

GENETIC RESPONSES TO CLIMATE IN *PINUS CONTORTA*: NICHE BREADTH, CLIMATE CHANGE, AND REFORESTATION

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Abstract. Fundamental plant–environment relationships were revealed by analyses of 20-yr height and survival of 118 populations representing two subspecies of *Pinus contorta* growing in common gardens at 60 environmentally disparate test sites in British Columbia. The approach involved (1) preparing models that described the general climate of British Columbia, (2) developing population-specific response functions driven by predicted climate variables, (3) developing general transfer functions that predict performance from the climatic distances over which populations were transferred, and (4) interpreting the results in terms of niche breadth, effects of climate change on adaptedness of populations, and reforestation in a changing environment.

Polynomial regression models used physiographic descriptors to predict seven climate variables from normalized records of 513 weather stations. Values of R^2 ranged over 0.80–0.97 for thermal variables and 0.54–0.61 for precipitation variables. Validations with independent data from 45 stations were strong and suggested that the models were generally free of bias within the limits of the original data.

Response functions describing the height or survival of each population were developed from quadratic regressions using predicted climate variables for each test site. Mean annual temperature and mean temperature in the coldest month were the most effective variables for predicting population height, while the ratio of summer temperature to summer moisture was the best predictor of survival. Validation of the response functions with independent data from two additional test sites produced values of R^2 between actual and predicted values that were as high as 0.93 for height and 0.73 for survival. The results demonstrated that natural populations have different climatic optima but tend to occupy suboptimal environments. Nevertheless, the general transfer functions showed that optimal growth and survival of the species as a whole is associated with the null transfer distance.

These seemingly anomalous results suggest that the same processes thought to determine the distribution of species control the distribution of genotypes within species: (1) environmental selection to produce a broad fundamental niche, and (2) density-dependent selection to produce a relatively narrow realized niche within which most populations are relegated to suboptimal environments. Consequently, the steep geographic clines typical of *P. contorta* seem to be driven more by density-dependent selection than by environmental selection. Asymmetric gene flow from the center of distribution toward the periphery is viewed as a primary regulator that provides the fuel for both environmental and density-dependent selection and thereby indirectly perpetuates suboptimality.

The response functions predict that small changes in climate will greatly affect growth and survival of forest tree populations and, therefore, that maintaining contemporary forest productivities during global warming will require a wholesale redistribution of genotypes across the landscape. The response functions also provide the climatic bases to current reforestation guidelines and quantify the adjustments necessary for maintaining adaptedness in planted trees during periods of small ($\sim 1^\circ\text{C}$) temporal temperature shifts.

Key words: climatic gradients; climate models; climate response functions of populations; fundamental niche vs. realized niche; genetic variation; global climate change; microevolution; niche breadth; *Pinus contorta*; population differentiation; reforestation in a changing environment; responses to a changing environment.

INTRODUCTION

A concept fundamental to ecology and biogeography is that climate is the primary factor controlling the

broad-scale distribution of organisms (Tuhkanen 1980, Woodward 1987). Yet, despite a few exceptions (see Brown and Gibson 1983), the subject is only superficially understood (Woodward 1987, Prentice et al. 1992). Recent interest, spurred largely by potential impacts of a warming climate, centers on describing the distribution of recurring plant associations from either

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mechanistic (e.g., Prentice et al. 1992) or correlative (e.g., Tchebakova et al. 1994) models that use climate variables as predictors. Plant responses to climate, however, are individualistic. Therefore, species with similar ecological requirements respond differently to changing conditions (Brubaker 1988, Betancourt et al. 1990, Huntley 1991). Because species themselves are composed of populations genetically attuned to differing environments (see Clausen et al. 1940), understanding the role of climate in controlling plant distributions must accommodate ecological genetics, a field devoted to the ecological bases for genetic differentiation of populations.

As developed by Turesson (1922), genecologic principles state that plant populations will express adaptations to the environments from which they originated, even when cultivated in common gardens. The principles, developed primarily from herbaceous annuals and perennials, were extended to forest trees, which are the subject of the present paper. This extension was based on Langlet's (1936) demonstration that genetic variation among natural populations of *Pinus sylvestris* L. was arranged along clines that paralleled Scandinavian climates. Driven by the economic necessity of assuring that planted trees were adapted, genecological research on forest trees was spawned in abundance by Langlet's work (see Langlet 1971, Morgenstern 1996). Some of this research has culminated in models that use physiographic variables to describe genetic variation across environmentally heterogeneous landscapes (e.g., Campbell 1987, Rehfeldt 1989a). The validity of such models, however, depends on the plausible assumption that physiographic variables are surrogates for the environmental variables that operate in natural selection, but that are difficult to observe. In this paper, we focus on environmental rather than physiographic descriptors of genetic variation by employing regional climate models (Booth 1990, Rehfeldt 1995) to describe the growth and survival of *Pinus contorta* Dougl. ex Loud. populations in British Columbia. The term "provenance" is used to designate a geographic location; "population" refers to the individuals at that location and their offspring.

Genetic structure of *P. contorta*

With a distribution spanning 33° of latitude (Fig. 1) and 3900 m of elevation, the wind-pollinated *P. contorta* occurs as a natural component of the coastal, montane, subalpine, and boreal forests of western North America (Wheeler and Critchfield 1985). Environmental heterogeneity across this immense distribution is accommodated in part by the existence of four subspecies (*P. c.* ssp. *latifolia* [Engelmann] Critchfield; ssp. *contorta* [Dougl. ex Loud.] Critchfield; ssp. *murrayana* [Greville and Balfour] Critchfield; and ssp. *bolanderi* [Parlatore] Critchfield), each of which inhabits a different portion of the species' range (Fig. 1; Critchfield 1957). As shown in common garden studies, ge-

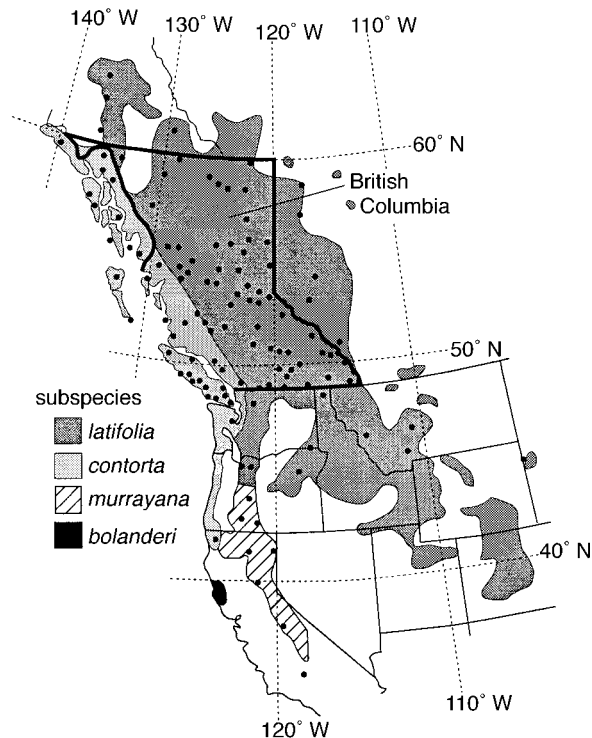


FIG. 1. Map of western North America locating the populations sampled (●) and the geographic distribution of *Pinus contorta* and its subspecies (adapted from Wheeler and Critchfield 1985).

netic variation among populations within subspecies tends to be large and arranged along steep altitudinal and latitudinal clines for characters conveying adaptation to the abiotic (e.g., Moore 1984, Ying et al. 1985, Rehfeldt 1988, Sorensen 1992, Ying and Liang 1994, Xie and Ying 1995) and biotic (e.g., Rehfeldt 1987, Ying and Hunt 1987, Yanchuk et al. 1988, Wu et al. 1996) environments. The clines are discernable even when assessed in Sweden (Lindgren et al. 1976) or when studied with allozymes (Wheeler and Guries, 1982a, Yeh et al. 1985).

As with most organisms (Brown and Gibson 1983), genetic variation among populations of *P. contorta* is characterized by strong negative relationships between growth potential and the relative harshness of the physical environment inhabited by a population (Rehfeldt 1980, 1983, 1987, 1989b). Rehfeldt (1987), for instance, presented a simple correlation of $r = -0.82$ between population means for 7-yr field height and freezing tolerance tested in the laboratory, and a correlation of 0.85 between height and tolerance to needle diseases. Clines in adaptive traits, therefore, tend to be interdependent. As a result, genetically similar populations recur across the landscape in association with the recurrence of similar environments (Rehfeldt 1988).

Despite pronounced differentiation of populations, genetic variability within populations tends to be high

for a variety of growth, developmental, morphologic, and physiologic traits (Rehfeldt 1985, 1989b, Xie and Ying 1995), as well as for allozymes (Yeh and Layton 1979, Wheeler and Guries 1982b, Yeh et al. 1985).

Goals and objectives

The primary objective of this paper is to develop climatic predictors of 20-yr growth and survival of *P. contorta* populations planted in an ecologically diverse array of field tests established and maintained by the British Columbia Forest Service. This program, hereafter referenced as the "Illingworth tests", included 142 populations and encompassed 60 field test sites that employed a common experimental design. These long-term field tests thus meet the strategic requirements (Landsberg et al. 1995) for an empirical modeling of forest responses to a variable climate. To this end, the Illingworth tests are of incomparable scope.

Over the years, the populations under study have demonstrated differential tolerance to stem rusts (*Cronartium coleosporioides* Arth. and *Endocronartium harknessii* Y. Hiratsuka), needle casts (*Lophodermella concolor* Dearn), and breakage caused by the load of accumulated snows (Ying et al. 1985, Ying and Hunt 1987, Yanchuk et al. 1988, Wu et al. 1996). Consequently, 20-yr height and survival of these populations measure adaptedness to both the biotic and abiotic environment. While survival measures adaptedness directly, the height realized in a particular environment is the phenotypic expression of an innate growth potential modified by adverse environmental effects that have accumulated in time. In addition, for forest trees in general, and for *P. contorta* in particular, the tallest individuals not only have an advantage in competition for light, water, and nutrients, but also tend to be of highest fecundity (Koch 1987).

The primary goal is addressed by developing empirically based models that (1) describe the general climate of British Columbia and its periphery from physiographic predictors, (2) predict population-specific response from estimated climatic effects, and (3) describe the performance of subspecies from climate transfer distances. Because height and survival are direct components of fitness, modeled responses can be used to estimate the climatic conditions for which growth and survival are optimal. The results pertain to topics dealing with the distribution of genotypes across the landscape, niche breadth, the effects of a changing climate on adaptedness of populations, and reforestation in a variable climate. The use of fitness-related responses allows the results to be applied directly to niche concepts without invoking assumptions between fitness and performance (Austin and Austin 1980).

Throughout this paper, the term "niche" refers to the Hutchinsonian multidimensional hypervolume (Hutchinson 1958), in which each dimension represents a climate variable across which a population is distributed. The "fundamental niche" represents that por-

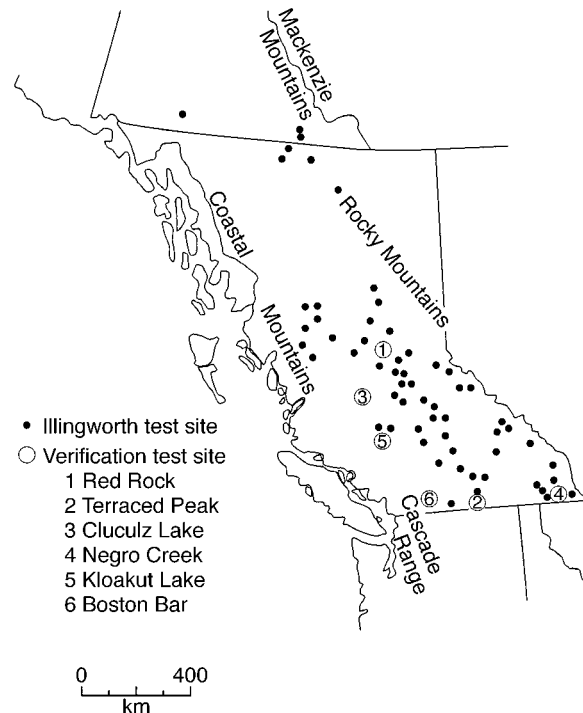


FIG. 2. Location of the test sites (●) in the Illingworth program and plantations suitable for verifying population response functions.

tion of the environmental gradient within which existence is possible, while the "realized niche" reflects the proportion of the fundamental niche that is actually occupied. In the present study, niche concepts are considered at the level of the population, subspecies, and species.

MATERIALS AND METHODS

Field tests

In 1974, field tests were established at 60 sites (Fig. 2) with one-year-old seedlings grown from seeds collected in 142 natural populations (Fig. 1). The populations represented much of the geographic distribution of *ssp. latifolia* and *ssp. contorta*, but also included populations of *ssp. murrayana*. The program favored *ssp. latifolia* because of its economic importance to the forest industry of British Columbia, and, consequently, test sites (Fig. 2) were selected to represent the ecological distribution of *ssp. latifolia* in the province (see Illingworth 1978).

Of the 142 populations originally sampled, 126 were represented after 20 yr on at least five sites, the minimum considered for these analyses. Implementing the procedures we describe required eliminating an additional eight populations, largely because of a lack of environmental diversity among the test sites on which these populations had been planted. Of the remaining 118 (Fig. 1), 101 are from either British Columbia or

its periphery; 79 are *ssp. latifolia*, 33 are *ssp. contorta*, and six are *ssp. murrayana*.

Because of practical limitations on the size of long-term experiments with forest trees, a subset of the populations was planted at each site. On the average, each of the 118 populations was planted on 33 sites, although 20 populations were on <20 sites, and 14 were on >50. The subset allocated to a planting site included all populations proximal to that site, but the representation of populations decreased as the distance between the site and the provenance increased. A planting site contained an average of 53 populations.

The experimental design at each planting site consisted of two randomized complete blocks within which populations were represented by nine seedlings. The trees were spaced at 2.5 m, and the plantings were cleaned periodically to remove ingrowth of competing trees and shrubs. Mortality due to intertree competition has only recently begun in the fastest growing plantings. As an experiment designed to incorporate intensive culture to limit environmental noise but retain much of the complexity of natural systems, the Illingworth tests are well-suited (see Holt and Gaines 1992, Loehle and LeBlanc 1996) for assessing the climatic factors that control the distribution of genotypes across the landscape.

The present analyses consider population means for 20-yr height and survival, both of which reflect adaptiveness to the biotic and abiotic environment. Subspecies were classified by Ying and Liang (1994) and correspond to Wheeler and Critchfield (1985).

Weather records

Weather records were accumulated from 513 stations (Fig. 3) that were either from British Columbia or its periphery. Data from Canadian stations had been normalized for 1951–1980 (British Columbia Ministry of Environment 1980), while those from 58 United States stations were summarized from daily records available from Earthinfo (1994) for 1950–1995. Data from the United States were used only when ≥ 20 of records were available after discarding those years missing >20% of the daily observations. Stations peripheral to British Columbia were included to assure that the resulting climate models described general patterns across provincial boundaries rather than being precisely fit to data from stations nearest to the boundaries.

For the purposes of describing geographic variation in the climate, it was unfortunate that the distribution of weather stations is skewed toward population centers. Only 35% of the stations were from north of 54° N, and only 64 stations were from elevations >1000 m, 61 of which were south of 54° N. Nevertheless, the stations represent the main distribution of *P. contorta* in British Columbia, particularly for those regions where forest management is currently practiced.

Seven variables were selected from the weather records for describing general temperature and precipi-

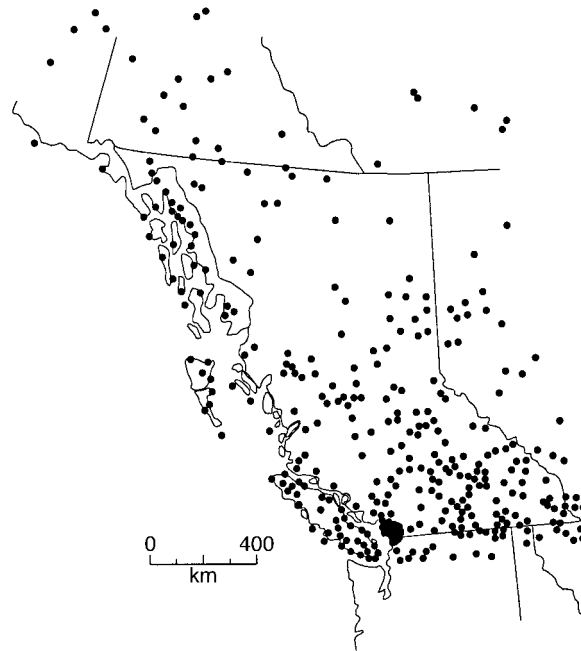


FIG. 3. Location of 513 weather stations (●) from which climatic data were used for developing climate models.

tation regimes: mean annual temperature, mean temperature in the coldest month, mean temperature in the warmest month, mean annual precipitation, mean precipitation in the summer months (May–September), mean number of days without a freezing temperature, and the average duration of the frost-free period.

An attempt was made to represent climate as multivariate vectors described by principal components. However, because of missing data, multivariate analyses would have required the elimination of data from 26 weather stations. Because nearly all of these stations were either or both from the north and from high elevations, their elimination was not tenable. Our approach, therefore, is to consider climate in a space of n dimensions, each of which is univariate.

Statistical analyses

Statistical analyses included regressions for developing climate models, population response functions, and general transfer functions. All statistical analyses used software of the SAS Institute (1985).

Climate models.—The hypothesis underlying the development of climate models is that variation in the climate occurs geographically, and, therefore, elements of the climate can be predicted from geographic descriptors. Regression models were developed according to the general procedures of Rehfeldt (1991):

- 1) Derive independent variables from the direct and transformed effects of latitude (LT), longitude (LN), and elevation (EL). Transformations included the synthetic variables NW (the product of LT and LN) and SW (the ratio of LT to LN), both of which produced

TABLE 1. Simple correlations among climate variables used to describe population responses.

