Interspecific and Intraspecific Variation in *Picea engelmannii* and its Congeneric Cohorts: Biosystematics, Genecology, and Climate Change

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Abstract

Rehfeldt, Gerald E. 2004. **Interspecific and intraspecific variation in *Picea engelmannii* and its congeneric cohorts: biosystematics, genecology, and climate change.** Gen. Tech. Rep. RMRS-GTR-134. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research. 18 p.
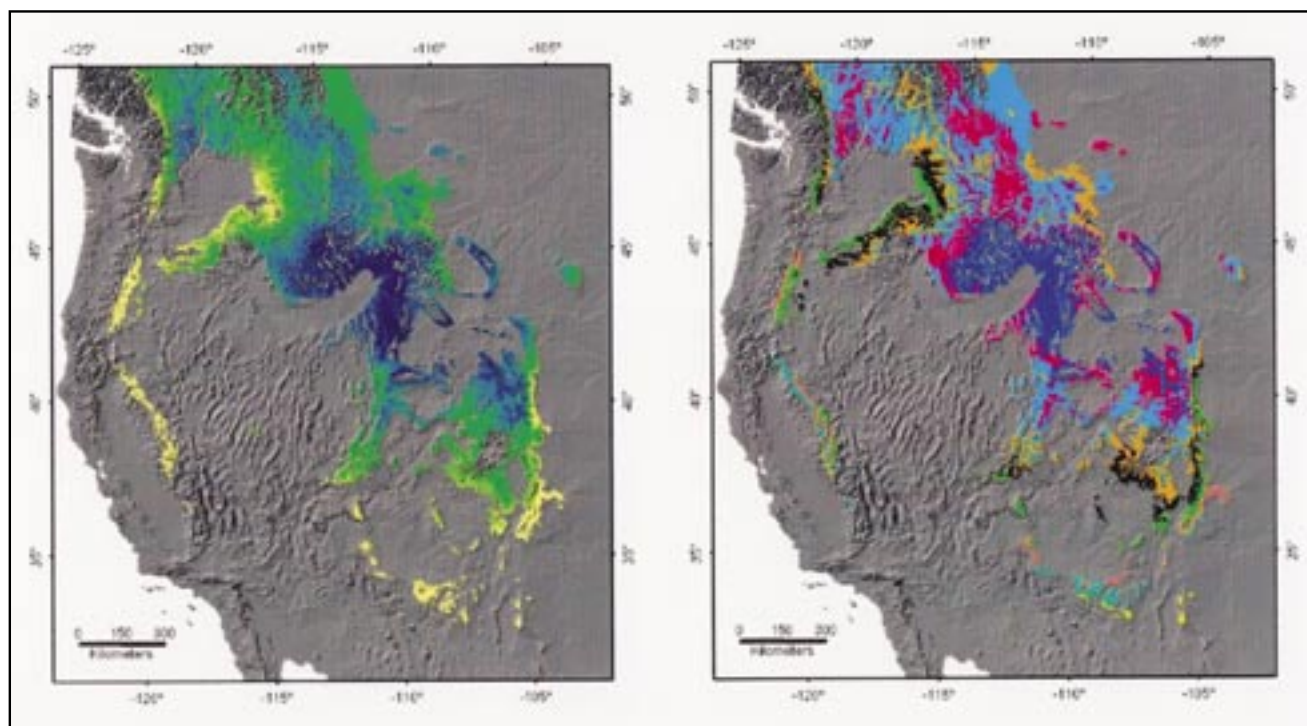
A series of common garden studies of 336 populations representing *Picea engelmannii, P. pungens, P. glauca, P. mexicana*, and *P. chihuahuana* provided as many as 13 growth and morphologic characters pertinent to biosystematics and genecology. Canonical discriminant analyses discretely segregated populations of *P. pungens* and *P. chihuahuana* while positioning *P. engelmannii* populations along a continuum anchored by Southwestern United States populations at one extreme and those classified as hybrids of *P. engelmannii* with *P. glauca* on the other. A population of *P. mexicana* was closely aligned with Southwest populations of *P. engelmannii*, while populations of *P. glauca* were intermixed with and peripheral to those identified as hybrid. While consistent with most taxonomic treatments of these taxa, the analyses nonetheless suggested that Southwestern United States populations should be considered as a variety of *P. engelmannii* that most likely should include *P. mexicana*.

Genecological analyses detected ample genetic variation among the 295 populations in the *P. engelmannii* complex. The analyses demonstrated that populations were distributed along clines driven primarily by the winter temperature regime of the provenance. For northern populations, summer temperatures also became a key factor in accounting for genetic differences among populations. Analyses also detected clines for the 19 *P. pungens* and 23 *P. glauca* populations.

An assessment of the effects of global warming according to the IS92a scenario of two general circulation models demonstrated for the current century: (1) an increasingly favorable climate for *P. pungens* as its distribution moves upward in elevation throughout much of the Great Basin, Colorado Rockies, and mountain islands of the Southwest; (2) a widespread reduction in the areal extent of *P. engelmannii* in the inland Northwestern United States to the extent that *Picea* may become rare in the local flora; (3) extirpation of *P. glauca* from the Black Hills and Cypress Hills; and (4) a widespread redistribution of genotypes across the landscape as contemporary populations adjust genetically to change.

Key words: common garden studies, quantitative traits, climatic clines, response to climate

The Author

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Acknowledgments

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Introduction

Picea engelmannii Parry ex Engelm. dominates subalpine forests throughout much of the Interior West of North America. Yet this broad-ranging species maintains such complex inter- and intra-specific relationships with its congeneric cohorts that it remains genetically an enigma. To the north, hybridization and introgression between *P. engelmannii* and *P. glauca* (Moench) Voss is so prevalent (Daubenmire 1974, Ogilvie and von Rudloff 1968, Rajora and Dancik 1999, Taylor 1959) that much of the *Picea* of Interior British Columbia is considered to be hybrid (Roche 1969). Toward the south, *P. engelmannii* frequently co-occurs with the montane *P. pungens* Engelm. Although the phenotypic resemblance between these species is so close that hybrids have been reported (Taylor and others 1975), careful studies have failed to uncover incidences of natural hybridization (Ernst and others 1990, Kossuth and Fetchner 1973, Mitton and Andalora 1981). Of the *Picea* of Mexico, moreover, one, *P. mexicana* Martinez, is so similar phenotypically (Taylor and Patterson 1980, Taylor and others 1994) and molecularly (Ledig and others 2004, Sigurgeirsson and Szmidt 1993) to *P. engelmannii* that its nomenclature is disputed; yet, a second, *P. chihuahuana* Martinez, is regarded as a distinct taxonomic entity by a unanimous consensus of the same authors.

At the intraspecific level, genetic variation among *P. engelmannii* populations is arranged along geographic clines (Rehfeldt 1994). Populations from the mildest climates at low elevations tend to have high growth potential and low tolerance to the cold, while those from the severe environments at high elevation display high cold tolerance and low growth potential. The clines are sufficiently steep that on average, populations separated by about 400 m of elevation tend to be genetically different. Although genetically similar populations tend to recur across the landscape presumably in association with the recurrence of similar climates, populations from the high mountains of the Southwestern United States nonetheless differ from those to the north to such an extent that they may deserve subspecific recognition (Ledig and others 2004, Rehfeldt 1994). For this paper, these southern populations are considered to be the species' southern ecotype (fig. 1) and are referenced as southwest *P. engelmannii*.

This paper deals with the biosystematics, genecology, and response to climate change of populations of seven taxa: *P. engelmannii*, southwest *P. engelmannii*, *P. glauca*, hybrids of *P. engelmannii* and *P. glauca*, *P. pungens*, *P. mexicana*, and *P. chihuahuana*. The focus, however, is on the taxa of the *P. engelmannii* complex: *P. engelmannii*, southwest *P. engelmannii*, and hybrid derivatives of *P. engelmannii* with *P. glauca*. A portion of these objectives were dealt with previously for populations of the Central Rocky Mountains (Rehfeldt 1994).

The analyses are based on genetic variation in quantitative traits expressed in common gardens. Assumptions fundamental to the analyses and interpretations are:

- Climate is the primary factor controlling the distribution of organisms (Brown and Gibson 1983, Woodward 1987).
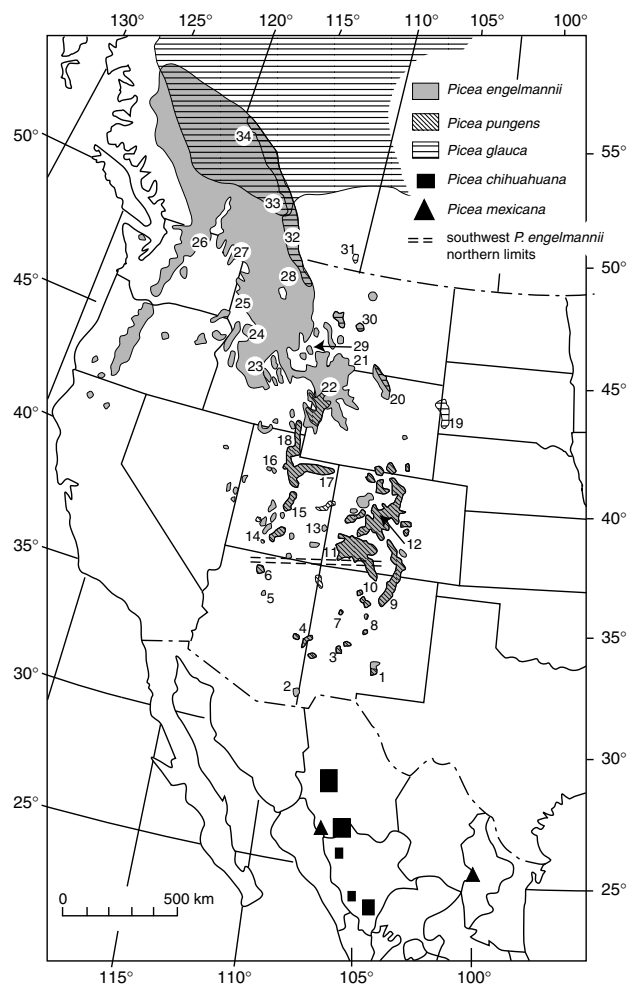

Figure 1—Distributions of *Picea engelmannii*, *P. pungens*, *P. mexicana*, and *P. chihuahuana*; the southwestern portion of the transcontinental range of *P. glauca*; the zone of hybridization and introgression between *P. engelmannii* and *P. glauca*; and the approximate boundary between *P. engelmannii* and southwest *P. engelmannii*. Numbered localities are referenced in the text and span the range of populations sampled.

- Niche space is a multidimensional hypervolume (Hutchinson 1958) whose limits are controlled by a balance between climatic tolerances and competition (Arthur 1987).

- Genotypes tend to occur in those environments where they can be competitively exclusive (Arthur 1987, Miller 1967).

- Climatic limits of distribution remain constant during periods of climate change (Box and others 1999).

The same principles controlling the distribution of species also operate intraspecifically to control the distribution of genotypes within populations (Rehfeldt and others 1999).

