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Assessing Population Responses to Climate in *Pinus sylvestris* and *Larix* spp. of Eurasia with Climate-Transfer Models

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Abstract

Weibull regression models were used to relate height and survival of Eurasian populations of Scots pine (*Pinus sylvestris* L.) at age 13 and three species of larch (*L. sukaczewii* Dylis, *L. sibirica* Ledeb., and *L. gmelinii* (Rupr.) Rupr.) at age 12 to the difference in climate between their provenance and a planting site. Univariate models using five climate variables as predictors all were statistically significant ($p < 0.01$), and all but the pine survival functions received strong verification with independent data. The models showed that the growth and survival of most populations of the pine and each species of larch are enhanced when populations are transferred from their provenance to warmer climates. The results are consistent with the view that most populations occur in climates that are suboptimal, the degree of which is directly related to the severity of the climate. Because of this, projected responses to a climate-change scenario of the Hadley Centre were highly variable geographically. Short-term plastic responses tended to be strongly negative for the least severe climates and strongly positive for the most severe. Long-term evolutionary responses primarily reflected extirpation and immigration for the species of larch but showed additionally for the pine that the accommodation of global warming will require a redistribution of genotypes throughout the species' range.

Key words: climate change responses, climatypes, genetic variation, reforestation, seed transfer guidelines

Introduction

The seminal work of Langlet (1936) stimulated a series of studies collectively demonstrating most species of forest trees to be composed of genetically different populations that are distributed as clines along geographic gradients. Because geographic clines invariably parallel climatic gradients, such clines have been interpreted as genetic responses to climate. Geographic variables, therefore, tend to be viewed as surrogates for climatic factors that operate in natural selection but are difficult to observe. With the current availability of climatic data, it is now possible to assess directly the relationship between genetic variation and climate (e.g., Rehfeldt *et al.* 1999*b*, 2002). Studies have shown, for instance, that clines in both lodgepole pine (*Pinus contorta* Doug. ex Loud.) and Scots pine (*Pinus sylvestris* L.) indeed reflect climatic gradients, but that most populations tend to inhabit suboptimal climates. While these results pertain to the seed zones and seed transfer guidelines used in reforestation, they also predict that a changing climate will initiate a redistribution of genotypes across the landscape (Rehfeldt *et al.* 2001, 2002). Response to change, therefore, becomes much more complex than mere shifts in geographic distributions (Davis and Shaw, 2001).

Approaches to predicting genetic responses to climate in forest trees commonly use data from long-term provenance tests. In such tests, populations have been transferred from the climate of their provenance to that of a planting site. The tests, therefore, can be considered as climate-change experiments. In this paper we develop response functions driven by the difference between the climate of the planting site and that of the provenance (e. g. Schmidtling 1994, Carter 1996, Persson 1998). Such climate-transfer functions have the advantage over traditional approaches in that populations need not be planted at more than one site for their performance to be usable. The approach, therefore, is ideal for assemblages of heterogeneous data from disparate tests. Interpretations, however, are based on transfer distances and, therefore, are indirect and are not population-specific.

This paper deals with populations of Scots pine and three species of larch (*L. sukaczewii* Dylis, *L. sibirica* Ledeb., and *L. gmelinii* (Rupr.) Rupr.) that had been tested in a series of provenance tests throughout the Soviet Union. The primary objective of this study is to develop and interpret climate-transfer functions. Because these analyses involve in part the same Scots

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pine data that were used to develop population-specific response functions driven directly by climate variables (Rehfeldt *et al.* 2002), a second objective involves comparing predictions made by the two approaches. A third objective is to use the climate-transfer functions for a climatic definition of climatypes, the climatic ecotypes (Turesson 1925) that comprise species. A fourth objective is to assess and compare the impact of climate-change on species that have distributions of much different breadth in Eurasia. The interpretation of our analyses are centered on the view (see Brown and Gibson 1983, Woodward 1987) that climate is the primary factor controlling the distribution of organisms, with other ecologic factors (e. g. soils, insects, and diseases) being secondary.