Climate variable	MTCM	MTWM	MAP	MSP	NFFD	FFP	AH:M	SH:M	TD
Annual temperature (MAT)	0.95	0.61	0.40	0.11	0.89	0.83	0.02†	0.18	−0.81
Cold month temperature (MTCM)		0.34	0.56	0.28	0.90	0.82	−0.18	−0.03 ^a	−0.95
Warm month temperature (MTWM)			−0.20	−0.37	0.35	0.43	0.53	0.64	−0.04 ^a
Annual precipitation (MAP)				0.86	0.52	0.52	−0.67	−0.60	−0.66
Summer precipitation (MSP)					0.23	0.26	−0.61	−0.70	−0.43
Days without frost (NFFD)						0.96	−0.26	−0.02 ^a	−0.82
Frost-free period (FFP)							−0.21	0.00 ^a	−0.73
Annual heat:moisture index (AH:M)								0.86	0.36
Summer heat:moisture index (SH:M)									0.23
Temperature differential (TD)									

Note: Degrees of freedom varied in the range 455–511.

† Not statistically significant ($P > 0.05$).

grids capable of accounting for climate patterns that are oblique to LT and LN. For all analyses, LT and LN were first transformed by subtracting 48 and 110, respectively.

2) Screen the independent variables by stepwise multiple regression. Potential models were evaluated according to statistical significance of the model as a whole, statistical significance of individual coefficients, the Mallows statistic, and patterns displayed by the residuals (Draper and Smith 1981).

3) Plot elevation and geographic patterns of variation in predicted values to assure that the models were intuitively sensible.

4) Plot residuals against predicted values to evaluate bias.

Although seven models were considered for each climate variable, all were variations on a polynomial model that screened 26 independent variables: the first three powers of LT, LN, NW, and SW, combined with $NW \times LT$, $NW \times LN$, $SW \times LN$, and $SW \times LT$, which together were capable of accommodating sinusoidal geographic patterns; the first two powers of EL for accommodating nonlinear altitudinal patterns; and the products of LT, LN, NW, and SW with the first two powers of EL to accommodate interactions between elevation and geographic location.

The regression model was of the following general form:

$$Y_i = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \dots + \beta_k X_{ki} + e_i$$

where Y_i is a climate variable specific to station i , β 's are regression coefficients, X 's are the geographic independent variables, and e is the residual.

Analyses validating the best fitting models were made with independent data from 38 weather stations (British Columbia Ministry of Environment 1980) that were normalized after the current analyses were completed. These were within the following ranges, thereby sampling much of the province: elevation, 97–1707 m; longitude, 116–135° W; and latitude 49–61° N. Nevertheless, not represented were coastal climates, the absence of which reduced the total range of variation for many variables. To test the models against a balanced matrix of independent variables, data from seven

coastal stations (EL < 25 m), spaced at ~2° intervals of LT, were added to the validation data set from the original database. Linear regressions of observed values on the predicted, and residuals (observed minus predicted) on the predicted, were made for the seven climate variables.

Population response functions.—To develop functions that predicted height and survival of populations in relation to environmental gradients (see Roberds et al. 1990), the climate models were used to describe the climate at each of the 60 test sites according to the seven variables. From the seven, three additional variables were calculated: (1) an annual heat: moisture index, the ratio of the mean annual temperature to the meters of annual precipitation; (2) a summer heat: moisture index, the ratio of the mean temperature in the warmest month to meters of summer precipitation; and (3) a temperature differential, the difference between the mean temperature in the warmest month and the mean temperature in the coldest month. For calculating the ratios, 10 was added to the mean annual temperature (as reported in °C) to assure that all values would be positive.

Although our approach is correlative, no attempt was made to screen an exhaustive list of variables that plausibly could be related to differential responses of populations. Instead, the variables we used included descriptors of the general mildness of the climate, its coldness, warmth, and wetness. The intent of the two ratios is to index the amount of precipitation available for plant growth, and the temperature differential is an index to the degree by which the climate is influenced by either maritime or continental air masses. The variables can be calculated readily from daily records of temperature and precipitation, and all have been used at various times by plant geographers, climatologists, or physiologists (Tuhkanen 1980). To be sure, some of these variables are strongly interrelated (Table 1). For those accustomed to working with degree-days, a nonlinear regression of degree-days (5°C base) on mean annual temperature produced from our database a value of $R^2 = 0.81$ (Appendix Table A1).

A quadratic regression model was used to fit each

climate variable to the height and survival of 126 populations:

$$Y_{ij} = \beta_0 + \beta_1 X_j + \beta_2 X_j^2 + e_{ij}$$

where Y_{ij} is the mean height or survival of population i at a planting site j ; β 's are regression coefficients; and X_j is a predicted environmental variable for planting site j . This model produced 2520 univariate response functions with 2–54 error degrees of freedom (126 populations, 2 dependent variables, and 10 independent variables). Response functions were discarded when $P > 0.1$.

This approach assumes that climate is the primary factor controlling the measured responses. In regions where edaphic or other environmental effects either dominate or confound climatic patterns, alternative approaches may be more appropriate for isolating climatic effects. For instance, Schmidtling (1994) standardized dependent variables to account for strong edaphic effects that countered climatic patterns. Another approach might involve fitting constants to account for qualitative environmental effects (Draper and Smith 1981).

To be sure, functions other than the quadratic (e.g., normal, Weibull, or Beta; see Johnson and Kotz 1970) that are asymptotic at zero and can be either symmetrical or asymmetrical are the most appealing conceptually. Alternate functions, however, require assumptions about symmetry and the nature of the inflection points for which little experimental evidence exists for natural systems (Austin and Austin 1980). Although test sites in the Illingworth program were spread across the ecological distribution of *P. contorta* in British Columbia, the data were not adequate to define the inflection points. As will be obvious in the material we present, the 60 test sites could not fully sample the fundamental niche of each population, and, therefore, assumptions concerning the shape of the response curves would not be supportable. Sixty test sites may be an impressively large number of common gardens, but they were insufficient for assessing differences in the shape of population-specific response functions.

Response functions were validated with two independent data sets, each of which had a different group of populations in common with the Illingworth tests. The first, analyzed by Xie and Ying (1995), involved the 20-yr height and survival of populations growing at Red Rock (Fig. 2). This site, at an elevation of 620 m, is geographically central in the province and ecologically central to the distribution of *P. contorta*. The planting had 53 populations in common with the Illingworth tests, but only included ssp. *latifolia*. The 53 ranged 457–1661 m in elevation and 49–61° N in latitude. The second data set involved unpublished data from Terraced Peak, an ecologically marginal site for *P. contorta* located at high elevation (1830 m) near the southern border of the province (Fig. 2). Although originally part of the Illingworth tests, the data were ex-

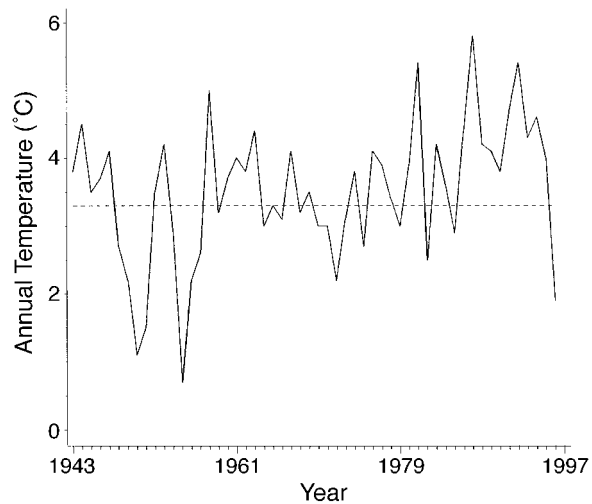


FIG. 4. Mean annual temperature at Prince George (located near Red Rock; Fig. 2) plotted by year. Horizontal dashed line is the normalized mean.

cluded from the analyses of Ying et al. (1985) because of exceptionally poor tree growth and survival resulting from a variety of environmental effects. This test included 45 populations from British Columbia and its periphery, four of which were ssp. *contorta*. For validations at this ecologically marginal site, predicted survivals that were ≤ 0 were equated to zero. Response functions were validated by examining regressions of residuals on the predicted values and of observed values on the predicted.

A comparison was made between the climate inhabited by a population and that associated with its optimal growth and survival. Because 20-yr height and survival are composite traits that reflect adaptedness at a test site, the y - and x -axis coordinates of the vertex (maximum point) of the response functions defined the optimal performance and the optimal climate, respectively. Provenance climate was available from the climate models. The significance of the difference between the inhabited and optimal climates (provenance climate minus optimal climate) was tested with a t test of paired observations for each of the climate variables. These differences, however, are biased to some extent by the recent climate of western Canada, which has been warmer than that of the normalized data base (Gullet and Skinner 1995). In interior British Columbia, where the Illingworth tests are located, the climate during the last 30 yr has averaged 0.4°C warmer in mean annual temperature than the normalized mean (Fig. 4; Spittlehouse et al. 1994). To adjust for this, scaling the regressions of Table A1 through a data point allowed either the site or provenance climate to be altered. No adjustments were necessary for precipitation variables.

The significance of the difference between the provenance climate and the optimal climate was tested before and after adjusting for the warm climate of recent

years. Simple correlation was used to relate the discrepancy between the provenance and the optimum climates to the latitude and elevation of the provenance.

General transfer functions.—The response functions pertain to specific populations. A topic related to whether or not populations occupy their optimal environments concerns the distance that native populations should be transferred along an environmental gradient to achieve optimal growth and productivity of the species as a whole. To address this topic, general transfer functions (Campbell 1974) were developed according to the following model:

$$Y_{ijk} = \beta_0 + \sum_i [\beta_{1i}w_iTD_{ijk} + \beta_{2i}w_i(TD_{ijk})^2] + \Delta w_i + \sum_j (\gamma_j Z_{jk}) + e_{ijk}$$

where $i = 1, 2$; $1 \leq j \leq 88$; $1 \leq k \leq 60$; Y_{ijk} is mean height or survival of population j from subspecies i planted on site k , expressed as a percentage of the plantation mean; Δ , γ , and β are regression coefficients; w_1 is a constant for coding subspecies that equals one if population j is *ssp. contorta*, but otherwise equals zero; w_2 is a constant for coding subspecies that equals one if population j is *ssp. latifolia*, but otherwise equals zero; Z_{jk} is a constant for coding population j at site k that equals one for all observations for population j , but otherwise equals zero; TD_{ijk} is the distance along the environmental gradient that population j in subspecies i was transferred (test site climate minus provenance climate) to site k after adjusting (Table A1) all but the precipitation variables for a recent mean annual temperature that is warmer by 0.4°C than those in the normalized data base; and e_{ijk} is the residual. Height and survival were expressed as a percentage of the plantation mean to produce functions that were not age-specific and to remove the main effects of test sites.

This regression thus fit a quadratic curve for each subspecies. Each population was represented by a constant that provided a unique vertex, although the shape of the curve was the same for all populations within a subspecies. Inverting a matrix that includes constants requires that one level of each effect represented by constants be included within β_0 , the intercept (Draper and Smith 1981). To prevent singularity of inverted matrices, the effects of *ssp. latifolia* and one population were included within β_0 . Constants were used to code populations so that the effects of the populations planted on the most sites did not disproportionately weight the resulting functions. Because the calculation of transfer distance required climate predictions at both the planting site and the provenance, only those populations originating from areas served by the climate models (Fig. 3) were used. In total, 88 of the populations were suited to these analyses; *ssp. contorta* was represented by only 20 populations that nonetheless were distributed from a latitude of 49–60° N. Because transfer distance was calculated by subtracting the

provenance climate from that of the planting site, negative values represent a transfer from a mild or moist site to one that would be either cooler or drier.

From these regressions, a general transfer function was adopted that used as the intercept (β_0) the average effect of a population: $[\beta_0 + \sum_j (\beta_0 + \gamma_j)]/n$, where n is the total number of populations (68 for *ssp. latifolia* and 20 for *ssp. contorta*). Because one degree of freedom was available for each population transferred to each site, the general transfer functions were based on 2804 observations; each population had been planted on (transferred to) a mean of 31.9 sites. Because 20-yr height and survival are fitness related, the x -axis coordinate of the vertex of the general transfer function estimates the distance along an environmental gradient that populations of a subspecies should be moved for optimal growth or survival of the subspecies as a whole.

The general transfer functions were validated with data from two studies involving four planting sites that were not part of the Illingworth tests. One, described by Ying et al. (1989), involved the 20-yr height and survival of 29 populations growing on two test sites (Fig. 2): Cluculz Lake (900 m elevation) and Negro Creek (1300 m elevation). Of the 29 populations, only five had been included in the Illingworth tests. The populations spanned the transition from *ssp. contorta* to *ssp. latifolia*, but only four populations represented *ssp. contorta*. Because one observation was available for the transfer of a population from its provenance to a planting site, this test provided 58 observations for validating the general transfer functions. The second test (Ying 1991) involved the 15-yr height and survival of 55 populations of *ssp. latifolia* planted at two sites (Fig. 2): Kloakut Lake (1520 m elevation) and Boston Bar (980 m elevation). In the original analysis of this test, the planting at Boston Bar was subdivided into its components, Anderson River and Scuzzy Creek, but, because of their geographic proximity, the sites are considered herein as a single planting at Boston Bar. The populations were all from either British Columbia or its periphery (Fig. 1), but all were common to the Illingworth tests. Because not all populations were planted at all sites, this test provided only 84 additional observations, making available 142 for validating the general transfer functions.

The primary objective for developing the general transfer functions was to relate the position of the vertex to transfer distance. Validations, therefore, were made simply by regressing observed values on the predicted for data combined from the two suitable data sets. Although these data sets dealt with trees of different ages, the effects of age as well as the main effects of the planting environment were removed from the analyses by using percentages of the plantation mean as dependent variables. Analyses were made on data for all populations and for only those of *ssp. latifolia*.

TABLE 2. Degrees of freedom (df), number of independent variables (N), and goodness of fit (R^2) for the best fitting climate models.

Dependent variable	df	N	R^2
Annual temperature	512	10	0.97
Cold month temperature	512	9	0.96
Warm month temperature	512	10	0.84
Annual precipitation	508	12	0.61
Summer precipitation	508	9	0.54
Days without frost	464	6	0.90
Frost-free period	502	6	0.80

Note: All regressions were significant at $P < 0.01$.

Applications

The response functions and general transfer functions are well-suited for estimating the effects of changing climates on forest growth and survival and for developing reforestation guidelines that are intended to limit poor adaptation of planted trees.

Changing climates.—Response functions were used to predict the height and survival of populations for (1) the current climate, (2) the current climate increased by 3°C in mean annual temperature, (3) the current climate increased by 5°C in mean annual temperature, and (4) a future climate as predicted for global climate change by the United Kingdom general circulation model of Wilson and Mitchell (1987). Heights and survivals were predicted for locations in southern, central, and northern British Columbia. In predicting responses by altering mean annual temperature, other thermal variables were altered according to the relationships in Table A1; precipitation was held constant. Because as many as 10 response functions were available for each population, rankings were based on the mean response of the three largest predictions to guard against possible bias from extrapolation. Survival was equated to zero if either the current or future climates were outside the range of climates inhabited by *P. contorta* in British Columbia. The contemporary limits of distribution were defined by the predicted climates of British Columbia provenances (Fig. 1). Height was equated to a value of zero if either predicted survival or height was < 0 .

Reforestation guidelines.—The goal of reforestation is to establish a new generation of trees with optimal growth and adaptedness. Doing this requires output from the general transfer functions to be implemented by forest managers. For practical purposes, therefore, genetic variability should be described with geographic rather than climatic predictors. The steps taken for doing this involved the following: (1) using the equations in Table A2 to generate a database of climate variables for a series of geographic locations defined by LT, LN, and EL; (2) predicting the height and survival for a target location from the general transfer function using a transfer distance of zero; (3) surrounding predictions for the target with a confidence interval; (4) calculating the x -axis coordinates for the points defining the in-

tersection of the transfer function with the confidence interval, and (5) screening the database for all locations with predicted climates lying within the intervals defined by the x -axis coordinates for all of the climate variables.

RESULTS

Climate models

Regression models were particularly effective in describing gradients in temperature from geographic predictors (Table 2). Values of R^2 for the mean annual temperature and mean temperature in the coldest month, for instance, approached 1.0. Models, however, were less effective in describing geographic patterns of precipitation, most likely because precipitation is strongly influenced by local orographic effects. Nevertheless, even for precipitation variables, the regressions still accounted for more than one-half of the variance among stations. Regression equations are presented in Table A2, and a program is available from the authors for predicting climate variables within British Columbia.

The climate models were verified with independent data from 38 stations supplemented by seven coastal stations from the original database (Table 3). Regressions of the observed data on the predicted (Fig. 5A) were statistically significant ($P < 0.01$) for all variables and produced values of R^2 as high as 0.87 (Table 3). Most encouraging were the high values of R^2 for mean annual precipitation and mean summer precipitation, the two variables with the weakest functions (Table 2). As illustrated for the mean temperature in the warmest month (Fig. 5B), regressions of residuals on predicted values generally were not significant, although a weak relationship was detected for mean summer precipitation (Table 3, Fig. 5C). The models tended to overestimate summer precipitation when it was high, thus producing a negative relationship ($R^2 = 0.10$) between the residual and longitude (Fig. 5D). Otherwise, lack of a relationship between residuals and predicted values

TABLE 3. Goodness of fit (R^2) for regressions validating climate models with normalized data from 45 weather stations. Statistics are presented for the regression of the observed on the predicted, and the residual (observed minus predicted) on the predicted.

Variable	Regression model	
	Observed on predicted	Residual on predicted
Annual temperature	0.87**	0.00
Cold month temperature	0.87**	0.00
Warm month temperature	0.61**	0.01
Annual precipitation	0.76**	0.03
Summer precipitation	0.77**	0.12*
Days without frost	0.79**	0.01
Frost-free period	0.66**	0.00

* Significance at $0.05 > P > 0.01$.

