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Components of Adaptive Variation in *Pinus contorta* from the Inland Northwest

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RESEARCH SUMMARY

Genetic variation among 83 populations of *Pinus contorta* from the Northern Rocky Mountains of the United States was studied with 7-year-old trees planted in three contrasting environments. Analyses of nine traits reflected adaptation to biotic and abiotic environments and revealed clinal patterns of differentiation that were elevationally steep but geographically gentle. In particular, populations from relatively mild environments had the highest growth potential but suffered the most snow damage when planted at high elevations. Populations from high elevations were most susceptible to needle cast when transferred to low elevation. And populations transferred the greatest geographic distances suffered the most from infestations of mites. Regression models present adaptive landscapes that mirror elevational and geographic gradients in climate.

Components of Adaptive Variation in *Pinus contorta* from the Inland Northwest

G. E. Rehfeldt

INTRODUCTION

Adaptive differentiation is discernible either directly as differential fitness in contrasting environments or indirectly as genetic responses that parallel environmental gradients. In *Pinus contorta* Dougl., for example, four geographic races are distinguished both morphologically (Critchfield 1957) and enzymatically (Wheeler and Guries 1982). Critchfield (1980) reviewed numerous studies that provide direct and indirect evidence of differential adaptation of races to climates as diverse as those of the northern Pacific Coast, the Sierra Nevada, the interior Rocky Mountains, and the Canadian subarctic.

In *P. contorta* spp. *latifolia*, the subject of this paper, genetic variation among populations is pronounced. Canadian populations, native to a region of dissected plateaus, are arranged along gentle clines that follow climatic gradients across 18° of latitude from the Yukon to southern British Columbia (Hagner 1970; Lindgren and others 1976; Ying and others 1985). In the mountains of Idaho (Rehfeldt 1983a), Utah (Rehfeldt 1985a), and Oregon (Stoneman 1985), population differentiation occurs along steep elevational clines that parallel the environmental changes associated with altitude. Whether geographic or elevational clines predominate, populations from mild environments express a high innate growth potential and low cold hardiness, while those from severe environments display a low growth potential and high hardiness.

Adaptive clines result from environmental selection of phenotypes that, for long-lived trees, develop in environments of extreme temporal heterogeneity. Adaptedness, therefore, has many component traits. A consideration of the interrelationships among components inspired Lande (1982) to argue that negative genetic correlations are often obscured phenotypically but commonly set the limits on microevolution. In trees, for example, negative genetic correlations relate growth potential and cold hardiness within families of both *Pseudotsuga menziesii* (Mirb.) Franco and *P. contorta* (Rehfeldt 1984). This means that an assessment of adaptive differentiation requires an understanding of component traits and their interrelations. Lande (1982) stressed that this understanding is particularly necessary for fields such as forestry where the traits of agronomic importance—growth and yield—are also major components of fitness.

The present study of *Pinus contorta* assesses genetic variability among populations, relates genetic variability to adaptive differentiation, and presents adaptive landscapes for the Inland Northwest.

DISTRIBUTION, ECOLOGY, AND DEMOGRAPHY

Adaptive variation must be interpreted according to the spatial environmental heterogeneity within the region of study (fig. 1). The climate of the Inland Northwest varies from the continental in the east to that with a coastal component in the west (Daubenmire and Daubenmire 1968; Pfister and others 1977). This general trend is reflected not only in gradients of temperature and precipitation (fig. 2), but also in the composition and distribution of plant communities (Daubenmire and Daubenmire 1968; Pfister and others 1977; Steele and others 1981). Superimposed on general climatic gradients are the topographic microclimates associated with mountainous terrain. Extreme environmental heterogeneity thus develops from a climatic transition that occurs across a series of rugged mountain ranges.

In the Rocky Mountains, *P. contorta* displays such a broad ecological distribution that it is capable of growing in almost any forest environment (Pfister and Daubenmire 1973). As an early successional species, the pine is common in a variety of plant communities that include associations dominated at maturity by *Tsuga heterophylla* (Raf.) Sarg. on mesic sites, *Pseudotsuga menziesii* (Mirb.) Franco on dry sites, and *Abies lasiocarpa* (Hook.) Nutt. on cold sites (Daubenmire and Daubenmire 1968; Pfister and others 1977; Steele and others 1981). The species forms large continuous populations on subalpine sites at elevations up to 3,000 m and in frost pockets on valley floors as low as 600 m.

Natural populations of *P. contorta* tend to be established in cycles (Lotan and others 1985). Greatly simplified, these cycles involve (1) wildfire, (2) profuse even-aged reproduction of as much as 500,000 seedlings/ha from either open or serotinous cones (Tackle 1959), (3) intense natural thinning, which can leave as few as 1,000 trees/ha by age 80 (Tackle 1959; Benson 1982; Vyse and Navratil 1985), and (4) epidemics of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Amman and others 1973; Shrimpton and Thomson 1983), which supplement the competitive mortality to provide the fuel for (5) wildfire.