The species of larch considered herein are largely allopatric (Abaimov *et al.* 1998). *L. sukaczewii* is distributed primarily in European Russia, *L. sibirica* in western and central Siberia, and *L. gmelinii* in eastern Siberia and Russia's Far East. Where distributions come into contact, species tend to interbreed. By contrast, Scots pine, recognized taxonomically as a single species with seven geographic varieties (Pravdin 1964, Iroshnikov 1977), is distributed throughout most of Eurasia. The distribution of Scots pine itself thus encompasses a similar range of climatic variability as is accommodated collectively by three species of larch.

The climate varies tremendously across the vast distribution of these species (see Alisov 1956). In the Baltic States of the northern portion of eastern Europe, the climate is submaritime with cool summers (700 degree-days>5°C) and only moderately cold winters. To the southwest in Belorussia or Ukraine, the climate is relatively mild and warm with precipitation sufficient for maintaining conifer and mixed conifer-deciduous forests. Toward the east in southwestern Russia, a hot climate (2400 to 2700 degree-days>5°C) with dry summers and cold winters supports vegetation that is largely steppe. To the north and east but still in European Russia, the climate is warm in the summer with moderately cold winters (January mean temperatures of about –12°C) that become increasingly colder (-16°C) toward the Ural Mountains that generally separate Europe from Asia. Precipitation throughout this region is sufficient to support deciduous, mixed conifer-deciduous, and conifer forests. In Siberia, January mean temperatures average -17 to -22°C in the west but gradually decline to -45 °C deep inside the Asian continent. In Yakutia, for instance, a fiercely continental climate with a summer-winter temperature difference of 60°C produces the most severe climates in the world. Nonetheless, Siberian summers are sufficiently warm (1000 to 1400 degree-days>5°C) to support conifer forests. Precipitation, however, declines toward the east, averaging only 200 to 300 mm in Yakutia, and as a result, the distribution of forests in Yakutia is limited more by low precipitation than by the cold. Russia's Far East has a monsoonal climate that is cold in the winter (–28°C), warm in the summer (1500 degree-days>5°C), and moist (650 mm annual precipitation). This combination is favorable for the development of richly diverse conifer and mixed conifer-deciduous forests.

Materials and methods

The height and survival of Scots pine and larch provenances were collated from published works dealing with provenance tests established in the latter half of the 20th Century. Pine data were available from 36 test sites (Iroshnikov 1977; Kouzmina 1999; Shutyaev and Giertych 1997, 2000). Larch data were available from 8 sites (Gursky and Dobrovolsky 1967, Deriujkin 1969, Makarov 1999, Dementiev 1969). Pine test sites differed by as much as 18.9°C in mean annual temperature, 2250 degree-days>5°C, and 27.7°C in the mean temperature in the coldest month; and larch test sites by 9.5°C in mean annual temperature, 790 degree-days>5°C, and 20.5°C in the mean temperature in the coldest month. Each test site contained a broad range of provenances from the species' distributions in Eurasia. Pine data were available from 313 populations for the analyses of height and 228 populations for the analyses of survival. For larch, heights and survivals were available for 130 populations, 63 of *L. sibirica*, 42 of *L. gmelinii*, and 25 of *L. sukaczewii*. For the pine, a subset of about 44 populations were planted at each site, and for larch, the subset averaged 30 populations. This sample of populations represented the distributions of these species reasonable well, except, perhaps, for the coldest provenances of *L. gmelinii*, a species of the permafrost (Abaimov *et al.* 1998).

Of the trials of Eurasian populations of Scots pine and larch that have been established in North America, four were suitable for verifying hypotheses developed from Eurasian data. One trial involved a transcontinental series of eight plantings that tested 80 pine populations. Unpublished data on 13-yr height and survival from these trials was supplied by Drs. K. C. Carter, University of Maine, Orono, Maine, USA; C. A. Mohn, University of Minnesota, Minneapolis, Minnesota, USA; and N. K. Dhir, Alberta Sustainable Resource Management, Edmonton, Alberta, Canada. A second dealt with 26-yr performance of 49 pine populations growing at a single location in North Dakota, USA (Cunningham 1973; Cunningham and Van Haverbeke 1991), and a third provided 14-yr performance of 22 pine populations at twelve sites in Quebec, Canada (Beaudoin 1996). The fourth tested the 15-yr performance of 10 populations of larch (1 of *L. sibirica*, 1 of *L. gmelinii*, and 8 of *L. sukaczewii* at four sites in Alberta, Canada (see Rehfeldt *et al.* 1999*a*).