** Significance at $P < 0.01$.

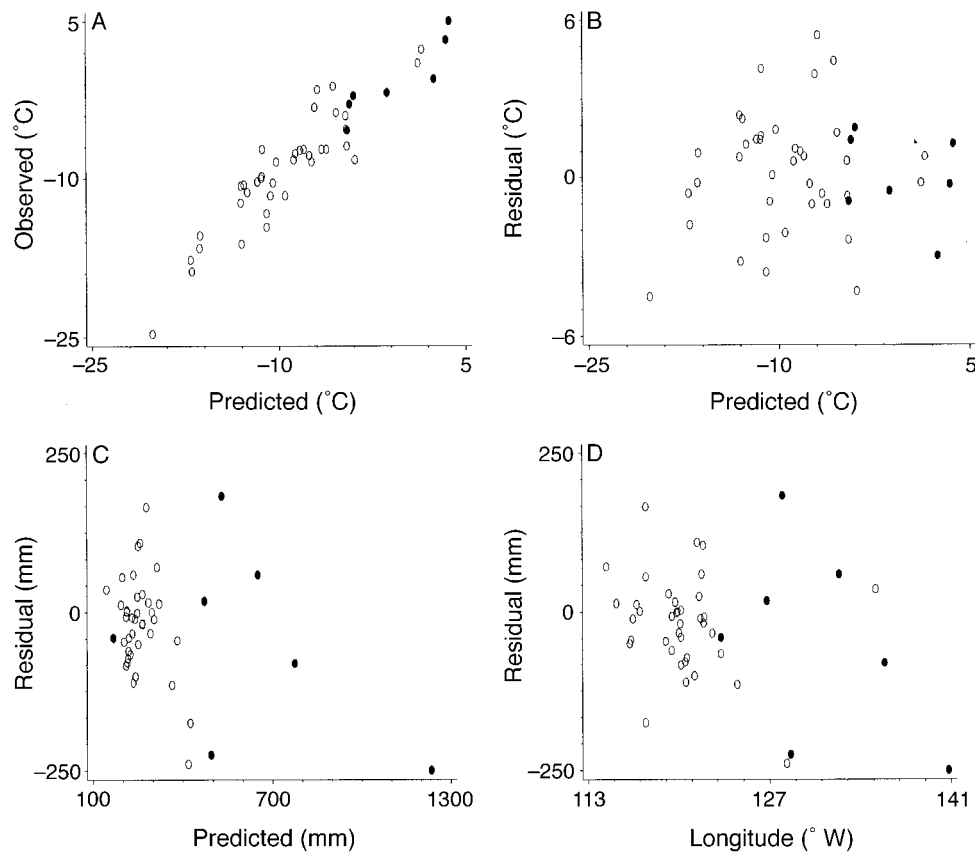


FIG. 5. Scatter plots illustrating the verification of climate models with independent data from 35 inland locations (open symbols) plus seven locations from coastal stations (solid symbols). (A) Observed mean temperature in the coldest month plotted against predicted values. (B) Residuals (observed minus predicted) for the mean temperature in the warmest month plotted against the predicted values. (C) Residuals of mean summer precipitation plotted against the predicted values. (D) Residuals of mean summer precipitation plotted against the longitude of the weather station.

suggested that most models were without bias across the range of the available data.

Geographic patterns described by the models are illustrated in Fig. 6 for predicted values along latitudinal transects at three longitudes. The latitudinal transect at 117° W crosses the Rocky Mountains from the south and enters a dissected plateau at about 54° N. Elevations within the plateau rarely exceed 700 m and decline toward the north. The models describe prominent effects of elevation on temperature and precipitation within the Rockies. As these mountains are approached, precipitation increases slightly, only to fall within their rain shadow. However, at a given latitude, high elevations tend to receive more precipitation than low elevations. The models also show that mean annual temperatures in the south decrease by $\sim 5^{\circ}\text{C}$ across an altitudinal range of 800 m, corresponding nicely to expected adiabatic lapse rates (see Rosenberg 1974) of $\sim 6^{\circ}\text{C}/1000$ m. In the north, altitudinal gradients in mean annual temperature are reduced greatly, largely because the coldest winter and warmest summer temperatures occur at the lowest elevations. However, the exponential increase in precipitation predicted for the

highest elevations (Fig. 6) is an anomaly that reflects an absence of weather stations above 600 m for $\text{LT} > 55^{\circ}$ N when $\text{LN} \approx 117^{\circ}$ W.

The transect at 125° W begins at sea level, crosses both the Coastal and the Rocky Mountains, and terminates in the Mackenzie Mountains of the Yukon. The models illustrate maritime effects on temperature and precipitation, the increasingly cold and continental climate to the north, and a rain shadow of the Coastal Mountains between the latitudes of 51° N and 54° N (Fig. 6). Altitudinal effects on temperature are similar to those for $\text{LN} = 117^{\circ}$ W as are predicted effects for mean annual precipitation. Thus, the exponential increase (Fig. 6) predicted for high elevation precipitation at $\text{LT} > 55^{\circ}$ N reflects an absence of high altitudinal weather stations in the north. Another anomaly that is not readily explained is for precipitation predicted at 300 m to exceed that for both 700 and 1100 m when $\text{LT} \approx 52^{\circ}$ N (Fig. 6).

The transect at $\text{LN} = 133^{\circ}$ W follows sea level up to $\text{LT} \approx 55^{\circ}$ N, crosses a coastal mountain range, and terminates in the valleys of the Yukon, which drain toward the north. Although gradients in the mean an-

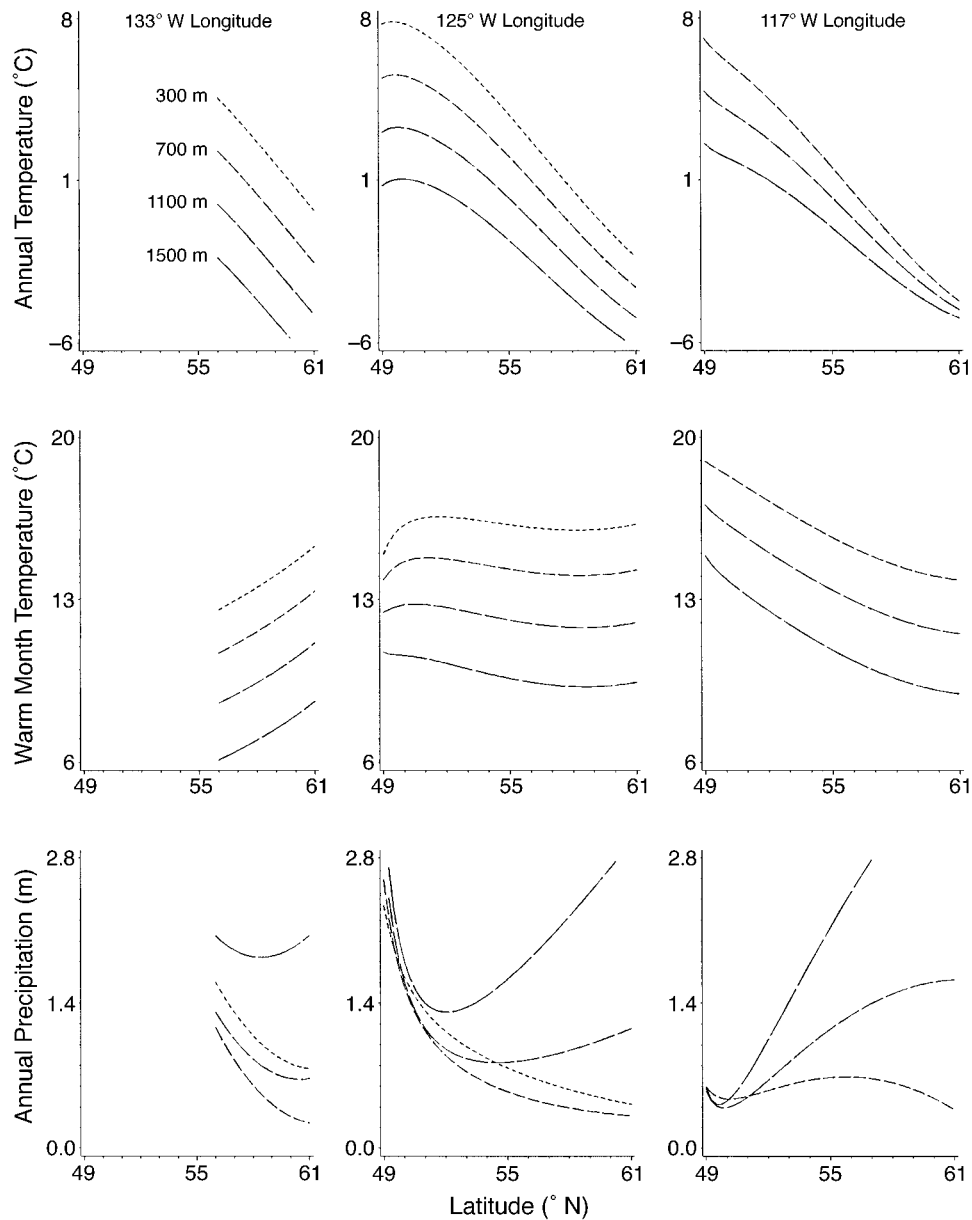


FIG. 6. Patterns of geographic variation in three climate variables (rows) plotted for latitudinal transects (x-axes) for three longitudes (columns) and four elevations (dashed lines). Longitude is noted in the heading, and the length of dash marks code elevations of 300 m (shortest dash), 700 m, 1100 m, and 1500 m (see upper left). Regression lines are truncated to approximate actual physiography (e.g., EL > 0 does not exist when LN = 133° W and LT < 55° N; and EL < 300 m does not exist for LN = 117° W when LT < 61° N).

nual temperature along this transect generally reflect the effects of altitude and latitude, the mean temperature in the warm month is strongly influenced by the moderating effects of the ocean and thus increase toward the north. Precipitation gradients, like those for the high latitudes at LN = 125° W, undoubtedly were influenced by the distribution of the weather stations. At LN > 132° W and LT < 60° N, only three stations exist at EL > 500 m, and none occur at EL > 1000 m. Although the models describe a decrease in precip-

itation as the arid north is approached, the altitudinal gradients are particularly suspicious.

Of the variables not shown, patterns for the mean temperature in the coldest month mirrored those of the mean annual temperature; those for the mean summer precipitation followed the pattern for mean annual precipitation, except that the effects of the rain shadow of the Coastal Mountains were less pronounced; and those for the number of days without frost and the length of the frost-free season followed the pattern illustrated for

TABLE 4. Maximum and minimum environmental conditions across which subspecies occur as predicted (Appendix Table A2) for 101 populations of *P. contorta* from British Columbia and its periphery.

Climate variable	Units	Provenances					
		Subspecies <i>latifolia</i>		Subspecies <i>contorta</i>		Test sites	
		Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
Annual temperature	°C	-6.1	6.9	2.1	9.5	-3.2	5.1
Cold month temperature	°C	-31.6	-6.1	-10.6	4.2	-22.2	-8.4
Warm month temperature	°C	9.9	18.7	12.1	17.3	10.9	17.3
Annual precipitation	mm	202.2	1378.0	920.3	3102.7	244.0	1106.0
Summer precipitation	mm	97.2	464.5	256.5	863.1	151.0	401.0
Days without frost	d	57.9	200.6	160.9	317.9	103.0	171.0
Frost-free period	d	32.0	126.5	98.3	213.9	38.0	101.0
Annual heat:moisture index†	...	5.5	36.4	5.9	14.9	7.1	35.7
Summer heat:moisture index	°C/m	24.5	143.8	15.1	67.3	29.2	84.1
Temperature differential	°C	20.2	45.6	10.0	23.1	21.6	36.1

† Units are a transformation of °C/m.

the mean annual temperature, except that the clines flattened as elevation increases.

Fig. 6 thus demonstrates that the climate models produce intuitively plausible descriptions of general climatic gradients across British Columbia. However, the figure also demonstrates that the precision of the climate models is dependent on the location of the weather stations. Because of the potential for bias when polynomial models are used to extrapolate, the errors of prediction associated with the high elevations in the north are obvious and perplexing. In the contemporary climate, *P. contorta*'s upper altitudinal limits are reached at ~ 1200 m in the north, and, therefore, bias produced by the models should not invalidate our analyses. One should also recognize that these climate models describe general patterns across a broad geographic tract. Local effects such as those associated with frost pockets, aspect, and orography will not necessarily be described.

In our presentations, climates that are predicted from these models (Appendix Table A2) are frequently treated as if they were empirical. Readers should be aware that our references to climates, climatic effects, or climatic gradients refer to predictions from the climate models.

Population response functions

To the extent that the sample of 101 populations from British Columbia and its periphery is representative of the geographic distribution of *P. contorta* in the province, the climate models can be used to estimate the provincial limits of the species' realized niche. Table 4 thus provides the climatic limits for the widespread distribution of *P. contorta* and two of its subspecies. The realized niche of *P. contorta* in British Columbia spans climates differing by > 35°C in mean temperature in the coldest month, 3 m in mean annual precipitation, and 180 d in the length of the frost-free season. In comparison to the realized niche of spp. *latifolia*, that of ssp. *contorta* strongly reflects the maritime climate to which it is native.

Because the Illingworth tests concentrated on ssp. *latifolia*, the test sites encompassed a relatively high proportion of the realized niche of ssp. *latifolia* in British Columbia (Table 5): 64% for mean annual temperature, 94% for warm month temperature, 54% for the mean temperature in the coldest month, and 73% for the mean annual precipitation; the most notable deficiency was a lack of representation of the coldest climates (Table 4). For the British Columbia distribution

TABLE 5. Number of response functions (*N*), the average goodness of fit (*R*²), the mean optimal environment, and the range in optimal environments among populations for 10 climate variables controlling the 20-yr height and survival of populations.

Climate variable	20-yr height				Survival			
	<i>N</i>	<i>R</i> ²	Optimum	Range	<i>N</i>	<i>R</i> ²	Optimum	Range
Annual temperature	96	0.63	3.8	8.0	61	0.40	2.1	7.6
Cold month temperature	84	0.65	-12.6	17.0	53	0.42	-10.7	19.6
Warm month temperature	56	0.36	16.5	3.7	20	0.43	13.3	4.1
Annual precipitation	90	0.46	611.4	475.4	61	0.41	753.7	694.0
Summer precipitation	89	0.54	267.5	231.0	63	0.43	306.0	138.8
Days without frost	77	0.55	162.4	133.4	67	0.41	140.5	144.7
Frost-free period	76	0.37	90.6	87.2	24	0.42	63.4	35.9
Annual heat:moisture index	60	0.33	26.0	17.7	35	0.41	16.6	17.1
Summer heat:moisture index	94	0.50	58.1	28.7	67	0.43	47.4	39.8
Temperature differential	86	0.61	27.1	15.2	57	0.42	23.0	15.8

Notes: Functions that opened upward (Fig. 7) were ignored. Units for the optimum and the range are listed in Table 4.

of the species as a whole, the test sites encompassed only $\sim 50\%$ of the realized niche for the thermal variables and only $\sim 30\%$ for precipitation variables, largely because of an absence of test sites in maritime climates. On the average, the sites encompassed 64% of the realized niche of *ssp. latifolia*, but only 46% of that combined for both subspecies.

It is well-documented that a single population of *P. contorta* can grow and survive on only a portion of the environmental gradient occupied by the species as a whole. As will be apparent in the illustrations presented, the broad range of environments sampled by the test sites (Table 4) provided opportunities for niche breadth of individual populations to be evaluated even though test sites did not fully sample the ecological distribution of either subspecies. For these evaluations, it is pertinent to note that niche concepts are often evoked in biogeographical research on the distribution of species in relation to physical environments (Brown and Gibson 1983) and, most recently, in modeling responses to global warming (Loehle and LeBlanc 1996). Although niche concepts are often treated as more hypothetical than real, the Illingworth tests offer a unique opportunity to quantitatively evaluate niche breadth.

Of the 2520 response functions that were calculated, 45% were discarded because statistical significance was at $P > 0.1$. Culling the nonsignificant regressions left 1372 functions, eliminated eight populations, and left 118 populations for further consideration. In total, 105 populations had significant response functions for 20-yr height, 97 for survival, and 82 for both. Only one population of *ssp. murrayana* had a statistically significant response function for 20-yr height.

A paring of the original number of response functions by 45% reflects either directly or indirectly that populations were not tested on the same set and number of sites. In many cases, a low number of observations led to a lack of statistical significance and to the rejection of a function. In other cases, climate variables were influential for some populations but not for others. In still other cases, climate variables chosen by us were only weakly related to growth and survival. Regardless of the reasons, response functions were not necessarily available for predicting height and survival of each population for all climate variables. For the British Columbia populations of *ssp. latifolia* that were being emphasized in the Illingworth tests, an average of 8.8 functions were available for predicting population height, while 5.6 functions were available for predicting survival.