These demographic cycles have pronounced effects on the genetics of populations. First, adaptive traits will include all traits that either directly or indirectly influence the expression of growth potential and thereby determine which trees are living when fires occur. And second, populations are frequently established on the same sites on

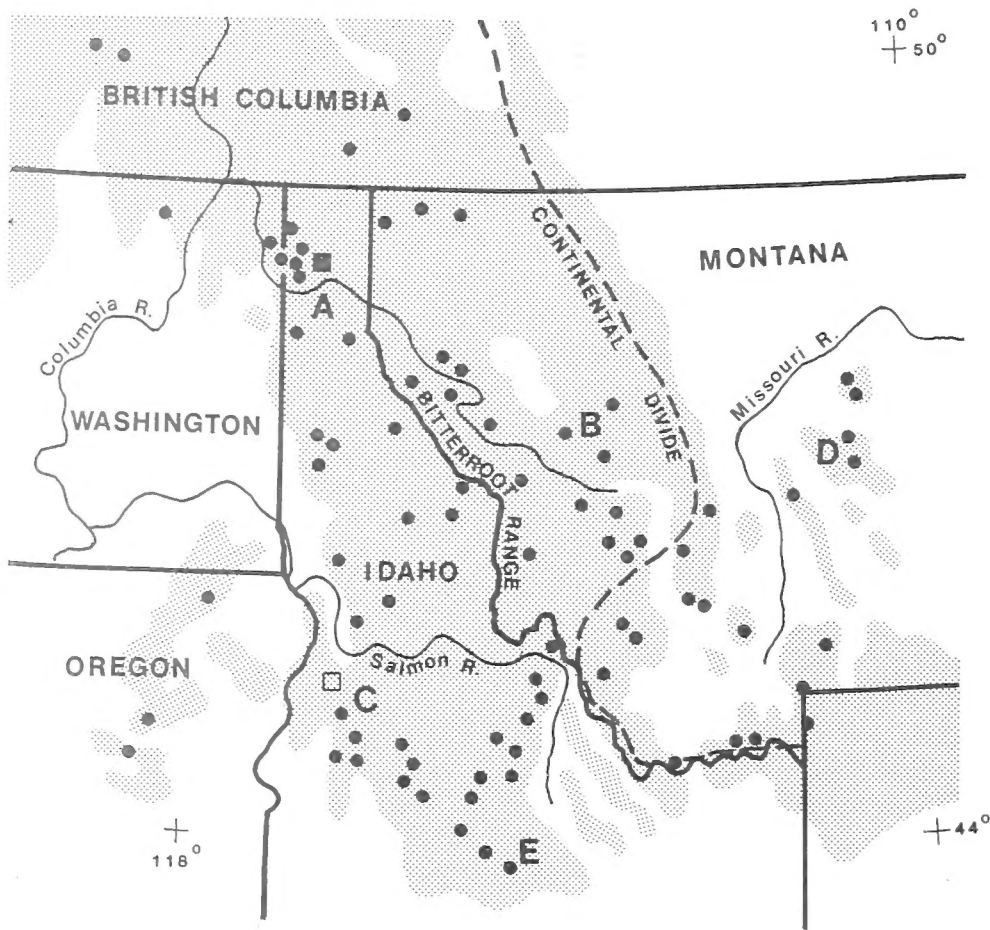


Figure 1—Distribution (shading) of *Pinus contorta* (from Little 1971) within the Northern Rocky Mountains, and location of populations sampled (dots). Letters A to E locate the elevational clines of figure 3. □ = Lost Valley, ■ = PREF.

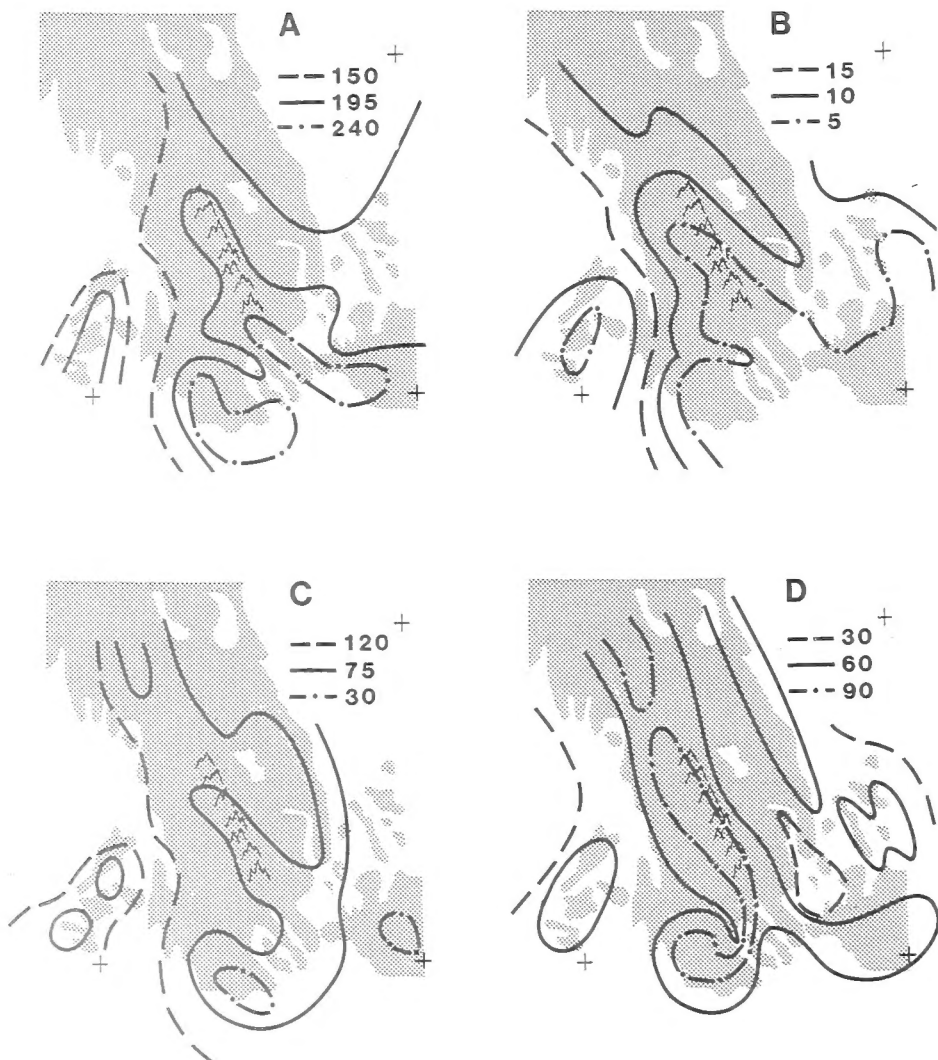


Figure 2—Climatic isopleths in relation to the distribution of the species (shading) and location of the Bitterroot Range (symbols) for (A) mean annual number of days with temperatures lower than 0 °C, (B) mean annual days with temperatures greater than 30 °C, (C) average annual frost-free period, and (D) mean annual precipitation (cm) (U.S. Department of Commerce 1968).

which ancestral populations grew, and therefore coadaptive complexes of traits can readily be perpetuated once such complexes arise.

