prior effects. These values thus can reflect adaptation to a particular environment in a short period of time. The variables PRDEV and WRDEV reflect 4-yr height as if all individuals had been the same height in yr 2. Because of spring frost damage at the beginning of the third growing season at Silver City, SCDEV3 reflects the effects of spring frost injury on the third-year growth of trees from a common height at yr 2; and SCDEV4 reflects the growth that occurred in yr 4 independently of the frost damage that occurred at the beginning of yr 3.

Greenhouse tests—Seedlings from each population were grown for 6 mo in plastic containers (740 cm^3) in a shadehouse at Moscow, Idaho. The experimental design consisted of nine seedlings growing in row plots in each of three blocks. Trays of containers containing three plots were transferred into an unheated greenhouse for the winter months and, in early March of the second growing season, 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 of the terminal shoot was well under way. Thereafter, each seedling was measured twice each week until elongation of the preformed shoot was complete.

Periodic measurements allowed shoot elongation of individual trees to be modeled with a logistic function with a hyperbolic time term (Rehfeldt and Wykoff, 1981):

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

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 produced by this function allowed calculation of six variables that were used to describe the pattern of shoot elongation of individual trees (Table 2). Additional measurements produced five more variables that reflected growth and development in the greenhouse environment.

TABLE 2. *Description of the variables analyzed*

Variable[a]	Description
PRHT4	Age 4 height
PRDIA	Age 3 diameter
PRDEV	Deviation from regression of 4-yr height on 2-yr height
PRCL	Scores of the color (green = 0 or blue = 1) of the succulent shoot
PRRTO	Ratio of the 3-yr height to the 3-yr diameter
PRLL	Leaf length from a fascicle near the center of the 3-yr terminal shoot
PRLW	Leaf width from a fascicle near the center of the 3-yr terminal shoot
PRLNM	Average number of leaves in ten fascicles distributed throughout the 3-yr terminal shoot
SCHT4	Age 4 height
SCSF	Scores (1 to 4) of damage to elongating shoots from a spring frost in year 3
SCDEV3	Deviation from regression of 3-yr height on 2-yr height
SCDEV4	Deviation from regression of 4-yr height on 3-yr height
WRHT4	Age 4 height
WRDEV	Deviation from regression of 4-yr height on 2-yr height
WRWI	Death of foliage from winter desiccation during years 2 and 3
WRLL	Leaf length from a fascicle near the center of the 3-yr shoot
WRDEAD	Score of mortality at any age
GHEL	Length of the terminal shoot produced in year 2
GHS2	Initiation of elongation: the day by which the 2-yr terminal shoot had elongated 2 mm
GHS8	Start of elongation: the day by which the 2-yr terminal shoot had elongated 8 mm
GHEN	Cessation of elongation: the day by which all but 2 mm of elongation had occurred
GHDR	Duration of elongation: the number of days between the initiation and cessation
GHRT	Elongation per day during the period for which 20% to 80% of the shoot elongated
GHHT2	Age 2 height
GHDIA	Age 2 diameter at the soil surface
GHLL	Average length of leaves from ten fascicles distributed through the 2-year terminal shoot
GHLNM	Average number of leaves in 10 fascicles distributed through the 2-yr terminal shoot
GHRTO	Ratio of the 2-yr height to the 2-yr diameter

[a] First two letters of variable code the test site: PR = Priest River, SC = Silver City, WR = Window Rock, and GH = Greenhouse.

Patterns of variation—Population differentiation was assessed from analyses of variance (SAS Institute, 1985, using Type III estimable functions), which were performed according to the following model of random effects:

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

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_{ij} 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 experi-

mental error becomes the variance appropriate for testing differences among populations. For these analyses, the harmonic mean of observations per plot was 9.92 at Priest River, 9.70 at Silver City, 8.62 at Window Rock, and 8.84 in the greenhouse.

An attempt was made to reduce the number of dimensions about which differentiation was being expressed by using principal component analyses (SAS Institute, 1985) on the data from each test site. However, differentiation of populations was so pronounced that the principal component analysis allowed the number of variates for which populations differed significantly to be reduced by only 8. Because of this, because the use of principal components results in a loss of information (Johnson and Wichern, 1982), and because principal components often are impractical in the general application of regression models, subsequent analyses involved only the original variates.

Multiple regression techniques were used to develop a general model of genetic variation according to procedures detailed earlier (Rehfeldt, 1989):

1) Deriving independent variables from latitude (LT), longitude (LN), and elevation that could serve as surrogates for the complex three-dimensional environmental gradients that have operated in natural selection. For the present analyses, independent variables included the first and second powers of elevation and the first, second, and third powers of LT, LN, LT × LN and LT ÷ LN. The latter two of these variables produced a grid from northwest to southeast and from northeast to southwest, respectively;

2) screening the independent variables by stepwise regression, the best model of which was judged relative to statistical significance, the Mallows statistic, and patterns displayed by the residuals (Draper and Smith, 1981);

3) refining a stepwise model with multiple regression to develop the most parsimonious model;

4) and finally, plotting elevational and geographic patterns of variation to assure that the models were sensible biologically.

A fifth step, verification of the model, could not be attempted because independent data were not available.

Models were developed for ponderosa pine by excluding populations of Apache and Arizona pine. This left 95 populations for the regression analyses. Excluding seedlings from Barfoot that had leaf characteristics of Arizona pine removed nine trees from greenhouse tests, three from Priest River tests, three from Silver City, and none from Window Rock where winter injuries and mortality had decimated the Barfoot population.

Rates of differentiation along geographic or elevational clines were interpreted relative to the least significant difference (Steel and Torrie, 1960) among populations at the 20% significance level (lsd 0.2). Values of lsd were used because stepwise models developed from numerous independent variables are subject to overfitting and overparameterizing (Draper and Smith, 1981). The use of lsd guarded against accepting fallacious results. The 20% significance level was used to guard against accepting no differences among populations when differences actually exist (type II errors); such errors provide the greatest potential for faulty interpretations when models are applied. Values of lsd were calculated from the interaction of blocks and populations in the analysis of variance.

Using lsd to assess rates of differentiation intuitively suggests that interpretations are dependent on sample sizes and experimental errors (uniformity of cultural conditions). However, because the cones from ten trees had been bulked, variances within plots are composed not only of environmental effects at the planting site, but also of genetic variances within populations. Consequently, lsd would still reflect the genetic variances within populations even if samples were large and the control of microenvironmental effects was complete.

Interrelation among species—Canonical discriminant analyses (SAS Institute, 1985) were used to assess multivariate relationships among species. These analyses were performed separately on data from each test site. They used observations on individual seedlings from each of the populations of Apache and Arizona pines, five populations of ponderosa pine, and the Barfoot population. The five ponderosa pine populations were geographically proximal and elevationally similar to the Arizona pine, Apache pine, and Barfoot population. Of the five, three came from the Mogollon Rim and one each came from the Tularosa and Pinaleno Mountains (Fig. 1). These analyses also used all trees from Barfoot, regardless of leaf morphology. Barfoot was of particular interest because the performance of its progenies suggested that the parental population was either a hybrid swarm or a mixture of Arizona and ponderosa pines.