Of the 1372 significant functions, 208 were of the types shown in Fig. 7. As illustrated for the Flathead population, one of these types involved functions that opened upward. This type ordinarily occurred when the assortment of sites on which the population was tested happened to span a limited range of climates. A second type, illustrated by the Albreda population (Fig. 7B), produced a curve with a vertex beyond the realized

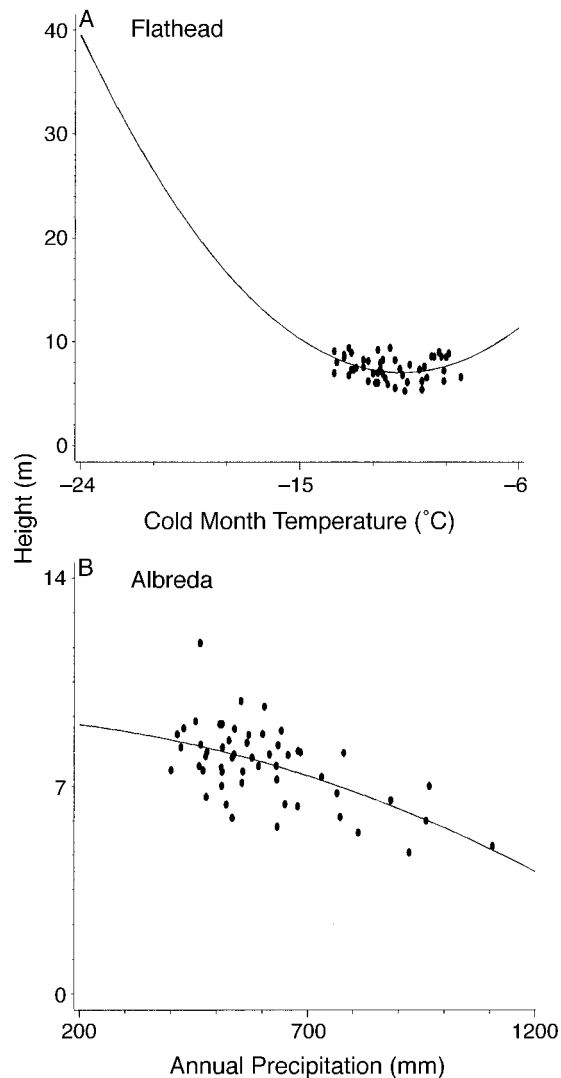


FIG. 7. Response functions for 20-yr height plotted in relation to observed data illustrating for the Flathead population (A) a function opening upward, and for the Albreda population (B) a function with a vertex occurring outside the range of environmental conditions under which *P. contorta* occurs in British Columbia.

niche of the species in the province (Table 4). The maximum growth for Albreda, for instance, is predicted to occur in a climate with a mean annual precipitation of -122 mm. Many of the functions that were discarded because of a lack of statistical significance at $P > 0.1$ were similar to those of Fig. 7. Both anomalies could have been avoided if each population had been tested in environments capable of severely limiting its growth and survival. In our presentations, these two types of functions (Fig. 7) are used only for interpolation.

Table 5 summarizes statistics associated with the population response functions. This table shows, for instance, that of the 105 populations for which response functions were available for predicting 20-yr height,

96 had functions using mean annual temperature as a predictor. These 96 functions had mean $R^2 = 0.63$; the vertex of the function occurred on the average at 3.8°C ; and the range among populations for the temperature associated with the vertex spanned 8°C . Because 20-yr height and survival are fitness related, the optimal climate is defined by the x -axis coordinate of the vertex of the response function. Statistics for survival are based on the 97 populations for which response functions were available.

Of the total number of response functions, 61% predicted 20-yr height, and these functions had mean $R^2 = 0.49$ (Table 5). Functions predicting survival had mean $R^2 = 0.40$. Based on both frequency (N) and mean R^2 , the mean annual temperature, mean temperature in the coldest month, and temperature differential seem to be the most influential in predicting 20-yr height; the mean temperature in the warm month, the length of the frost-free season, and the annual heat : moisture index seem to be the least influential. Functions predicting survival had relatively uniform values of R^2 , but the number of populations for which significant response functions were available (N) suggests that the number of days without a freezing temperature and the summer heat : moisture index were the most effective; the mean temperature in the warm month and the length of the frost-free season were the least effective.

The optimum environment for 20-yr height or survival for the species as a whole was calculated for British Columbia as the average across all populations of the x -axis coordinate for the vertex of the response functions. On the average, therefore, the tallest trees are expected in an environment with a mean annual temperature of $\sim 3.8^\circ\text{C}$, a mean temperature in the cold month of -12.6°C , and summer precipitation of ~ 268 mm (Table 5). In general, the species' optimum for survival is slightly more maritime than the optimum for growth: lower mean annual temperature, warmer mean temperature in the cold month, cooler mean temperature in the warmest month, higher precipitation, and a lower temperature differential.

In defining niche breadth in terms of the Hutchinsonian hypervolume, it is pertinent to determine whether the mean optimal climate for *P. contorta* in British Columbia is a compromise among the univariate optima of Table 5 or whether all optima could occur at a single geographic locality. A search of the weather data located a station at Kersley (LT = 52.8°N , LN = 122.4°W , and EL = 671 m) that approached the climatic optima (Table 5) for 20-yr height: mean annual temperature = 3.9°C , temperature in the coldest month = -11.2°C , temperature in the warmest month = 15.6°C , annual precipitation = 520 mm, summer precipitation = 252 mm, number of frostless days = 163 d, frost-free period = 86 d, and temperature differential = 26.8°C . A similar search for stations with climates approximating the survival optima produced the Nanika River Hatchery (LT = 54.1°N , LN = 127.5°W , and EL =

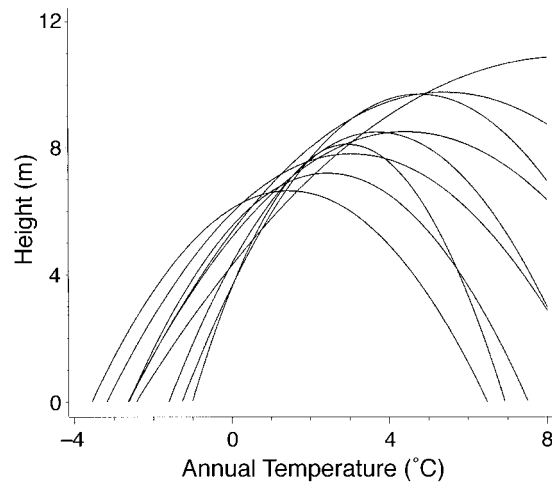


FIG. 8. Response functions using mean annual temperature as a predictor of height for nine populations that represent a variety of responses for *ssp. latifolia*.

704 m) which is west (more maritime) of Kersley. For this station, mean annual temperature was 2.1°C , annual precipitation was 723 mm, and temperature differential was 23.7°C .

The optimum climate for the growth and survival of individual populations varied greatly about the mean optimum for the species (Table 5). Differences among populations are readily illustrated in Fig. 8 by nine response functions that use the mean annual temperature as a predictor. Functions selected for this figure illustrate several aspects of the species' genetic structure: differences among populations for growth potential (y -axis coordinate of the vertex) and tolerance to cold (x -axis coordinate of the vertex), and the negative relationship between growth potential and cold hardiness.

In addition, the breadth of the curves (distance between the roots) suggests that populations are capable of growth and survival across a broad range of environments. These curves (Fig. 8), coupled with the scatter plots of Fig. 9, thus suggest that populations have an extremely broad fundamental niche. Although difficult to estimate precisely from ≤ 60 data points, the fundamental niche of these populations appears to approach 10°C in mean annual temperature, an amount that exceeds the temperature differential expected across 1000 m of elevation (see Rosenberg 1974). A fundamental niche of this size would mean that the array of seedlings produced from natural wind pollinations within a single population would be capable of collectively inhabiting approximately two-thirds of the realized niche estimated for *ssp. latifolia* across its entire range in British Columbia (Table 4). A lack of test sites within the distribution of *ssp. contorta* precluded even rough estimates of niche breadth for this subspecies.

Validation of response functions.—At Red Rock, a

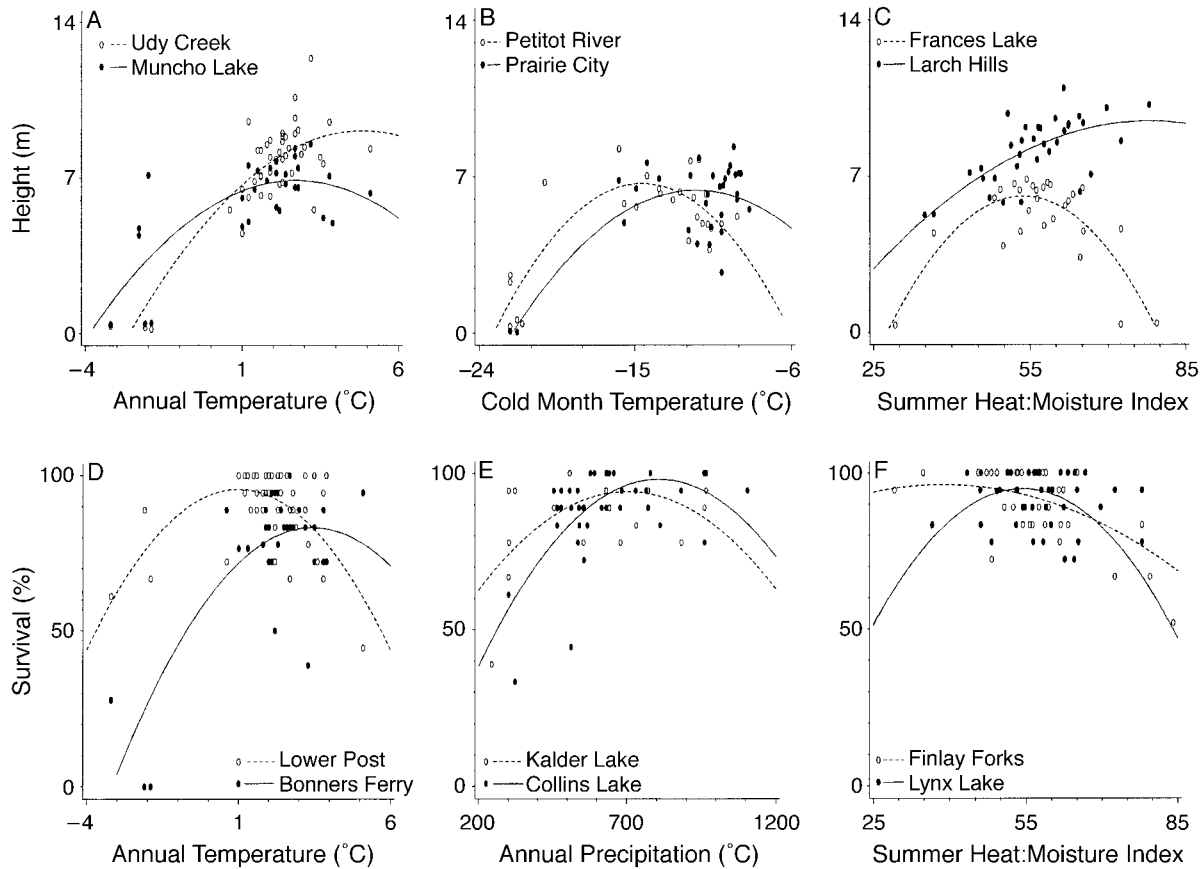


FIG. 9. Response functions for *ssp. latifolia* populations plotted in relation to the observed data illustrating differential climatic adaptation between pairs of populations. (A–C) relate 20-yr height to climate; (D–F) relate survival to climate.

site that is geographically central for *P. contorta* in British Columbia, mean height was 8.4 m, but that of individual populations ranged 4.8–10.6 m. The regressions of actual on predicted height were statistically significant for all climatic predictors, with functions using the mean annual temperature, mean temperature

in the coldest month, length of the frost-free period, and the temperature differential all accounting for >90% of the variance in the actual 20-yr height (Table 6). Nevertheless, for all functions, except those using mean summer precipitation as a predictor, residuals were not independently distributed with respect to the

TABLE 6. Number of populations (*N*) represented by a climatic predictor and the goodness of fit (R^2) for regressions of (1) the actual response on the predicted value, and (2) the residual on the predicted value for data from Red Rock.

Response function predictor	<i>N</i>	Height regressions		<i>N</i>	Survival regressions	
		Actual on predicted	Residual on predicted		Actual on predicted	Residual on predicted
		R^2	R^2		R^2	R^2
Annual temperature	52	0.90**	0.16**	27	0.17*	0.00
Cold month temperature	39	0.93**	0.61**	24	0.25*	0.04
Warm month temperature	40	0.83**	0.25**	8	0.58*	0.23
Annual precipitation	49	0.76**	0.26**	28	0.02	0.03
Summer precipitation	49	0.65**	0.02	29	0.07	0.02
Days without frost	37	0.44**	0.44**	28	0.42**	0.18*
Frost-free period	47	0.92**	0.41**	12	0.73**	0.33
Annual heat:moisture index	33	0.78**	0.34**	17	0.08	0.34*
Summer heat:moisture index	52	0.84**	0.41**	30	0.18*	0.01
Temperature differential	49	0.92**	0.50**	26	0.44**	0.09

* Significance at $0.05 > P > 0.01$.

** Significance at $P < 0.01$.

TABLE 7. Number of populations (N) represented by a climatic predictor and the goodness of fit (R^2) for regressions of (1) the actual response on the predicted value and (2) the residual on the predicted value for data from Terraced Peak.

Response function predictor	Height regressions			Survival regressions		
	N	Actual on predicted	Residual on predicted	N	Actual on predicted	Residual on predicted
		R^2	R^2		R^2	R^2
Annual temperature	51	0.15**	0.50**	28	0.02	0.24**
Cold month temperature	37	0.53**	0.43**	26	0.14	0.01
Warm month temperature	42	0.39**	0.58**	12	0.47*	0.51**
Annual precipitation	48	0.45**	0.69**	34	0.36**	0.19**
Summer precipitation	48	0.49**	0.69**	31	0.44**	0.23**
Days without frost	38	0.21**	0.69**	30	0.03	0.35**
Frost-free period	42	0.16**	0.71**	14	0.59**	0.17
Annual heat:moisture index	38	0.39**	0.25**	17	0.01	0.18
Summer heat:moisture index	52	0.58**	0.58**	35	0.28**	0.01
Temperature differential	38	0.19**	0.34**	23	0.38**	0.07

* Significance at $0.05 > P > 0.01$.** Significance at $P < 0.01$.

predicted values. The response functions tended to overestimate the height of short populations and underestimated the height of the tallest.

Survival at Red Rock averaged 85% but ranged 48–97% for individual populations. While several of the regressions of actual survival on predicted survival were statistically significant, those using the number of days without frost and the temperature differential as predictors had relatively high frequencies (N) and produced functions with relatively high values of R^2 (~0.43). However, when the number of days without frost was used as an independent variable, residuals were not independent of the predicted values (Table 6). When predictions were based on functions driven by the length of the frost-free season, R^2 relating observed and predicted heights was exceptionally high, but the power of the test was low, because the appropriate response functions were available for only 12 populations in the Red Rock planting.

At Terraced Peak, a site ecologically marginal for *P. contorta*, trees averaged 4 m in 20-yr height with population means ranging 1.5–5.2 m. Response functions that used as predictors the mean summer precipitation, summer heat:moisture index, and mean cold month temperature accounted for the most variance in actual heights (Table 7). Values of R^2 approached 0.6, but, like the Red Rock analyses, relationships between the residuals and predicted values were strong. For Terraced Peak, the relationships were negative for all climatic predictors, which meant that the response functions overestimated height when high and underestimated it when low.

Survival of populations at Terraced Peak spanned 0–100%. Validation of survival response functions (Table 7) showed that those functions that used as predictors the mean annual precipitation, the mean summer precipitation, the temperature differential, and the summer heat:moisture index appeared to be the most effective. Predictions from functions driven by precipitation, however, were not independent of the residuals; these

functions tended to underestimate high survival and overestimate low survival. When the length of the frost-free season was the independent variable, R^2 relating observed and predicted survival was high, but significance tests had few degrees of freedom.

The validations thus provide strong support for the capability of the response functions to estimate the relative height and survival of populations on sites with much different climates. Nevertheless, strong relationships between the residuals and predicted values demonstrated bias in the models. The patterns displayed by the residuals, however, were conflicting: at the ecologically extreme site, response functions tended to overestimate the height of tall trees and underestimate the height of short trees, but, at the ecologically central site, the same functions underestimated the height of tall trees while overestimating the height of the shortest. These conflicting results suggest that if performance were considered across a full spectrum of sites suitable to *P. contorta*, the averages should be free of bias. The conflicting patterns displayed by the residuals probably reflect environmental effects such as those associated with soils, aspect, or short-term climate that are independent of the general long-term climates of the normalized database. Because our objectives involve responses to climate on which edaphic effects are superimposed, the validations can be considered as strongly supportive.

Adaptation vs. occurrence.—The broad range of climatic conditions associated with the optimal growth and survival of populations (Table 5, Fig. 8) corroborates the many research results of Ying and his collaborators (see *Literature cited*) demonstrating that British Columbia populations of *P. contorta* are genetically attuned to much different environmental conditions. Differential adaptation is illustrated in Fig. 9 for pairs of populations selected to demonstrate first, genetic variation, and second, its ecologic basis.

As shown in Fig. 9A, the Muncho Lake population exhibits the short stature and low temperature optimum

TABLE 8. Mean differences between the climate inhabited by a population and the optimum climate, number of observations (N), and the level of significance of a t test of paired observations calculated for 20-yr height and survival of *ssp. latifolia* populations before and after adjusting for the warm climate of recent years. Negative values denote an optimum that is warmer, wetter, more continental, or has greater heat per unit of moisture than the inhabited climate.

Climate variable	20-yr height			Survival		
	N	Mean differences		N	Mean differences	
		Unadjusted	Adjusted		Unadjusted	Adjusted
Annual temperature	66	-2.4**	-2.8**	31	-0.5	-0.9**
Cold month temperature	52	-2.7**	-3.6**	26	-1.8	-2.6**
Warm month temperature	36	-1.8**	-2.0**	8	0.9	1.8
Annual precipitation	55	19.7	-16.1	41	-106.0**	-141.9**
Summer precipitation	64	-7.0	-13.6	41	-37.4**	-43.7**
Days without frost	50	-23.3**	-26.9**	37	2.2	-1.3
Frost-free period	57	-17.5**	-20.7**	11	-1.6	-3.1
Annual heat:moisture index	40	-4.9**	-4.2**	22	1.9	2.6
Summer heat:moisture index	67	-1.6	-0.4	41	6.3**	7.2**
Temperature differential	58	1.5*	2.1**	26	2.5**	3.2**

Note: Units are listed in Table 4.