Thus, a broad ecological distribution, a unique cycle of population establishment, and occupancy of an extremely heterogeneous environment make *P. contorta* an ideal species for studying adaptedness, the degree by which individuals are physiologically attuned to their environment.

MATERIALS AND METHODS

Genetic variation was studied in seedlings from 83 populations (fig. 1) that represented the geographic and ecological distribution of *P. contorta* in the Northern Rocky Mountains. Populations ranged in elevation from 640 to 2,700 m and represented habitat types as diverse as the *Tsuga heterophylla/Pachistima myrsinites* on moist sites and the *Abies lasiocarpa/Vaccinium scoparium* in subalpine communities.

Because of pronounced genetic heterogeneity within populations (Rehfeldt 1985b; Ying and others 1985), cone collections were conducted in a manner to assure that subsequent seedling populations would represent a large number of parental trees. Thus, about 250 wind-pollinated cones, each containing about 25 viable seeds, were selected from several squirrel caches in each population. Genetic diversity was further assured by selecting a variety of cone morphologies, sizes, and colors from each cache.

Seedlings were grown for 6 months in plastic containers (65 cm³) in a shadehouse at Moscow, ID (lat. 48.5° N., long. 116.7° W.). In the fall, seedlings were planted at three locations (fig. 1): at 640 m and 1,500 m elevation on the Priest River Experimental Forest (PREF), and at 1,500 m in Lost Valley. The experimental design consisted of a random allocation of linear seedling plots within rows of a rectangular planting. A plot comprised eight seedlings from each population. Nine plots represented each population at PREF sites, and six plots represented each population at Lost Valley. Thus, 72 seedlings represented each population at both PREF sites while 48 represented each population at Lost Valley. The spacing of seedlings within and between rows was: 0.5 m and 1 m, respectively, at PREF 640; 0.5 m and 0.5 m at PREF 1,500; and 1 m and 1 m at Lost Valley.

Intensive culture at PREF included control of competing vegetation, gophers, and white grubs. The site at 640 m was irrigated once during years 2 and 3. No control of extraneous environmental effects was provided at Lost Valley. Variable cultural regimes and spacing of trees in different physical environments sample a range of conditions under which populations exist naturally. Survival was 76 percent at PREF 640, 83 percent at PREF 1,500, and 65 percent at Lost Valley.

Periodic measurements or scores provided the following variables:

1. Mean height for each plot after 3 years.
2. Height of individual trees after 7 years.
3. Adjusted height: the 7-year height of individual trees adjusted by regression on 5-year height.
4. Late growth of trees at PREF: the amount of the 7-year, predetermined shoot that elongated after the date

when the uppermost leaves of the shortest trees were approximately 2 cm long (June 4 at 640 m; July 3 at 1,500 m).

5. Needle cast: the proportion of 6-year leaves of individual trees at PREF 640 that were infected with *Lophodermella concolor* (Dearn.) Darker, scored in July of year 7 with values of 1 to 5, which coded <5 percent, 25 percent, 50 percent, 75 percent, or >95 percent infected leaves.

6. Mites: the presence or absence of *Trisetacus camp-nodus* Keifer (Hunt 1981) on 7-year shoots of individual trees at PREF 640.

7. Shoot borers: the presence or absence of *Eucosma sonomana* Kearfott on the 7-year shoots of individual trees at PREF 640.

8. Frost injury: presence or absence of spring frost injury to the developing 7-year shoot at PREF 640.

9. Snow damage: scored in the spring of year 7 as the presence or absence of basal injuries of individual trees at PREF 1,500 sufficient to expose the inner bark.

Population differentiation was assessed with data from individual trees for all variables except snow damage, frost injury, mites, and shoot borers, for which the proportion of injured trees in each plot was analyzed. Allometric traits were transformed to logarithms because variances were proportional to the square of mean values. Scores of needle cast were transformed to \sqrt{X} to normalize distributions. Three-year height was not subjected to rigorous analysis but was used only for correlation.

Statistical analyses followed a general model of unweighted means (Steel and Torrie 1960):

$$Y_{ijkl} = \mu + s_i + p_j + sp_{ij} + d_{k(ij)} + e$$

where Y_{ijkl} = the performance of the l th tree of the k th plot of the j th population at the i th planting site, μ = the overall mean, s = the effect of the planting site, p = the effect of the population, sp = the interaction of sites and populations, d = the effect of plots within populations and sites, and e = the residual.