RESULTS

The results consider first, variation among populations of ponderosa pine, and second, biosystematic implications.

Population differentiation—Differences among populations were detected ($P < 0.05$) for all but one variable, with the effects of populations accounting for at least 40% of the total variance for ten of the variables (Table 3). Because of the experimental design that was used, weak effects for blocks (Table 3) meant that the intraclass correlation for the effects of populations approximates the ratio of the total genetic variance to the phenotypic variance. The size of these intraclass correlations, therefore, attests to pronounced differentiation of populations.

The strongest effects of populations were associated with the cessation of shoot elongation (GHEN), the duration of elongation (GHDR), and number of leaves per fascicle (PRLNM and GHLNM), variables for which population effects accounted for as much as 72% of the total variance. For most of the variables, however, much of the total variance was associated with sampling errors that are composed of microenvironmental effects at the test site and genetic variances within populations. Since genetic variances for many of these traits tend to be pronounced (Rehfeldt, 1992), large sampling errors also can be expected. The deviation from regression of 4-yr height on 2-yr height at Window Rock (WRDEV) was the only variable for which no differences were detected among populations, a result suggesting that growth potential (innate ability to produce and assimilate photosynthate in the absence of environmental effects that mask the ge-

TABLE 3. *Mean of all ponderosa pine populations, range of mean differences among populations, and results of analysis of variance. Results of the anlayses of variance are presented as intraclass correlations, the ratio of the variance component for the indicated effects to the sum of all components*

Variable	Units	Mean	Range		Source of variance			
			Maximum	Minimum	Blocks	Populations	Experimental error	Sampling error
PRHT4	cm	81	97	58	0.07**	0.40**	0.02**	0.51
PRDIA	mm	17	21	14	0.07**	0.41**	0.06**	0.47
PRDEV	cm	0.0	11	−11	0.01**	0.14**	0.06**	0.80
PRCL	Score	0.8	1.0	0.4	0.00	0.10**	0.00	0.89
PRRTO	cm/mm	2.9	3.4	2.5	0.02**	0.22**	0.09**	0.67
PRLL	cm	17	19	14	0.03**	0.26**	0.04**	0.67
PRLW	mm	1.7	1.8	1.6	0.04**	0.17**	0.08**	0.71
PRLNM	Count	3.1	3.2	2.0	0.00	0.72**	0.02**	0.26
SCHT4	cm	57	85	28	0.03**	0.41**	0.11**	0.46
SCSF	Score	2.2	2.8	1.5	0.01**	0.13**	0.04**	0.82
SCDEV3	cm	0	7	−4	0.01	0.13**	0.11**	0.76
SCDEV4	cm	0	10	−10	0.07**	0.15**	0.19**	0.60
WRHT4	cm	26	33	19	0.01**	0.22**	0.16**	0.61
WRDEV	cm	0	5	−4	0.06**	0.03	0.25**	0.66
WRWI	%	27	92	0	0.05**	0.19**	0.06**	0.70
WRLL	cm	7	8	5	0.16**	0.03*	0.23**	0.58
WRDEAD	%	11	35	0	0.04**	0.09**	0.16**	0.71
GHEL	mm	134	175	71	0.00	0.40**	0.05**	0.55
GHS2	d	4	6	3	0.01*	0.03*	0.15**	0.82
GHS8	d	8	11	7	0.00	0.07*	0.19**	0.74
GHEN	d	38	50	29	0.01**	0.50**	0.02	0.48
GHDR	d	34	46	25	0.01**	0.46**	0.02	0.51
GHRT	mm/d	6	8	4	0.00	0.23**	0.04*	0.73
GHHT2	mm	240	319	130	0.00	0.40**	0.07**	0.54
GHDIA	mm	6	9	4	0.01**	0.41**	0.06**	0.53
GHLL	cm	14	167	106	0.00	0.20**	0.04*	0.76
GHLNM	Count	3.1	3.4	3.0	0.00	0.61**	0.02*	0.37
GHRTO	mm/mm	38	44	30	0.01*	0.15**	0.19**	0.65

* Significance of F-value at $0.05 > P > 0.01$.
** Significance of F-value at $P < 0.01$.

notype) had been masked in the rigorous environment (Table 1).

The degree of differentiation among populations is illustrated readily by the variables describing shoot elongation. In the greenhouse, shoot elongation of individual trees was completed between 17 and 62 d after the greenhouse was warmed. This meant that seven to 19 observations were available for the logistic regressions that described shoot elongation of individual trees nearly perfectly: values of R^2 ranged from 0.93 to essentially 1.0, averaging 0.99.

Because shoot elongation is one of a sequence of developmental events that must be completed within the frost-free season, different patterns of shoot growth illustrate adaptation to heterogeneous environments. As shown in Fig. 2, differences in the start of elongation were small, but differences in the rate, duration, cessation, and amount of elongation were pronounced. In this figure, the high growth potential and long duration of shoot growth of trees from the Bradshaw Mountains (locality E) describes a population from the lowest elevation (1,700 m) sampled in the study. The remaining graphs are for populations from about the same elevation (2,300–2,700 m) but different geographic localities. In contrast to southern populations, those from the north (e.g., San Juan Mountains [locality B] or Markagunt Plateau [locality A]) combined an early cessation of elongation with low growth potentials.

Multiple regression models accounted for statistically significant ($P < 0.01$) proportions of the variance among populations for all variables (Table 4). Values of R^2 were as high as 0.85, averaging 0.58. For only eight of the variables did regression models account for less than half of the variance among populations. These results thus demonstrate that much of the variation follows systematic

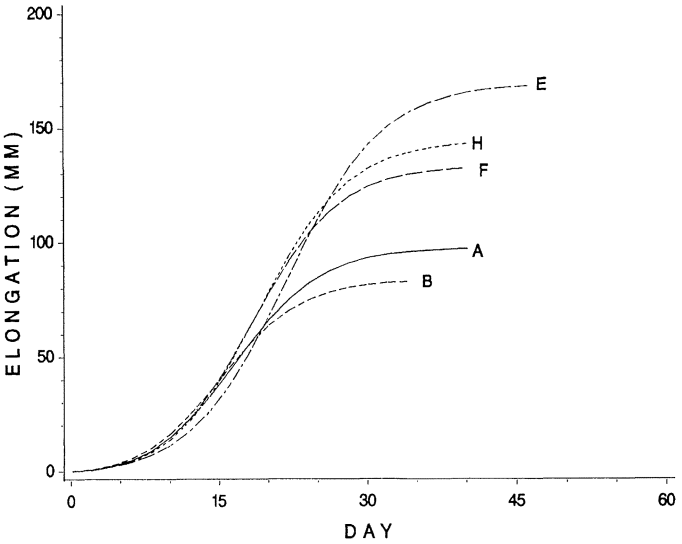

Fig. 2. Mean cumulative shoot elongation of seedlings from six localities identified in Fig. 1.