* Significance of t at $0.05 > P > 0.01$.

** Significance of t at $P < 0.01$.

expected of populations adapted to severe environments, while the stature and optima exhibited by the Udy Creek population suggest adaptation to mild climates. Although both of these populations are from approximately the same elevation, Muncho Lake is in the far north (LT = 59.1° N) while Udy Creek is much farther south (LT = 53° N). Fig. 9B illustrates response functions of two populations exhibiting the low growth potentials typical of populations adapted to severe environments. The optima for these two populations, however, occur in much different temperature regimes. The Petitot River population is from northeastern British Columbia and achieves optimal growth at colder winter temperatures than the Prairie City population, which originated from a high elevation (1500 m) in the Cascade Range of the United States (LT = 44.5° N). In Fig. 9C, the slowly growing population at Frances Lake comes from the Yukon Territory (LT = 61.2° N) and achieves its greatest height at a lower value of the summer heat:moisture index than the fast-growing population from Larch Hills, which is near the eastern edge of the rain shadow of the Cascade Range (LT = 50.7° N).

Illustrations in Fig. 9 for survival follow similar patterns. In Fig. 9D, the population at Lower Post (LT = 60° N) achieves its best survival at much cooler temperatures than genotypes from Bonners Ferry, which is from a relatively low elevation (1000 m) in the inland west of the United States (LT = 48.5° N, LN = 116.5° W). In Fig. 9E, both populations are from about the same latitude (54° N), but Collins Lake is from the western portion of the province where precipitation is higher than in the central region inhabited by Kalder Lake genotypes; peak survival of Collins Lake genotypes occurs at a higher mean annual precipitation than those of Kalder Lake. And finally, in Fig. 9F, Lynx Lake (LT = 53.5° N) is from the warm, relatively dry central interior, while Finlay Forks (LT = 56° N) is in

the Rocky Mountains to the north; the highest survival of the Finlay Forks population thus occurs at a lower summer heat:moisture index than that for Lynx Lake.

Fig. 9 thus demonstrates adaptive differences among populations that are related to their climate of origin. One is led, therefore, to expect that the environment occupied by a natural population should be near the optimum for its growth and survival. However, the Udy Creek population (Fig. 9A) occurs naturally in an environment that has a mean annual temperature of 2.4°C, while that of Muncho Lake is -2.5°C. Both populations, therefore, occupy environments that are ~4°C colder than their respective optimum for growth. This observation led to an examination of the relationship between the optimal climate and the climatic regime under which the populations actually occur. In Table 8 for *ssp. latifolia* and in Table 9 for *ssp. contorta*, mean differences have been calculated as the provenance climate minus the optimum; negative numbers occur when the optimum climate is either warmer or wetter, has more heat per unit moisture, or is more continental than the provenance environment. Also shown in these tables are the results of t tests of paired observations that address the probability that the differences between the inhabited and optimal environments differ from zero. Statistics are presented before and after adjusting for the warmth of the recent climate.

For *ssp. latifolia* (Table 8), the t tests show that native populations tend to occupy environments that are colder and more continental, have shorter frost-free periods, and have less heat per unit moisture on an annual basis than the environments in which optimal growth occurs. Data adjusted for the warmth of the recent climate produces even a greater differential than the unadjusted data, but both suggest that the difference is between 2 and 3°C in mean annual temperature. For survival, Table 8 shows that native populations of *ssp. latifolia* are occupying climates that are somewhat

TABLE 9. Mean differences between the climate inhabited by a population and the optimum climate, number of observations (N), and the level of significance of a t test of paired observations calculated for 20-yr height and survival of *ssp. contorta* populations before and after adjusting for the warm climate of recent years. Positive values denote an optimum that is cooler, drier, more maritime, or has less heat per unit of moisture than the inhabited climate.

Climate variable	20-yr height			Survival		
	N	Mean differences		N	Mean differences	
		Unadjusted	Adjusted		Unadjusted	Adjusted
Annual temperature	12	1.9*	1.5	11	4.7**	4.3**
Cold month temperature	8	9.9**	9.1**	9	7.3**	6.5**
Warm month temperature	5	-2.6*	-2.8*	6	0.2	0.1
Annual precipitation	12	1342.0**	1306.1**	14	1426.5**	1390.6**
Summer precipitation	13	276.4**	275.4**	15	292.7**	292.1**
Days without frost	11	77.8**	69.8**	13	95.4**	85.9**
Frost-free period	9	62.9**	56.1**	6	110.2**	96.2**
Annual heat:moisture index	6	-13.3**	-13.4**	10	-5.7**	-5.7**
Summer heat:moisture index	11	-27.3**	-27.5**	17	-18.8**	-19.1**
Temperature differential	8	-8.7**	-8.1**	5	-8.6**	-8.0**

Note: Units are listed in Table 4.

* Significance of t at $0.05 > P > 0.01$.

** Significance of t at $P < 0.01$.

colder and drier with more summer heat per unit moisture than the optimum. When both responses are considered, the optimum appears to be considerably warmer and slightly wetter than the inhabited climate. Nevertheless, considerable variance exists among these estimates. The range among populations for the difference between the mean annual temperature of the provenance and the optimal was from -9 to $+3^{\circ}\text{C}$.

While the data presented in Table 8 were being prepared, it became obvious that the discrepancy between the inhabited climate and the optimum climate for thermal variables was related to population latitude (Fig. 10). When based on predictions from response functions for 20-yr height, simple correlations (r) with ab-

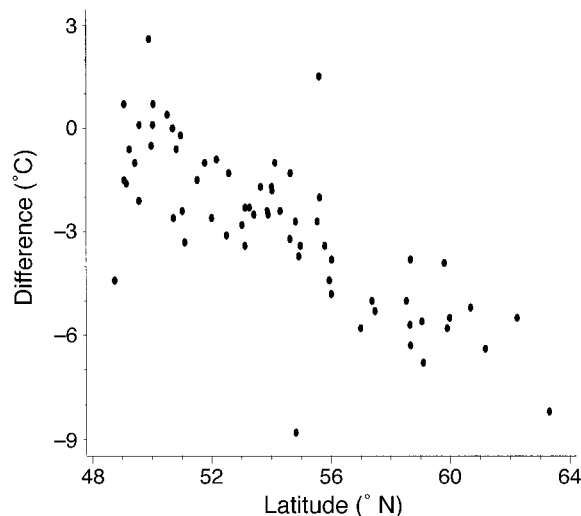


FIG. 10. Discrepancy between the mean annual temperature of the inhabited environment and that of the optimal environment plotted by population latitude. Discrepancies are based on response functions that describe 20-yr height of *ssp. latifolia*. Negative values denote an optimum that is warmer than the inhabited environment.

solute values ranging 0.77–0.84 related population latitude with the discrepancy between the inhabited and optimal mean annual temperature, mean temperature in the coldest month, average temperature differential, and average number of days without a freezing temperature. Although several statistically significant correlations were found between population elevation and several of the discrepancies, all were weaker ($r \approx -0.4$) than those involving latitude and, therefore, were interpretable as latitudinal effects indirectly mediated through elevation (elevation of valley floors decrease as latitude increases). The correlations in general, and Fig. 10 in particular, show without doubt that the size of the discrepancy increases with distance north. Populations in the south tend to occur in climates that are only 0.5°C below their optima for the mean annual temperature, while populations from north of $LT = 60^{\circ}\text{N}$ tend to occupy climates $\sim 7^{\circ}\text{C}$ colder than their optima (Fig. 10). A similar assessment based on predictions from survival functions leads toward the same conclusions, although absolute values of the coefficients were lower.

Even though similar assessments for *ssp. contorta* were hindered by the low statistical power associated with fewer observations (Table 9), the t tests overwhelmingly showed that, of those populations capable of growing in inland climates, optima were $\sim 10^{\circ}\text{C}$ cooler in mean temperature in the coldest month, nearly 1.3 m lower in mean annual precipitation, and $\sim 8^{\circ}\text{C}$ higher in mean summer–winter temperature differential than the climates actually inhabited. Because of the size of these differences, interpretations remained the same regardless of whether climates were adjusted for the recent warmth. Nevertheless, in contrast to *ssp. latifolia*, populations of *ssp. contorta* tend to be occupying climates that are much warmer and wetter than their optima.

These analyses have shown that the height and sur-

TABLE 10. Goodness of fit (R^2) for general transfer functions and their validation with independent data. Validation tests were made with and without data from four populations of *ssp. contorta*.

Climate variable	20-yr height			Survival		
	Transfer function	Validation		Transfer function	Validation	
		All data	<i>ssp. latifolia</i>		All data	<i>ssp. latifolia</i>
Annual temperature	0.67**	0.60**	0.23**	0.25**	0.05**	0.00
Cold month temperature	0.67**	0.72**	0.45**	0.29**	0.00	0.06**
Warm month temperature	0.54**	0.61**	0.05**	0.20**	0.09**	0.16**
Annual precipitation	0.57**	0.56**	0.09**	0.25**	0.01	0.00
Summer precipitation	0.53**	0.57**	0.05**	0.25**	0.04*	0.02
Days without frost	0.60**	0.46**	0.03	0.22**	0.06**	0.00
Frost-free period	0.54**	0.55**	0.01	0.20**	0.04*	0.02
Annual heat:moisture index	0.53**	0.61**	0.03*	0.22**	0.04*	0.03
Summer heat:moisture index	0.53**	0.67**	0.21**	0.27**	0.00	0.02
Temperature differential	0.64**	0.70**	0.37**	0.30**	0.00	0.08**

* Significance at $0.05 > P > 0.01$.** Significance at $P < 0.01$.

vival of populations adapted to different environments can be predicted from response functions driven by climatic variables. The response functions also suggested that seedlings produced from natural populations of *ssp. latifolia* exhibit a broad fundamental niche, despite the fact that the populations exhibit much different climatic optima. Finally, the analyses again raise the possibility (Namkoong 1969) that, despite repeated demonstrations of clines paralleling environmental gradients, natural populations of forest trees do not necessarily occupy their environmental optima.

General transfer functions

The general transfer functions predicted height or survival (as a percentage of a plantation mean) for each subspecies from quadratic models of transfer distance along each of 10 climate gradients. Because transfer distance was calculated as test site climate minus prov-

enance climate, negative values would represent the transfer of a population from a warmer or wetter climate to one cooler or drier. Table 10 shows that all regressions were statistically significant ($P < 0.01$), producing values of R^2 that ranged 0.53–0.67 for height and 0.20–0.30 for survival. The best predictors of height were transfers in units of the mean annual temperature, mean temperature in the coldest month, and temperature differential. The best predictors of survival were transfer distances in units of the temperature differential, mean temperature in the coldest month, and summer heat : moisture index.

Effects of subspecies were statistically significant ($P < 0.01$) for all climate variables and are illustrated by differences in (1) the height of the vertex along the y-axis, which reflects the greater growth potential of *ssp. latifolia* in inland environments (Figs. 11 and 12), and (2) the position of the vertex along the x-axis,

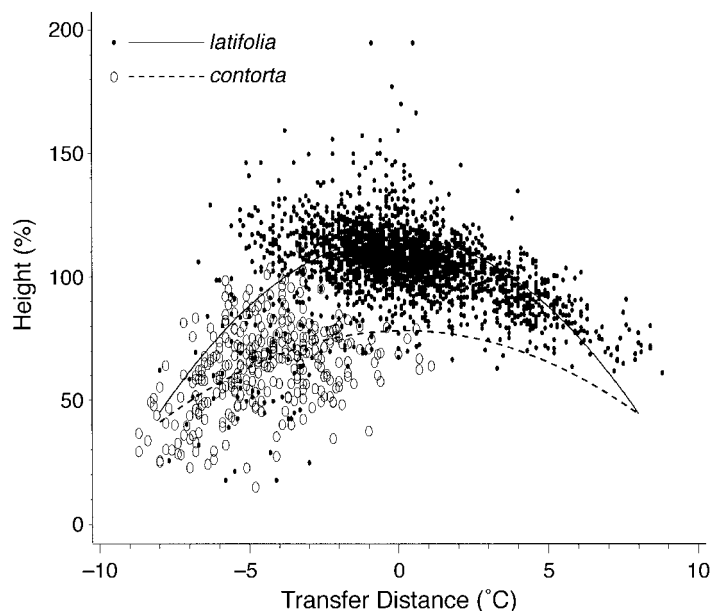


FIG. 11. The 20-yr height (percentage of plantation mean) of *ssp. latifolia* and *ssp. contorta* plotted by transfer distance (planting site mean minus the provenance mean) in units of the mean annual temperature. Regression lines are values predicted by the general transfer function. Positive values of transfer distance denote transfers into a warmer climate than the provenance.

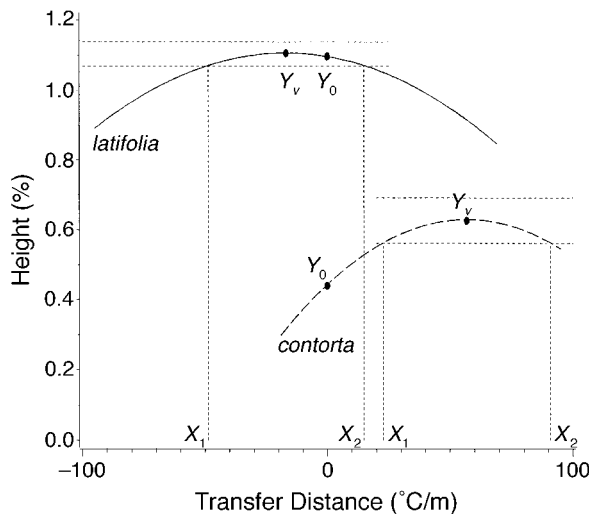


FIG. 12. General transfer functions predicting 20-yr height as a percentage of the plantation mean from transfer distance in units of the summer heat : moisture index for two subspecies of *P. contorta*. Statistics illustrated are Y_0 and Y_v , predicted values at the null transfer ($X = 0$) and at the vertex of the function, respectively; the 95% confidence intervals for Y_v ; and the x -axis coordinates (X_1 and X_2) for the intersection of the lower confidence interval of the vertex with the response function. Positive values of transfer distance denote transfers to climates that are warmer per meter precipitation than the provenance.

which illustrates the preference of ssp. *contorta* for maritime climates (Fig. 12). The quadratic coefficients lacked significance for only two regressions: the prediction of 20-yr height of ssp. *contorta* from mean annual precipitation and the from the length of the frost-free period.

When data from both subspecies were considered (Table 10), validations were strong for height functions, but were weak for survival functions. Even after eliminating the four populations of ssp. *contorta*, the validations still provided strong support for four of the height functions, while support for the survival functions was improved but remained weak.

Statistics produced from the general transfer functions are of particular interest in understanding the factors controlling the distribution of genotypes across the landscape. While Fig. 11 illustrates the fit of the regressions, Fig. 12 illustrates the relationship between the vertex of the function and the null transfer ($X = 0$) in terms of statistical precision. These analyses ignore functions such as those in Fig. 7 that could not be interpreted: for ssp. *latifolia*, the prediction of survival from transfers in units of summer precipitation; and for ssp. *contorta*, the prediction of height from transfers in units of mean annual precipitation and the prediction of survival from transfers in units of the mean temperature in the warmest month, the number of days without frost, the length of the frost-free period, and the annual heat : moisture index.

According to Fig. 12, the response Y for a population

of ssp. *latifolia* has a maximum value at the vertex ($Y_v = 1.103$) where $X = -16.9$. At the null transfer distance of $X = 0$, the predicted response, Y_0 , is 1.094. The confidence interval ($\alpha = 0.05$) about Y_v is ± 0.035 and is illustrated in the figure by the horizontal hashed lines. Y_0 occurs within the confidence interval of Y_v and, therefore, does not differ significantly from it. Of the confidence intervals, the lower interval has interpretative value because it intersects with the transfer function at two points: $X_1 = -47.8$, and $X_2 = 14.1$. Because Y_0 does not differ from Y_v , the interval between X_1 and X_2 therefore, 20-yr height should be optimal when populations are transferred zero units along a gradient of the summer heat : moisture index. Because X_1 and X_2 are associated with the 95% confidence limits about Y_v , populations separated from X_v by distances of ± 30.9 units ($[X_2 - X_1]/2$) will be genetically different with a probability of 0.95.

For ssp. *contorta*, Y_0 (Fig. 12) lies outside the confidence interval of Y_v (the interval between X_1 and X_2 does not include zero) and, therefore, the optimal growth of this subspecies should be achieved by transferring populations to environments that are warmer per unit of precipitation than those in which they occur naturally.

Table 11 shows that the results and conclusions illustrated by Fig. 12 for ssp. *latifolia* are consistent for all climate variables: values of Y_0 and Y_v were so similar that the intervals between X_1 and X_2 include the null transfer distance. Therefore, optimal growth and survival for this subspecies should occur when populations are not moved from the climatic conditions under which they occur naturally. For ssp. *contorta*, however, transfer distances associated with optimal performance are substantial. For instance, optimal growth of populations should be obtained with transfers of >22.8 units but <90.9 units in the summer heat : moisture index (Table 12, Fig. 12). Transfers of this magnitude would result in ssp. *contorta* being moved to sites customarily inhabited by ssp. *latifolia* (Table 4). Such transfers might optimize the growth of ssp. *contorta* but would be counterproductive to the growth and productivity of the species as a whole.

We emphasize that the results for ssp. *contorta* apply only to populations capable of surviving at those inland sites on which they happened to be tested. In maritime environments, populations of ssp. *contorta* achieve a greater height than those of ssp. *latifolia* (Ying and Liang 1994). If data were available that included a full range of ssp. *contorta* populations tested on both maritime and inland sites, general transfer functions for this subspecies might also peak near the null transfer.