Methods

Experimental Materials

Seeds that had received natural wind pollinations were obtained from 336 populations, 200 *P. engelmannii*, 32 southwest *P. engelmannii*, 63 *P. engelmannii – P. glauca* hybrid derivatives, 23 *P. glauca*, 16 *P. pungens*, and one each of *P. mexicana* and *P. chihuahuana*. Identification of all taxa except southwest *P. engelmannii* was based on taxonomic characters of the parental populations. In the experience of the author, distinguishing mature *P. pungens* and *P. glauca* from *P. engelmannii* is unambiguous, but distinguishing hybrids from either *P. glauca* or *P. engelmannii* is extremely difficult. No phenotypic keys exist for southwest *P. engelmannii*, the distribution of which is based on the research results of Rehfeldt (1994).

The intent of this sampling was to thoroughly represent the ecologic and geographic distribution of the *P. engelmannii* complex from 32 °N to 54 °N latitude; provide a representative sample of the *P. pungens* distribution; sample enough *P. glauca* in Western North America to provide a bridge to *P. engelmannii*; and simply include *P. mexicana* and *P. chihuahuana.* Most of the seeds were obtained from squirrel caches in native populations, but those from Canada were from reforestation stores of either the British Columbia Ministry of Forests or Alberta Sustainable Resource Management. The procedures customarily used to procure these seeds assured that each population was represented by a large number of parental trees.

Experimental Procedures

Genetic variation among populations was compared in four independent studies:

- Study 1 consisted of 37 populations from Southwestern United States.

- Study 2 consisted of the 103 Intermountain populations of Rehfeldt (1994).

- Study 3 consisted of 135 populations from the Inland Northwestern United States.

- Study 4 consisted of 73 populations from Western Canada.

This meant that study 1 consisted largely of southwest *P. engelmannii*; studies 2 and 3 largely of *P. engelmannii*; and study 4 largely of *P. glauca* and *P. glauca-P. engelmannii* hybrids. To provide a means of comparing results of independent studies initiated in different years, the studies contained either nine or 14 populations in common with one of the studies conducted previously. Each taxon was represented by one or more of the common populations.

Experimental procedures used for all studies followed those of Rehfeldt (1994) and involved assessing differences among populations for (1) patterns of shoot elongation during the second growing season in a shadehouse-greenhouse complex at Moscow, ID, and (2) growth, development, and cold hardiness of 4-year trees growing in field tests established at high (1,500 m) and low (970 m) elevations near Priest River, ID.

For assessing patterns of shoot elongation, nine seedlings representing each population were grown in 740 cm^3 containers arranged in a randomized complete block design for each of three blocks. Seeds were sown directly into the containers, which were kept in a greenhouse for the duration of the germination period. The containers were transferred to a shadehouse (50 percent shade) in June for the duration of the first growing season but were returned to the greenhouse for the duration of the winter. Winter temperatures were maintained above freezing. In March of the second growing season, greenhouse temperatures were set at 20 (±4) °C during the day, and then were allowed to cool to a minimum of 10 °C at night with no supplemental lighting.

Periodic measurements were made of shoot elongation during the second growing season; a modified logistic model was fit to the elongation of each tree, and estimates were made of the initiation, cessation, rate, and amount of elongation from the logistic model (see Rehfeldt 1994). These variables plus 2-year height were then available for assessing genetic differences among populations. In assessing patterns of shoot elongation, measurements were begun on the day when the greenhouses were warmed, usually March 1.

Field tests were established in a randomized complete block design with 10 seedlings representing each population in each of three blocks. The tests were maintained for 4 years, during which time data were collected on growth, winter injuries, mortality, foliage color, and needle length. The tests provided as many as eight variables for assessing population differentiation.

Patterns of shoot elongation were assessed on all seedlings in each of the four studies. Field tests, however, were established at both elevations for studies 1 and 2, but the high elevation site was abandoned for study 3 because the climate at this elevation was not severe enough to injure the northern populations being tested. In study 4, populations were compared for only the pattern of shoot elongation. These irregularities in the experimental approach meant that a different assortment of variables was available for assessing population differentiation in each of the studies; in fact, only the six variables describing shoot elongation were available for all populations (table 1).

In the analyses described below, metric variables were transformed to logarithms because variances

Table 1—Number of populations tested (parentheses) and intraclass correlations for the main effects of populations expressed as a percentage of the sum of all variance components from four studies of the three taxa included in the *Picea engelmannii* complex. F-values for tests of significance for the effects of populations were statistically significant (p<0.01) for all intraclass correlations greater than 7 percent.

Test site and variable	Study 1 (37)	Study 2 * (103)	Study 3 (125)	Study 4 (59)
Greenhouse				
total elongation	48	17	43	42
start of elongation	29	7	17	21
cessation of elongation	52	19	37	47
duration of elongation	54	17	43	51
rate of elongation	12	11	35	25
2-year height	43	23	48	44
Priest River, 970 m				
4-year height	52	39	45	-
winter injuries	11	7	-	-
blue foliage	0	17	-	-
needle length	-	-	22	-
Priest River, 1500 m				
4-year height	8	27	-	-
winter injuries	10	0	-	-
mortality	33	-	-	-
healthy	21	-	-	-

* From Rehfeldt (1994)

were proportional to population means. Except where noted, all statistical analyses used the algorithms of SAS Institute (1985).

Scaling and Joining Multiple Data Sets

To assess genetic variation in response to climate across the entire geographic distribution of the *P. engelmannii* complex, population means were corrected for the effects of studies. Table 2 illustrates the mean values of three variables for a subsample of populations in common among studies. Differences between values for the same population represented in disparate studies illustrate the necessity of scaling the data before combining datasets. Table 2 shows that the effects of studies were most apparent for populations of southwest *P. engelmannii*, but that the ranking of populations remained constant between studies despite the differential effects of studies.

The scaling process followed that of Rehfeldt (1989, 1999) and involved adjusting population means according the standardized normal deviate of the performance of populations in common between studies. In the present analyses, logarithmic transformations produced homogenous variances between studies, which meant that population means could be used directly for scaling as long as the adjustments were made within taxa. Only those six variables describing patterns of shoot elongation were measured in all studies (table 1) and, therefore, were suited for these procedures.

In scaling population means between studies, those for study 4 were adjusted to those of study 3 according to the difference in performance of nine populations common to both studies; the resulting data set was then adjusted to those of study 2 according to the difference in performance of a different set of nine populations that were in common; and this data set in turn was adjusted to those of the study 1 according to the performance of 14 populations in common between the studies. Because adjustments were done separately for each taxon, *P. mexicana* and *P. chihuahuana* were

Table 2—Mean values of three variables for a sample of populations common to the independent studies. All populations are *P. engelmannii* except where noted.

Population number	Amount of elongation (mm)				Duration of elongation (days)				Cessation of elongation (day)			
	Study: 1	2	3	4	Study: 1	2	3	4	Study: 1	2	3	4
1	-	50	64	69	-	22	25	22	-	31	38	33
3	-	54	66	-	-	20	23	-	-	31	37	-
8	-	65	76	-	-	24	27	-	-	35	41	-
37	90	49	-	-	27	20	-	-	38	31	-	-
45	72	43	-	-	24	21	-	-	35	31	-	-
467	-	-	104	92	-	-	33	29	-	-	44	39
512	-	-	53	60	-	-	21	22	-	-	37	32
492††												
62**	127	60	-	-	48	31	-	-	54	40	-	-
108**	101	55	-	-	31	22	-	-	39	32	-	-
60**	128	71	-	-	62	51	-	-	62	52	-	-
61†	146	81	-	-	67	50	-	-	73	58	-	-
67†	156	76	-	-	76	47	-	-	80	56	-	-
447§	-	-	61	64	-	-	28	27	-	-	41	37

** Southwest *P. engelmannii*
† *P. pungens*
†† *P. glauca* x *P. engelmannii* hybrid
§ *P. glauca*

excluded from the adjusted data set. Note, however, that excluding the latter two taxa does not constrain interpretation of subsequent results because the available climate data from Mexico was not sufficient for estimating provenance climate.

Developing Climate Surfaces

Meeting the objectives required estimates of climate variables describing the provenance of each population. To this end, monthly averages of daily temperatures (minimum, maximum, and mean) and sums of daily precipitation, normalized for the period 1961 through 1990, were obtained for approximately 2,200 weather stations in Western United States (U.S. Department of Commerce 1994) and Southwestern Canada (Environment Canada 1994). However, most of the long-term stations were established for agronomic purposes and, therefore, poorly represented remote forested locations. To better represent the climate of provenances under test, daily temperature and precipitation records were obtained from Earthinfo (1994) for an additional 805 stations that (a) had a record period of at least 5 years for temperature and 7 years for precipitation and (b) had valid records (missing no more than 3 days) for all months. Data from these additional stations were adjusted to the normalized database by using the average of monthly deviations from the three closest stations within the database. The procedures gave approximately 3,000 observations for monthly means of the four variables for the area from 31° to 51° N latitude to 102° and 125° W longitude. Climate data sufficient for these purposes were not available for Northern Mexico.

Thin plate splines (Hutchinson 2000) were used to develop climate surfaces that would provide estimates of the 48 monthly climate variables for a geographic location, specified by latitude, longitude, and elevation. The splines were first fit to the normalized database from which 10 percent of the observations had been withheld to provide independent data for verification. As indicated by (a) the relationship between the predicted and observed values, and (b) the deviation of the regression coefficient of the observed on predicted values from a value of 1.0, verification of the approach was superb, especially for temperature variables. In fact, the worst fitting regression of predicted values on the observed was for August precipitation for which R^2 was 0.88, the regression coefficient was 0.9937 and the intercept was 8.84 mm.

Following verification, the data used for verification were returned to the normalized database and thin plate splines were refit. Statistical output from the splines showed that 95 percent confidence interval for predicted point was (a) 1.5 to 2.0 °C for average and maximum temperature, (b) about 3 °C for minimum temperature, and (c) about 25 mm of winter precipitation or 10 mm of summer precipitation.

Seventeen descriptive statistics of relevance in plant biology (see Tuhkanen 1980) were then calculated from the point estimates of monthly temperature and precipitation for the provenances represented in this study:

- Mean annual temperature.
- Mean temperatures in the coldest month.
- Minimum temperatures in the coldest month.
- Mean temperatures in the warmest month.
- Maximum temperatures in the warmest month.
- Annual precipitation.
- Summer (April through September) precipitation.
- Summer to winter temperature differential.
- Degree-days greater than 5 °C.
- Degree-days less than 0 °C.
- Annual moisture index (ratio of degree-days greater than 5 °C to mean annual precipitation).
- Summer moisture index (ratio of degree-days greater than 5 °C to mean summer precipitation).
- Julian dates of the last freeze (50 percent probability) of spring.
- Dates of the first freeze of autumn.
- Length of the frost-free period.
- Sum of degree-days greater than 5 °C that accumulate during the frost-free period.
- Julian date on which the sum of degree-days greater than 5 °C reached 100.