TABLE 4. *Results of multiple regression analyses. Geographic patterns of variation are keyed to Fig. 4. All regressions were statistically significant at probabilities less than 0.01*

Dependent variable	R^2	Independent variables	Pattern of genetic variation				
			Elevation cline			Geographic cline	
			Sign	Slope	Shape	Slope	Direction
PRHT4	0.85	6	Negative	Steep	Nonlinear	Steep	South to North
PRDIA	0.82	5	[a]	Steep	Nonlinear	Steep	South to North
PRDEV	0.59	3	Positive	Steep	Nonlinear	Steep	South to North
PRCL	0.49	8	Negative	Shallow	Linear	Shallow	Southwest to Northeast
PRRTO	0.52	3	Negative	Steep	Linear	Shallow	North to South
PRLL	0.75	6	Negative	Steep	Nonlinear	Moderate	South to North
PRLW	0.23	3		[b]		Shallow	Northeast to Southwest
PRLNM	0.64	7	Negative	Shallow	Nonlinear	Shallow	South to North
SCHT4	0.85	3	Negative	Steep	Linear	Moderate	South to North
SCSF	0.54	8	Positive	Moderate	Linear	Moderate	Northeast to Southwest
SCDEV3	0.63	4	Negative	Steep	Linear	Moderate	Southwest to Northeast
SCDEV4	0.50	2		[b]		Moderate	South to North
WRHT4	0.71	3	Negative	Shallow	Linear	Moderate	South to North
WRDEV	0.20	3		[b]		Shallow	Southeast to Northwest
WRWI	0.79	3		[b]		Steep	South to North
WRLL	0.40	2	Negative	Shallow	Linear	Shallow	Southeast to Northwest
WRDEAD	0.26	3	Positive	Shallow	Linear	Shallow	Southwest to Northeast
GHEL	0.83	4	Negative	Moderate	Linear	Steep	South to North
GHS2	0.16	5	[a]	Shallow	Nonlinear	Shallow	Southeast to Northwest
GHS8	0.27	6	[a]	Shallow	Nonlinear	Moderate	Southwest to Northeast
GHEN	0.83	5	Negative	Moderate	Linear	Steep	South to North
GHDR	0.84	5	Negative	Moderate	Linear	Steep	South to North
GHRT	0.66	4		[b]		Moderate	South to North
GHHT2	0.83	5	Negative	Moderate	Nonlinear	Moderate	South to North
GHDIA	0.83	5	Negative	Moderate	Nonlinear	Steep	South to North
GHLL	0.60	7	Negative	Moderate	Linear	Moderate	South to North
GHLNM	0.55	5	[a]	Shallow	Nonlinear	Moderate	South to North
GHRTO	0.44	5	Negative	Shallow	Linear	Shallow	North to South

[a] No general sign.
[b] No elevational cline.

patterns that regression models are remarkably capable of describing. Regression equations are available from the author.

The models described genetic variation as occurring along both elevational and geographic clines (Table 4). Elevational clines (Fig. 3) were detected for all but five of the variables and exhibited a variety of shapes, slopes, and signs. Ten variables exhibited nonlinear elevational clines, all of which were of shape similar to those of PRHT4 and PRDEV in Fig. 3. While the sign of the elevational cline is directly interpretable for linear clines, only a general cant describes the slope of nonlinear clines; thus, the general relationship for PRHT4 is negative and that for PRDEV is positive (Fig. 3). The strength of a cline was interpreted relative to lsd 0.2: for clines of steep slope, differences equal to lsd 0.2 are expected to occur between populations within the same geographic locality that are separated by less than 300 m of elevation; for those of moderate slope, 300 to 500 m; and for those of shallow slope, more than 500 m.

Together, the clines illustrate declining growth potential as the elevation of the population increases. Thus, the duration of developmental events, height-diameter ratios, leaf lengths, and tree heights were negatively related to elevation. In addition, as elevation increased, the color of succulent shoots tended to change from blue-green toward green, the number of leaves per fascicle decreased, damage from the spring frost at Silver City increased, and mortality at Window Rock increased.

Nonlinear elevational clines typified the general response of many variables measured at Priest River, a site to which some populations were transferred north as much as 17° of latitude. While linear clines commonly related growth potential to elevation (see GHHT2 and GHLL, Fig. 3), populations from the mildest environments (lowest elevations) evidently were incapable of fully expressing their growth potential at the northern site. Yet, populations from the middle and high elevations seemed to be unaffected. As a result, the populations from high elevations had the most growth from a common 2-yr height (PRDEV). The nonlinear cline for 4-yr height (PRHT4), therefore, resulted first from a difference in growth potential among populations and second from a difference in the degree that the potential was masked.

Rates of differentiation along linear clines are readily interpreted in relation to lsd 0.2. For the 4-yr height of trees at Silver City (SCHT4), the variable with the steepest linear cline, populations in the same locality that were separated in elevation by about 300 m tended to be genetically different. This variable, incidentally, integrated genetic differences in growth potential with those controlling tolerance to spring frosts. Frost injury to populations from high elevations accentuated the differences in height that accrue according to the negative relationship between growth potential and elevation.

Rates of differentiation along the nonlinear clines, however, depend on the elevations at which comparisons are made. The results for 4-yr height at Priest River (PRHT4),