Multiple regression models were used to relate genetic variation to the elevation and geographic location of the seed source. Independent variables included elevation, latitude, longitude, northwest departure, southwest departure, and their squares. Northwest and southwest departures were derived by rotating the grid of latitude and longitude by 45°. Geographic variables were nested within four geographic regions that had proven useful in previous analyses (Rehfeldt 1980; Rehfeldt and Wykoff 1981): Idaho north or south of the Salmon River, and Montana east or west of the Continental Divide (fig. 1). However, the geographic regions were not represented by dummy variables because such variables force continuous genetic variation to be described discontinuously. Interactions of elevation and geographic variables were not considered because preliminary analyses indicated that the effects of elevation could be described by similar regression coefficients in all geographic regions. Thus, 34 independent variables were screened by a stepwise regression model for maximizing R^2 (SAS 1982) according to the general model:

$$Y_i = \beta_0 + \beta_1 E_i + \beta_2 E_i^2 + \sum_{j,k} \gamma_{jk} X_{ijk} + \sum_{j,k} \delta_{jk} X_{ijk}^2$$

where Y_i is the performance of population i ; E_i is the elevation of population i ; X_{ijk} is geographic variable k for population i in geographic region j ; and $\beta_0, \beta_1, \beta_2, \gamma_{jk}$, and δ_{jk} are regression coefficients, $j = 1 \dots 4$, $k = 1 \dots 4$.

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

RESULTS

Environmentally diverse planting sites strongly influenced growth and development of seedlings (table 1). While the average tree at PREF 640 was 106 cm tall, that at PREF 1,500 and Lost Valley was only 76 cm and 62 cm, respectively. Values for adjusted height imply that, even if all trees had been the same height at age 5, by age 7 those at PREF 640 would still have been about 10 cm taller than trees on the other sites. Main effects of test environments are also expressed by the occurrence of snow damage only at high elevations and by the relatively high incidence of needle cast, shoot borers, and frost injuries at low elevation. Environmental effects on late growth also were pronounced; similar stages of shoot elongation occurred about 1 month later at PREF 1,500 than at PREF 640.

In these heterogeneous planting environments, mean differences between populations were statistically significant for all traits except adjusted height (table 1). Pronounced effects of populations were associated with mean differences as large as 55 cm in 7-year height, 5 cm in late growth, 78 percent in leaves infected with needle cast, and 65 percent in number of trees exhibiting snow damage. Weak effects of populations were evident for mites, spring frost damage, and shoot borers largely because of low incidence for each variable. Thus, mites occurred on only 10 percent of the trees, but as many as 33 percent of the trees from one population were infested. The proportion of trees damaged from a spring frost was only 2 percent, but mean values for populations ranged up to 11 percent. And the incidence of shoot borers for most populations was incidental (<5 percent), but 19 percent of the trees were injured in one of the British Columbia populations.

Interactions of provenances and test environments were also significant for all variables measured on more than one site (table 1). Interactions for late growth and 7-year height obviously represented a scale effect because simple correlations of population means for the same variable at different sites ranged from 0.80 to 0.92. The interaction for adjusted height most likely resulted from various maladaptations that have accumulated between ages 5 and 7 and have differentially affected the height of populations at each planting site. This interaction is clarified by subsequent analyses that consider adjusted height at each test site as separate traits.

Simple correlations (table 2) describe a relationship between the height of populations at ages 3 and 7 that is nearly perfect ($r = 0.94$). Other extremely strong correlations (table 2) show that the tallest populations at ages 3 and 7 also (1) produced the most 7-year elongation after midsummer (late growth) regardless of test site, (2) grew the most from a common height at age 5 when planted at low elevation, (3) suffered little needle cast and few injuries from spring frost when planted at low elevation, but (4) were the most susceptible to snow damage at high elevations. Populations that were short also had little late growth, suffered the least snow damage, but were most susceptible to needle cast at low elevations. Table 3 illustrates that the tallest populations suffered the most injury from autumn freezing tests (Rehfeldt 1980) and displayed the greatest growth and longest duration of elongation in studies of the periodicity of shoot elongation involving 2-year-old trees (Rehfeldt and Wykoff 1981).

Regression models for relating variation among populations to the elevation and geographic location of the seed source were not only statistically significant for all variables but also accounted for over 80 percent of the genetic variance in five variables (table 4). These models, however, included between 10 and 20 independent variables and were therefore subject to overfitting, the fitting of variables to individual samples rather than to the group (Draper and Smith 1981). Consequently, biological significance of the results is judged with respect to the least significant difference (Steel and Torrie 1960) at the 95 percent level of probability, $lsd (.05)$, calculated from analyses of variance and presented in figure 3.

Table 1—Results of analyses of variance expressed as intraclass correlations. σ_E^2 , σ_P^2 , σ_{PE}^2 , $\sigma_{D(P)}^2$, and σ_W^2 are variance components associated with the effects of environments and populations, interaction, plots in populations, and error variance within plots. σ_T^2 is the sum of all components

Variable	σ_E^2/σ_T^2	σ_P^2/σ_T^2	σ_{PE}^2/σ_T^2	$\sigma_{D(P)}^2/\sigma_T^2$	σ_W^2/σ_T^2
7-year height	0.39**	0.16**	0.03**	0.12**	0.30
Adjusted height	.72**	-.00	.12**	.05**	.11
Late growth	.05**	.29**	.20**	.05**	.41
Needle cast		.52**		.07**	.41
Mites		.05**		.95	
Shoot borer		.05**		.95	
Spring frost injury		.09**		.91	
Snow damage		.40**		.60	

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

Table 2—Matrix of simple correlation coefficients among mean values for 83 populations.
 Absolute values greater than 0.21 or 0.26 are statistically significant at the 5 and 1 percent levels of probability, respectively