While the derivation of the first eight of these variables is straightforward from the monthly estimates, the algorithms and their verification for the latter nine are available from the author.

Biosystematic Analyses

Because of the experimental design, two canonical discriminant analyses were needed to assess the relationships among taxa. The first analysis used data from study 1 and allowed discrimination among populations of *P. engelmannii, P. pungens,* southwest *P. engelmannii, P. mexicana,* and *P. chihuahuana* for 13 characters—six measured in the greenhouse and seven measured in the field (table 1). Although it is impossible to represent genetic variation with a sample of single population, *P. mexicana* and *P. chihuahuana* are carried through these analyses to provide a general assessment of their relationships to their congeneric cohorts.

The second discriminant analysis dealt with *P. engelmannii, P. glauca,* and the hybrids. The analyses used data from studies 3 and 4 and used only the six variables describing patterns of shoot elongation within the corrected data set. Both discriminant analyses were performed on the standardized matrix.

Analyses of Genetic Differentiation Within Taxa

Differentiation among the 295 populations representing the *P. engelmannii* complex was assessed with univariate analyses of variance of each variable measured in each study (table 1). Statistical tests used in these analyses are presented in detail in Rehfeldt (1994) where the degree of genetic variation was expressed as intraclass correlations, the ratio of the

variance component for the effects of populations to the sum of all variance components.

Variance components were also calculated for analyses of the 16 *P. pungens* populations and the 23 *P. glauca* populations.

Genecological Models

In assessing patterns of genetic variation among populations in relation to climate, preliminary examinations revealed several associations that were both strong and nonlinear. To facilitate nonlinear regression analyses, the 17 original climate variables were scaled to values between 0 and 1:

$$X_i' = (X_i - X_{min})\left[(X_{max} - X_{min})^{-1}\right] \qquad [1]$$

where X' is the transformed value of a climate variable for provenance i; and X_{max} and X_{min} are the largest and smallest values, respectively.

A simple quadratic model was used for an initial screening of the relationship between scaled climate variables and genetic variation of all variables of table 1. The primary intent of this screening was to examine the consistency of responses across studies. This screening showed that the same combination of dependent and independent variables produced the highest R^2 in all studies, and of the independent variables, the cessation, duration, and amount of shoot elongation were the variables with the strongest relationships to climate. This meant that the analytical approach could be simplified without constraining interpretations by assessing clinal patterns of genetic variation with the corrected data set containing the six variables describing shoot elongation of all populations.

The preliminary screening also showed that of the independent variables, degree-days less than 0 °C and mean temperature in the coldest month consistently produced the strongest relationships with the six dependent variables. The relationships, however, were strongly nonlinear for all dependent variables except the rate of shoot elongation. To accommodate the nonlinear patterns, the following model was fit for the cessation and duration of shoot elongation:

$$Y_i = b_1 e^{b_2 X_i^{b_3}} \qquad [2]$$

where Y is the cessation or duration of shoot elongation of population i; X is the transformed value of mean temperature in the coldest month of population i; e is the base of natural logarithms; and the b's are regression coefficients. Values of X were transformed according to [1].

For 2-year height and amount of shoot elongation, the appropriate model was:

$$Y_i = e^{\left(b_1 + b_2 X_i^{b3}\right)} \qquad [3]$$

where X is the transformed value of degree-days less than 0 °C with other symbols defined in [2].

And for the start of shoot elongation, the appropriate model was:

$$Y_i = b_1 + b_2 X_i + b_3 X_i^{b_4} \qquad [4]$$

with the symbols described in [3].

To find the best fitting combination of predictors for describing genetic variation in response to climate in general, values predicted by [2, 3, and 4] were treated as transformations of the independent variable in a stepwise linear regression model that screened, for each of the six dependent variables, a total of 35 independent variables—the first and second powers of the 17 original variables plus the variable transformed according to [2, 3, or 4]. Rates of differentiation along a cline were interpreted relative to a confidence interval (CI) calculated from the standard error of the mean ($s_{\bar{x}}$) at $\alpha = 0.2$. The confidence interval indicates the amount by which two predicted values must differ before one is reasonably sure that the differences are real. A relatively high level of probability (0.2) was used to reduce the possibility of accepting no differences among populations when differences actually exist. Such errors (type II) have the greatest potentials for making poor decisions when models are applied to practical problems. The approach is directly suited for assorting populations into climatypes, the climatic ecotypes of Turesson (1925).

Effects of Climate Change

Assessing the effects of a change in climate on the distribution of taxa and adaptedness of populations required, first, an estimation of the climatic limits of each taxon. To this end, a canonical discriminant analysis was made using the 17 derived climate variables to segregate five taxa—the three of the *P. engelmannii* complex, *P. pungens,* and *P. glauca*. Because the present studies sampled only a small portion of the transcontinental distribution of *P. glauca*, climate data from an additional 38 Alberta provenances were included in the discriminant analysis. These supplemental data were provided by N. K. Dhir, Alberta Sustainable Resources, Edmonton, Alberta. Climatic limits of taxa were inferred from those of their constituent populations. The canonical coefficients could then be used to determine site suitability: a locality was deemed suitable for a taxon if each of the four canonical variates calculated from the climate at that locality fell within the taxon's limits (see Box and others 1999).

Next, a climate database was developed that was representative of the contemporary altitudinal distribution of the taxa. This database was produced by generating an altitudinal sequence of sites at 50 m intervals for each of the 36 localities numbered in figure 1. The thin plate splines described above were then used to estimate for each site the monthly means for the minimum, maximum, and average temperature and precipitation. These variables were then converted to the 17 derived variables being used to drive the models of genetic variation.

To update this database for the effects of global warming, monthly output from General Circulation Models (GCM) produced by the Hadley Centre and the Canadian Centre for Climate Modelling and Analysis

was summarized for the region of study. The scenarios chosen were HadCM3GGa1 of the Hadley Centre (Gordon and others 2000) and CGCM2_ghga of the Canadian Centre (Flato and Boer 2001), both of which address the IS92a scenario (1 percent per year increase after 1990) of the International Panel on Climate Change (IPCC 2001). For each, monthly means for the minimum, average, and maximum temperature and precipitation were obtained for the normalization period (1961 through 1990) and for three future decades, those beginning in 2030, 2060, and 2090.

GCM output was used to calculate the monthly change in climate between the normalization period and future decades for those grid cells that underlie figure 1. The change in climate expected at each provenance represented in the present studies could then be calculated by a weighted average of change expected at each cell center lying within 500 km of the provenance. The inverse of the distance of the provenance to the cell center was used for weighting. Because the two GCMs use different grid sizes, weighted means were calculated for each GCM and were averaged to estimate the change in climate of each provenance. Estimated climates of the future were then converted to the 17 derived variables being used to drive the models of genetic variation.

In the third step, genecological models of genetic variation were used to predict for all locations in the database the six variables describing patterns of shoot elongation for the contemporary climate and for three decades of the future. This database could then be queried for the effects of climate on the adaptedness of a population at any specific targeted locality. To estimate the geographic distribution of populations expected to be genetically suited to the contemporary climate at a specific locality, one (1) selects a target locality, (2) determines which taxa are suitable for the target, (3) predicts genetic responses for the suitable taxa from the models of genetic variation, (4) attaches confidence limits to each prediction, and (5) searches the database of contemporary climates for all locations expected to be inhabited by genotypes whose responses fall within the confidence intervals calculated for the target. To estimate future effects, one merely uses, in step 5, the database of future climates instead of that of contemporary climates.

Two Euclidean measures of distance were calculated to provide an indication of the suitability of a selected population to the climate at a targeted locality. One was a genetic distance (*GD*):

$$GD = \sqrt{\left[\sum\left(\frac{d_i}{CI_i}\right)^2\right]n^{-1}} \qquad [5]$$

where *d* is the difference in genetic responses in trait *i* between that predicted for the climate at the targeted locality and that of a population represented in the database; *CI* is the confidence interval ($\alpha = 0.2$) surrounding population means for trait *i*; and *n* is the number of traits, equal here to 6.

The second was a climate distance (*CD*):

$$CD = \sqrt{\left(\sum g_i^2\right)n^{-1}} \qquad [6]$$

where *g* is the difference between climate variable *i* scaled according to [1] at the targeted location and that of a population represented in the database; and *n* is the number of climate variables. All derived variables were used for these calculations, and, therefore, *n* = 17.

Results

Biosystematics

The canonical discriminant analysis based on 13 variables (table 1) measured on five taxa in study 1 produced a primary vector that accounted for 46 percent of the variance among taxa; a second accounting for 42 percent; a third for 10 percent; and a fourth for 3 percent. The position of the taxa with regard to the first three canonical vectors (fig. 2) shows that (1) *P. chihuahuana* is readily separated from all other taxa; (2) *P. pungens* can also be separated from all other taxa; and (3) *P. engelmannii*, southwest *P. engelmannii*, and *P. mexicana* tend to form a continuum anchored by *P. engelmannii* at one extreme and by southwest *P. engelmannii* at the other with *P. mexicana* peripheral and somewhat disjunct. The fourth vector was inconsequential.

The second discriminant analysis considered 290 populations of *P. engelmannii*, *P. glauca*, and their hybrids; was based on the dataset that had been corrected for the effects of studies; and used, therefore, only the six variables describing shoot elongation. The first canonical vector accounted for 86 percent of the variance among groups and the second 14 percent. The scatter of data points according to these vectors (fig. 3) demonstrates that the three taxa can be separated on average, but not discretely. Not surprisingly, populations labeled as hybrid generally were positioned intermediate between parental taxa.

Population Differentiation

Analyses of variance detected abundant genetic variation among the 295 populations representing the *P. engelmannii* complex (table 1). Differentiation was most pronounced in study 1, which contained a mixture of *P. engelmannii* and southwest *P. engelmannii* genotypes; was nearly as pronounced in studies 3 and 4, composed of *P. engelmannii* and *P. engelmannii – P. glauca* hybrids; and was the least in study 2, composed primarily of the *P. engelmannii* populations analyzed previously (Rehfeldt 1994).

Table 1 shows clearly that population differentiation is most pronounced for either variables describing shoot elongation or seedling height in the low elevation field test. This means that the absence in studies 3 and 4 of data from either or both of the field test sites should not constrain interpretations.