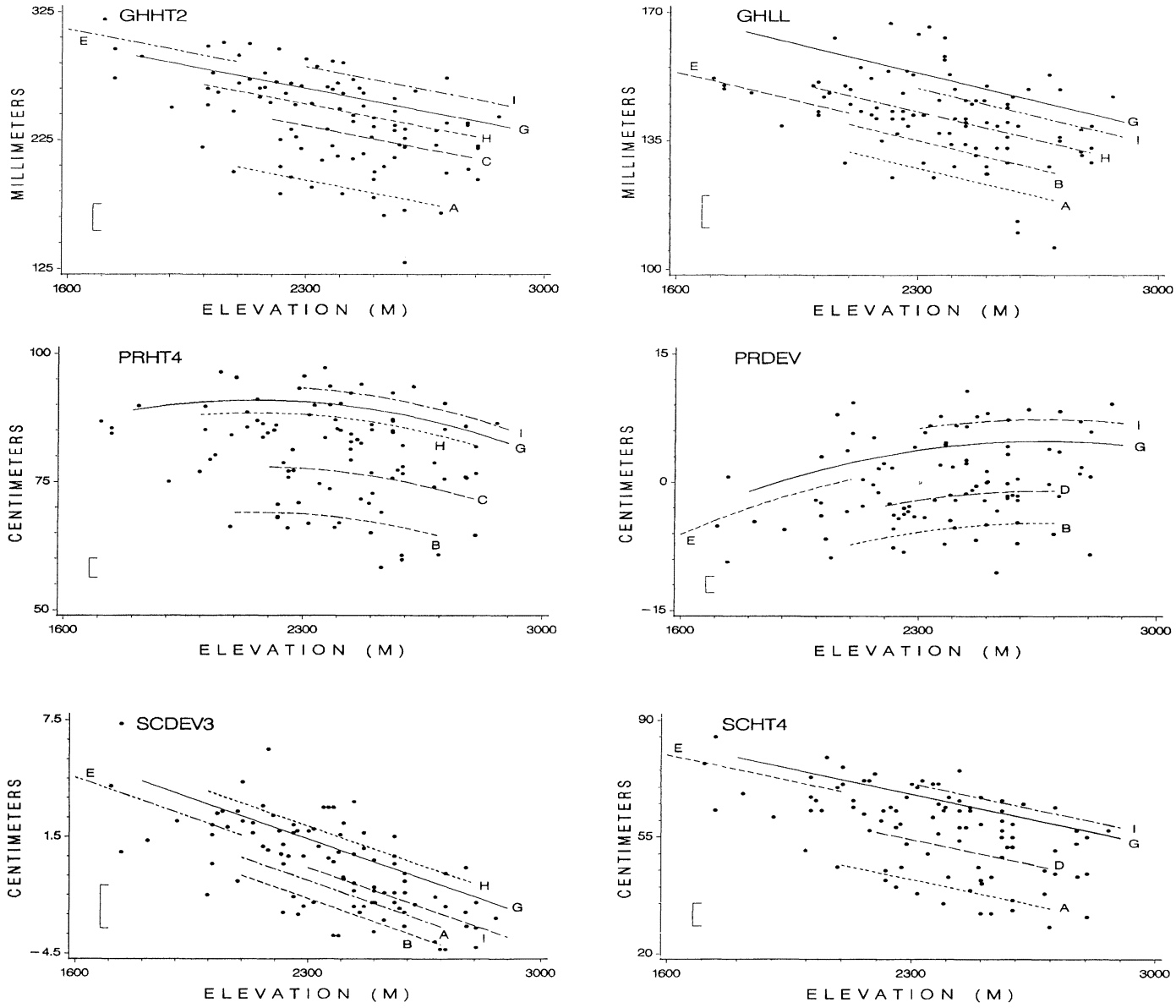

Fig. 3. Mean performance of ponderosa pine populations for six variables plotted according to the elevation of the seed source. Variables are referenced in Table 2. Each regression line represents a geographic locality identified in Fig. 1, and the bracket near the origin quantifies lsd 0.2.

for instance, imply differentiation of populations from high elevations (>2,400 m) when separated by about 220 m of elevation, but suggest little differentiation among populations from lower elevations. Similarly, analyses of growth from a common 2-yr height at Priest River (PRDEV) suggest differentiation among populations from low elevation (<2,300 m) if separated by at least 220 m of elevation, but imply little differentiation among the populations at higher elevations.

The models thus suggest that elevation and, therefore, length of the frost-free period are closely related to genetic differentiation. This means that at localities such as the Tularosa Mountains (locality G, Fig. 1) where the elevational distribution of ponderosa pine is broad (Fig. 3), genetic differentiation across the landscape is pronounced.

A geographic component to genetic variation was detected in all of the variables (Table 3), and is illustrated in Fig. 3 by regression lines of different intercept. This component is shown in detail for six variables in Fig. 4 where genetic variation among populations predicted for an elevation of 2,400 m is represented by isopleths. In this figure, the interval between isopleths equals ½ lsd 0.2. This means that populations separated by a geographic distance equaling two intervals are expected to differ at about the 20% probability level. Geographic patterns for other variables are documented in Table 4 where the slope of the cline is described as steep when the distance between isopleths averages less than 50 km, moderate when averaging between 50 and 100 km, and shallow when averaging more than 100 km. Here also, in describing the direction of a cline, the geographic direction listed first is that toward which highest values are predicted.

Although geographic patterns were detected for all variables, the model for the growth from a common 2-yr

