

Historic, archived document

Do not assume content reflects current scientific knowledge, policies, or practices.

199.4
F7644
cop. 2

United States
Department of
Agriculture

Forest Service

Intermountain
Research Station
Ogden, UT 84401

Research Paper
INT-356

January 1986



Ecological Genetics of *Pinus contorta* in the Upper Snake River Basin of Eastern Idaho and Wyoming

G. E. Rehfeldt

CURRENT SERIAL RECORDS

APR 9 '86

USDA
NATIONAL LIBRARY
OF AGRICULTURE

THE AUTHOR

G. E. REHFELDT is a plant geneticist at the Intermountain Research Station's Forestry Sciences Laboratory in Moscow, ID. He has been studying the ecological and quantitative genetics of Rocky Mountain conifers since 1968.

RESEARCH SUMMARY

Genetic differentiation of 60 populations of *Pinus contorta* primarily from eastern Idaho and adjacent Wyoming was assessed in three studies involving (1) growth and development in field environments, (2) the periodicity of shoot elongation in the greenhouse, and (3) freezing tolerance in the laboratory. Genetic differentiation between populations was observed for traits that included 3-year height, leaf length, freezing tolerance, and the pattern of shoot elongation. Regression models related as much as 83 percent of the variation between populations to the elevation and geographic location of the seed origin. Elevational clines were particularly steep. Consequently, if maladaptation is to be controlled in artificial reforestation, seed transfer should be restricted severely for elevation but geographically may be relatively liberal. Detailed practical guidelines will be presented separately.

Ecological Genetics of *Pinus contorta* in the Upper Snake River Basin of Eastern Idaho and Wyoming

G. E. Rehfeldt

INTRODUCTION

Ecological genetics is devoted to exploring the ecological bases for adaptive differentiation between populations. In lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), differentiation of populations from both Canada (Lindgren and others 1980; Hagner 1980; Ying and others 1985) and the United States (Rehfeldt 1985b) is related to the geographic origin and elevation of the seed source. Adaptive clines, however, reflect environmental gradients. As a result, clines in British Columbia reflect the relatively gentle environmental gradients associated with a region of dissected plateaus. But in the rugged Rocky Mountains of the United States, adaptive clines tend to be steep for a variety of traits that include growth potential, morphology, and cold hardiness (Rehfeldt 1980, 1983), patterns of shoot elongation (Rehfeldt and Wykoff 1981; Stoneman 1985; Rehfeldt 1985a), and resistance to insects and diseases (Hoff 1985). Regardless of geographic region, populations appear as physiological specialists for relatively small segments of the environmental gradient.

Steep adaptive clines have direct relevance to forest management. Artificial reforestation carries the implicit goal of maximizing productivity while maintaining adaptedness. Steep clines require that seed for reforestation be transferred only short distances along the environmental gradient if maladaptation and resultant losses in productivity are to be controlled.

The present study is part of a series that (1) examines adaptive variation between lodgepole pine populations, (2) relates patterns of variation to geography, topography, physiography, and climate, and (3) develops seed transfer guidelines for reforestation.

MATERIALS AND METHODS

The study of population differentiation included seedlings from 60 populations, 51 of which represented the geographic distribution and ecologic amplitude of the species in the upper Snake River Basin (fig. 1). Additional populations from peripheral areas provided a link to other studies in this series: four were from the Wasatch Mountains of Utah and southeastern Idaho;