In analyses not presented, population differences were also detected among the 15 *P. pungens* populations of study 1. Particularly strong were population effects for 4-year height at the low elevation test site and for 2-year height measured in the greenhouse, but all variables describing the pattern and amount of shoot elongation were
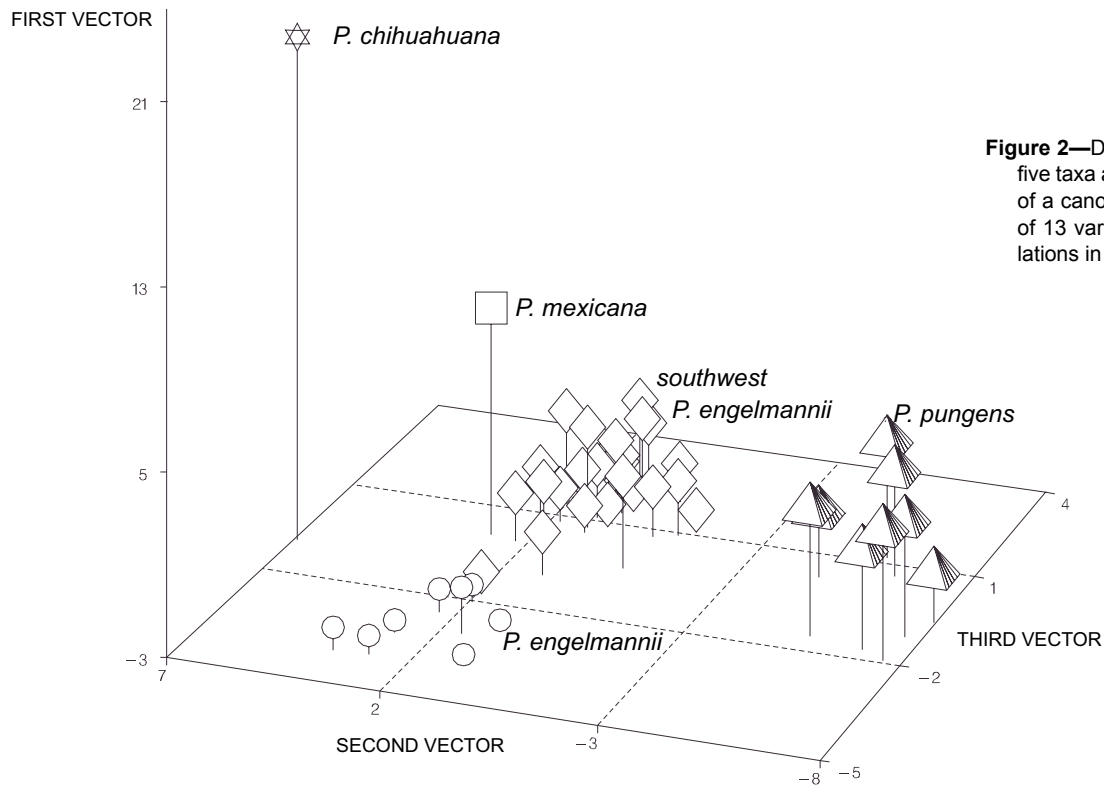
Figure 2—Dispersion of populations of five taxa along the first three vectors of a canonical discriminant analysis of 13 variables measured on populations in study 1 (table 1).
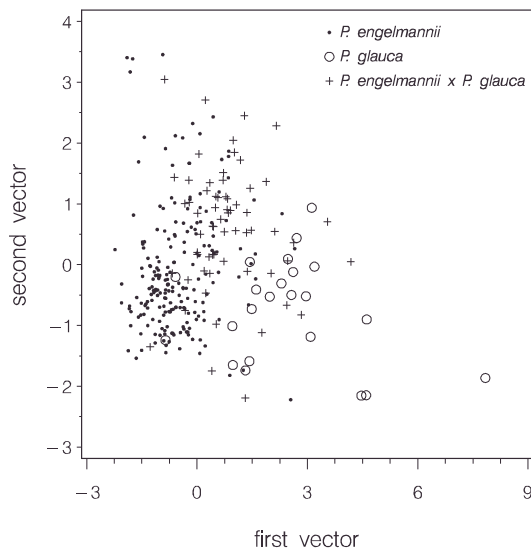

Figure 3—Dispersion of three taxa along the first two vectors of a canonical discriminant analysis of six variables describing patterns of shoot elongation measured in populations of studies 3 and 4 (table 1).

statistically significant ($p < 0.0001$). Differences among populations also were apparent among the 13 populations of *P. glauca* for all variables measured in study 4.

Climatic Clines Within Studies

Despite the disparate composition of the four studies, univariate relationships of climate variables to the performance of populations from the *P. engelmannii* complex were surprisingly consistent across studies (table 3). The strongest relationships invariably involved the cessation, duration, and amount of elongation, all

of which were measured in the greenhouse on 2-year trees. Relationships between genetic variation in these variables and climate tend to be strong, with climate accounting for as much as 76 percent of the variation among populations (table 3). Univariate relationships also suggest that in the south (studies 1 and 2), genetic differentiation is most closely related to climate variables reflecting winter temperature, but toward the north (studies 3 and 4), summer temperatures also become important descriptors.

The consistency of these results implies that the same primary factors are molding genetic variation throughout the distribution of the three taxa that

Table 3—Combination of dependent and independent variables with the strongest univariate relationships to provenance climate for populations in the *P. engelmannii* complex.

Study	Dependent variables	Independent variables	Maximum R^2
1	cessation, duration, and amount of elongation	degree-days<0ºC, mean temperature in coldest month, mean annual temperature	0.76
2*	cessation and duration of elongation	degree-days<0ºC, mean temperature in coldest month, mean annual temperature, date when degree-days>5ºC summed to 100	0.70
3	duration of elongation, 4-yr height in low elevation test site	degree-days<0ºC, mean minimum temperature in coldest month, mean annual temperature, degree-days>5ºC, date when degree-days>5ºC summed to 100, sum of degree-days>5ºC during frost-free period	0.60
4	cessation and duration of elongation	degree-days>5ºC, degree-days<0ºC, mean annual temperature, date when degree-days>5ºC summed to 100, sum of degree-days>5ºC during frost-free period	0.71

* From Rehfeldt (1994)
Note: all values of R^2 statistically significant at p < .0001

compose the *P. engelmannii* complex. Because (1) the variables for which genetic variation was the most pronounced (table 1), and (2) the variables for which relationships with climate are the strongest (table 3) are derived from measurements of shoot elongation, subsequent analyses could deal solely with the corrected data set. Nonetheless, before results using the corrected data set can be accepted unequivocally, some assurance is required that the methods employed in merging data sets did not inadvertently introduce bias.

Effects of Scaling and Joining Datasets

In scaling and joining data collected in disparate studies, correction factors were used that consisted of the difference in performance between the same populations represented in different studies. However, to develop correction factors for each taxon, all of the available data were required. This meant that no independent tests could be made for judging the effectiveness of the procedures (see Rehfeldt 1989).

Three observations nonetheless are pertinent: First, of the 32 possible comparisons between adjusted and actual means, adjusted means on average were within 3 percent of the actual mean for the start and end of shoot elongation; 4 percent for the duration of shoot elongation; 6 percent for the amount of shoot elongation and 2-year height; and 7 percent for the rate of elongation. Second, the mean difference between the actual and adjusted values was smaller on average than the standard error of the mean. And third, in regressions of observed means on adjusted means for these 32 observations, values of R^2 ranged from 0.88 (rate of elongation) to 0.99 (cessation of elongation); regression coefficients were essentially 1.0, ranging from 0.96 to 0.99; and intercepts were essentially zero (5 mm for 2-year height, 1.5 mm for amount of shoot elongation, 0.2 days for the duration of elongation, 0.4 days for the cessation of elongation, 0.5 days for the start of elongation, and 0.14 mm/day for the rate of elongation). Although not conclusive, these comparisons are consistent with the tests of Rehfeldt (1989); both suggest

that when careful experimentation is conducted under similar conditions, these independent data sets can be scaled according the performance of common populations without incorporating bias but yet producing errors of estimate that are quite small.

Climatic Clines of the P. engelmannii Complex

Regressions relating climate to genetic variation among the 295 populations representing the *P. engelmannii* complex used the corrected data and, therefore, deal with only those six variables describing patterns of shoot elongation. Figure 4 shows the relationship between the total amount of elongation and degree-days less than 0 °C modeled according to [3]. For this relationship, degree-days less than 0 °C accounts for 62 percent of the variance in the amount of elongation. The relationship is decidedly nonlinear: as the winter of the provenance becomes more severe, the amount of shoot elongation exhibited in the mild climate of a common garden diminishes. But the cline is much less steep for severe climates than for mild climates. The clines relating winter temperatures to the cessation and duration of shoot elongation and to 2-year height are essentially the same as that shown in figure 4. As the winter climate of the provenance becomes more severe, growth potential is reduced in response to a shortened growth period, and these characteristics are expressed even when the populations are grown in the mild climates of common gardens.

Genetic variation in the start of shoot elongation also showed a primary relationship with degree-days less than 0 °C, with the dependent variable accounting for approximately 34 percent of the variance in the start of elongation. The relationship was driven largely by populations of southwest *P. engelmannii,* which initiated shoot elongation the earliest and originated from provenances with mild winters. Differences among the *P. engelmannii* and hybrid populations from colder climates to the north were not related to the coldness of winters of the provenance.
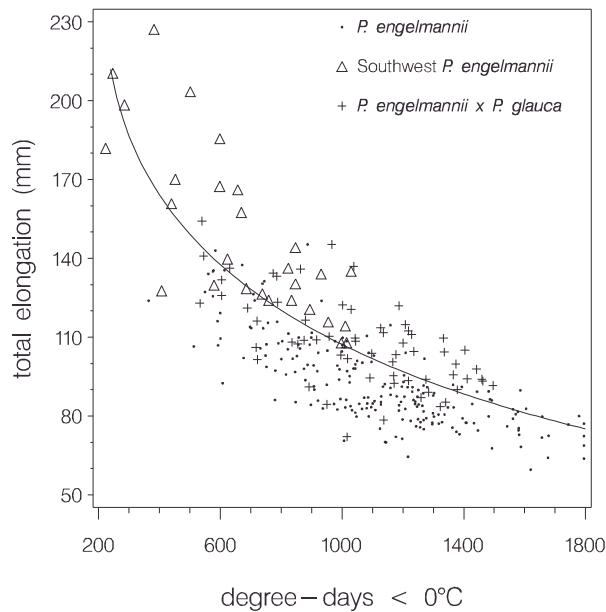
Figure 4—Population means for the amount of shoot elongation of taxa of the *P. engelmannii* complex plotted according to degree-days less than 0 °C of the provenance. The univariate regression model (line) accounts for 62 percent of the variance in the dependent variable.

The primary cline relating the rate of shoot elongation to climate was essentially a linear response associated with either the Julian date of the last spring frost (R^2 = 0.30) or degree-days more than 5 °C that accumulate during the frost-free period (R^2 = 0.28). Slow rates of elongation were exhibited in common gardens by populations from climates where the last frost of spring customarily occurs early in the spring; and high rates typified populations from provenances where the degree-days accumulating within the frost-free season are high.

Rates of differentiation along univariate clines can be judged in relation to the standard error of the mean.

For figure 4, for example, the confidence interval (α = 0.2) about a population mean for amount of elongation is ±0.0802 mm in units of logarithms. When converted to the original units of measure, a standard error of this size would mean that for two populations to differ at a reasonable level of probability (α = 0.2), the mean difference in elongation must be at least 12 mm for populations with low innate growth potential (for example, 75 mm total elongation) or by 24 mm for populations with high growth potential (for example, 150 mm elongation). It follows, therefore, that two genetically different populations tend to originate in provenances differing by about 110 degree-days less than 0 °C if growth potential is low or about 90 degree-days if growth potential is high (fig. 4). The clines relating 2-year height to degree-days less than 0 produced a similar conclusion, but the cline for the start of elongation produced much broader intervals particularly for populations from cold climates where differentiation was difficult to detect.