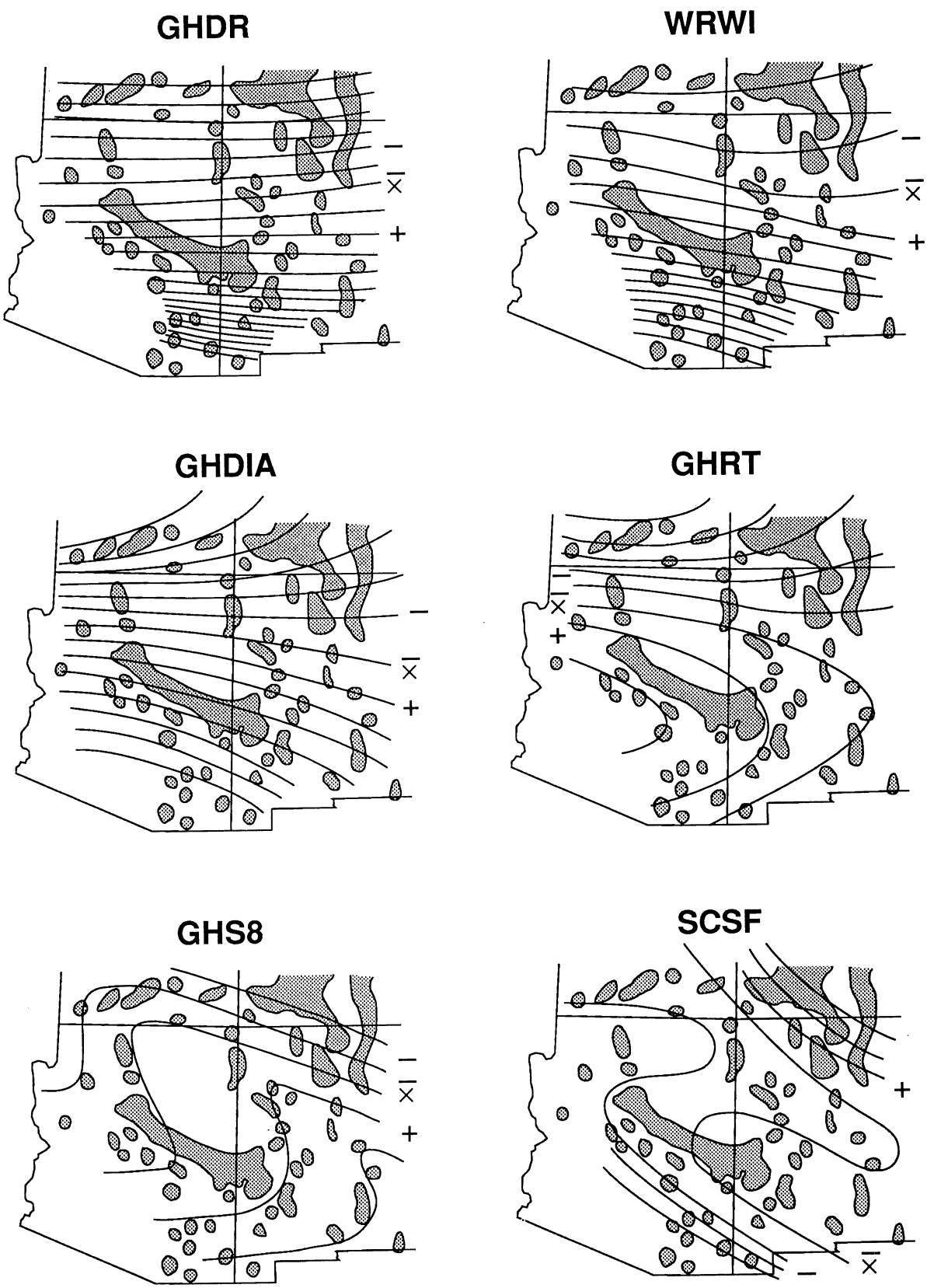

Fig. 4. Geographic patterns of variation for six variables predicted by regression models for populations at a common elevation (2,400 m). Isopleths connect populations of similar performance, and the interval between isopleths equals ½ lsd 0.2. The mean isopleth ($\bar{X}$) along with the positive (+) and negative (−) deviations from the mean are marked. Variables are referenced in Table 2.

TABLE 5. *Simple correlations of selected variables with all variables. Only those coefficients with an absolute value greater than 0.30 are presented. All coefficients are statistically significant at probabilities less than 0.001*

	GHDR	WRWI	SCDEV3	PRLL	PRCL	GHLNM
PRHT4	0.85	0.71	0.48	0.81	0.47	0.42
PRDIA	0.83	0.70	0.30	0.76	0.38	0.58
PRDEV	0.57	0.59		0.51		0.56
PRCL	0.46	0.48	0.50	0.43	1.00	
PRRTO	0.35		0.69	0.33	0.46	−0.31
PRLL	0.70	0.62	0.39	1.00	0.42	0.30
PRLW						
PRLNM	0.49	0.53		0.32		0.81
SCHT4	0.81	0.64	0.75	0.75	0.56	
SCSF			−0.58		−0.42	
SCDEV3	0.44	0.35	1.00	0.39	0.50	
SCDEV4	0.63	0.53		0.57		0.49
WRHT4	0.71	0.48	0.59	0.68	0.40	
WRDEV						
WRWI	0.75	1.00	0.35	0.62	0.48	0.53
WRLL	0.47	0.39	0.40	0.58		
WRDEAD	0.38	0.46				0.30
GHEL	0.91	0.70	0.46	0.74	0.48	0.40
GHS2						
GHS8	0.30					
GHEN	0.99	0.75	0.46	0.71	0.45	0.49
GHDR	1.00	0.75	0.45	0.70	0.46	0.49
GHRT	0.65	0.50	0.41	0.65	0.39	
GHHT2	0.82	0.61	0.58	0.72	0.55	
GHDIA	0.88	0.76	0.44	0.72	0.47	0.53
GHLL	0.59	0.49	0.36	0.72	0.40	
GHLNM	0.49	0.54		0.30		1.00
GHRTO						−0.43

height at Window Rock (WRDEV) failed to predict differences that exceeded lsd 0.2. This variable, moreover, was the only variable for which the effects of populations lacked statistical significance. Of the 27 remaining variables, 18 exhibited geographic patterns that were described by latitudinal clines or variations thereon (Table 3); four of these latitudinal clines are presented in Fig. 4. All but two of the latitudinal clines were inclined toward the south; for only the ratios of height to diameter (PRRTO and GHRTO) were the largest values (least stocky trees) found to the north. Together, these clines illustrate that when populations from the same elevation are compared, growth potential decreases as latitude increases and the length of the frost-free period decreases. As a result, variables as different as the duration of shoot elongation in the greenhouse (GHDR) and winter injuries at Window Rock (WRWI) can exhibit patterns that are nearly identical (Fig. 4).

While latitudinal clines were the strongest of the geographic patterns, two secondary patterns were also evident. The strongest of these secondary patterns (Fig. 4) occurred across an axis from northeast to southwest and showed that populations from the Rocky Mountains were the earliest to begin shoot elongation in the greenhouse (GHS8) and were the most susceptible to damage from the early spring frost at Silver City (SCSF and SCDEV3). Another weak pattern (not presented) occurred from southeast to northwest and also tended to separate populations from the Rocky Mountains from those of the Southwest.

Clines involving both elevation and latitude were prominent in regression models for 16 of the variables. This implies that many of the variables were strongly intercorrelated (Table 5), a result common in studies of population differentiation in ponderosa pine (Rehfeldt, 1986a, b, 1990).

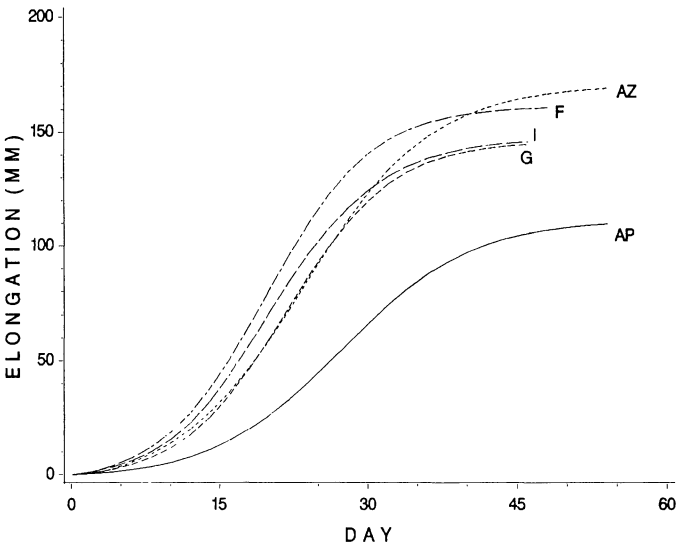

Fig. 5. Mean cumulative shoot elongation of seedlings of Arizona pine (AZ), Apache pine (AP), and three populations of ponderosa pine, keyed to Fig. 1. The populations of ponderosa pine were geographically proximal and elevationally similar to those of the other species.

Biosystematic implications—Some of the effects of populations detected by the analysis of variance (Table 3) result from differences between ponderosa, Apache, and Arizona pines. Differences among these species are readily illustrated by patterns of shoot elongation (Fig. 5). Apache pines tended to start elongation the latest, elongated at the slowest rate, and elongated the least, despite having a long duration of shoot growth. Seedlings of Arizona pine coupled a high rate of elongation with a long duration to achieve the highest growth potential. Seedlings of ponderosa pine grew at a rapid rate but ceased elongating early.