To test whether the optimal transfer distance differed between northern and southern populations of ssp. *latifolia*, the statistics of Table 11 were recalculated for populations either north or south of $LT = 54^\circ N$. The results indicated no differences between the groups,

TABLE 11. Statistics (see Fig. 12) produced from the general transfer functions that predict height or survival (percentage of the plantation mean) of *ssp. latifolia* from the distance along 10 environmental gradients over which populations were transferred from their provenance to the planting site.

Climate variable	Height				Survival			
	Y_0	Y_v	X_1	X_2	Y_0	Y_v	X_1	X_2
Annual temperature	1.158	1.158	-1.6	1.6	1.003	1.005	-4.8	3.1
Cold month temperature	1.146	1.147	-2.8	3.9	1.026	1.027	-8.5	5.9
Warm month temperature	1.087	1.098	-5.1	1.6	1.024	1.024	-5.0	5.2
Annual precipitation	1.103	1.117	-248.9	838.9	0.958	0.962	-769.4	426.3
Summer precipitation	1.104	1.121	-77.4	359.4
Days without frost	1.094	1.094	-24.1	22.6	1.017	1.021	-59.2	33.2
Frost-free period	1.088	1.090	-36.6	23.2	0.993	0.994	-56.7	42.1
Annual heat:moisture index	1.069	1.084	-31.0	8.5	0.970	0.972	-17.5	27.3
Summer heat:moisture index	1.094	1.103	-47.8	14.1	1.047	1.065	-18.0	79.9
Temperature differential	1.074	1.076	-5.2	2.9	1.017	1.019	-6.1	8.4

Notes: Estimates are made from coefficients calculated after adjusting for the warmth of the recent climate. Response functions opening upward were ignored. Y_0 = predicted values at $X = 0$; Y_v = predicted value at the vertex; X_1 and X_2 are the x -axis coordinates of the intersection of the response function and the lower confidence interval ($\alpha = 0.05$) of Y_v ; units for the x -axis coordinates are in Table 4.

and, therefore, the null transfer seems appropriate to *ssp. latifolia* throughout the province.

Like the results of this study, the works of Schmidting (1994) and Carter (1996) also show that the null transfer for 11 species in eastern North America is not always associated with optimal growth. While productivity of *Pinus taeda* L. and *Abies balsamea* (L.) Mill. apparently would benefit from transfers of about +4°C along gradients in the mean minimum temperature, that of *Acer rubrum* L. could be optimized from transfers of -5°C along the same gradients. Likewise, the growth and productivity of *Fraxinus americana* L. would be enhanced by the northward transfer of populations (Roberds et al. 1990, Carter 1996), but that of *Pinus sylvestris* would be increased by southward transfers (Persson 1994). It is plausible, therefore, for the null transfer to be appropriate for *ssp. latifolia*, but not for *ssp. contorta*.

The statistics produced by the general transfer functions also are suitable for estimating the breadth of a

population's realized niche. According to Table 11, there is a 95% certainty that populations of *ssp. latifolia* are genetically different if they inhabit environments differing by as much as 3.2°C in mean annual temperature or by 6.7°C in the mean temperature in either the warmest or coldest month. These estimates, however, are based on levels of probability designed to reduce type I errors, concluding that differences are real when they are not. For estimating the size of a population's realized niche, the type II errors, accepting no differences when they actually exist, are equally serious. An arbitrary approach, used frequently by two of the present authors (see, for example, Rehfeldt [1989a] or Ying et al. [1989]) for making practical decisions while accommodating both types of errors, simply involves using a higher level of probability ($\alpha = 0.2$) for accepting differentiation. Resulting statistics thus provide an environmental interval beyond which genetic differentiation is reasonably certain, but within which differentiation is largely absent.

TABLE 12. Statistics (see Fig. 12) produced from the general transfer functions that predict height or survival (percentage of the plantation mean) of *ssp. contorta* from the distance along 10 environmental gradients over which populations were transferred from their provenance to the planting site.

Climate variable	Height				Survival			
	Y_0	Y_v	X_1	X_2	Y_0	Y_v	X_1	X_2
Annual temperature	0.661	0.661	-2.9	3.2	1.041	1.046	-4.0	2.4
Cold month temperature	0.616	0.632	-8.4	2.1	1.111	1.139	-8.7	2.3
Warm month temperature	0.591	0.668	-1.0	16.5
Annual precipitation	1.163	1.287*	-1079.5	-29.1
Summer precipitation	0.052	1.075*	-787.4	-405.5	1.612	1.614	-170.3	204.8
Days without frost	0.818	0.854	-31.1	128.8
Frost-free period	0.697	0.700	-73.2	51.3
Annual heat:moisture index	0.505	0.616*	6.5	50.5
Summer heat:moisture index	0.440	0.626*	22.8	90.9	1.212	1.216	-21.5	13.0
Temperature differential	0.554	0.570	-3.1	10.0	1.142	1.163	-2.3	7.7

Notes: Estimates are made from coefficients calculated after adjusting for the warmth of the recent climate. Response functions opening upward were ignored. Y_0 = predicted value at $X = 0$; Y_v = predicted value at the vertex; X_1 and X_2 are the x -axis coordinates of the intersection of the response function and the lower confidence interval of Y_v ; units for the x -axis coordinates are in Table 4.

* Y_0 significantly ($P = 0.05$) different from Y_v .

TABLE 13. Values of the x -axis coordinates of the intersection of the general transfer function with the lower confidence interval of the vertex (X_1 and X_2 , Fig. 12) for ssp. *latifolia* calculated from confidence intervals about Y_v at $\alpha = 0.2$.

Climate variable	20-yr height		Survival	
	X_1	X_2	X_1	X_2
Annual temperature	-1.2	1.2	-4.0	2.4
Cold month temperature	-2.1	3.2	-7.0	4.4
Warm month temperature	-4.4	0.8	-4.0	4.2
Annual precipitation	-150.5	740.5	-646.3	303.2
Summer precipitation	-31.6	313.6
Days without frost	-20.1	18.7	-50.7	24.9
Frost-free period	-31.0	17.6	-48.2	33.5
Annual heat:moisture index	-27.1	4.6	-13.5	23.2
Summer heat:moisture index	-42.7	9.0	-8.8	70.7
Temperature differential	-4.5	2.2	-4.8	7.1

Note: Units are listed in Table 4. Calculations could not be performed for response functions opening upward.

Recalculating X_1 and X_2 (Fig. 12) for ssp. *latifolia* using $\alpha = 0.2$ for the confidence intervals of Y_v produced, for example, environmental intervals ($X_2 - X_1$) of 2.5°C for mean annual temperature, 5.3°C for the mean temperature in both the warmest and coldest months, 891 mm in mean annual precipitation, and 38 d in the number of nights without frost (Table 13). Note that the intervals between X_1 and X_2 include the null transfer regardless of whether $\alpha = 0.05$ (Table 11) or $\alpha = 0.2$ (Table 13). To us, the values in Table 13 represent a reasonable estimate of the realized niche for populations of ssp. *latifolia* in British Columbia. Meaningful estimates of niche size for ssp. *contorta* were precluded by an array of test sites that incompletely represented the ecological distribution of this subspecies.

Applications

Changing climates.—The population response functions (Figs. 8 and 9) were used to predict the height of the 105 populations for which functions were available;

19 of these populations had no survival functions. Percentile rankings, according to the predicted 20-yr heights of selected populations, are given in Table 14 for three locations, all of which are for an elevation of 1200 m. This elevation would be at or near the upper altitudinal distribution of *P. contorta* in northern British Columbia, but would be at the lower altitudinal distribution in the south. Table 14 lists only those populations that occurred in the upper fifth percentile for any of the climatic regimes. Rankings are shown for the current climate ($\Delta T = 0$), the current climate augmented by an increase in the mean annual temperature by 3°C ($\Delta T = 3$), and $\Delta T = 5$. In altering the climate by increasing the mean annual temperature, climate variables other than precipitation were changed according to the relationships in Appendix Table A1.

Populations expected to be in the upper fifth percentile for 20-yr height at the central site (Table 14) in the current climate are all ssp. *latifolia* that are geographically proximal to the site, but from elevations that are slightly lower than the site itself (600–1100

TABLE 14. Percentile rankings according to 20-yr height of selected populations predicted for three locations and three levels of change (ΔT) in the contemporary mean annual temperature. Only those populations that occur in the upper fifth percentile (top 5%) for any of the temperature regimes are listed.

Southeast†				Central‡				Northwest§			
ΔT				ΔT				ΔT			
Population	0	+3	+5	Population	0	+3	+5	Population	0	+3	+5
46	5	10	10	65	5	10	25	59	5	50	70
57	5	10	15	24	5	15	40	28	5	10	40
14	5	5	10	25	5	40	70	106	5	10	50
42	5	5	5	62	5	10	15	66	5	30	45
72	5	5	5	106	5	40	50	35	5	30	50
63	10	5	5	105	10	5	10	24	15	5	10
147	10	5	5	44	15	5	25	25	15	5	30
15	10	10	5	17	20	5	15	142	20	5	20
				101	50	5	15	62	10	5	5
				72	80	5	5	65	10	5	5
				14	35	20	5	44	30	15	5
				147	50	10	5	1	40	15	5
				63	45	35	5	17	40	15	5
				46	70	35	5				

† LT = 50°, LN = 117°, EL = 1200 m.

‡ LT = 55°, LN = 124°, EL = 1200 m.

§ LT = 59°, LN = 131°, EL = 1200 m.

m). In a climate that warms by 3°C, however, a completely different array is expected to compose the upper fifth percentile. The new array consists of populations from either (1) low elevations (~600 m) near the site, or (2) southern latitudes (50°–52° N) and slightly lower elevations (600–900 m). In a climate that warms by 5°C, the array expected for the upper percentile is composed of southern populations, two of which (numbers 120 and 147) are from the United States with a third being *ssp. contorta* (number 83). The response functions also predict that if the genotypes best suited to each temperature scenario actually occupy the site, growth of *P. contorta* will be maintained at levels typical of the species in the contemporary environment; survival, however, should decrease by ~25%.

Of the populations expected to compose the upper fifth percentile at the southeastern site in the contemporary climate, number 42 is geographically proximal to the site, but the remainder are from moderate elevations (~1000 m) in south central locations. In the southeast, an increase in the mean annual temperature of either 3°C or 5°C is not expected to alter greatly the array of populations in the upper fifth percentile. Rather than reflecting a broad adaptability of southern populations, however, these projections more likely result from either or both of the following: (1) a deterioration of the physical environment suitable to *P. contorta*, and (2) few populations in the Illingworth tests from low elevations in warm climates. Environmental deterioration, for instance, may be reflected in a 10% reduction in growth and survival at $\Delta T = 3$ and $\Delta T = 5$, even if the most appropriate genotypes are actually present at the site. In fact, at $\Delta T = 5$, the lowest elevations supporting *P. contorta* are expected to be at 1000 m, which is only 200 m below the targeted site. The possibility that unsampled populations suitable to warm climates may exist to the south is suggested by the occurrence in the upper fifth percentile at $\Delta T = 3$ and $\Delta T = 5$ of population number 147, originating from an elevation of 1000 m in the interior west of the United States (LT = 48.75° N, LN = 116.5° W).

At the northwestern site (Table 14), three of the populations expected in the upper fifth percentile for the contemporary climate (numbers 28, 35, and 66) originate in the north, while the remaining two are from moderately high elevations (~1150 m) from south central regions. In a warming climate, the composition of the upper fifth percentile is expected to change greatly. At $\Delta T = 3$, populations from low elevations (700–900 m) at middle latitudes (53–56° N) are represented in the new array, while at $\Delta T = 5$, the shift is to populations from even farther south (49–53° N). Productivity in the north, unlike that in the central and southern locations, is projected to increase by ~40% if the best suited genotypes actually occur at the appropriate sites. Survival, however, is expected to decline by ~25% at both $\Delta T = 3$ and $\Delta T = 5$.

Models that predict response to a changing climate

readily accommodate forecasts of global warming as predicted by the various general circulation models. Of the models, the United Kingdom model (UKMO) of Wilson and Mitchell (1987) tends to predict the largest effects (see Cooter et al. 1993) and, therefore, was used herein to illustrate possible intraspecific responses. According to UKMO, British Columbia can expect an increase in mean annual temperature of ~6°C south of LT = 58° N, but, within latitudes of 58–60° N, temperatures should additionally increase by ~1°C per degree of latitude. Although precipitation should remain relatively constant, ratios of temperature to precipitation should increase markedly. For the present, we are ignoring possible effects of elevated CO₂ on growth and productivity, which could be as large as 5% for *P. contorta* (Higginbotham et al. 1985).

Effects of climate change according to UKMO can be addressed as either transitory effects on the current forest, or long-term effects on the forest composition, growth, and productivity of future generations. In Table 15, predicted height and survival are presented for (1) populations in the upper fifth percentile for height in contemporary environments, (2) the same populations as if they had grown in the climate predicted by UKMO, and (3) the populations expected to be in the upper fifth percentile after global warming. In comparison with the first of these estimates, the second reflects transient effects, and the third predicts long-term effects.

For the southeastern location, the response functions predict that the populations most suitable for the lowest elevations (<1000 m) in the contemporary environment will not survive global warming (Table 15). For these low elevations, the climate is expected to shift outside the range of conditions (Table 4) under which the species occurs in British Columbia today. Whether populations exist to the south that are capable of inhabiting these climates is problematic. For elevations >1000 m, the effects of global warming would depend on the array of genotypes that might inhabit the site. If the populations that are best suited for the contemporary climate continue to occupy these sites after climate change, the 20-yr height at 1300 m is expected to drop by 33%, while that at 1600 m would be expected to decline by 11%; survival would be expected to decrease by 30–40%. However, if the genotypes best suited to the new climates occupy the sites, 20-yr height at 1300 m should be reduced by 20% from that of today, while that at 1600 m would remain about the same; survival, however, is still expected to decline by 30–40%.

Projections for the central location show large reductions in 20-yr height (30–55%, depending on elevation) and concomitant losses in survival (8–25%), if the populations most suitable for contemporary environments would occupy their present locations after global warming. If the populations best suited to the future climates actually occur on the appropriate sites, growth and productivity should remain about the same

TABLE 15. Predicted 20-yr height (m) and percentage survival of populations expected to be in the upper fifth percentile (top 5%) at 12 locations.

Location	UKMO projected climate					
	Current climate		Top 5% in current climate		Top 5% in future climate	
	Height	Survival	Height	Survival	Height	Survival
Southeast, 700 m	8.74	69	...	0	...	0
Southeast, 1000 m	8.89	73	...	0	...	0
Southeast, 1300 m	8.77	85	5.84	45	6.96	47
Southeast, 1600 m	7.66	91	6.85	60	7.56	63
Central, 700 m	8.49	89	5.73	78	7.37	64
Central, 1000 m	7.74	94	3.45	86	7.66	71
Central, 1300 m	7.16	75	3.35	52	7.03	53
Central, 1600 m	...	0	...	0	7.08	49
Northwest, 700 m	7.82	71	6.96	82	7.95	52
Northwest, 1000 m	6.22	69	5.82	83	7.61	67
Northwest, 1300 m	...	0	...	0	6.49	61
Northwest, 1600 m	...	0	...	0	...	0

Notes: Projections are made for both the contemporary environments and future environments, corresponding to the predictions of the UKMO model of global climate change (Wilson and Mitchell 1987). Southeast, central, and northwest are defined in Table 14.

as in the contemporary climate; survival, however, is expected to decrease by ~20%. Largely because of the entry of high elevation sites (≤ 1700 m) into the land base climatically suitable for *P. contorta*, future productivity in the central portion of the province could increase. However, whether the altitudinal distribution could expand depends on edaphic factors, which are supplemental to climate and genes.

At the northwestern location, global climate change should have the least impact on the existing forests, largely because northern populations currently occupy environments that are much colder than their optima (Fig. 10). Thus, global warming is expected to reduce the 20-yr height of populations best suited to the contemporary environment by $\leq 10\%$ while increasing survival by ~12%. If the genotypes best suited to the changed conditions inhabit the appropriate sites, height at elevations < 1000 m is expected to increase up to 20%. Still, concomitant reductions in survival could be as high as 20% at the lowest elevations. Table 15 also suggests the possibility of a shift in the species' upper altitudinal limits.

These results show that a changing climate will have dramatic effects on growth and productivity of the *P. contorta* forests of British Columbia. The effects originate with population-specific responses that are keyed to different climatic optima. As a result, shifts in climate produce a change in the array of genotypes that are best suited for a given location.

Reforestation.—For *P. contorta*, a genetic structure in which variability is maintained within populations, despite pronounced differentiation of populations, produces the realized niches estimated (Table 13) for ssp. *latifolia* populations by the interval between X_1 and X_2 (Fig. 12). Using $\pm(X_2 - X_1)/2$ as a confidence interval for a target location provides an environmental interval across which genetic differences among populations

are a reasonable possibility, but within which differentiation is largely absent.

When the climate intervals associated with the realized niches of Table 13 were converted into geographic units, the calculations showed that, for the southeast, populations from near the valley floor (EL < 1000 m) must be separated by only ~280 m of elevation before one is reasonably certain of genetic differentiation, but, at EL > 1400 m, populations must be separated by ~450 m. In the central portion of the province, the altitudinal interval associated with differentiation varies between 400–560 m depending on the target elevation, while, in the north, where the altitudinal distribution of the species encompasses only ~600 m, elevation becomes inconsequential to genetic differentiation. Similar calculations showed the latitudinal intervals to range 2.1–3.0° (depending on LN and EL), while longitudinal intervals were ~8° in the south but only 7° in the north.

These results suggest that, for reasonable assurance of genetic differentiation, populations in the same mountain range must be separated by ≥ 300 m of elevation, or populations from the same elevation must be separated by $\geq 2^\circ$ of latitude and 7° of longitude. A conservative estimate of the size of a tract of land, within which little or no differentiation is expected but across which differentiation is likely, is ~250 km of latitudinal distance by 400 km of longitudinal distance (~100 000 km²). The tract would include ~300 m of elevation for the mild environments in the south; 400 m for both the middle latitudes and for the high altitudes in the south; and ~500 m in the north.