The same reasoning applied to the univariate clines—that is, relating rates of change in the cessation and duration of elongation to mean temperature in the coldest month—also produced estimates of 0.6 °C and 2.2 °C by which populations from either warm or cold provenances, respectively, must be separated before one can be reasonably certain (α = 0.2) of genetic differentiation. The cline for the rate of elongation suggested that genetically different populations originate from provenances differing by at least 20 days in the date of the last spring frost and about 600 degree-days more than 5 °C that accumulate across the frost-free period.

Genetic differentiation in response to multiple climatic effects was assessed for populations of the *P. engelmannii* complex with stepwise regression, the best fitting models of which produced values of R^2 between 0.54 and 0.83 (table 4). The dependent variables for which climatic clines were the steepest were the cessation and duration of shoot elongation. Although the regression models include as many as five independent variables, most described the severity of the winter. This result also corroborates those obtained from univariate regressions done within studies (table 3) that show

Table 4—Independent variables for the best fitting multiple regression models of genetic variation in variables describing patterns of shoot elongation in populations of the *P. engelmannii* complex on provenance climate.

Dependent variable	R²	Independent variables
start of elongation	0.54	degree-days<0ºC, mean minimum temperature in coldest month, April – September precipitation
rate of elongation	0.62	date of last spring frost, date of first fall frost, mean minimum temperature in coldest month, mean maximum temperature in warmest month
cessation of elongation	0.81	degree-days<0ºC, mean minimum temperature in coldest month, mean temperature in the coldest month, mean maximum temperature in warmest month
duration of elongation	0.83	degree-days<0ºC, mean minimum temperature in coldest month, mean temperature in the coldest month, mean maximum temperature in warmest month, summer – winter temperature differential
2-year elongation	0.78	degree-days<0ºC, mean maximum temperature in warmest month, length of the frost-free period, date when degree-days>5ºC summed to 100
2-year height	0.72	degree-days<0ºC, mean temperature in coldest month, mean maximum temperature in warmest month

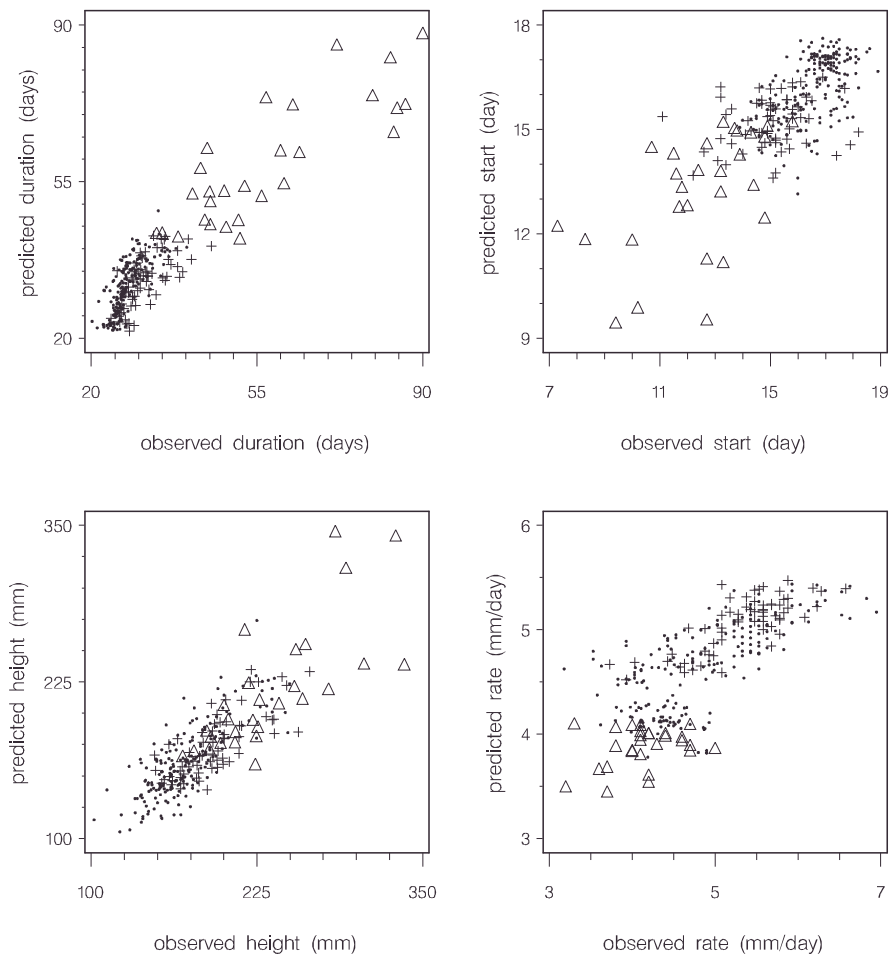Note: all values of R^2 statistically significant at $p < .0001$

Figure 5—Plots of population means for the *P. engelmannii* complex against values predicted by multivariate regression models of the duration (upper left), start (upper right), and rate (lower right) of shoot elongation and 2-year height (lower left) on climate variables. The regressions account for 83, 54, 62, and 72 percent of the variance in the dependent variable, respectively. Symbols correspond to figure 4.

relationships of genetic variation to summer temperatures to be secondary. Relationships between predicted and observed values are shown in figure 5 for four of the variables.

Climatic Clines in P. pungens and P. glauca

Even though few populations of *P. pungens* and *P. glauca* were tested, their performance shows without doubt that climatic clines within these species are much different from those of the *P. engelmannii* complex (fig. 6). Climate variables most strongly related to genetic variation in *P. pungens* included degree-days less than 0 °C, mean temperature in the coldest month, the summer-winter temperature differential, and summer precipitation. Although populations of both the *P. engelmannii* complex and *P. pungens* are arranged along clines driven by winter temperatures, the cline for the *P. engelmannii* complex is of much steeper slope than that for *P. pungens* (fig. 6).

For *P. glauca*, the summer-winter temperature differential, the Julian data at which the annual degree-day greater than 5 °C sum reached 100, length of the frost-free period, Julian date of the last spring frost, and mean temperature in the coldest month were the climate variables most closely associated with variation among populations. These clines, therefore, are driven by much
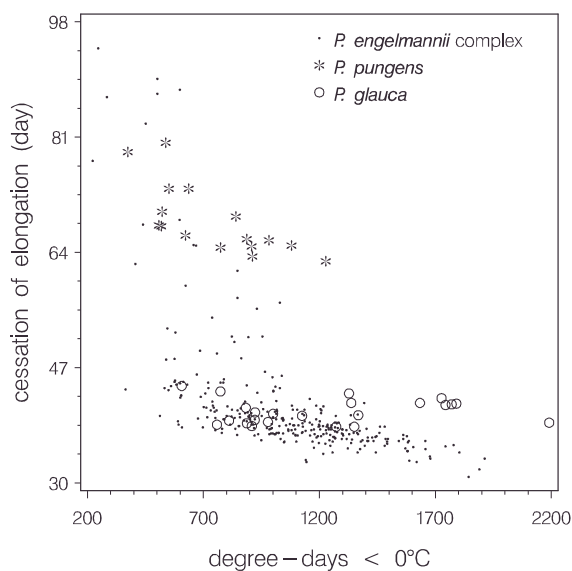

Figure 6—Population means for cessation of shoot elongation of the *P. engelmannii* complex, *P. pungens*, and *P. glauca* plotted according to the degree-days less than 0 °C of the provenance.

different climate variables than those of *P. pungens* and the *P. engelmannii* complex. Figure 6, in fact, shows that variation in cessation of shoot elongation for populations of *P. glauca*, unlike that of its congeneric cohorts, is not arranged along clines paralleling winter temperatures. While winter temperatures were most closely related to the start of shoot elongation in *P. glauca*, on the whole, genetic differentiation within the species was most closely related to the summer-winter temperature differential of the provenance.

Interpreting Genetic Variation Along Multiple Climatic Clines

Because the distribution of genotypes along multiple climate gradients deals as much with the distribution of taxa as with populations, a discriminant analysis for separating the five taxa, the three of the *P. engelmannii* complex, *P. pungens*, and *P. glauca*, was made using the 17 climate variables as discriminators. The analysis produced a first canonical vector accounting for 60 percent of the variance among the five taxa; a second for 27 percent; a third for 7 percent; and a fourth for 5 percent. The results are illustrated in figure 7 (left and right). These illustrations show that while most taxa are separated along the first and second vectors, *P. pungens* tends to be separated from both southwest *P. engelmannii* and *P. engelamnnii* along the third vector. As expected for taxa that can cooccur, the segregation of the taxa is not complete. Nonetheless, populations labeled as hybrids between *P. engelmannii* and *P. glauca* segregated into positions intermediate between populations of the two parental species.

The discriminant functions when used in conjunction with the climatic limits of the taxa can be used to construct a climatic envelope (see Box and others 1999) within which genecological models can be interpreted. Modeled population responses for the duration of shoot elongation (table 4), for instance, are mapped in figure 8 within the climatic envelope of the *P. engelmannii* complex on a 1 km (0.0083 degrees) grid (Globe 1999).
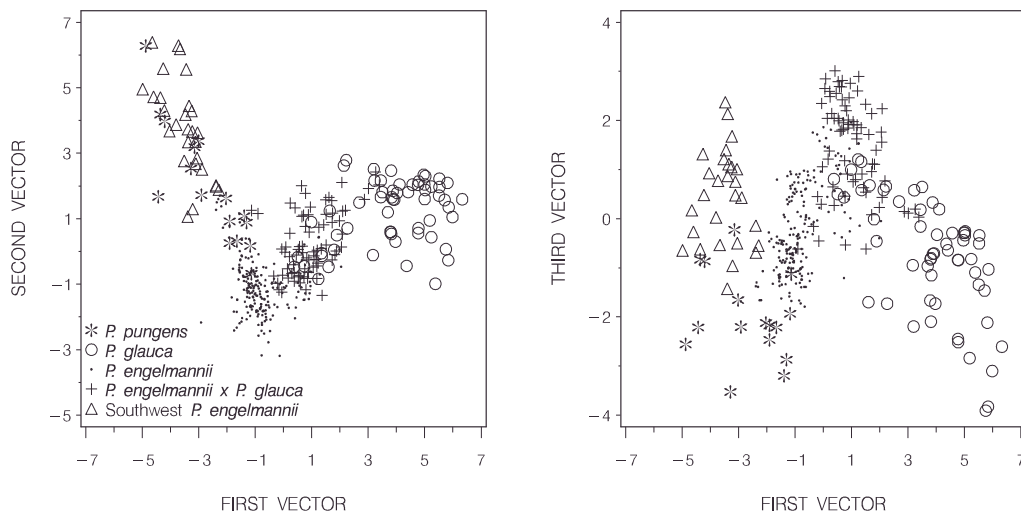