A comparison of mean values of seedlings representing the three species and the Barfoot population (Table 6) shows, first, the numerous traits that differentiate Apache and ponderosa pines. Apache pine's lower growth potential, longer leaves, slower rates of shoot elongation, and stockier form are prominent. Differences between the population of Arizona pine and those of ponderosa pine center on Arizona pine's higher leaf counts, narrower leaves, and slightly higher growth potential. It follows, therefore, that seedlings of Arizona pine differed from those of Apache pine in nearly all characters measured. The trees from Barfoot, however, minus those trees with leaf morphologies of Arizona pine, differed from ponderosa pine for about one-half of the characters that separated Arizona pine and ponderosa pine. These same trees, moreover, differed from ponderosa pine for three of the characters that separated Apache pine from ponderosa pine.

The canonical discriminant analyses produced two eigenvalues that accounted for at least 90% of the variance among the four groups discussed above. In fact, for all

TABLE 6. *Mean values for seedlings from five populations of ponderosa pine as compared to those of the Arizona pine, Apache pine, and Barfoot populations. For populations other than ponderosa pine, only those means are presented that deviate from ponderosa pine by an amount greater than lsd 0.01. The populations of ponderosa pine were geographically proximal and elevationally similar to those of the other groups*

Variable	Units	Apache pine	Arizona pine	Ponderosa pine	Barfoot
PRHT4	cm	68.1	105.5	90.8	
PRDIA	mm	25.0		18.9	
PRDEV	cm		7.9	0.9	9.8
PRCL	Score	0.66	1.00	0.89	1.00
PRRTO	cm/mm	1.7		3.0	2.6
PRLL	cm	21.3		18.5	
PRLW	mm		1.1	1.7	1.5
PRLNM	Count		4.57	3.04	3.30
SCHT4	cm	56.2		68.7	
SCSF	Score	1.3		2.1	
SCDEV3	cm	0.7		1.7	
SCDEV4	cm	12.0	13.5	−0.9	
WRHT4	cm	17.1		28.8	
WRDEV	cm			−1.1	
WRWI	%	95.0	95.2	56.4	92.5
WRLL	cm			7.0	
WR DEAD	%		92.5	21.0	
GHEL	mm	111.5		153.6	
GHS2	d	6.9		4.0	
GHS8	d	13.6		8.6	
GHEN	d	51.4	52.3	42.9	48.8
GHDR	d	44.5	47.8	38.9	44.8
GHRT	mm/d	4.2		7.0	
GHHT2	mm	190.7		276.8	
GHDIA	mm	9.4		7.5	9.3
GHLL	cm			15.7	
GHLNM	Count	3.29	4.86	3.09	3.67
GHRTO	mm/mm	20.7		37.2	29.8

but the Window Rock data set, the first two eigenvalues accounted for at least 96% of the variance between groups. In Fig. 6, scores for each seedling are plotted for the first two canonical variables for Priest River and greenhouse data. Only about one-half of the plots are presented for ponderosa pine, although the range and density of plotted values are accurately depicted. Discriminant scores for data from Silver City and Window Rock are not presented because the results were of lesser resolution. While it may seem anomalous for the two least natural of the test sites to provide the results of greatest resolution, one must recall that 1) Arizona and Apache pines performed poorly in the harsh environment at Window Rock, and 2) the leaf characters and ratios of height to diameter that prominently distinguished the species (Table 6) were not measured at Silver City.

For both the Priest River and greenhouse data sets, the discriminant function nicely separated the three species. On the one hand, the greenhouse data suggested that the Barfoot population is a mixture of ponderosa and Arizona pines, the two of which could be separated by leaf morphology. Thus, the three individuals from Barfoot that had leaf morphologies of Arizona pine fell within the cluster of Arizona pines (Fig. 6). But on the other hand, the distribution of Barfoot trees for Priest River data implied introgression that may even implicate Apache pine. Noteworthy is one seedling that displayed a leaf morphology of Arizona pine but otherwise resembled ponderosa pine.

DISCUSSION

When grown in environmentally disparate common gardens, seedling populations representing the Ponderosae of the Southwest exhibited genetic differences for 27 of the 28 morphological and developmental traits analyzed. While some of this variation was due to interspecific differences, most reflected genetic differentiation among the 95 populations of ponderosa pine that were studied.

Population differentiation—Mathematical models were remarkably successful in describing patterns of genetic variation across the landscape. Because intercorrelations among traits were strong, similar patterns of variation

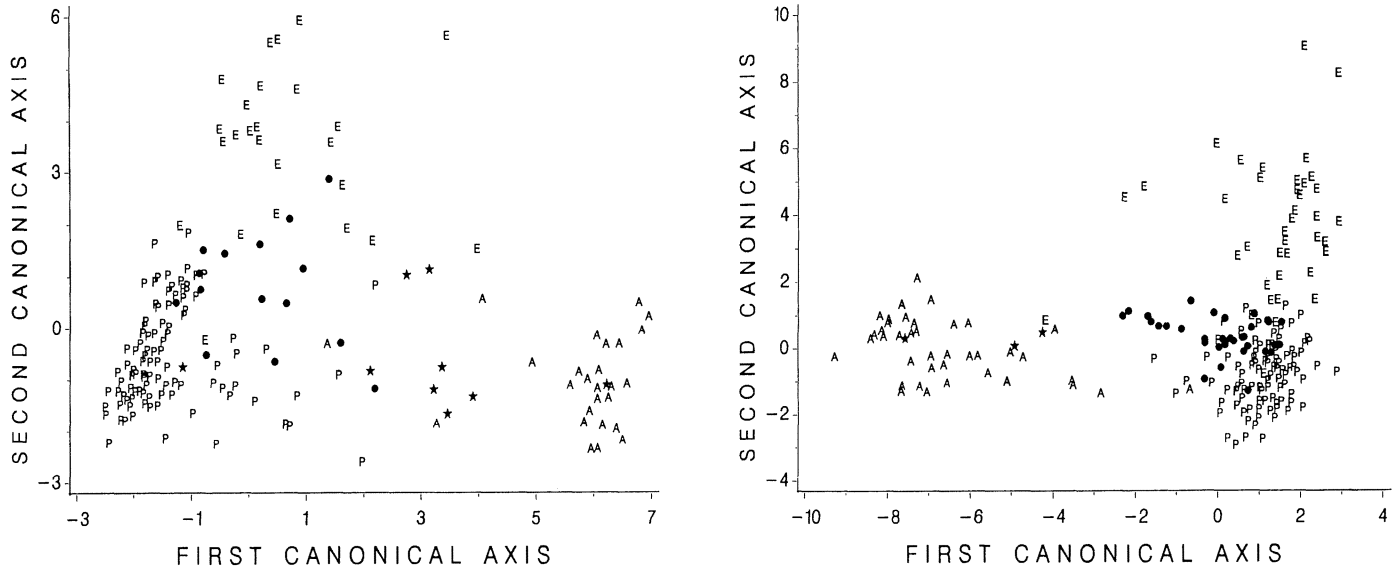

Fig. 6. Results of canonical discriminant analyses for greenhouse studies (left) and Priest River tests (right). P = ponderosa pine; A = Arizona pine; E = Apache pine; asterisk = Barfoot trees with leaf morphologies of *P. arizonica*; circle = other Barfoot trees.

were evident. The most prominent patterns implicated elevation and latitude, two variables whose relation to environmental factors is well known.