Variable	Codes	HT7	AH1	AH2	AH3	LG	NC	M	SB	FI	SD
3-year height	HT3	0.94	0.82	-0.40	0.14	0.88	-0.84	-0.29	0.36	-0.43	0.74
7-year height	HT7		.89	-.26	.29	.94	-.85	-.26	.44	-.41	.72
Adjusted height											
PREF 640	AH1			-.19	.29	.92	-.93	-.26	.41	-.43	.78
PREF 1,500	AH2				+.00	-.13	.31	.24	.02	.13	-.33
Lost Valley	AH3					.25	-.17	.04	.14	-.06	.16
Late growth	LG						-.86	-.20	.45	-.41	.68
Needle cast	NC							.29	-.41	.39	-.76
Mites	M								.09	.14	-.30
Shoot borer	SB									-.12	.23
Frost injury	FI										-.34
Snow damage	SD										

Table 3—Correlation of 30 population means from field tests with laboratory tests of freezing injury (Rehfeldt 1980) and greenhouse evaluations of the periodicity of shoot elongation (Rehfeldt and Wykoff 1981). Coefficients of absolute value greater than 0.35 and 0.45 are statistically significant at the 5 and 1 percent levels, respectively

Variable	Freezing injury	Shoot elongation				
		Amount	Initiation	Rate	Duration	Cessation
3-year height	0.82	0.81	-0.19	0.67	0.79	0.79
7-year height	.81	.80	-.22	.63	.82	.81
Adjusted height						
PREF 640	.75	.62	-.22	.40	.81	.80
PREF 1,500	.32	-.19	-.30	-.25	-.22	-.27
Lost Valley	.09	.17	.25	.16	.14	.18
Late growth	.85	.80	-.26	.61	.81	.80
Needle cast	-.77	-.59	.18	-.42	-.76	-.76
Mites	-.01	-.14	.29	-.03	-.11	-.06
Shoot borer	-.43	.19	-.20	.06	.42	.41
Spring frost injury	.27	-.55	.30	-.48	-.53	-.50
Snow damage	.52	.59	-.17	.47	.69	.69

Table 4—Results of stepwise multiple regression analyses presented as standard errors (s) and coefficients of determination (R^2)

Dependent variable	Independent variables	R^2	s
	Number		
7-year height	10	0.89**	0.0654
Adjusted height			
PREF 640	13	.86**	.0350
PREF 1,500	15	.50**	.0197
Lost Valley	16	.45**	.0273
Late growth	13	.91**	.1878
Needle cast	13	.88**	.1113
Mites	20	.41**	.0536
Shoot borers	13	.41**	.0258
Spring frost injury	15	.40**	.0203
Snow damage	18	.80**	.0740

**Statistical significance at the 1 percent level.

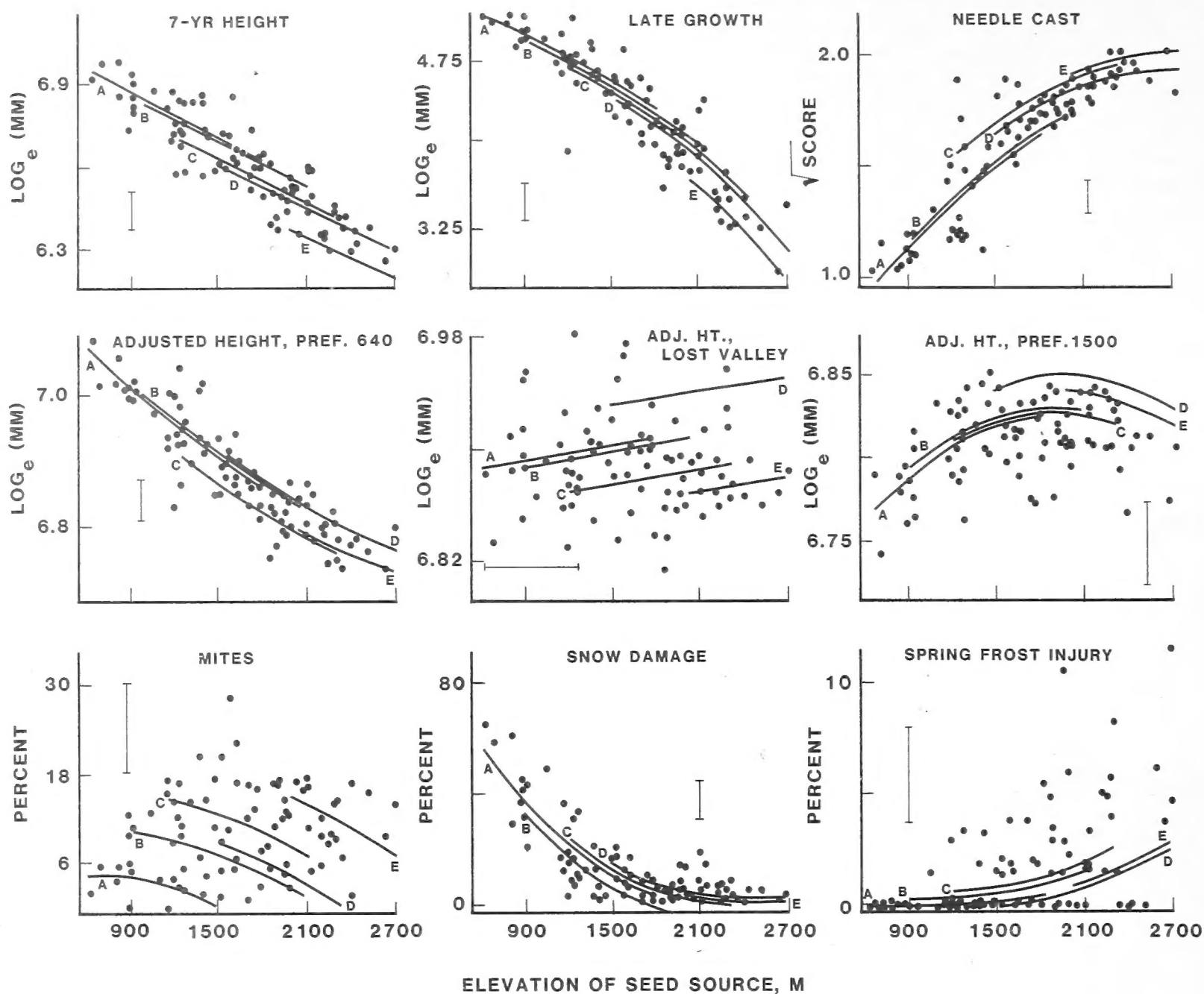


Figure 3—Population means for six variables plotted by elevation of the seed source. Localities A to E are keyed to figure 1. The length of each regression line reflects elevational distributions at each locality. Brackets quantify *lsd* (0.05).