Figure 7—Dispersion of populations of five taxa along the first two vectors of a canonical discriminant analysis (left) and the first and third vectors (right) using 17 variables describing provenance climate.
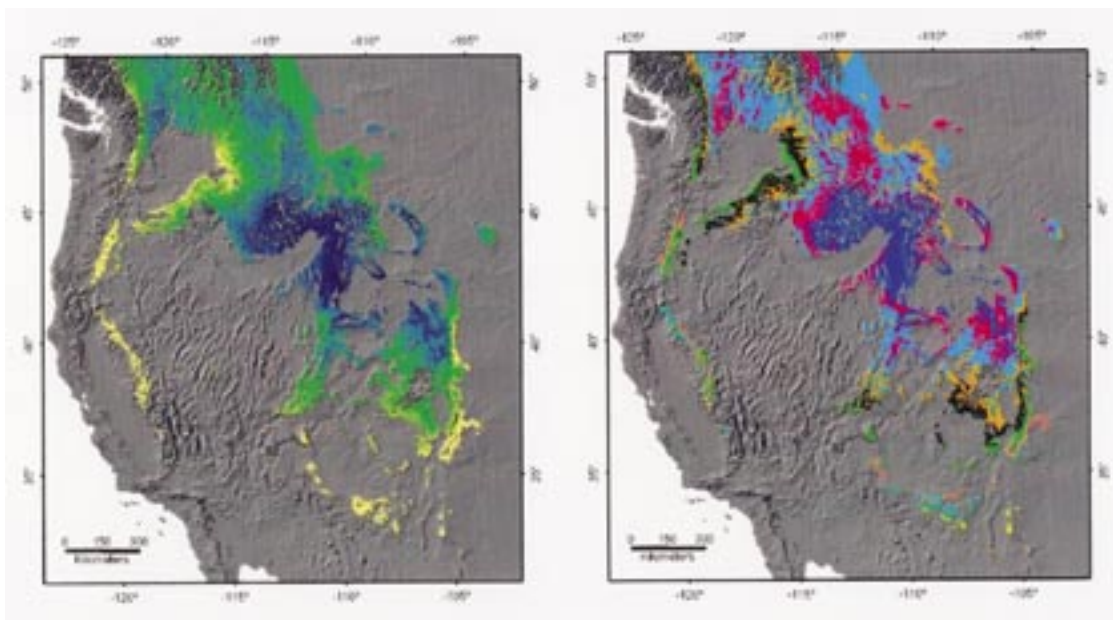

Figure 8—Mapped patterns of genetic variation in the duration of shoot elongation predicted for populations of the *P. engelmannii* complex. Left: continuous variation from 21 days (dark blue) to 79 days (light yellow). Right: nine classes of breadth equal to the confidence interval ($\alpha = 0.2$) surrounding mean.

In figure 8, a map of continuous variation described by the model can be compared with that for nine geographic groups composed of genetically similar populations.

Figure 8 nonetheless illustrates univariate cline described by multiple climatic effects. To assess genetic variation across the landscape according to all six response variables, the regression models of table 4 were used to make queries into a climate database to locate extant populations expected to have patterns of shoot elongation that are genetically compatible with the climate at a targeted location. As an example, consider a target at an altitude of 3,000 m in southwestern New Mexico (location 3, fig. 1) that is currently inhabited by southwest *P. engelmannii*. This population is relatively isolated (fig. 1) in a region where populations have a high growth potential and, therefore, clines are steep (fig. 4). As a result, genotypes compatible (for example, within ±CI at $\alpha = 0.2$ for all six predicted responses) with the climate at this location are expected to be found at a few isolated locations peripheral to location 3: in east-central Arizona (location 4) at an altitude of 2,900 m, in central New Mexico (location 8) at 2,900 to 3,000 m elevation, and in northern New Mexico (location 9) at 2,800 m (table 5).

In the severe climates in the north, clines tend to be less steep than in the south (fig. 4), and as a result, populations expected to be genetically compatible with the climate at a targeted site (table 5) are more widespread than in the south. At location 20, for instance, the climate at an altitude of 2,250 m should be suitable for genotypes that are distributed across a region so vast as to include populations occurring as distant as 2,500 km (table 5, fig. 1). Broad adaptability of northern populations of the *P. engelmannii* complex is also evident for targeted sites at localities 24 and 33.

Because clines are steeper for mild climates than for severe, populations best suited genetically to the climate at high elevations tend to be more widespread than those compatible with low elevation climates (for example, 1,350 m altitude at location 24 versus 1950 m at the same location). Also noteworthy in table 5 is that (1) either *P. pungens* or southwest *P. engelmannii* should be suited for the selected elevations at locations 10 or 14 even though the former is best suited for southwest *P. engelmannii* and the latter for *P. engelmannii*, (2) either hybrid or *P. engelmannii* genotypes should be suited to localities 20 and 33, (3) *P. engelmannii*, hybrid, or *P. glauca* populations are suited for the target site at location 32, (4) only *P. glauca* is suited for the Cypress Hills (location 31) of Southwestern Alberta and the Black Hills (location 19) of South Dakota, and (5) the same elevations at localities 32 and 33, which are on the eastern and western slopes of the Rocky Mountains, have climates so diverse that the best suited genotypes are from entirely different complements. For future reference, note that in table 5, populations capable of similar response to the climate at a targeted locality are within 0.75 units of genetic distance, and these similar populations should recur in climates within 0.25 units of climate distance.

The relationships of table 5 can be mapped for the *P. engelmannii* complex by classifying the continuous patterns of genetic variation for each of the six response variables (fig. 8) and mapping unique combinations of the classes as climatypes (fig. 9 and 10). Three of the largest climatypes are mapped in figure 9. Of these, the largest, colored yellow, occurs at altitudes of about 900 to 1,300 m in Alberta, 1,800 to 2,400 m in Idaho, 2,000 to 2,500 m in Utah, and 2,300 to 3,100 in Colorado; the climatype of the Northwest (pink) occurs at altitudes from 900 to 1,500 m on both sides of the Columbia

Table 5—Locations (number codes in **bold face**, keyed to figure 1) and their altitudes (m) containing genotypes expected to be genetically compatible with the contemporary climate of the targeted locality. Compatible genotypes are *P. engelmannii* except as noted.

Targeted locality	Location of compatible genotypes						
	1	2	3	4	5	6	7
3: 3000	**3**: 3050-3150 *	**8**: 2900-3000*	**9**: 2800-2850 *	**4**: 2900 *			
10: 3000	**10**: 2950-3100 *	**10**: 2950-3000 †	**5**: 2950 *	**7**: 3200 *	**6**: 2700*		
14: 2800	**14**: 2750-2850	**14**: 2750-2850 †	**15**: 2750-2850	**15**: 2750†			
12: 3200	**12**: 3100-3300	**14**: 3250-3300	**15**: 3200-3250	**17**: 2900-2950	**20**: 2500		
17: 2900	**17**: 2800-2950	**16**: 2850-2900	**23**: 2100-2250	**15**: 3200	**12**: 3200	**20**: 2350	
20: 2250	**20**: 2150-2300 ††	**24**: 2000-2200	**16**: 2700-2750	**17**: 2650-2750	**21**: 2200-2250	**32**: 1750-1800	**12**: 2900-2950
24: 1350	**24**: 1300-1600	**25**: 1250-1500	**27**: 1100-1150	**28**: 1100-1150			
24: 1950	**24**: 1800-2050	**25**: 1700-1800	**26**: 1400-1550	**27**: 1500	**28**: 1550	**32**: 1650-1700	
31: 1450	**31**: 1150-1500§						
32: 1250	**32**: 1300-1400 ††	**32**: 1200-1250§	**30**: 1650-1700§	**21**: 1850§	**28**: 1150		
33: 1250	**33**: 1100-1350††	**34**: 700-1050††	**28**: 1400-1500	**27**: 1450	**24**: 1750		

Note: also compatible for targeted location **20** are: **21**: 2150 ††, **15**: 3000, **14**: 3150, and **12**: 2900†
* Southwest *P. engelmannii*
† *P. pungens*
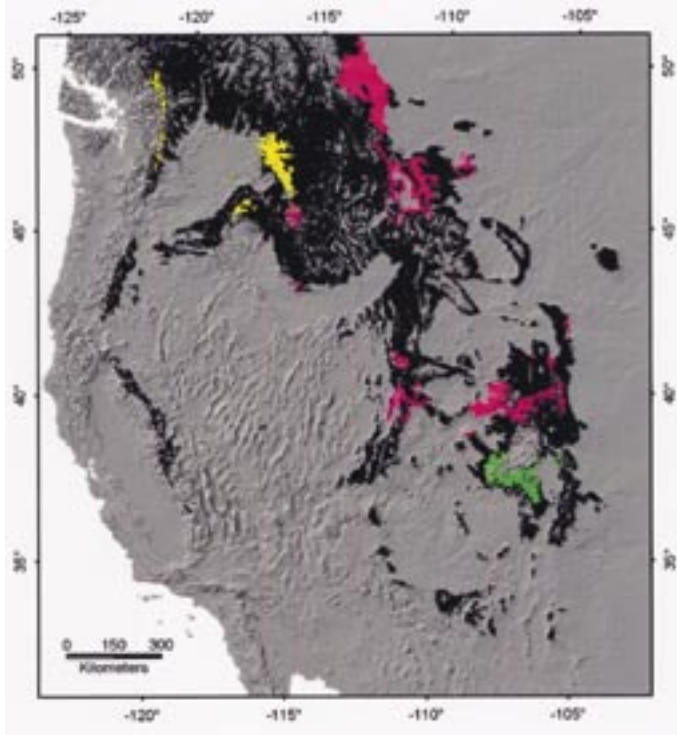†† *P. glauca* x *P. engelmannii* hybrid
§ *P. glauca*

Figure 9—Three climatypes of the *P. engelmannii* complex superimposed on the taxon's climatic distribution in Western United States and Southwestern Canada.

for Colorado), both regions are dominated by only a few. For Idaho and Montana, for instance, 20 climatypes account for approximately 75 percent of the distribution of the *P. engelmannii* complex, while two of these account for about 20 percent. For Colorado, the 20 largest climatypes account for about 80 percent of the taxon's total distribution while one of these alone accounts for 12 percent.

Climate Change

The estimates of global warming used for these analyses were derived from the average of predictions by the Hadley and Canadian Models for the IS92a scenario. At a longitude of 114 °W, the change in mean annual temperature projected by the average of the two models for the decade beginning in 2030 is +1.9 °C for a latitude of 35 °N and +2.5 °C for a latitude of 50 °N; +3.5 °C and +3.7 °C, respectively, for the decade beginning in 2060; and +4.4 °C and +5.0 °C, respectively, for the decade beginning in 2090. Although calculated in percentages, changes in precipitation equate roughly to +17 mm, +10 mm, and +65 mm for the decades of 2030, 2060, and 2090, respectively, at 35 °N; and +55 mm, +96 mm, and +105 mm in the three decades at 50 °N.