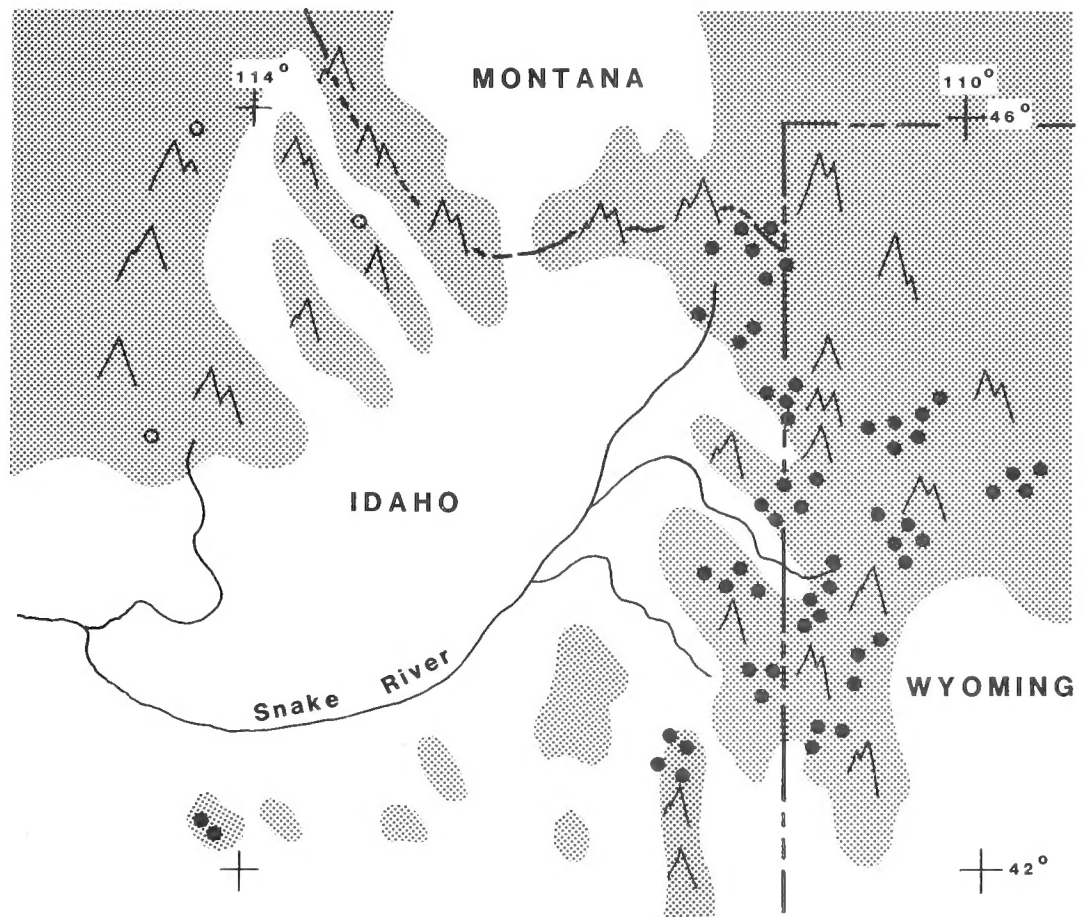


Figure 1.—Geographic distribution of *Pinus contorta* (shading according to Little 1971) within the region of study and location of populations.

three were from the lower Snake River basin of central Idaho; and two were from a small disjunct population from Deadline Ridge in south-central Idaho (fig. 1). Seedlings from the 60 populations were used in separate studies of (1) growth and development in field environments, (2) periodicity of shoot elongation in a greenhouse, and (3) cold hardiness in the laboratory. Because cone collections, experimental procedures, and statistical analyses are detailed in the first paper of this series, which involved populations from the Wasatch and Uinta Mountains of Utah (Rehfeldt 1985a), only an outline of these procedures follows.

Growth and Development

One set of seedlings from each of the 60 populations grew for 6 months in plastic containers (10 in³) in a shadehouse at Moscow, ID (lat. 48.5° N., long. 116.7° W.). In the fall, seedlings were transplanted into two environments, 2,200 and 5,000 feet elevation, at the Priest River Experimental Forest, 150 miles north of Moscow. Eight seedlings, spaced at 1.0 foot and 0.5 foot at low and high elevation sites, respectively, were planted in row plots, separated by 1.5 feet and 1.0 foot at the respective sites. Three blocks were established at each site, and both plantings were maintained under intensive culture.

The performance of each seedling was described by four variables for which differentiation of Utah populations had been pronounced: (1) height—seedling height after 3 years; (2) late growth—amount of the 3-year predetermined shoot that elongated after the fourth week of elongation in the respective environments; (3) leaf length—the length of a leaf near the center of the 3-year shoot; and (4) adjusted height—3-year height adjusted by regression on 2-year height. By representing the increment from a common 2-year height, adjusted height is relatively independent of previous environmental (such as transplanting shock) and genetic effects and thereby is capable of reflecting adaptation of populations to a particular environment for a single growing season.

In addition, scores were made for the presence or absence of injury from a freeze (16 °F) that occurred in mid-May at the low-elevation site. Injuries ranged from death of the developing shoot to reductions in internode lengths near the shoot tip.

To account for heterogeneous variances at the two test environments, data were transformed to standard normal deviates (Steel and Torrie 1960) for each test site and the deviates were analyzed according to a model of random effects. The model estimated: (1) main effects for test environments, blocks within environments, and populations; (2) the interaction of populations × environments; (3) an experimental error, composed of the interaction of populations × blocks within environments; and (4) a residual error. As a result of the transformations, mean squares associated with the main effects of test environments were zero. A harmonic mean of 7.20 reflected the number of seedlings representing each population in each block.

Injury from the spring frost was analyzed according to a model of random effects, which estimated main effects for blocks and populations, plus an error.

Periodicity of Shoot Elongation

Another set of seedlings grew for 1 year in plastic containers (45 in³) in a shadehouse at Moscow. Nine seedlings from each population grew in each of three blocks. In early March of the second growing season, seedlings were moved into a greenhouse before shoot elongation had begun. Greenhouses were maintained under natural lighting; temperatures were about 75 °F during the day and 55 °F at night. All seedlings were measured three times each week until elongation of the preformed bud had ceased.

As described by Rehfeldt and Wykoff (1981), shoot elongation of individual trees was expressed mathematically by a logistic function that included a hyperbolic time term. Regression statistics allowed calculation of the following variables for describing periodicity of shoot elongation of individual seedlings: (1) initiation of growth—the day on which 0.1 inch of cumulative growth had occurred; (2) cessation of growth—the day on which all but 0.1 inch of growth had occurred; (3) duration of growth—the number of days between initiation and cessation; (4) rate of growth—elongation per day during the period of maximum elongation; and (5) total elongation.

Population differentiation was assessed according to least squares analyses of random effects that estimated main effects for populations and blocks, the interaction of populations × blocks, and an error. A harmonic mean of 8.81 reflected the number of seedlings representing each population in each block.