Figure 3 illustrates steep elevational clines for five variables. The higher the elevation of the seed source, the lower the 7-year height, the less the late growth, the greater the needle cast, and the less the snow damage. And, if all trees at PREF 640 had been the same height after 5 years, the height of populations at age 7 still would have been distributed according to elevational clines. Moreover, the model for adjusted height at PREF 1,500 (fig. 3) shows that populations from about the same elevation as the 1,500-m planting site have grown the most from a common height at age 5.

Elevational clines for mites, spring frost injury, and adjusted height at Lost Valley are so gentle that they are biologically insignificant. The model for shoot borers is not presented because it was fit primarily to the population for which 19 percent of the trees were infested.

Because elevation and geography are not independent of each other, geographic patterns of variation can be described either as (1) performance at a constant elevation or (2) performance at a base elevation, the lowest elevation that the species occurs at a given locality. Figure 3 shows that populations at the base elevations for localities A and E, for example, differ tremendously for most traits. But most of these differences arise because populations at base elevations occupy much different positions along the elevational cline (fig. 3).

Nevertheless, geographic variation at a constant elevation was significant for five of the variables (fig. 3). In all cases, however, the differences barely exceeded *lsd* (.05). Therefore, geographic clines for a constant elevation can be described by the relatively gentle clines of figure 4. In this figure, geographic patterns are depicted by isopleths

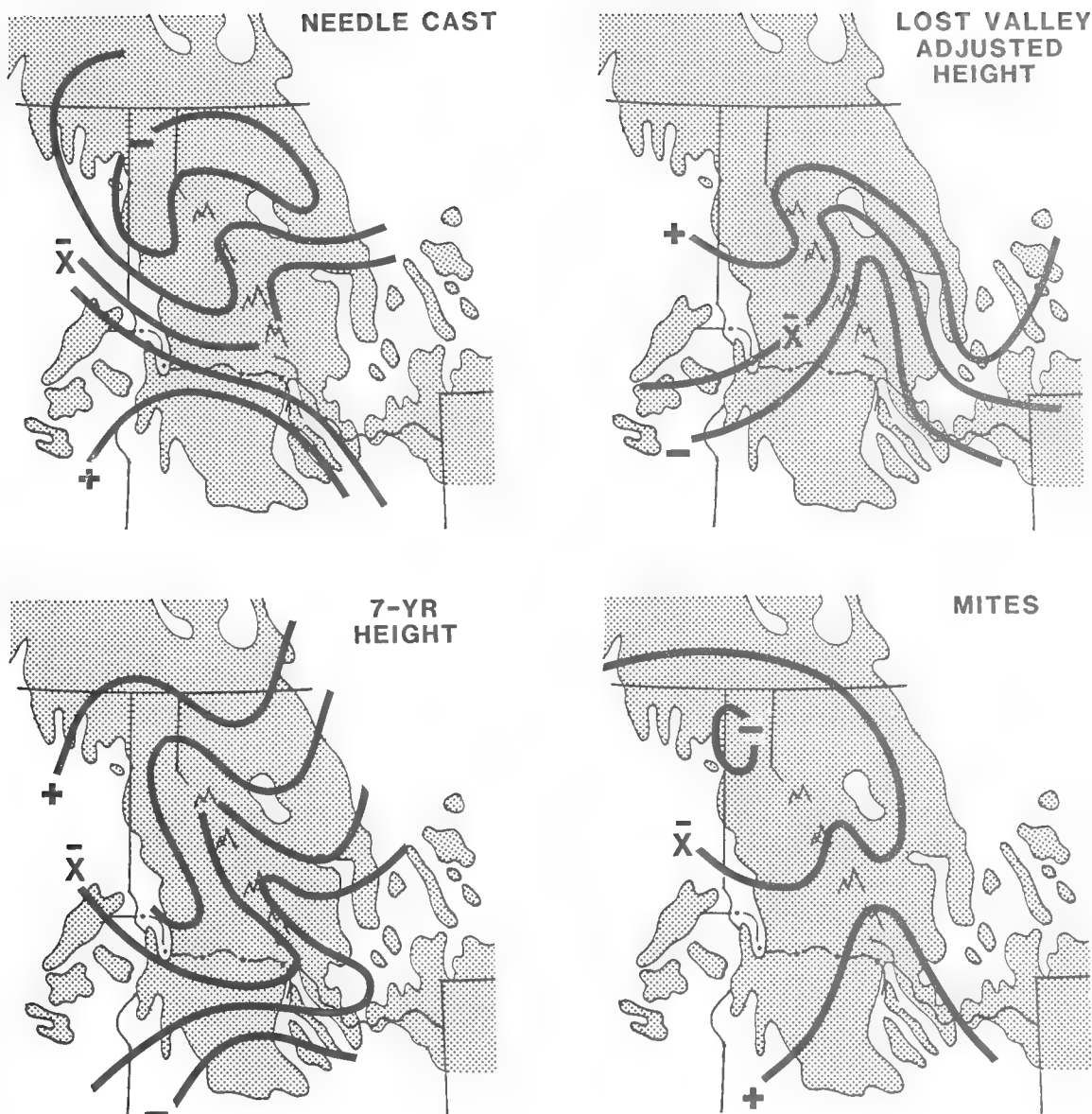


Figure 4—Geographic patterns that are independent of elevation as predicted by regression models. Patterns are relative to the distribution of the species (shading), the Bitterroot Range, and the Salmon River. Isopleths are positioned relative to the mean value (\bar{x}) with an interval scaled to $1/2sd$ (0.05).