After changing the climate at a target location according to averages of GCM output, one then can identify the contemporary populations that should be the best suited for novel climates. Table 6 provides examples for the same target locations used for table 5. At location 3, for instance, the combined increase in temperature and precipitation should produce a climate beyond current climatic limits of distribution for southwest *P. engelmannii* and *P. pungens*. The analyses imply further that the climate should not be suitable for *Picea* at locations 1 and 2 by 2030 and at location 4 by 2060. By 2090, the southern limits of both southwest *P. engelmannii* and *P. pungens* are expected to be at locations 7 and 8 (fig. 1). One must note, however, that the suitability of *P. chihuahuana* and *P. mexicana* for the

Basin; while the third (green) is common from 2,700 to 3,600 m in the Southwest. Grid cells within each of these climatypes are expected to be of similar climate and therefore should support similar genotypes.

In figure 10, the assortment of climatypes is mapped for Idaho and western Montana (left) and Colorado (right). Although these maps delimit a relatively large number of climatypes (103 for Idaho and Montana; 87
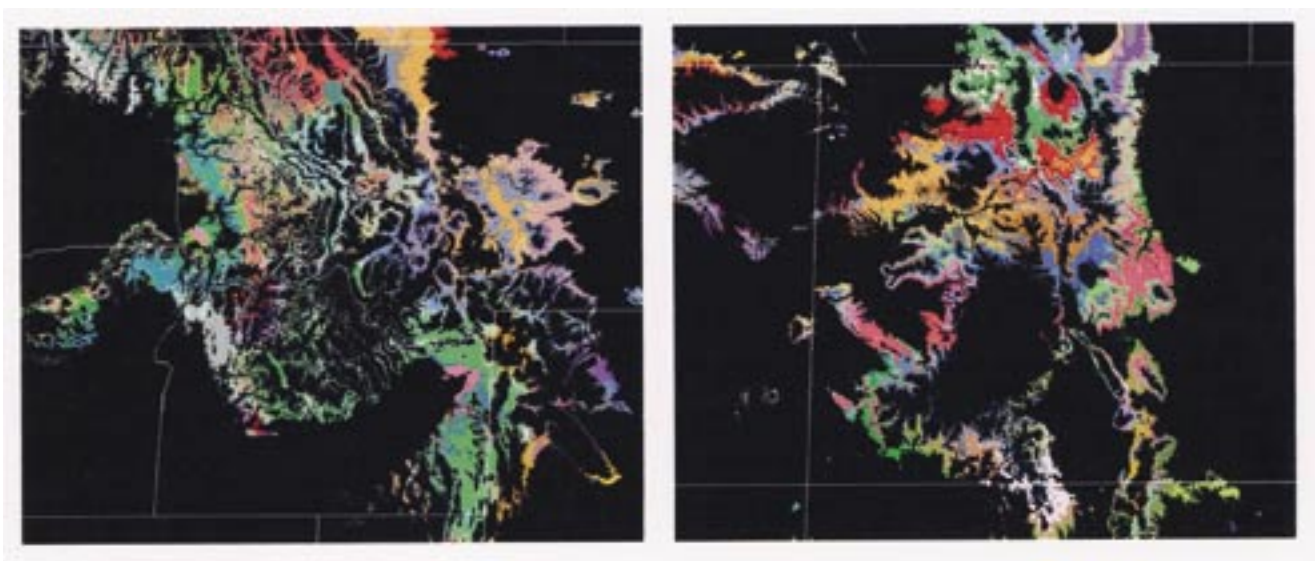

Figure 10—Distribution of climatypes of the *P. engelmannii* complex in Idaho and western Montana (left) and Colorado (right).

novel climates at these southern locations could not be assessed.

In another example, at 2,800 m at location 14, the climate should become more suitable to *P. pungens* than to *P. engelmannii* by 2030 and should remain so throughout the remainder of the century. Yet, as the climate warms, the best suited populations of *P. pungens* are shown to currently reside farther and farther to the south. By 2090, the best suited genotypes for this site currently inhabit 2,600 m elevation at location 3, about 600 km to the southeast. By 2060, *P. pungens* should be the dominant member of the genus on the plateaus of central and southern Utah (locations 13, 14, 15, and 17).

By contrast, at 3,000 m at location 10, a climate that today is suitable for southwest *P. engelmannii* should remain suitable throughout the century. Nonetheless, the contemporary location of the best suited genothypes shifts toward the south as the climate changes. At the end of the century, in fact, the best suited genotypes for the novel climate at this location reside today at the southern limits of the taxon's distribution, nearly 700 km away.

Elsewhere, at 3,200 m at location 12, the climate of 2,030 should become best suited to populations of *P. engelmannii* from lower elevations and milder climates. After 2060, however, the climate at this site should become more suitable for *P. pungens*, the best suited genotypes of which currently reside at lower elevations 400 km to the south.

Toward the north at location 20, the novel climate of 2030 should be best suited to hybrid genotypes from slightly lower elevations, but beyond 2060, the climate should be more suitable for populations of *P. glauca*. For location 32, a transition from *P. engelmannii* to *P. glauca* also is expected by 2060, but by 2090 the climate should no longer be suited for the genera. Quite similarly, the populations of *P. glauca* that currently inhabit mid elevations in the Cypress Hills (location 31, fig. 1) and the Black Hills (location 19) should remain suitable for the novel climate of 2030, but by 2090, the climate at all elevations should be unsuitable for the genera.

In the northwest part of the region, the projected changes in climate should produce responses that are now expected: (1) a zone of extirpation moving from low to high elevations as the climate warms and (2) a change in the genotypes best suited to the novel climate to those that today occupy milder climates at lower elevations. Thus, at 1,350 m at locality 24, the best suited genotypes for 2030 currently reside at 1,000 m elevation slightly to the north where the climate is somewhat milder. By 2060, the site should no longer be suitable for *Picea*. But at an elevation of 1,950 m at the same general locality, *P. engelmannii* should be suited throughout the century. Yet the contemporary location of the genotypes best suited to the new climates shifts from the contemporary site to the low elevations at the northern tip of the Cascade Range (location 26) by the end of the century.

The effects of a changing climate at location 24 (table 6) tend to be repeated at locations 26, 27, 33, and 34. However, by the end of the century at site 35, the northernmost site used for these examples, *P. glauca* should be the best suited taxon up to an elevation of about 1,500 m, beyond which hybrid populations currently inhabiting milder climates to the south become best suited. This suggests that by the end of the century in the northwest portion of the region of study, taxa of the *P. engelmannii* complex should become a rarity, occupying only the highest elevations and coldest sites.

Effects of global warming on the *P. engelmannii* complex are illustrated in figure 11 where the current and future distributions of a single climatypes are superimposed on the climatic distribution of the complex. As shown in this figure, the distribution toward the end of the current century is expected to be reduced by about 89 percent as climates suited for this complex are pushed upward and northward. The altitudinal displacement is

Table 6—Contemporary location (codes in **bold face**, keyed to figure 1) and their altitudes (m) containing genotypes expected to be the best suited for future climates predicted according to the IS2a scenario of two GCMs. All locations are assumed to be inhabited by *P. engelmannii* except where noted.

Target locality	2020-2029		2060-2069		2090-2099	
	Population location	Genetic distance	Population location	Genetic distance	Population location	Genetic distance
3: 3000	--	---	--	---	--	---
10: 3000	**7:** 2850 *	0.30	**8:** 2800 *	0.60	**2:** 2950 *	0.99
14: 2800	**9:** 2700 †	0.86	**6:** 2500 †	0.42	**3:** 2600 †	0.88
12: 3200	**14:** 3050	0.61	**9:** 2750 †	0.90	**10:** 2550 †	0.35
17: 2900	**16:** 2500	0.71	**11:** 2600 †	0.81	**10:** 2500 †	0.53
20: 2250	**21:** 1850 ††	0.76	**30:** 1600 §	0.92	**19:** 1300 §	0.90
24: 1350	**25:** 1000	0.89	--	---	--	---
24: 1950	**27:** 1500	0.70	**27:** 1100	0.92	**26:** 600	0.85
31: 1450	**19:** 2000 §	0.36	---	---	---	---
32: 1250	**25:** 1000	1.08	**19:** 1200 §	1.23	---	---
33: 1250	**28:** 1100	0.34	**24:** 1300	0.72	---	---

* Southwest *P. engelmannii*
† *P. pungens*
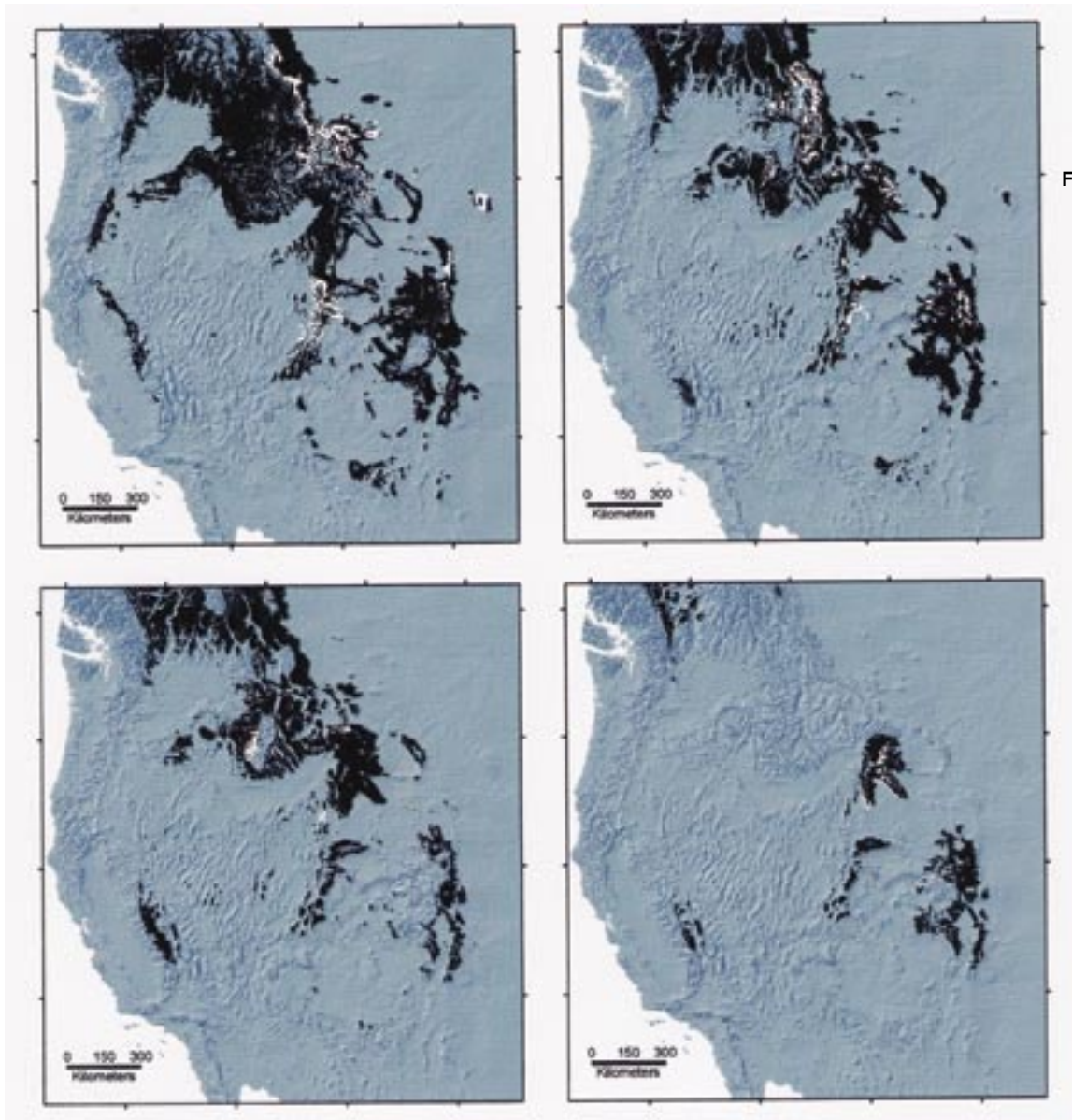†† *P. glauca* x *P. engelmannii* hybrid
§ *P. glauca*