Cold Hardiness

To estimate the relative cold hardiness of populations in early autumn, laboratory tests of freezing tolerance were made according to the general procedures of Levitt (1972). Mature leaves were collected in late September from near the center of the 3-year shoot of trees planted at 5,000 feet elevation in the study of growth and development.

Four sets of eight leaves were collected from each eight-tree plot; each set contained one leaf from each tree. One set of leaves from each plot was exposed to one of four test temperatures (−4 °F, −6 °F, −10 °F, and −12 °F) by cooling at the rate of 10 °F/h. Injured leaves were identified visually by the presence of discolored and flaccid tissue (Rehfeldt 1980). Population differentiation for the proportion of injured leaves from each plot was assessed from a model of random effects that allowed estimation of main effects for populations, blocks, and test temperatures; three two-way interactions; and a residual.

Patterns of Variation

Geographic patterns of genetic variation were assessed from a series of regression analyses that fit independent variables describing the origin of populations to the array of population means. Because the primary purpose of these analyses was to describe genetic patterns of variation for the upper Snake River Basin, regression analyses considered only the 51 representative populations. The sequence of regression analyses concentrated first on the relationship between performance and eleva-

tion of the seed source, and second on geographic patterns of variation that were independent of elevation. Adequacy of a model was judged according to the goodness of fit (R^2), residual variance ($s_{y,x}$), and geographic or ecologic patterns displayed by residuals (Draper and Smith 1966).

Elevational models considered both a linear and quadratic relationship between performance and elevation of the seed source. Deviations from the best fitting elevational regressions were then used as dependent variables for considering geographic patterns of variation that were independent of elevation. The geographic model included four independent variables, plus their squares: latitude, longitude, northwest departure, and northeast departure. The latter two variables were obtained by rotating the grid of latitude and longitude by 45° . Thus, eight independent variables were included in the model, which was fit with a stepwise regression program for maximizing R^2 (Barr and others 1979). Finally, for those variables in which both the elevational and geographic models had been significant, elevation of the seed source was added to the independent variables of the best fitting geographic model in order to estimate the joint determination of performance by geography and elevation.

RESULTS

Because each study was autonomous, the results of each are presented separately but are considered jointly in establishing patterns of genetic variation.

Growth and Development

The effects of planting environment on growth and development of seedlings were pronounced for all traits (table 1). Compared to trees growing at high elevation, trees at low elevation were much taller and had longer leaves. In addition, late growth, defined as the proportion of the predetermined shoot that elongated after the fourth week, was measured approximately 5 weeks earlier at low elevation than at high and therefore was affected tremendously by the environment. Adjusted heights show that even if all trees had been the same height at age 2, those growing at low elevation would still have been tallest after 3 years.

For nearly all variables, the range in population mean values was considerably different at the two planting environments (table 1). For these ranges to differ greatly illustrates the heterogeneous variances that required adjustment before statistical analyses were made.

By accounting for more than 20 percent of the total variance, effects of populations were pronounced for 3-year height and injury from a spring frost (table 2). These strong effects are illustrated by mean differences between populations of as much as 0.8 foot in height and 50 percent in trees injured by frost. On the average, trees damaged by frost were 3.2 inches shorter after 3 years than uninjured trees from the same population. Relatively weak effects for late growth are likely due to the relatively late stage of elongation at which measurements were begun: the average tree produced only 10 percent of the 3-year shoot as late growth. Consequently,

Table 1.—Mean values according to test environment and range of population means in each environment

Variable		Mean values		Range in population means	
		2,200 ft	1,500 ft	2,200 ft	5,000 ft
Late growth	(inches)	1.1	0.7	0.8	0.4
Leaf length	(inches)	2.9	2.7	1.1	0.8
Height	(inches)	17.1	13.9	12.2	5.8
Adjusted height	(inches)	16.2	14.7	5.7	1.8
Frost injury	(percent)	22	—	56	—

Table 2.—Results of analyses of variance for growth and development presented as intraclass correlations, the ratio of individual variance components to the sum of all components

Source of variance	Variable				
	Late growth	Leaf length	Height	Adjusted height	Frost injury
Environments	0	0	0	0	0
Blocks in environment	0.03**	0	0.02**	0	0
Populations	.06**	0.08**	.36**	0.02*	0.20**
Environment × population	0	.02	.01	.09**	—
Experimental error	.07**	.07	.03**	.04**	.79
Within plots	.84	.83	.57	.84	—

*Statistical significance of the F-value at the 5 percent level of probability.

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

mean values for populations ranged from only 0.7 to 1.2 inches. Significant effects of populations in leaf length reflected mean differences as large as 0.8 inch. And finally, the significant effects of populations for adjusted height show that populations would have differed in 3-year height even if all trees had been the same height at age 2, even though 2-year height accounted for 64 percent of the variance in 3-year height of individual trees.

Significant interactions of populations and environments were detected only for adjusted height; consequently, main effects for this variable were significant with a rather low level of probability (table 2). The interaction was caused by (1) a lack of differences between populations in the environment at high elevation, combined with (2) statistically detectable differences at low elevation. Consequently, subsequent analyses for adjusted height use only those data from the low-elevation site.