Practical recommendations from these estimates might be that seeds of ssp. *latifolia* produced in natural populations should be transferred from their origin $\pm 1^\circ$ of latitude, $\pm 3.5^\circ$ of longitude, or ± 150 m of elevation, if elevations are low and in the south; ± 200 m of el-

evation at either middle latitudes or high elevations in the south; or ± 250 m of elevation in the north. If managers chose to develop discrete zones that best account for the continuous genetic variation, the zones should be similar in size to the tract estimated above. These recommendations are remarkably similar in direction, but somewhat broader in extent, than those produced from models employing physiographic descriptors of genetic variation for contiguous areas in the interior west of the United States (Rehfeldt 1983, 1987, 1988) and for British Columbia itself (Ying et al. 1985, Ying et al. 1989, Ying 1991).

At the very least, patterns of genetic variation described by the climate models provide the ecologic basis for the guidelines currently in use. However, models with physiographic predictors apply to static climates, while those using climatic predictors can accommodate a variable climate. If the mean annual temperature were to increase merely by 1°C, reforestation guidelines should shift. Calculations similar to those made here show that, instead of transfers that are symmetrical about a target's location, the appropriate transfer would be from 0.2° south to 2.1° north, from 6° east to 1.5° west, and from 40 m downward to 360 m upward (depending on LT and LN of the target).

DISCUSSION

The results demonstrated the effective use of polynomial models to describe general patterns of variation in the climate across a large and diverse geographic region. The models were used to develop climate response functions for individual populations of *P. contorta* that predicted the 20-yr height or survival of populations. Consistent with the abundant previous studies of genetic variation in this species, the response functions showed that different populations achieved maximal growth and survival in much different climates.

In relating genetic differentiation to climatic gradients, it is tempting to compare the relative effectiveness of climate variables in describing differentiation. In the case of the Illingworth tests, however, the fact that each population was not tested in all environments tends to confound such comparisons. Still, Tables 6 and 10 demonstrate consistently strong effects for only a few of the climate variables. Judging by R^2 and the number (N) of populations for which a climate variable was an effective predictor of response, the best predictors of 20-yr height are the strongly intercorrelated set (Table 1) of the mean annual temperature, mean temperature in the coldest month, and the temperature differential. For survival, the heat:moisture indices and the temperature differential seemed to be the best predictors.

The response functions are based on correlations between field performance and predicted climates. Causal mechanisms, therefore, undoubtedly have been obscured by both the errors of prediction and an imprecise knowledge of how climate interacts with physiology to control responses. Strong validations notwithstand-

ing, predictions beyond the range of the data therefore become tenuous (Loehle and LeBlanc 1996). In fact, bias resulting from extrapolation with our correlative models could have been responsible for the weaker validations of response functions for data from the ecologically extreme site at Terraced Peak (Table 7) than from Red Rock (Table 6). Nevertheless, in our applications of these functions, some extrapolation was required. For the validity of such projections, it is fortunate that the Illingworth test sites (1) spanned about one-half of the environmental heterogeneity encountered in British Columbia by *P. contorta* as a whole and ~65% for ssp. *latifolia* (Table 4), (2) encompassed the fundamental niche of many populations, and (3) presented one or more sites in climates sufficiently extreme to anchor a tail of the symmetrical response functions of many other populations close to the x-axis (Fig. 9). As a result, extrapolation to climates not represented in the Illingworth program became feasible. Compare, for instance, the functions for Larch Hills and Finlay Forks (Fig. 9C and F, respectively), which are poorly suited for extrapolation, to those of the other functions in the figure.

Distribution of populations

This study, along with numerous previous studies of genetic variation in *P. contorta*, shows that the remarkably broad ecological amplitude of this species (Table 4) results from genetic variation among and within subspecies that tends to be continuously distributed across the landscape. The species and its subspecies, therefore, are composed of numerous populations (Ying et al. 1985, Rehfeldt 1988, Ying 1991, Ying and Liang 1994), each of which is adapted to only a portion of the environmental conditions across which the species is distributed (Fig. 9). Continuous variation among populations reflects small changes in allele frequencies across the environmental gradients (Wheeler and Guries 1982a, 1982b, Yeh et al. 1985).

Nevertheless, despite rampant population differentiation, 20 yr of field performance on an environmentally disparate array of test sites have demonstrated that the adaptability of individuals and the populations they compose is high. This high adaptability is an expression of an extremely broad fundamental niche (Figs. 7, 9, 11, and 12, Table 11) that may approach 10°C in mean annual temperature. Our view of the fundamental niche, however, is based on the performance of planted trees. Planting circumvents the rigors of the first growing season when seedlings are the most vulnerable to environmental effects (see Campbell 1979). Even though an estimate of the breadth of the fundamental niche provided by this study is probably inflated, a niche that even approaches 10°C in mean annual temperature attests to either or both a remarkably high plasticity of individuals (see Bradshaw 1965, Spitze and Sadler 1996) and high genetic variances within populations (Rehfeldt 1985, Xie and Ying 1995).

The present results unquestionably demonstrated (Fig. 9) differential adaptation of populations to climate, and the differences among populations seemed to conform to genecological principles. Thus, populations inhabiting cold climates tended to be slow growing and tended to achieve their optimal growth and survival under colder temperature regimes than fast growing populations from mild climates. These results, coupled with repeated documentation of steep clines in *P. contorta*, led toward the expectation that natural populations would occur in those environments optimal for their growth and survival. To the contrary, our results showed that native populations of *ssp. latifolia* tend to be found in environments that are cooler than their optimum for growth and drier than their optimum for survival (Table 8). The discrepancy between the inhabited and optimal environments, moreover, was more pronounced for northern populations than for southern (Fig. 10). For *ssp. contorta*, the inhabited environment tends to be warmer, wetter, and more maritime (Table 9) than the optimal as expressed on inland sites.

Despite these findings, the general transfer functions suggested that the optimal growth and survival of *P. contorta* as a whole are achieved by accepting the null transfer. Carter (1996) also observed little difference between predicted performance at the vertex of the transfer function and that for the null transfer (Y_v vs. Y_0 ; Fig. 12), and from this concluded that the adaptation of natural populations was optimal. For us, such a conclusion is incompatible with our demonstration that native populations of *P. contorta* tend to occupy suboptimal environments. Understanding the environmental bases governing the dispersion of genotypes across the landscape requires accommodating these seemingly anomalous results.

To this end, a consideration of the joint effects of environmental selection and density-dependent selection is appropriate. Fig. 9A shows that genotypes from the northern population of Muncho Lake have a cooler temperature optimum than Udy Creek genotypes, which originate in a much milder environment to the south. The figure also illustrates the well-known negative relationship between innate growth potential (Y_v) and cold tolerance for terrestrial plants in general (see Brown and Gibson 1983) and for *P. contorta* in particular (Rehfeldt 1980, 1983, 1987, 1989b). Despite their adaptive differences, genotypes from both the Muncho Lake and Udy Creek populations grow (and survive) nicely in environments with a mean annual temperature of $\sim 2^\circ\text{C}$ (Fig. 9A), the temperature associated with the optimal growth of the Muncho Lake population. However, even though the same environment is suboptimal for the Udy Creek population, genotypes from Udy Creek would be expected to be ~ 1.5 m taller after 20 yr than those from Muncho Lake (Fig. 9A). Because 1.5 m at age 20 is not trivial, there is little doubt that in a mixed planting, density-

dependent selection would favor Udy Creek genotypes even though the climate is the optimum for the Muncho Lake population. In fact, Fig. 9A shows that in only those environments with mean annual temperature $<0.5^\circ\text{C}$ would genotypes from Muncho Lake be taller than those from Udy Creek and thereby survive self thinning. Density-dependent selection would relegate Muncho Lake genotypes to suboptimal environments.

Our results thus suggest that environmental selection establishes a broad fundamental niche from which density-dependent selection, self thinning, and competitive exclusion carve out a realized niche spanning only $\sim 2.5^\circ\text{C}$ in mean annual temperature (Table 13). Consistent with the processes described by Arthur (1987), adaptation and competition, the factors thought to control the distribution of species (Miller 1967, Brown and Gibson 1983, Loehle and LeBlanc 1996), apparently control the distribution of individuals, populations, and subspecies within *P. contorta*. The views of Brown and Gibson (1983) seem particularly appropriate: "... in gradients of physical stress such as increasing cold, aridity, or soil salinity, terrestrial plants that are adapted to tolerate the harsh conditions typically have slow growth rates so that they are competitively excluded from more equitable environments by faster growing species."

An explanation of our results that includes density-dependent selection is particularly suited to *P. contorta*, a species in which profuse reproduction after disturbance typically results in many thousands (e.g., 500 000) of seedlings per hectare (Tackle 1959) that will be reduced to as few as 1000/ha by age 80 yr (Tackle 1959, Benson 1982, Vyse and Navratil 1985). As populations undergo self thinning, the shape and position of the response functions should change with regard to the environmental gradient. In a mixed planting, competitive exclusion will force the vertices of the response functions for populations such as Muncho Lake to shift toward the suboptimal conditions under which native populations occur. In time, the curves should become narrower as the difference between the roots (values of X when $Y = 0$) decrease and thereby obscure the breadth of the fundamental niche. In a mixed planting at advanced ages, therefore, researchers quite likely would observe a smaller fundamental niche, a smaller realized niche, less disparity between the fundamental and realized niches, and a smaller difference between the optimum environment and the inhabited environment than are shown by the present analyses. Because the Illingworth tests have begun self thinning only recently in only the fastest growing plantations, age 20 yr was ideal for assessing optimality and niche breadth.

Fig. 13 graphically illustrates the view provided by the Illingworth tests of the joint effects of environmental selection and density-dependent selection on the growth or survival of *P. contorta* populations. The response (height or survival) of populations along an

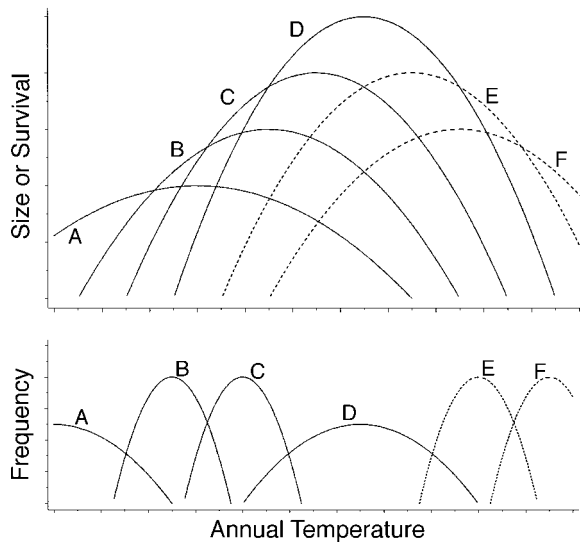


FIG. 13. Diagrammatical representation of the response of populations (fundamental niche) to gradients in the mean annual temperature (top), and the frequency of occurrence (realized niche) of populations across the same gradient (bottom).

environmental gradient is diagrammed at the top of this figure, and the frequency with which those populations occur along the same environmental gradient is on the bottom. An integral component of this view is the opposing clines in growth potential and cold hardness that are basic to the genetic structure of the species.

According to this view, a broad fundamental niche is defined for each population by environmental selection that promotes adaptation of populations to a heterogeneous environment. Populations, therefore, have a fundamental niche that encompasses only a portion of the environmental gradient occupied by the species. Density-dependent selection during the processes of self thinning then carves out a realized niche from that portion of the fundamental niche where a population is competitively exclusive. Because populations adapted to more equitable climates will have a higher growth potential, most populations are competitively excluded from their ecologic optimum. The realized niche, therefore, tends to be suboptimal, occurring for *ssp. latifolia* populations in environments that are colder than the optima and for *ssp. contorta* populations in environments that are more maritime than their optima. By illustrating the losses in growth that would occur if each population actually inhabited the ecologic optima, Fig. 13 also shows why optimal productivity occurs under the null transfer. As applied to populations within species, Fig. 13 reconciles the philosophical arguments among Ellenberg (1953), Ernst (1978), and Austin (1982) pertaining to possible discrepancies between ecological and physiological optima of plant species: populations do indeed occupy suboptimal environments. Our results and their interpretation thus support the belief of Harper (1964) that the reaction of plants

to their neighbors is one of the most critical elements of autecology.

Exceptions to this general view (Fig. 13) are expected on three fronts. First, the natural system is subject to sampling errors. As a result of the contingencies of evolutionary history, bottlenecks in population size, founder effects, vagaries of pollination ecology and cone production, or shifting environmental gradients, the most appropriate genotypes may not be available when a site is colonized. Consequently, the degree of suboptimality is variable (Fig. 10).

A second exception would involve populations such as D, which comprise genotypes with the highest innate growth potentials (Fig. 13). Like all populations, D would have a broad fundamental niche. Population D, however, also would have a broad realized niche arising from the competitive advantage provided by its innate growth potential; it would be the D genotypes that competitively exclude B and E from their optima and relegate them to suboptimal conditions. D genotypes, therefore, initiate the cascading effects of competitive exclusion that relegate other populations to suboptimal environments. Population D thus would have a realized niche that encompasses a higher proportion of its fundamental niche than populations peripheral to it. The distribution of D genotypes, moreover, should be symmetrical about the ecologic optimum, and for D, therefore, there should be little difference between the inhabited and optimal environments (Fig. 10). In forest management, incidentally, sites inhabited by D become earmarked as those on which a species reaches its best growth and productivity (highest site index). As shown for *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco (Monserud and Rehfeldt 1990) and illustrated in Fig. 13, site index is as much a genetic response as it is an attribute of the site. Without D genotypes, highest site indices would be associated with vertex of either C or E.

A third exception would involve populations at the margin of a species' distribution. Population A (Fig. 13), for instance, would comprise the species' most cold-hardy genotypes. Because of this, no other *P. contorta* genotypes could exclude A in environments of increasing coldness. The actual limits of A's distribution and, therefore, that of the species would occur where either (1) environmental conditions exceed the plasticity of individuals, or (2) genotypes of other species are competitively exclusive. To the extent that the limits of distribution are not controlled through competitive exclusion by other species, A genotypes, for much different reasons than D, would also have a realized niche that encompasses a relatively high proportion of its fundamental niche. This broad realized niche of marginal populations provides at least a partial explanation of why genetic diversity in marginal populations of *P. contorta* is somewhat reduced, but certainly not impoverished (Yeh and Layton 1979). However, because of an inflated realized niche that is skewed away from the ecologic optimum, genotypes

within peripheral populations, such as A, exhibit a discrepancy (Fig. 10) between the ecologic optima and inhabited environment that is larger than for populations toward the center of the distribution (B or C). Because this discrepancy is strongly related to latitude, but not to altitude, it would also appear that the upper altitudinal distribution of *P. contorta* is determined primarily by competitive exclusion by other species, while the northern limits reflect a lack of appropriate genetic variability.

Although Fig. 13 accounts for the present results within the framework of the genetic structure of the species, the natural forces that would interact to maintain such a system are not intuitively obvious. On the one hand, the suboptimality of natural populations is readily accommodated in the concepts of adaptational lags (Mátyás and Yeatman 1992), migrational lags (Davis and Botkin 1985), or vegetation inertia (Smith 1965, Pielou 1991). These concepts become an attractive explanation of the greater discrepancy in the north between the inhabited and optimal environments than in the south (Fig. 10) when considered in light of post-glacial migrations: *P. contorta* has been present in southeast British Columbia for nearly 12 000 yr (MacDonald and Cwynar 1991) but has arrived near the northern terminus of its current range within the last 500 yr (MacDonald and Cwynar 1985). These concepts, however, deal with transitory effects that can be overcome in a few generations. If suboptimality were transient and readily overcome, the vertices of the general transfer functions should have counterbalanced the degree of suboptimality (Tables 8 and 9). Because the null transfer was associated with optimal growth and survival, neither adaptational lags, migrational lags, nor vegetation inertia satisfactorily account for our results.

Accounting for the maintenance and perpetuation of the system illustrated in Fig. 13 requires a consideration of gene flow. Particularly appropriate are recent theoretical arguments (Garcia-Ramos and Kirkpatrick 1997, Kirkpatrick and Barton 1997) developed from models of gene flow in continuously distributed species exhibiting clinal variation in adaptive traits. In short, simulations showed that asymmetric gene flow from the center of distribution toward the periphery can prevent peripheral populations from evolving to their ecologic optima. In the view of these modelers, decreasing population densities toward the periphery leads to asymmetry. In forest trees, such effects would be accentuated by the temperature dependence of phenologic events that include the maturation of both male and female strobili. Gene flow, therefore, can become decidedly skewed along both temperature and density gradients.

For *ssp. latifolia*, asymmetric gene flow from equitable climates would produce in each population an array of seeds with genotypic distributions skewed toward greater growth potential and warmer temperature

optima than those of the parental generation. Asymmetric gene flow, therefore, readily accounts for the discrepancies between the inhabited environment and the ecologic optima (Fig. 10). Southern British Columbia is proximal to the center of the subspecies' distribution where gene flow is relatively symmetrical, and, therefore, populations tend to occupy environments that approach their ecological optima. Toward the periphery, however, gene flow becomes increasingly asymmetric, causing the discrepancy between the inhabited environment and the ecologic optima to increase. At the periphery, strongly asymmetric gene flow stymies microevolution, forces the terminus of the range, and maintains populations that are poorly adapted to the conditions they inhabit (Kirkpatrick and Barton 1997). The distribution of genotypes across the landscape (Fig. 13), therefore, can be viewed as being regulated primarily by asymmetric gene flow, which provides the fuel for environmental and density-dependent selection and thereby is indirectly responsible for suboptimality.