of relatively equal predicted performance for the mean elevation (1,625 m). Contouring was begun with the mean value, and the interval between isopleths was scaled to $1/2sd$ (.05). Thus, populations separated by two isopleths are expected to differ at about the 95 percent level of probability. The pattern for late growth duplicates that of 7-year height and is not presented.

When comparing populations from the same elevation, those from the north were the tallest and had the most late growth; populations from central Idaho were the shortest and exhibited little late growth. The percentage of trees infected with needle cast or infested with mites was directly related to the geographic distance that the seed was transferred to the planting site. Populations of highest adjusted heights at Lost Valley (1,500 m) tended to be from the north where growth potentials were highest.

DISCUSSION

The results illustrate differentiation of populations for numerous traits which together determine adaptedness, the degree by which populations are physiologically attuned to their environment. Genetic differentiation was readily detected experimentally, and patterns of genetic variation were closely associated with the elevation and geographic location of the seed source. Pronounced clines tend to typify genetic differentiation in montane populations of *P. contorta* spp. *latifolia* (Ying and others 1985; Rehfeldt 1983a, 1985a; Stoneman 1985).

That the clines reflect adaptation to natural environments is demonstrated both directly, as differential fitness in contrasting environments, and indirectly, as genetic responses that parallel environmental gradients. Thus, indirect support is provided by the steep elevational clines

that parallel a change of 80 days in the frost-free period across 1,000 m elevation (Baker 1944). Likewise, the geographic patterns of variation illustrated in figure 4 unmistakably parallel geographic climatic patterns of figure 2. As a result, geographic patterns of genetic variation are strongly influenced by the Bitterroot Range and Salmon River Drainage.

Thus, populations from mild environments exhibit a high innate growth potential that develops from a long duration of elongation. Those from severe environments exhibit the low growth potential and short duration of elongation expected in populations adapted to a short growing season. For these clines to reflect adaptive differentiation is unquestionable; rejection of such indirect evidence requires acceptance of an untenably improbable alternative: that the systematic patterns have developed randomly.

Although direct evidence for adaptive clines ultimately resides with the survival or death of individuals, the demographic cycles of population establishment in *P. contorta* endow an adaptive value to all traits that condition growth and development in a particular environment. Thus, direct support of adaptive clines is provided by the differential incidence of snow damage, needle cast, and mites, as well as by differences in growth potential itself. At high elevations, such as PREF 1,500 where snow accumulations commonly exceed 3 m, populations from mild environments suffered considerable damage from the snow. Mean differences calculated within populations showed that the 7-year shoot elongation of trees damaged by the snow was 22 percent less than that of trees not damaged. Consequently, damaged trees had an adjusted height that was 5 percent less than undamaged trees from the same population.

Similarly, needle cast is a disease most common in relatively humid valleys (Krebill 1975), and therefore, populations native to either high elevations or arid climates are rarely exposed to the disease. The present data, as well as those of Hoff (1985), show that populations from either high elevations or southern latitudes are much more susceptible to needle cast than populations from low elevations. Mean differences within populations depict a tremendous reduction in 7-year height for diseased trees. For each increase in the damage score of one unit—an increase of approximately 25 percent in infected leaves per tree—7-year height was reduced about 4 percent. This means that reductions in 7-year height between uninfected and severely infected trees from the same population would amount to nearly 17 percent. This reduction accrued largely from a corresponding reduction of 34 percent in shoot elongation during year 7.

Mites receive no recognition in pest surveys for Rocky Mountain conifers (Tunnock and others 1984; Gibson and others 1984). But when populations are transferred large geographic distances, infestations by mites increase substantially. Because mites generally deform terminal shoots, growth and development are affected greatly.

The components of adaptedness tend to be integrated by values of adjusted height. By representing growth from a common height at age 5, adjusted height was free of most genetic and environmental effects that had accrued up to that age. Consequently, the variable was capable of expressing adaptation of populations to particular environ-

ments over a short period. At low elevation, populations from mild environments had larger adjusted heights than populations from severe environments. A part of this difference was due to the high innate growth potential of populations from low elevation, and a part was due to the high susceptibility to needle cast of populations from high elevations. At PREF 1,500, populations from about 1,500 m had the largest adjusted heights; populations from extremely high elevations displayed an innately low-growth potential, while populations from low elevations suffered snow damage. At Lost Valley, however, environmental effects sufficient for adaptively differentiating populations evidently are only beginning to be expressed. Although southern populations of low growth potential displayed the smallest adjusted heights, superior performance of relatively local sources cannot yet be detected (fig. 3).

Adaptive differentiation is readily quantified from regression statistics. Table 5 shows that elevational clines are particularly steep for 7-year height, late growth, needle cast, and snow damage. Populations separated by 1,000 m are expected to differ by 16 cm (33 percent of the mean) in 7-year height largely because of a large difference in the amount of late growth. These same populations, when planted at low elevation, are expected to differ by 48 percent in leaves infected with needle cast. When planted at high elevation, they are expected to differ by 28 percent in trees damaged by the snow. Previous studies (Rehfeldt 1980) also predict that populations separated by 1,000 m will differ by 31 percent in trees damaged by a fall frost that causes a mean injury of 50 percent. Elevational clines are so steep that populations separated by merely 224 m tend to be genetically differentiated (95 percent level of probability) for late growth while those separated by 500 m are differentiated for numerous traits (table 5).