Periodicity of Shoot Elongation

The logistic function described periodicity of shoot elongation of individual trees nearly perfectly. Values of R^2 ranged from 0.94 to essentially 1.0 while averaging 0.99. Analyses of variance detected strong effects of populations for duration, rate, cessation, and amount of shoot elongation (table 3). These effects accounted for 21 to 38 percent of the total variance and are illustrated in figure 2. Differences between populations were as large as 15 days in cessation, 16 days in duration, 0.1 inch/day in rate, and 3.4 inches in the amount of elongation. Populations differed by only 0.8 day in the initiation of shoot elongation, and, consequently, no differences could be detected statistically.

Cold Hardiness

Effects of test temperatures dominated analyses of variance (table 4). These effects are associated with a range in injury from 36 percent at -4 °F to 78 percent at -12 °F. Effects of populations were significant but accounted for only 5 percent of the total variance. Mean differences between populations amounted to as much as 55 percent injury.

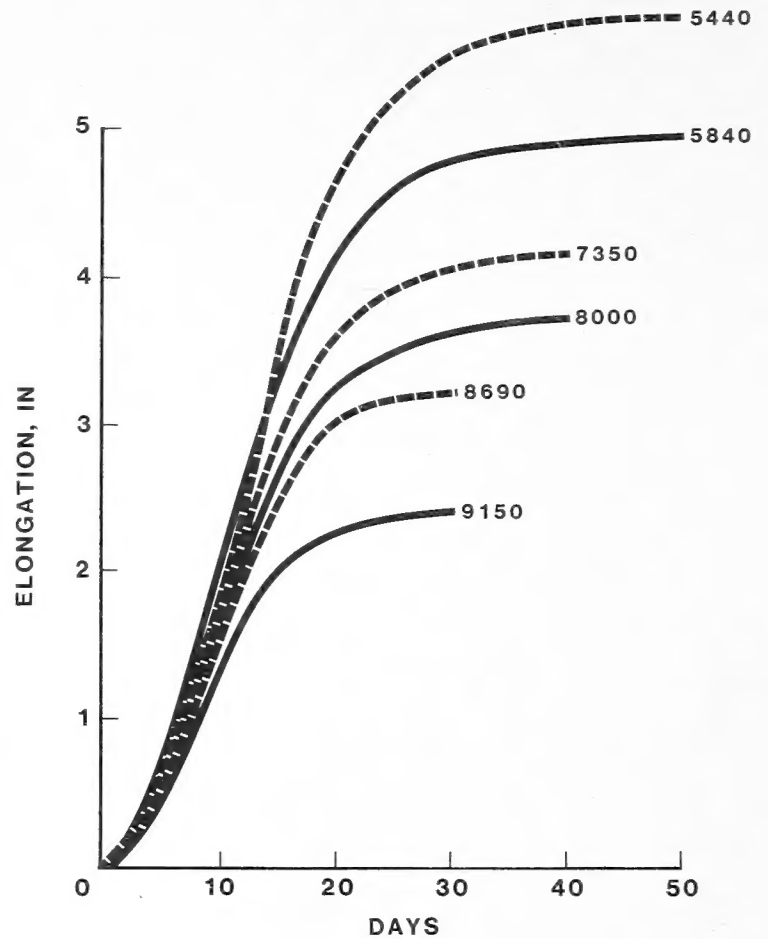


Figure 2.—Periodicity of shoot elongation for populations from a range of elevations (feet) that represented maximum differences in response.

Patterns of Variation

Elevation of the seed source had a pronounced effect on population performance (table 5, fig. 3). Elevational models accounted for more than 70 percent of the variance between populations for five variables and were statistically significant for all variables except the initiation of shoot elongation. As elevation increases, growth potential decreases, largely because of an associated decline in late growth and in the rate, duration, and cessation of shoot elongation. Leaf lengths also decline with

Table 3.—Results of analyses of variance for periodicity of shoot elongation presented as intraclass correlations, the ratio of a variance component to the sum of all components

Source of variance	Initiation	Duration	Rate	Cessation	Elongation
Blocks	0.10**	0.04**	0.03**	0	0.01
Populations	.02	.22**	.21**	0.23**	.38**
Interaction	.15**	0	.06	0	.03*
Within plots	.73	.73	.70	.77	.58

*Statistical significance of the F-value at the 5 percent level.

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

Table 4.—Results of analyses of variance of freezing tests presented as intraclass correlations, the ratio of a variance component to the sum of all components

Source of variance	Intraclass correlation
Blocks	0.06*
Temperatures	.21**
Populations	.05**
Populations × temperatures	0
Residual ¹	.68

*Statistical significance of the F-value at the 5 percent level.

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

¹Composed of the interactions involving blocks.

Table 5.—Coefficients of determination (R^2) for regression analyses relating genetic variation to geographic and physiographic variables

Variable	Elevational model		Geographic model	Combined model
	Linear	Quadratic		
Growth and development				
Late growth	0.26**	0.27**	0.04	—
Leaf length	.32**	.32**	.26*	0.49**
Height	.70**	.70**	.24*	.78**
Adjusted height (2,200 ft)	.50**	.53**	.31**	.66**
Frost injury	.21**	.22	0	—
Periodicity of shoot elongation				
Duration	.71**	.74**	.31**	.83**
Rate	.74**	.74**	.09	—
Cessation	.70**	.74**	.29*	.80**
Elongation	.78**	.79**	.19	—
Cold hardiness				
Injury	.13**	.13*	.33**	.43**

*Statistical significance at the 5 percent level of probability.