Correlated sets of traits apparently have resulted from parallel selection to produce coherent (sensu Clausen and Hiesey, 1960) genetic systems involving the components of an annual sequence of developmental events. This sequence begins with dehardening in the spring; includes shoot elongation, leaf expansion, bud development, diameter growth, and lignification; and concludes with cold acclimation. As described by Dietrichson (1964), the sequence has been molded to fit within a growing season of finite length, and, therefore, the duration of events tends to be intercorrelated. As a result, a diverse assortment of variables becomes correlated even though the traits might be measured in very different environments. In this case, the duration of shoot growth (GHDR), the number of leaves per fascicle (GHLNM and PRLNM), winter injury at Window Rock (WRWI), leaf lengths (PRLL and GHLL), stem color (PRCL), spring frost damage at Silver City (SCDEV3 and SCSF), and various expressions of growth potential are strongly intercorrelated. Because shoot growth in ponderosa pine is predetermined (Sacher, 1954), the pattern of shoot elongation can act as a surrogate for understanding the adaptation of the entire sequence to a heterogeneous environment.

Genetic variation that is systematically distributed along environmental gradients undoubtedly arises from natural selection. Selection apparently has molded a system of loosely intercorrelated traits that jointly adapt populations to the Southwest's spatially heterogeneous environments, a conclusion compatible with results of studies of the same species from the Colorado Plateau (Rehfeldt, 1990), the Inland Northwest (Madsen and Blake, 1977; Rehfeldt, 1991), the Sierra Nevada (Callaham and Liddicoet, 1961; Conkle, 1973), and the eastern slopes of the Rocky Mountains (Read, 1980, 1983).

Elevational clines have direct microevolutionary interpretations. As elevation increases, temperatures decrease, with a reduction in mean annual temperature of 1 C leaving 12 fewer frost-free days (Baker, 1944). Consequently, seedlings from populations distributed along an elevational gradient 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 relatively long period, and become large; populations adapted to short growing seasons cease development early and tend to be small. In the Southwest, an elevational interval of 1,000 m tends to be associated with a change of 90 frost-free days (Baker, 1944). As shown in this study, populations separated in elevation by about 220 m tend to be different genetically. This suggests that populations occupying environments that differ by 20 frost-free days tend to differ genetically. This conclusion is remarkably similar to that reached for the same variety on the Colorado Plateau (22 d) but is much less than that obtained for *P. p.* var. *ponderosa* in the Inland Northwest (35 d).

The latitudinal clines also seem to reflect adaptation to frost-free periods of variable length. Baker (1944) shows that for a constant elevation, the frost-free period differs by about 70 d between the San Juan Mountains and the Tularosa Mountains (Fig. 1). In Fig. 4, each isopleth represents ½ lsd 0.2, a value that equals the amount of differentiation expected between populations separated by 110 m (10 frost-free d) along the elevational cline. If, then, the latitudinal clines reflect differentiation associated with the frost-free period, there should be about seven isopleths separating the San Juan and Tularosa Mountains. Of the latitudinal clines in Fig. 4, nine isopleths separate these localities for GHDR, seven for WRWI, eight for GHDIA, and six for GHRT. Clearly, much of the variation associated with both latitude and elevation reflects adaptation to the length of the frost-free period.

Secondary geographic clines were much weaker than the latitudinal clines and tended to separate populations from the Rocky Mountains from those of the Southwest (see GHS8 and WRWI, Fig. 4). This separation was also apparent for populations from the Colorado Plateau (Rehfeldt, 1990) and seemed to reflect the transition from a climate dominated by winter–spring droughts in the Southwest to that characterized by summer droughts in the Rocky Mountains. Populations from the continental climate of the Rocky Mountains initiate shoot elongation rapidly while those from the Southwest initiate shoot activity more slowly. Because of this, southern Colorado populations were the most susceptible to damage from a late spring frost at Silver City (SCSF, Fig. 4).

Together, the elevational and geographic clines describe complex patterns across the landscape. Populations inhabiting the same elevation in different mountain ranges tend to be different genetically (Fig. 3). This also means that populations capable of similar responses are expected to recur at different elevations in different mountain ranges. For instance, populations capable of developing relatively long leaves (e.g., GHLL = 150 mm, Fig. 2) are expected at 1,750 m in the Bradshaw Mountains (locality E), 2,000 m in the Sacramento Mountains (locality H), 2,300 m in the Pinaleno Mountains (locality I), and 2,800 m in the Tularosa Mountains (locality G).

Examining the frequency by which populations that exhibit similar responses recur with respect to several variables is facilitated by using the regression model. Each regression equation can be used to generate a data base containing predicted values for the entire geographic and elevational distribution of ponderosa pine within the region of study. Then, by surrounding each observation in the data base with a confidence interval of ±½ lsd 0.2, populations readily can be grouped according to similar responses.

The expected recurrence of populations capable of similar responses is illustrated in Fig. 7 for six targeted populations (pyramids). For populations in the center of large continuous distributions (Tularosa Mountains [locality G] and Sangre de Cristo Mountains [locality C]) recurrence is widespread. But recurrence is considerably restricted for populations in isolated mountain ranges whether the locality is on the periphery (Bradshaw Mountains [locality E] and Sacramento Mountains [locality H]) or in the center (Defiance Plateau [locality D]) of the species distribution. For the isolated ranges in southeastern Arizona (Pinaleno Mountains [localityI]), however, recurrence is extremely limited (Fig. 7).