Even though Fig. 13 accounts for the statistics in Table 12 and is supported by theoretical arguments, the view we have of the relationship between the subspecies of *P. contorta* is based on survival of *ssp. contorta* populations at inland sites. Therefore, Fig. 13 quite likely is too simplistic. Indeed, contrary to the implications of the figure, in maritime environments populations of *ssp. contorta* attain 20-yr heights of 10 m (Ying and Liang 1994), thereby approaching the maxima for *ssp. latifolia* populations on inland sites (Figs. 8C and 9A). Consequently, niche space for populations of *ssp. contorta* quite likely is oriented along a vector oblique to the temperature gradient of Fig. 13. The performance of populations in response to multiple climate vectors could then be illustrated with bubbles of different height, half-submerged in a two-dimensional environmental grid. Fig. 13 then would represent a slice along only one dimension of the grid. Unfortunately, data have not yet been assembled for evaluating the climatic control of population distributions in *ssp. contorta*.

A distribution of populations as illustrated in Fig. 13 accounts for seemingly inexplicably disparate results between studies of genetic variation (genecological studies) and studies of adaptability (performance trials). Genetic variation among natural populations of *P. contorta* (Rehfeldt 1988, Xie and Ying 1995), like those in *Pseudotsuga menziesii* (Mirb.) Franco (Campbell 1979, Campbell and Sorensen 1978), has been described by relatively steep clines along geographic and physiographic gradients. Steep clines tend to prompt the conclusion that environmental selection is responsible for the clines and that adaptation is closely linked to the environment. Because emphasis is placed on detecting differentiation of populations, genetic variation is being studied in reference to the realized niche (Fig. 13, bottom), and the performance of a population is

considered relative to that of all other populations. For our data, therefore, a genecological assessment would detect genetic differences among populations located at $\sim 2.5^\circ\text{C}$ intervals along a gradient in the mean annual temperature. However, when adaptability and productivity are studied in natural environments, the performance across the fundamental niche (Fig. 13, top) is ordinarily assessed. Thus, analyses of *P. contorta* populations introduced to Scandinavia (Lindgren et al. 1993) and *Pseudotsuga menziesii* families widely planted in northwestern United States (Stonecypher et al. 1996) demonstrated a high adaptability to a broad range of climates that seemed (1) incongruous with the steep clines noted in genecological tests but (2) compatible with a broad fundamental niche. As illustrated in Fig. 13, those studying adaptability in terms of the fundamental niche receive a much different impression of ecological adaptation and microevolution than those studying genecology in reference to the realized niche.

Using niche theory to account for the ecologic distribution of populations within species is well supported by theoretical arguments describing the distribution of species (see Hutchinson 1958, Miller 1967, Brown and Gibson 1983, Loehle and LeBlanc 1996). Indeed, Arthur (1987) emphasized the parallels between interspecific competition and intergenotypic competition. The implications are direct for paleoecologists, ecophysiologicals, and plant geographers who interpret plant responses in relation to environmental gradients. Contrary to the views of many (see Huntley 1991), adjusting to temporal and spatial environmental heterogeneity in either static or changing climates deals as much or more with microevolution within populations as migration of populations. The fundamental force driving plant responses to the environment is the intraspecific interaction of genes and environment.

Climate change

Using the response functions to predict the effects of a changing climate on growth and productivity of *P. contorta* demonstrates that even small shifts in temperature will have widespread effects. Because the effects of global climate change are magnifications of effects caused by small climatic fluctuations, our discussion will concentrate on the former.

Together, Tables 14 and 15 illustrate disastrous impacts of the United Kingdom model's (UKMO) version of global warming on the current generation. As the climate warms, maladaptation increases (Y_0 becomes more distant from Y_v ; Fig. 12), and, as a result, 20-yr height and survival are expected to decline 10–55%. The impact, however, should be related to latitude. In the south, where the discrepancy between the inhabited and optimal environments is the least, the adverse effects of a warming climate will be the greatest. The smallest losses should occur in the north where contemporary populations are occupying climates much colder than their optima (Fig. 10). However, the degree

to which these predictions are applicable depends in part on the assortment of genotypes represented in the Illingworth tests. It is reassuring that others who have considered the genetic consequences of global warming have produced complementary results with a variety of species and methods. Mátyás (1994), for instance, projected 20% loss in the growth of *Pinus banksiana* Lamb. near its southern limits of distribution, and Beuker (1994) estimated gains in productivity in *Picea abies* L. Karst and *Pinus sylvestris* at latitudes north of 60° N. For species in eastern North America, Schmidting (1994) and Carter (1996) together demonstrated adverse effects of global warming on the growth and productivity of 11 species, while two are expected to have increased productivity.

Estimated effects of global warming on future productivity suggest that if genotypes and future climates are appropriately matched, growth and productivity of the *P. contorta* forests of British Columbia should increase (Table 15). If the appropriate edaphic requirements can be met, gains in productivity at high latitudes and elevations should overcompensate the losses projected for low elevations in the south. These results thus support the view that the northern temperate and boreal forests should become increasingly important sinks for atmospheric CO_2 (Sedjio 1992). Nevertheless, because the projected gains require genotypes and climates to be appropriately matched, reaping the potential benefits will be challenging.

Once initiated, global climate change is expected to be completed within a century (Wigley and Raper 1992), which can be less than a single generation for *P. contorta*. Adjusting to the change requires a redistribution of genotypes across the landscape (Table 14) in tree species known for exhibiting a delayed response to change (Brubaker 1986). To be sure, the genotypes best suited to future climates in central and northern British Columbia currently exist in the south, and the only natural means by which the appropriate genotypes can occur on northern sites is through either microevolution or migration. This creates the challenge. On the one hand, the outcome of evolutionary processes is problematic, particularly when large environmental changes occur within single generations (see Gerber and Dawson 1993). On the other hand, postglacial migrations of *P. contorta* across British Columbia occurred at a rate of $\sim 1^\circ$ of latitude per 900 yr (MacDonald and Cwynar 1985). Consequently, there seems little doubt that maintaining forest productivity in the face of global warming would require human intervention to assist the migration of genotypes to their most suitable climates. Despite British Columbia's enormous annual planting program of 107.6 million *P. contorta* seedlings (British Columbia Ministry of Forests 1997), the task of assisting migration throughout the province is staggering.

Also alarming is for survival estimates to decline independently of the projections for height, even if

genotypes are matched with the most suitable climates. Thus, Table 15 (as well as the data on which Table 14 is based) suggests that adjusting to either or both the transient and long-term effects of a warming climate will require accepting increased mortality. Three possibilities need to be considered. First, the rankings on which Tables 14 and 15 are based may be too strongly weighted toward growth responses. An index based, for instance, on the product of growth and survival (Marklund 1981) may be more appropriate. Second, increased mortality might result from a climate projected to warm while precipitation remains constant, thus altering the heat:moisture ratios that were influential in predicting survival. Although managers could readily adjust for increased mortality by planting trees at higher densities, the change in these ratios could also mean that conditions were becoming more suitable to species other than *P. contorta*. Third, the increased mortality may indicate that response functions are known for too few populations; genotypes better suited to future climates may exist but are yet to be located or tested. Regardless of the possibilities, it seems clear that maintaining optimal growth and productivity after pronounced shifts in the climate will require extraordinary human effort either to locate and transfer or to develop suitable populations.

Tables 14 and 15 illustrate the wholesale redistribution of genotypes that would have to accompany a warming climate if the productivity of the *P. contorta* forests were to be maintained. The results, therefore, strongly support the need to incorporate into models of vegetal response the ecological genetic principles governing intraspecific variation (Travis and Futuyma 1993). Regardless of their conceptual appeal (Loehle and LeBlanc 1996), process models (i.e., Woodward 1987, Prentice et al. 1992) that attempt to predict the response of individuals from environmental input (Dunham 1993) are faced with a formidable challenge. In fact, the task of accumulating intraspecific estimates of ecophysiological responses is so enormous that the correlative approaches (e.g., Tuhkanen 1980, Tchebakova et al. 1994, Monserud and Tchebakova 1996) appear to be the most feasible, despite their potential bias when used to extrapolate (Loehle and LeBlanc 1996).

Reforestation

Reforestation programs employ seed transfer guidelines to assure that genotypes are planted in the appropriate climates. Transfer functions that use climatic predictors readily demonstrate the climatic bases for the contemporary seed transfer guidelines that employ physiographic descriptors. These same functions represent flexible tools that allow forest managers to adjust guidelines when environmental gradients shift. As discussed in the previous section, moreover, population-specific response functions will be indispensable if artificial reforestation assumes a role in maintaining pro-

ductivity during or after pronounced changes in climate.

While seed transfer guidelines ordinarily are applicable to reforestation from seeds produced by natural populations, much of the future reforestation in British Columbia will involve seedlings that are products of breeding programs. To increase productivity while maintaining adaptedness, these programs attempt to raise the height of the vertex (Y_v) of the general transfer function (Fig. 12) without altering the function's roots (values of X when $Y = 0$). The implications of the present results are threefold. First, potential economic rewards for working with population D (Fig. 13) would be enormous. Genotypes from D are not only among the fastest growing, but also have a much broader realized niche than all but the ecologically marginal populations. Thus, the potential returns from selective breeding within D are unparalleled within a species. Second, the potential economic returns for breeding within populations such as B or C are limited by the small range of environments (i.e., a breadth of 2.5°C in mean annual temperature) within which these genotypes should be planted. Consequently, the cost-effectiveness of programs dealing with these populations will be questionable. Third, gains in productivity from breeding in B or C will be realized only if adaptedness is maintained. If gains in productivity are accompanied by a change in the roots, breeding is merely recombining genetic variability to convert, for instance, C genotypes to those of D. Breeders, therefore, need to be aware of possible inadvertent effects of breeding on adaptive characteristics when working with species in which population differentiation is pronounced.

Our results and their interpretations describe a natural system in which productivity of a species is optimized even though individual populations tend to occur in suboptimal environments (Fig. 13). However, the natural system is imperfect; sampling errors from a variety of sources commonly prevent genotypes from occurring in those environments where they are competitively exclusive. Whether using seeds produced in natural populations or from seed orchards, these sampling errors can be overcome with reforestation programs that rely on response functions to match genotypes to the appropriate climates.

CONCLUSIONS

Twenty-five years ago the British Columbia Forest Service established and has since maintained a comprehensive series of genecological tests of remarkably broad scope. The results of our analyses of 20-yr data have been used to address topics dealing with climatic control of plant distributions, effects of a changing climate, and reforestation.

The present results provide empirical evidence supporting the long-held theoretical argument that competitive exclusion complements environmental selection to control the distribution of genotypes both inter-

and intraspecifically. With asymmetric gene flow providing the fuel, density-dependent selection relegates most populations to suboptimal ecological conditions. As a result, the steep clines noted for species such as *P. contorta* seem to be driven more by density-dependent selection than by environmental selection. Although our results pertain directly to only *P. contorta*, it seems likely that the phenomena are widespread within ecological systems. With such findings, one can hope that the bonds between experimental ecology and evolutionary genetics are strengthened.

Despite the intuitive appeal and consistency of the results, methodological flaws exist, the effects of which, in retrospect, could be alleviated. To others tempted to undertake similar analyses, we offer two suggestions. First, from a climatologist, obtain hand-extrapolated climatic variables for critical locations not served by weather stations. Adding such data to the climate database not only would balance the geographic matrix of weather variables, but also allow climate to be described by multivariate vectors. Second, consider techniques that would force the tails of the response functions toward zero. Although the use of alternative functions might suffice, one might consider incorporating into the database values of zero growth and survival for environments beyond the fundamental niche of the species in the region of study.

The Illingworth program is providing a glimpse of fundamental relationships between plants and their environment. Yet, the rewards from this program are only beginning to accrue. Still to be considered are the implications of these data in evolutionary topics dealing with migration lags and adaptation lags. The tests themselves are ideal for understanding the genetic and environmental control of ecophysiological processes and would be nicely suited for validating process models. The current results have direct implications in managing gene resources to prevent inadvertent deterioration of genetic variability and in designing long-term experiments with forest trees. And finally, data already exist for developing climate response functions describing tolerance of populations to insects and diseases and for predicting growth and survival from a combination of environmental, geographic, and genetic effects. The latter predictions would allow empirical estimates of the effects of forest ecosystems in regulating atmospheric CO₂ in a changing climate. The authors have been privileged to participate in the fruition of this long-term program. Would that there were many more.

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APPENDIX

TABLE A1. Regression equation ($Y = a + b_1X + b_2X^2$) with associated number of observations (N) and goodness of fit (R^2) using mean annual temperature (MAT) and mean annual precipitation (MAP) as independent variables (X) to predict selected climatic variables (Y).

X	Y	N	R^2	a	b_1	b_2
MAT	Cold month temperature	513	0.90**	-16.969	1.9404	0.0
MAT	Warm month temperature†	513	0.38**	13.971	0.2248	1.8672×10^{-2}
MAT	Annual precipitation	509	0.16**	590.621	89.8416	0.0
MAT	Summer precipitation	509	0.03*	277.686	20.5723	-1.8455
MAT	Days without frost‡	465	0.85**	123.977	5.4486	1.3303
MAT	Frost-free period§	503	0.78**	61.717	4.0593	1.1305
MAT	Degree days >5°C	448	0.81**	922.626	53.8443	6.1437
MAP	Annual temperature	509	0.24**	1.674	0.0053	-9.9300×10^{-7}
MAP	Cold month temperature	509	0.42**	-16.258	0.0133	-2.3040×10^{-6}
MAP	Warm month temperature	509	0.04**	16.684	-0.0005	0.0
MAP	Summer precipitation	509	0.76**	151.352	0.0896	3.0133×10^{-5}
MAP	Days without frost	462	0.36**	137.978	0.1085	-1.8827×10^{-5}
MAP	Frost-free period	500	0.36**	64.054	0.0946	-1.6117×10^{-5}

* Significance at $0.05 > P > 0.01$.

** Significance at $P < 0.01$.

† Best-fitting regression is two-staged with Y constrained to 335.006 for $X > 6.5$.

‡ Best-fitting regression is two-staged with Y constrained to 118.401 for $X < -2$.

§ Best-fitting regression is two-staged with Y constrained to 58.073 for $X < -1.8$.

TABLE A2. Equations for predicting seven climate variables for British Columbia locations.

Mean annual temperature = $10.58 - (0.00603058 \times \text{EL}) + (0.00055086 \times \text{LTEL}) - (0.00002252 \times \text{NWEL})$ $- (0.44827860 \times \text{LT}) - (0.12219061 \times \text{LT}^2) + (0.00520826 \times \text{LT}^3) - (1.3 \times 10^{-7} \times \text{NW}^3) + (0.30811835 \times \text{SW})$ $+ (0.00141833 \times \text{NWLN}) - (0.02432959 \times \text{SWLN})$
Mean cold month temperature = $2.44 - (0.01241359 \times \text{EL}) + (3.44 \times 10^{-6} \times \text{EL}^2) + (0.00111278 \times \text{LTEL})$ $- (5.025 \times 10^{-5} \times \text{NWEL}) - (2.47544415 \times \text{LT}) + (0.01985806 \times \text{LN}^2) - (2.3 \times 10^{-7} \times \text{NW}^3)$ $+ (0.00153691 \times \text{NWLN}) - (0.00289851 \times \text{SWLN})$
Mean warm month temperature = $22.65 - (0.00419566 \times \text{EL}) - (9.1 \times 10^{-7} \times \text{EL}^2) + (0.00015534 \times \text{SWEL})$ $- (0.71328117 \times \text{LT}) + (0.00106834 \times \text{LT}^3) + (0.27682377 \times \text{LN}) - (0.02781342 \times \text{LN}^2) + (0.00551017 \times \text{SW}^2)$ $+ (0.00148437 \times \text{NWLN}) - (0.02584067 \times \text{SWLN})$
Mean annual precipitation = $2703.37 - (1.325891 \times \text{EL}) - (0.010659 \times \text{NWEL}) + (0.125826 \times \text{SWEL})$ $+ (0.000229 \times \text{LTEL}^2) - (16.688878 \times \text{LT}^2) - (474.405124 \times \text{LN}) + (25.458632 \times \text{LN}^2) + (43.041842 \times \text{NW})$ $+ (0.081641 \times \text{NW}^2) - (3.064043 \times \text{NWLN}) - (33.551654 \times \text{SWLT}) + (6.344387 \times \text{SWLN})$
Mean summer precipitation = $254.91 + (0.05649979 \times \text{LTEL}) - (0.03010864 \times \text{LNEL}) - (0.00528360 \times \text{NWEL})$ $+ (0.03345429 \times \text{SWEL}) - (0.04340429 \times \text{LT}^3) + (3.82 \times 10^{-6} \times \text{NWEL}^2) + (0.81672 \times \text{LN}^2)$ $- (35.93049382 \times \text{SW}) + (2.10766386 \times \text{SWLN})$
Mean number of days without frost = $312.93 - (0.20992685 \times \text{EL}) + (5.029 \times 10^{-5} \times \text{EL}^2) + (0.01644896 \times \text{LTEL})$ $- (0.00049496 \times \text{NWEL}) - (14.81915168 \times \text{LT}) + (0.10292992 \times \text{LN}^2)$
Mean frost-free period = $216.28 - (0.14224050 \times \text{EL}) + (3.471 \times 10^{-5} \times \text{EL}^2) + (0.00585152 \times \text{LTEL})$ $- (0.00245978 \times \text{LNEL}) - (8.85234423 \times \text{LT}) + (0.04526817 \times \text{LN}^2)$

Notes: The equations are suitable for $62^\circ \text{N} > \text{latitude} > 48.5^\circ \text{N}$ and $137^\circ \text{W} > \text{longitude} > 114^\circ \text{W}$. LT = latitude - 48; LN = longitude - 110; EL = elevation; NW = LT \times LN; SW = LN/LT; NWLT = LT² \times LN; NWLN = LN² \times LT; SWLN = LN²/LT; SWLT = LN/LT²; LTEL = LT \times EL; LNEL = LN \times EL; NWEL = NW \times EL; SWEL = SW \times EL; LTEL² = LT \times EL²; NWEL² = NW \times EL².