**Statistical significance at the 1 percent level of probability.

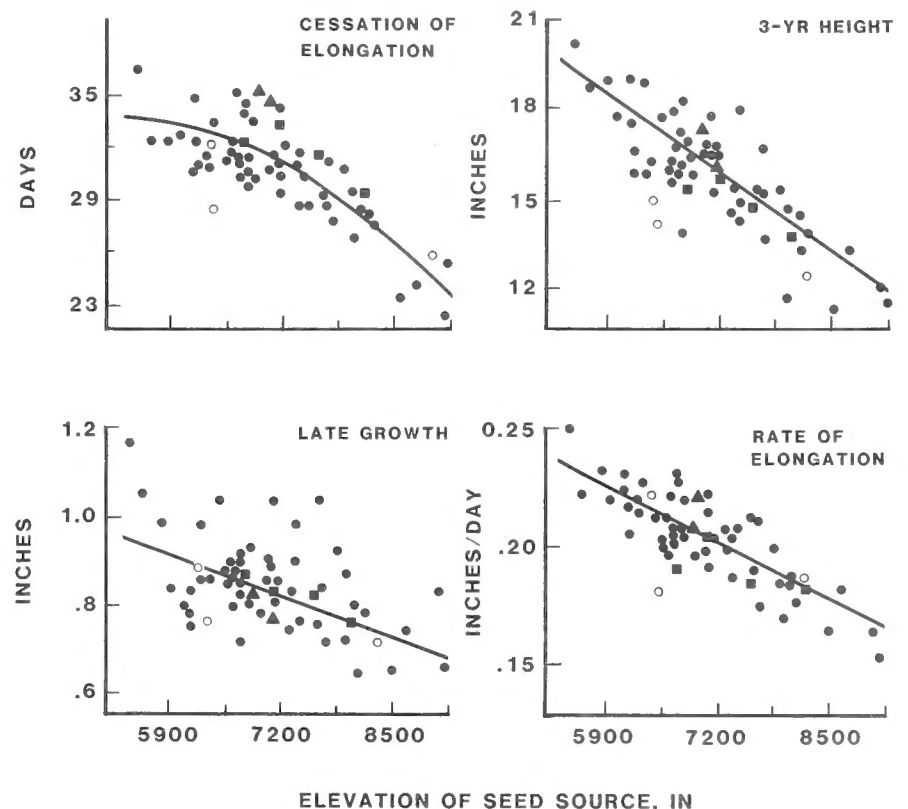


Figure 3.—Population means for four variables plotted by elevation of the seed source. Symbols code geographic origins: ● = Upper Snake River Basin; ○ = Lower Snake River, ■ = Wasatch Mountains, ▲ = Deadline Ridge.

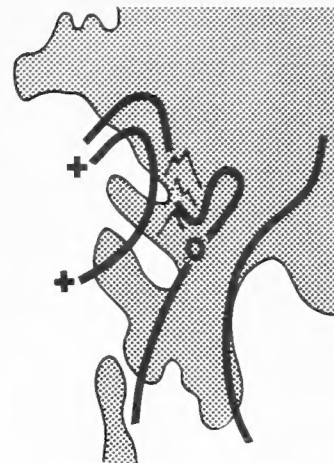
increasing elevation of the seed source, but freezing tolerance increases. The strong relationship between elevation and adjusted height indicates that, at the low elevational planting, populations from mild environments still would have been tallest even if all trees had been the same height at age 2. Quadratic models provided a significant reduction in the residual mean square of the linear model for only the cessation and duration of elongation.

The geographic model (table 5) was statistically significant for only half of the variables. At most, this model accounted for less than a third of the variance in the dependent variables that was not explained by elevation. Consequently, geography accounted for less than 25 percent of the variance among populations. Thus, elevational clines tend to be steep, and geographic clines are relatively gentle. Nevertheless, geographic variables plus elevation (the combined model) accounted for 43 to 83 percent of the variance of populations.

Geographic patterns of genetic variation that are independent of elevation are presented in figure 4 for several traits. These patterns were generated from values predicted by the geographic model. The contour interval is scaled to a value equaling half the least significant difference (Steel and Torrie 1960) between populations at the 80 percent level of probability [$\frac{1}{2} lsd(0.2)$]. Because values of *lsd* were calculated from the analysis of variance (table 2), contours represent about half the geographical distance associated with population differentiation at the 80 percent level of probability. Contouring was begun with the overall mean, the zero deviation from the elevational regression.