Practical uses of models of genetic variation are numerous and diverse (see Rehfeldt, 1991). For artificial reforestation, one can assume that the targeted locations

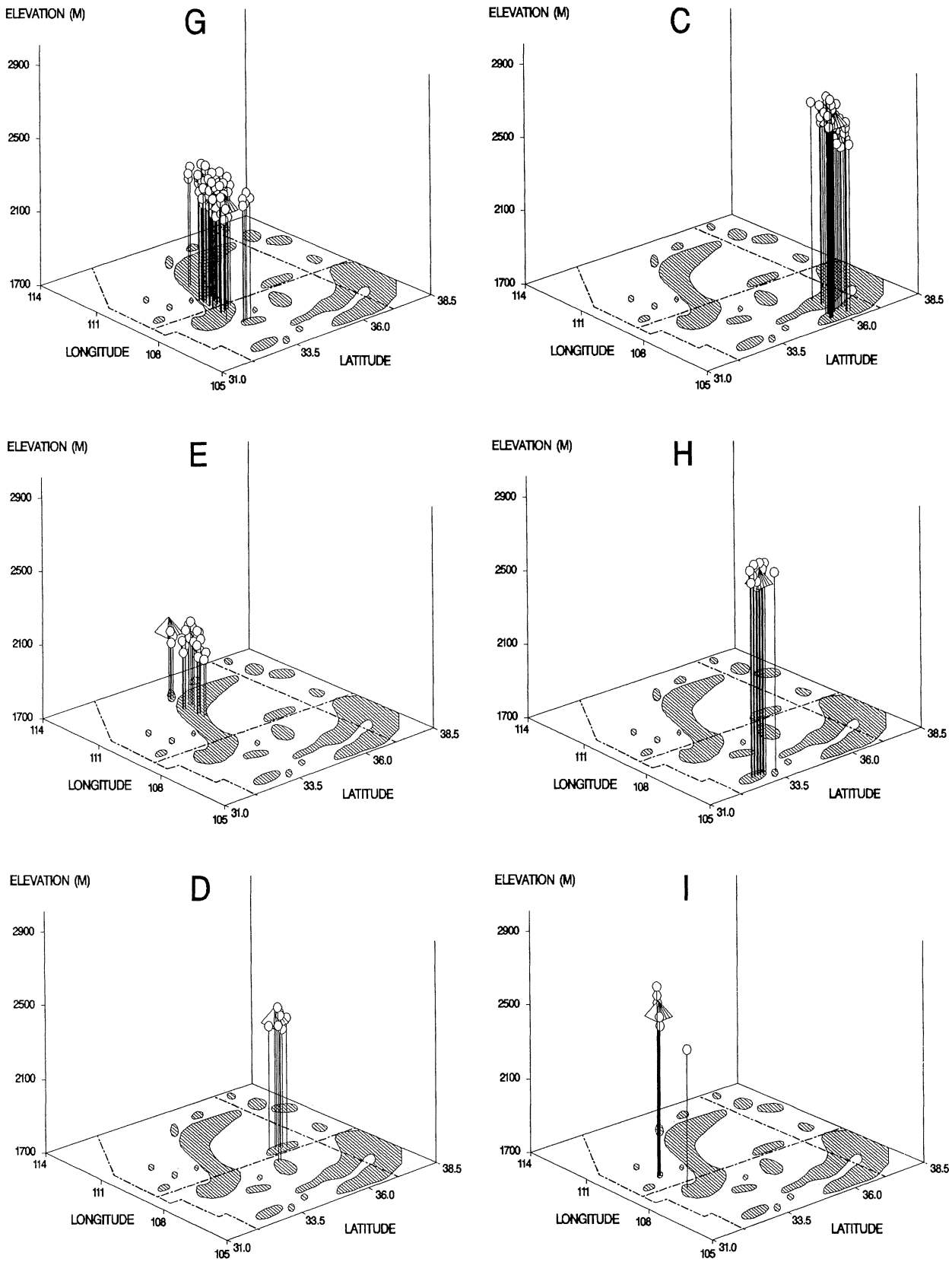

Fig. 7. Using models of genetic variation to locate populations (balloons) expected to exhibit responses in common gardens that are similar to those of a targeted population (pyramid). Letters key the general geographic locality (Fig. 1) of the target population.

represent either planting sites or seed production areas. The model can then be used to 1) locate sources of seeds that should be genetically compatible with the environment at the target, or 2) select planting sites for which seeds gathered from the targeted population should be adapted. The model might also be used to locate disjunct populations so unique genetically that gene conservation programs may be desirable as, for example, in the Pinaleno Mountains (locality I). Additional uses might include assessing the impact of climate change on the adaptedness of populations, understanding phenotypic variation, and delimiting seed orchards and breeding zones.

The usefulness of a model, however, depends on its credibility, and a first step in acquiring credibility involves verification. Unfortunately, independent data currently are not available for verifying the present model. Therefore, the model should be used with discretion. In addition, genetic variation might be occurring along clines independent of those already detected. This would mean that the recurrence of similar populations across the landscape is more restricted than the results imply. For this reason, functional models require periodic updating as additional mathematical descriptors become available. Finally, credibility requires that the appropriate species are ecologically suited to the elevations and localities for which predictions are made. This means that data bases must be firmly coordinated with the ecological distribution of the species; until physiographic predictors are replaced by environmental variables, models should not be used for extrapolation.

Nevertheless, the results attest to pronounced levels of genetic variation among populations of southwestern ponderosa pine. It seems reasonable to conclude that much of the variation has been molded by heterogeneous environments. Microevolutionary processes undoubtedly have been furthered by ponderosa pine's discontinuous distribution in the Southwest. Such distributions limit gene flow and thereby promote selective differentiation.

Biosystematic implications—Conkle and Critchfield (1988) separate the southwestern race of *P. p.* var. *scopulorum* from the Rocky Mountain race in southern Utah and southwestern Colorado. Yet the results of this study, like those from the Colorado Plateau (Rehfeldt, 1990), demonstrate continuous genetic variation along geographic and elevational gradients. To be sure, populations from southern Arizona and New Mexico differ tremendously from those in Utah and Colorado. While these differences may be sufficient to justify the racial classifications, the transition between races is unquestionably broad.

The results also support Peloquin's (1971) contention that introgression among species of Ponderosae is common in southeastern Arizona. While Peloquin reached his conclusions from phenotypic observations in natural populations, the present results suggest introgression from the performance of progenies from Barfoot. One might, moreover, interpret several of the patterns of geographic variation in ponderosa pine according to introgressive hybridization. As illustrated by the duration of shoot elongation in the greenhouse (GHDR) and winter injuries at Window Rock (WRWI) in Fig. 4, the slope of geographic cline for nine variables became the steepest in southeastern Arizona. Of these nine, the patterns for three variables could have been interpreted as introgression with Apache pine, while those for the other six variables could have been interpreted in terms of introgression with Arizona pine. Although logical, such interpretations must be tempered by the fact that only two ponderosa pine populations were sampled from the isolated ranges in southern Arizona, and the southernmost of these was Barfoot. Since Barfoot seems to be introgressed, it is likely that the change in the slope of geographic clines in southern Arizona was due to the fitting of the regression to the performance of Barfoot progenies rather than to widespread introgression.

Nevertheless, these results along with those of Peloquin support introgression, primarily involving ponderosa and Arizona pines but also implicating Apache pine. Yet the degree of hybridization, the amount and direction of gene flow, and the ecological genetics of species of the Ponderosae in the Southwest deserve a thorough examination.

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