The elevational cline, moreover, is the dominant cline (table 5). For those variables in which differentiation was pronounced (height, late growth, needle cast, and snow damage), the amount of differentiation associated with 1,000 m of elevation varies from half to twice that associated with 7° latitude at a constant elevation. Consequently, differentiation per unit distance is much greater along the elevational cline than along the geographic cline.

Nevertheless, both clines arise from environmental selection along climatic gradients. Because the frost-free period decreases by 80 days across an elevational interval of 1,000 m (Baker 1944), an average difference of only 18 days in frost-free period seems sufficient for inducing differentiation of populations for late growth, a variable reflecting tolerance to early fall frosts. Consequently, the steep elevational cline reflects the rapid change in frost-free period associated with elevation. And the gentle geographic cline arises from a gradual geographic gradient in the frost-free period.

These results have direct practical application. First, quantitative estimates of differentiation along adaptive clines define the risks involved with seed transfer in artificial reforestation. Reforestation goals involve increasing productivity while maintaining adaptiveness. To accomplish this, limits of seed transfer must reflect adaptive clines. The steep elevational clines described in this study

Table 5—Quantification of the percentage differences expected between populations located along elevational and geographic clines

Variable		Difference across 1,000 m elevation	Difference across 7° latitude	Elevational interval (m) associated with <i>Isd</i> (.05) ¹
7-year height	(cm)	16	28	463
Adjusted height				
PREF 640	(cm)	14	10	544
PREF 1,500	(cm)	6	5	2,461
Lost Valley	(cm)	3	12	4,735
Late growth	(cm)	7	6	224
Needle cast	(%)	48	38	354
Mites	(%)	5	14	2,519
Shoot borer	(%)	3	10	5,129
Spring frost injury	(%)	2	2	2,268
Snow damage	(%)	28	17	643

¹Calculated for linear regressions as the ratio [*Isd*(.05)]/*b* and for nonlinear regressions as the solution to the quadratic equation for elevations associated with $Y \pm \frac{1}{2}[Isd(.05)]$ at the mean geographic intercept.

imply that the elevational transfer of seeds should be greatly restricted, but the gentle geographic clines imply that the lateral movement of seeds can be relatively liberal. These conclusions are corroborated by others for the same species in adjacent geographic regions (Rehfeldt 1983a, 1985a; Stoneman 1985).

Regardless, there is little doubt that adaptive variation among populations of *P. contorta* reflects physiological specialization for relatively small segments of the environmental gradient. Specialized populations develop from a balance of environmental stimuli that harmoniously adjust the developmental cycle to the physical and biotic environment. By means of this specialized evolutionary mode, coadaptive traits have been designed by natural selection to overcome ecological problems as diverse as variable frost-free periods, insect infestations, and disease epidemics. Therefore, the large geographic and broad ecological distributions of this species result from the existence of innumerable populations, each of which is specialized. Perpetuation of specialized populations is readily facilitated by cycles of even-aged reproduction whereby individuals tend to become established on sites that supported their ancestors.

As evidenced by substantial genetic variances within populations (Ying and others 1985; Rehfeldt 1985b), specialization has not led to genetic uniformity. Although migration, mutation, and the founder effect undoubtedly contribute to intrapopulation variation, much of this variation likely results from variable selection pressures associated with environmental heterogeneity in time. For

long-lived stationary organisms, temporal heterogeneity not only is pronounced but also places a limit on the degree to which specialization can develop. Bryant (1976) noted that, if populations are to survive, the process of specialization cannot deplete the genetic variability required for accommodating environmental heterogeneity in time.

Forest trees of the Rocky Mountains have achieved adaptation to heterogeneous environments according to different modes. *Pseudotsuga menziesii*, like *P. contorta*, exhibits specialization, but *Larix occidentalis* Nutt. and *Pinus monticola* Dougl. are generalists: adaptive clines are relatively flat, and populations express a high fitness to a broad range of environments (Rehfeldt 1984). *Pinus ponderosa* Dougl. ex Laws., moreover, displays an intermediate mode. Thus, the specialist mode is characterizing species with broad ecological distributions while the generalist mode is characterizing species with relatively narrow distributions. Indeed, *P. contorta* and *Pseudotsuga menziesii* have greater botanical distributions and larger ecological amplitudes than any other western conifer; but the ecological distribution of *Pinus monticola* and *Larix occidentalis* is relatively small while that of *Pinus ponderosa* is intermediate (U.S. Department of Agriculture 1965). An understanding of the ecological genetics of species such as *Thuja plicata* Donn ex D. Don and *Tsuga heterophylla*, both of which have narrow ecological amplitudes and small geographic distributions, is necessary for assessing this apparent relationship between abundance and the adaptive mode.

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Rehfeldt, G. E. Components of adaptive variation in *Pinus contorta* from the Inland Northwest. Research Paper INT-375. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1987. 11 p.

Genetic variation among 83 populations of *Pinus contorta* from the Northern Rocky Mountains of the United States was studied with 7-year-old trees planted in three contrasting environments. Analyses of nine traits reflected adaptation of populations to the biotic and abiotic environments and revealed clinal patterns of differentiation that were elevationally steep but geographically gentle. Regression models present adaptive landscapes that mirror elevational and geographic gradients in climate.

KEYWORDS: genetic variation, population differentiation, microevolution, *Pinus contorta*

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