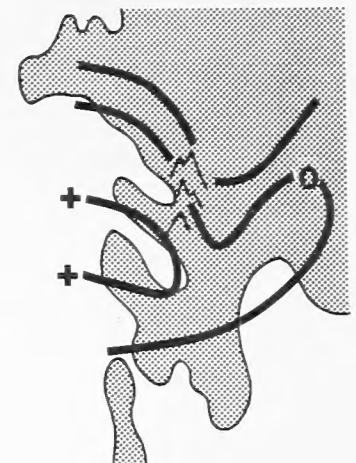
All variables for which the geographic model was significant presented similar patterns of genetic variation. Those variables selected for figure 4 illustrate patterns of greatest divergence. In general, populations in the west-central regions are of highest growth potential and lowest hardiness. From this area, growth potential decreases and hardiness increases in all directions. The general pattern, however, is influenced greatly by the rugged Teton Range. Populations of relatively high growth potential and low hardiness extend into the

DURATION OF ELONGATION



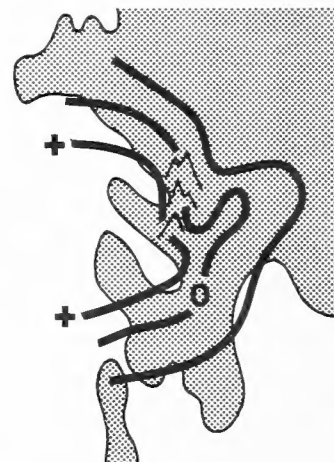
CI=0.9 DAYS

LEAF LENGTH



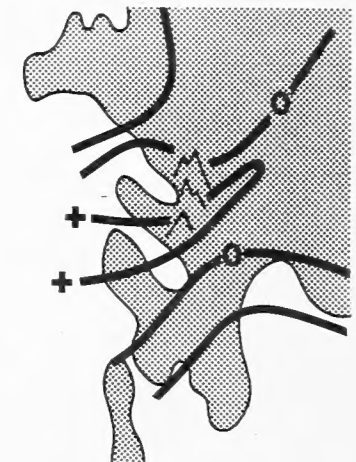
CI=0.08 INCHES

3-YEAR HEIGHT



CI=0.47 INCHES

FREEZING INJURY



CI=7 %

Figure 4.—Geographic patterns of variation that are independent of elevation. Shading marks the distribution of lodgepole pine in reference to the Teton Range. C.I. = the contour interval, which is scaled to a value of $\frac{1}{2} lsd(0.2)$. The zero contour represents the mean of all populations standardized for elevation.

Table 6.—Correlation matrix relating population means for all studies¹

Variable	Code	LL	H	AH	FI	I	D	R	C	EL	IN
Growth and development											
Late growth	LG	0.56	0.68	0.61	0.34	-0.24	0.54	0.61	0.53	0.61	0.13
Leaf length	LL		.62	.53	.33	-.27	.62	.59	.62	.64	.21
Height	H			.81	.56	-.21	.84	.87	.85	.90	.36
Adjusted height (2,200 ft)	AH				.44	-.32	.71	.71	.70	.75	.20
Frost injury	FI					.08	.42	.43	.43	.44	.27
Periodicity of shoot elongation											
Initiation	I						-.33	-.23	-.27	-.31	.10
Duration	D							.84	.99	.93	.27
Rate	R								.84	.97	.40
Cessation	C									.93	.28
Elongation	EL										.37
Cold hardiness											
Injury	IN										

¹Coefficients of absolute value >0.27 are statistically significant at the 5 percent level.

Table 7.—Average difference between the observed performance of peripheral populations and that expected from the elevational regressions

Variable		Lower Snake River	Wasatch Mountain	Deadline Ridge
Growth and development				
Late growth	(inches)	-0.07	-0.00	-0.07
Leaf length	(inches)	-.08	.05	.13
Height	(inches)	-2.48	-.71	.57
Adjusted height	(inches)	-.41	-.86	1.27
Frost injury	(percent)	-9.3	-8.7	-3.0
Periodicity of shoot elongation				
Initiation	(days)	0	-.1	.3
Duration	(days)	-1.9	1.6	3.3
Rate	(inches/days)	-.01	-.01	.01
Cessation	(days)	-1.8	1.6	3.6
Elongation	(inches)	-.35	-.02	.58
Cold hardiness				
Injury	(percent)	-3.1	-1.6	5.1

drainages east of the Tetons. Significant intercorrelations between variables (table 6) produce the similar elevational and geographic clines. Particularly noteworthy are the correlations among variables associated with growth potential. Whether measured in the field or greenhouse, these correlations were extremely strong ($r > 0.8$).

The performance of populations from geographic regions peripheral to the region of study is presented in table 7, relative to that expected for populations from the upper Snake River drainage at similar elevations. Populations from the Wasatch Mountains are of slightly lesser growth potential and slightly higher hardiness than populations from the upper Snake. But, the populations tested from the lower Snake were of considerably lesser growth potential and higher hardiness than those from the upper Snake. However, disjunct populations from Deadline Ridge are of higher growth potential and lesser hardiness than populations from similar elevations in the upper Snake.

DISCUSSION

Genetic differentiation between populations from the upper Snake River Basin, like that for populations from northern Idaho (Rehfeldt 1983), Utah (Rehfeldt 1985a), and Oregon (Stoneman 1985), occurs along relatively steep clines. Differentiation was detected for a variety of traits, most of which were intercorrelated. Strong intercorrelation of adaptive traits results from either or both genetic linkage and parallel selection. Regardless, coherence (Clausen and Hiesey 1960) typifies the system of genetic variability for a species such as lodgepole pine that is physiologically specialized for specific environments. Populations from mild environments display a high growth potential and relatively low hardiness; populations from severe environments express high hardiness and low growth potential. Adaptation can be viewed as a balance between selection for high growth potential in mild environments and selection for high cold hardiness in severe environments.