Figure 11—Distribution of a single climatypes of the *P. engelmannii* complex superimposed on the climatic distribution of the species for the contemporary climate (upper left), and the distribution of future climates suitable for the same climatype in the decades beginning in 2030 (upper right), 2060 (lower left), and 2090 (lower right).

expected to approach 1,000 m. As a result, only about 23 percent of the 2090 distribution will be inhabited continuously during the century, but approximately 80 percent of the 2090 distribution should be suitable climatically for climatypes that exist today.

Discussion

Biosystematics

Biosystematic relationships among the *Picea* taxa of Western North America are complex and confusing (see Ledig and others 2004). The present results join with those of numerous studies dealing with a broad spectrum of characters to readily distinguish *P. pungens* and *P. chihuahuana* from each other, from the taxa composing the *P. engelmannii* complex, and from *P. glauca*. The present results are also consistent with the prevailing view of widespread introgressive hybridization on the northern front between *P. engelmannii* and *P.*

glauca and show that the introgression tends to bridge the climates inhabited by the parental taxa.

Unanimity among researchers, however, does not exist concerning the southern front, where the taxonomic status of *P. mexicana* has been repeatedly questioned since its naming in 1961 (Martinez 1961). To be sure, all pertinent research has demonstrated a close relationship between *P. mexicana* and *P. engelmannii* in morphologic (Taylor and Patterson 1980, Taylor and others 1994), chemical (Taylor and Patterson 1980, Taylor and others 1994), and molecular (Sigurgeirsson and Szmidt 1993) characters. While Taylor and his coworkers (for example, Taylor and Patterson 1980) believed that *P. mexicana* should be recognized as a variety of *P. engelmannii*, Ledig and others (2004) believe that allozyme differences between the taxa are large enough to warrant the designation of separate species. Illustrative of the problem but providing no solution is figure 2, in which the *P. mexicana* population was aligned closely with, but peripheral to, populations of southwest *P. engelmannii*.

Also unclear is the taxonomic status of southwest *P. engelmannii*. While mean differences between this

taxon and *P. engelmannii* are real (Ledig and others 2004, Rehfeldt 1994, fig. 2), variances obviously overlap (fig. 4). On the one hand, the present results (for example fig. 2) could be used to support the view that southwest *P. engelmannii* merely represents the southern portion of the *P. engelmannii* cline. Yet, on the other hand, populations of the two taxa are arranged along clines of much different slope that presumably have been molded by different climatic effects (fig. 4). It seems reasonable, therefore, to view southwest *P. engelmannii* as a variety of *P. engelmannii*. A logical extension of this view would be to designate *P. mexicana* as the taxon at the southern tip of this cline.

Clines of the P. engelmannii Complex

Widely distributed species invariably face a broad range of climate variability. Indeed, for most of the *Picea* taxa considered herein, genetic differences among geographically disparate populations have been detected in common garden studies: *P. pungens,* for example, by Bongarten and Hanover (1986), *P. engelmannii* by Shepperd and others (1981) and Rehfeldt (1994), and *P. glauca* by Morgenstern (1996). In the present paper, however, clines in *P. engelmannii* were considered in relation to climatic rather than geographic gradients.

The results showed that the primary cline along which genotypes of the *P. engelmannii* complex are distributed is in relation to the winter temperature regime of the provenance, particularly for southern populations. A secondary cline was in relation to summer temperatures and seemed most pronounced for northern populations. These clines show that populations from the least severe climates, whether measured by either summer or winter temperatures, were the largest after 2 years, ceased elongation the latest, had the longest duration of elongation, elongated at the fastest rate, began elongation the earliest, and elongated the most. Other climate variables that appeared influential included: maximum temperature in the warmest month, length of the frost-free season, Julian date on which the degree-day greater than 5 ∞C sum reached 100, summer precipitation, and dates of first spring and last fall frosts.

Global Warming

Climate is the primary factor controlling the distribution of organisms (Brown and Gibson 1983, Woodward 1987). Organisms, therefore, will respond to a change in climate. In plants, the response can be of four different types (see Rehfeldt and others 2001): coping—the exploitation of physiological plasticity; extirpation—the mortality that accrues when the amount of change exceeds the capacity of the plastic physiological system to adjust; evolution—the changes resulting from the novel selection pressures; and immigration. Table 6 suggests that the IS92a climate change scenario will stimulate one or more of these responses in each and every population within the distribution of the taxa under study. Global warming, therefore, will have effects that transcend the margins of distribution where extirpation and immigration occur to include all populations

as genetic systems adjust to change (Davis and Shaw 2001).

According to the IS92a scenario, effects of global warming during the present century on *P. engelmannii* and its congeneric cohorts should be especially pronounced on four fronts (table 6). One front involves the northwest portion of the study area where extirpation is predicted for all taxa of the genera across hundreds (600 to 900) of meters of elevation. This level of extirpation essentially would remove *Picea* from the local flora except perhaps, for the coldest sites and those at the highest elevations (greater than 1,900 m). Thompson and others (2002) reached the same conclusions using much different procedures. A second front would involve extirpation in the mountain islands of the Southwest: by the end of the century, the southern limit of southwest *P. engelmannii* may, in fact, may have shifted 400 km to the north. As suggested by table 6, *P. pungens* is expected to take advantage of this widespread extirpation of the *P. engelmannii* complex, although the possibilities that *P. mexicana* and *P. chihuahuana* could fill the void remain unexplored. A third front involves the geographic isolates of *P. glauca* in the Black Hills of South Dakota and the Cypress Hills of Alberta where a changing climate should rapidly produce climates not suitable for *Picea*. And last, throughout much of the remaining areas, widespread extirpation is expected at low elevations as a warming climate forces upward the lower altitudinal limits.

To be sure, immigration of *Picea* taxa will be occurring concomitantly with the extirpation, but it seems doubtful that the immigration can be sufficient to offset the extirpation. On the one hand, an orderly migration of *P. glauca* toward the north and *P. pungens* toward higher elevations is readily envisioned. But on the other hand, the immigration opportunities for taxa of the *P. engelmannii* complex are limited largely because taxa of the complex currently inhabit the high elevations. In the north, moreover, the distribution of the complex abuts and intermixes with that of *P. glauca*. While the *P. engelmannii* complex is montane, *P. glauca* is a component of the boreal forests distributed across the continental climates of the northern latitudes. These continental climates are warmer in the summer than the montane climates inhabited by taxa of the *P. engelmannii* complex. Climate data, for instance, show that habitats occupied by *P. glauca* range up to 2,100 degree-days greater than 5 °C and 21 °C for mean temperature in the warmest month, while maximums for the same variables in the *P. engelmannii* complex are 1,700 degree-days and 18 °C, respectively. A warming climate in the north, therefore, should further increase the inhospitality of the contemporary boreal forests to taxa of the *P. engelmannii* complex.

One is led, therefore, to an independent corroboration of the conclusions of Thompson and others (2002): global warming should result in a large reduction in the distribution of the *P. engelmannii* complex. While the distribution of *P. glauca* may expand to the north, and *P. pungens* may become the dominant species of the genus in the Southwest and Great Basin, the opportunities for immigration of taxa of the *P. engelmannii* complex are greatly limited.

Extirpation and immigration notwithstanding, a portion of the region currently inhabited by taxa of the *P. engelmannii* complex should remain suitable for taxa of the complex throughout the century. Table 6 shows clearly, however, that those genotypes expected to be the best suited for the novel climates may today exist at large distances from the site of their future climatic optima. This means that accommodation of a warming climate by taxa of the *P. engelmannii* complex will not only involve extirpation and immigration, but also should result in a complete redistribution of genotypes across the landscape. This conclusion is precisely the same as those reached for *Pinus contorta* of Western North America (Rehfeldt and others 1999, 2001) and for *Pinus sylvestris* of Eurasia (Rehfeldt and others 2002). As argued for these pines, the process by which redistribution occurs most likely will involve selection and recombination in extant populations rather the migration. Calculations for the pines also suggest that the amount of change required to accommodate global warming is more than genetic systems are capable of achieving in a single generation of selection. Adjustment, therefore, may require as many as 10 generations and may take more than 1,000 years. Although data are not available for making similar calculations for *Picea*, there is no reason to expect the natural processes to differ greatly.

Practical Applications

An understanding of the adaptation of populations to heterogeneous environments has direct application in reforestation, the goal of which invariably includes producing for the future populations that are physiologically attuned to their environment. In a stable climate, this goal can be achieved by establishing geographic limits beyond which seeds from existing populations are not transferred. Although fundamentally sound, such geographically based guidelines are not suitable for extrapolation and, therefore, are not suitable (1) in regions where genetic variation is unexplored and (2) during periods of climate change. As demonstrated by the present results, climate-based seed transfer guidelines overcome such restrictions.

Table 5 can be considered as output from a prototype of an expert system for guiding seed transfer (see Monserud and Rehfeldt 1990). The expert system requires a database containing an extensive inventory of locations and their climates within the distribution of a species. From this database, queries can be made for the location of genotypes expected to be compatible with the climate at a specific planting site. According to table 5, for example, in the contemporary climate, seeds suitable for a planting site at low elevation at location 24 could come from an interval of 300 m surrounding the planting site, from slightly lower elevations in peripheral localities where the climate is somewhat more severe, or from higher elevations where the climate is more mild. Seeds suitable for a high elevation planting site at the same locality, however, could come from a broad range of sites, generally at high elevations where the climate

is similar. When the climate shifts, however, a different assortment of seeds becomes best suited to the same planting site. The seed lots best suited to these new climates readily can be selected by the expert system (see table 6).

Climate-based seed transfer guidelines, therefore, represent a flexible means for managers to approach the goal of establishing populations physiologically attuned to the future even during periods of climate change. As shown herein, converting geographically-based transfer guidelines to those that are climate-based merely requires recasting clines using climatic predictors.

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