Adaptive clines parallel environmental gradients. Temperatures and frost-free periods sharply decrease as elevation increases. Consequently, elevational clines are steep. On the average, populations separated by 3,000 feet elevation are expected to differ, for example, by 42 percent in 3-year height, by 20 percent in both spring and fall frost injury, and by 0.3 inch in leaf length.

A comparison of figures 4 and 5 shows that geographic patterns of genetic variation closely parallel environmental gradients in temperature but are poorly related to precipitation gradients. In fact, the geographic patterns presented in figure 4 nearly duplicate the environmental gradients represented by the length of the frost-free period (fig. 5). Patterns of genetic variation that arc to the east of the rugged Teton Range respond to the relatively mild climates that also extend east of this mountain range.

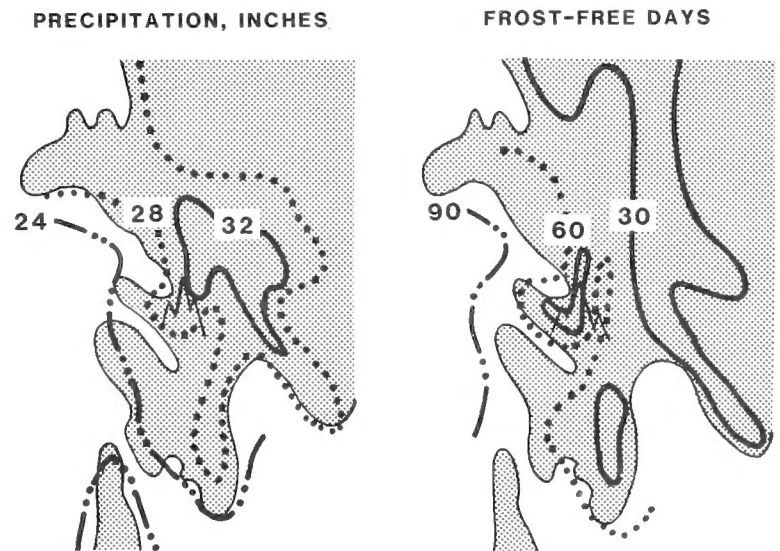


Figure 5.—Geographic patterns in precipitation and the frost-free period for the upper Snake River Basin (from U.S. Department of Commerce 1968).

Elevational clines are much steeper than the geographic. A comparison of these clines can be made by noting that in figure 4, each geographic band, situated between any two contours, is standardized for elevation. Each band is equivalent to the amount of genetic differentiation that occurs across 302 feet elevation for 3-year height, 315 feet for duration of elongation, 935 feet for leaf length, and 1,377 feet for fall freezing injury, respectively. Thus, in a region approximately 200 miles from north to south, the geographic clines (fig. 4) in those variables for which population differentiation was pronounced (table 5) are equivalent to the genetic differentiation that occurs within about 1,000 feet elevation at a single locality.

Patterns of adaptive variation between populations have direct implications in forest management. To limit maladaptation in planted trees, seed transfer guidelines must reflect adaptive variation. One estimate of an appropriate limit to seed transfer involves the smallest geographic or elevational interval across which differentiation can be detected (Rehfeldt 1979). This interval is estimated by the ratio $lsd(0.2)/b$, where b is the regression coefficient and $lsd(0.2)$ is derived from the analysis of variance as the least significant difference between population means at the 80 percent level of probability. (A rather low level of probability is used to avoid accepting no differences when differences actually exist.)

Elevational intervals associated with $lsd(0.2)$ include, for example, 604 feet for 3-year height, 738 feet for rate of elongation, 1,788 feet for late growth, and 2,752 feet for injury from fall freezing. These intervals suggest that the maximum elevational limits for biologically sound seed zones should not be much greater than 600 feet. This means that the transfer of seed from a single source should be limited to ± 300 feet. Nevertheless, con-

siderable genetic differentiation occurs across seed zones that occupy only 600 feet. These differences, for instance, amount to 9 percent in 3-year height and 5 percent in susceptibility to injury from the cold. Therefore, transfers of seeds beyond these limits can result in considerable productive losses in artificial reforestation.

Geographic patterns of variation (fig. 4) were scaled to a value of $\frac{1}{2} lsd(0.2)$, and therefore lateral transfers of seed should be limited to about ± 1 contour. This means that two geographic zones are sufficient for the upper Snake River Basin.

The appropriate size of seed zones should be practical operationally and economically. Thus, limits to seed transfer must accommodate biology, operational feasibility, and economics. When, however, administration demands an alteration in the guidelines proposed above, it should be remembered that each geographic band in figure 4 is equivalent genetically to a relatively small elevational interval within a band. Consequently, the geographic limits should be compromised. From the biological viewpoint, seed zones for the upper Snake River Basin should be considered as elevational zones with geographic stratification.

Regardless, populations of lodgepole pine from the drainages of the upper Snake River display patterns of genetic variation that typify the adaptation of the species to heterogeneous environments in other geographic localities. Populations appear to be physiologically attuned to specific environments, clines are steep, and genetic differences occur across relatively small environmental intervals. Differentiation between populations is easy to detect experimentally and is closely related to geography and elevation of the seed origin. Therefore, seed transfer in artificial reforestation should be greatly limited.

REFERENCES

- Barr, A. J.; Goodnight, J. H.; Sall, J. P. SAS user's guide, 1979 ed. Raleigh, NC: SAS Institute, Inc.; 1979. 494 p.
- Clausen, J.; Hiesey, W. M. The balance between coherence and variation in evolution. Proceedings, National Academy of Science. 46: 494-506; 1960.
- Draper, N. R.; Smith, H. Applied regression analyses. New York: John Wiley and Sons; 1966. 407 p.
- Hagner, M. Geographic variation in *Pinus contorta* and *Picea mariana* with respect to cone size, seedling growth rhythm and cotyledons. In: *Pinus contorta* as an exotic species. Proceedings IUFRO meeting 1980. Research Note 30. Garpenberg, Sweden: Swedish University of Agricultural Science; 1980: 83-102.
- Hoff, R. J. Susceptibility of lodgepole pine to the needle cast fungus *Lophodermella concolor*. Research Note INT-349. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1985. 6 p.
- Lindgren, K.; Lindgren, D.; Persson, A. Survival and height increment of *Pinus contorta*. In: *Pinus contorta* as an exotic species. Research Note 30. Garpenberg, Sweden: Swedish University of Agricultural Science; 1980: 103-132.
- Levitt, J. Responses of plants to environmental stresses. New York: Academic Press; 1972. 697 p.
- Little, E. J., Jr. Atlas of United States trees. Vol. 1. Conifers and important hardwoods. Miscellaneous Publication 1146. Washington, DC: U.S. Department of Agriculture, Forest Service; 1971. 9 p. 313 maps.
- Rehfeldt, G. E. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) populations. I. North Idaho and northeast Washington. *Heredity*. 43: 383-397; 1979.
- Rehfeldt, G. E. Cold acclimation in populations of *Pinus contorta* from the Northern Rocky Mountains. *Botanical Gazette*. 141: 458-463; 1980.
- Rehfeldt, G. E. Adaptation of *Pinus contorta* populations to heterogeneous environments in north Idaho. *Canadian Journal of Forest Research*. 13: 405-411; 1983.
- Rehfeldt, G. E. Ecological genetics of *Pinus contorta* in the Wasatch and Uinta Mountains of Utah. *Canadian Journal of Forest Research*. 15: 524-530; 1985a.
- Rehfeldt, G. E. Prospects for tree improvement in lodgepole pine. In: Baumgartner, D. M.; Krebill, R. G.; Arnott, J. T.; Weetman, G. F., eds. Lodgepole pine: the species and its management: Symposium proceedings; 1984 May 8-10; Spokane, WA; 1984 May 14-16; Vancouver, BC. Pullman, WA: Office of Conferences and Institutes, Cooperative Extension; 1985b: 55-60.
- Rehfeldt, G. E.; Wykoff, W. R. Periodicity of shoot elongation among populations of *Pinus contorta* from the Northern Rocky Mountains. *Annals of Botany*. 48: 371-377; 1981.
- Stoneman, C. Adaptation of lodgepole pine populations of south-central Oregon; a description of genetic variation based on seedling tests. Moscow, ID: University of Idaho; 1985. 97 p. M.S. thesis.
- Steel, R. G. D.; Torrie, J. H. Principles and procedures of statistics. New York: McGraw-Hill; 1960. 481 p.
- U.S. Department of Commerce, Environmental Data Service. Climatic atlas of the United States. Washington, DC. 1968. 80 p.
- Ying, C. C.; Illingworth, K.; Carlson, M. Geographic variation in lodgepole pine and its implications for tree improvement in British Columbia. In: Baumgartner, D.M.; Krebill, R.G.; Arnott, J.T.; Weetman, G.F., eds. Lodgepole pine: the species and its management: Symposium proceedings; 1984 May 8-10; Spokane, WA; 1984 May 14-16; Vancouver, B.C. Pullman, WA: Office of Conferences and Institutes, Cooperative Extension; 1985: 45-53.

Rehfeldt, G. E. Ecological genetics of *Pinus contorta* in the upper Snake River Basin of eastern Idaho and Wyoming. Research Paper INT-356. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station; 1986. 9 p.

Genetic differentiation of 60 populations of *Pinus contorta* primarily from eastern Idaho and western Wyoming was studied in field, greenhouse, and laboratory tests. Analyses of variables reflecting growth potential, morphology, cold hardiness, and periodicity of shoot elongation revealed population differentiation for a variety of traits. Regression models related as much as 83 percent of the variance of population means to the elevation and geographic location of the seed source. For genetic variation to be arranged along relatively steep environmental clines implies pronounced adaptive differentiation. As a result, seed transfer in reforestation should be restricted severely if maladaptation is to be controlled.

KEYWORDS: microevolution, adaptation, population differentiation, seed zones, seed transfer

INTERMOUNTAIN RESEARCH STATION

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

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

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

Station laboratories are located in:

Boise, Idaho

Bozeman, Montana (in cooperation with Montana State University)

Logan, Utah (in cooperation with Utah State University)

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

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

Ogden, Utah

Provo, Utah (in cooperation with Brigham Young University)

Reno, Nevada (in cooperation with the University of Nevada)