All analyses used normalized climate data (Gidrometeoizdat 1966-1970, Environment Canada 1994, United States Department of Commerce 1994). The climate of a planting site or provenance was inferred from that of the closest weather station, usually within 30 km. If no stations were within this limit, climate was interpolated from two or more stations.

Statistical analyses – Scots pine

In the data we assembled, heights had been measured and survival scored at ages between 7 and 21. While one can assume that survival at such ages is independent of size, heights required adjustment for age.

The adjustments were done in the three steps described in detail by Rehfeldt *et al.* (2002), and are only abbreviated here:

In the first step, a height-age relationship was developed with data from nine sites where repeated measurements of height were available:

$$[1] \qquad Y_{i\bullet} = b_0 + b_1(A * D)_i$$

where Y is the height of trees at planting site i averaged across all populations; $A*D$ is the interaction of age and degree-days>5°C for site i; and the b's are regression coefficients. Thirteen was adopted as the standard age.

In the second step, a mean height for each of the 36 planting sites was calculated for the standard age by forcing the regression line in [1] through the observed mean:

$$[2] \qquad Y''_{i\bullet 13} = Y_{i\bullet} + Y'_{i\bullet 13} - Y'_{i\bullet}$$

where Y'' is the estimated mean height at age 13 of all populations growing at site i; Y is the observed mean height of trees at planting site i at the observed age; and Y' is the mean height predicted from [1] at site i for either the observed age ($Y'_{i\bullet}$) or the standard age of 13 ($Y'_{i\bullet 13}$).

Third, genetic variation about the adjusted planting mean was restored with the use of standard normal deviates calculated for each population at the observed age. This standard deviate was considered to apply also to the standard age because coefficients of variation in our sample tend to remain stable. The mean height of a population at the standard age then was estimated by:

$$[3] \qquad Y''_{ij13} = Y''_{i\bullet 13} + \left[Y''_{i\bullet 13} \times \left(\frac{s_i}{Y_{i\bullet}} \right) \times \left(\frac{Y_{ij} - Y_{i\bullet}}{s_i} \right) \right]$$

$$[4] \qquad = Y''_{i\bullet 13} \times \left(\frac{Y_{ij}}{Y_{i\bullet}} \right)$$

where Y''_{ij13} is the estimated 13-year height of population i at site j; $Y''_{i\bullet 13}$ is estimated in [2];
s is the standard deviation of population means at site i;
and Y_{ij} and $Y_{i\bullet}$ are defined above.

The effectiveness of these procedures was assessed thoroughly by Rehfeldt *et al.* (2002) by comparing the percent error of actual and adjusted heights for independent data.

After being adjusted for a common age, the data were then suitable for developing climate-transfer regression models. Independent variables used for these models were the transfer distances between the planting site and the provenance (planting site climate minus provenance climate) for five climate variables: (1) growing degree-days>5°C; (2) degree-days<0°C; (3) an annual moisture index, the ratio of growing degree-days>5°C to mean annual precipitation; (4) mean annual temperature; and (5) Conrad's (1947) continentality index, a function of the summer-winter temperature differential and latitude. These five have been shown to be useful in previous analyses of genetic responses to climate (Rehfeldt *et al.* 1999*a*, 1999*b*, 2002).

To model responses to transfer distance, we adopt the prevailing view of population adaptation to climate: a climatic optimum exists for each population, but as the climate deteriorates from this optimum in either direction, growth and survival decrease. This view is supported by numerous theoretical and empirical works and forms the basis of contemporary approaches to limiting seed transfer in reforestation. While several mathematical functions are suitable for modeling such responses (*e.g.* Gaussian, beta, quadratic), the Weibull function (Johnson *et al.* 1994) was chosen because unlike other functions, it can be asymmetric about its vertex.

The Weibull function was originally conceived as a probability-density function suited to normal or skewed normal distributions (Johnson *et al.* 1994). To use this function, one merely fits it to mean values for a number of classes. As shown in Figure 1*a* and *b*, this function is well suited to our data regardless of whether classes are constructed uniformly along the x-axis (Fig. 1*a*) or are constructed according to frequencies (Fig. 1*b*). However, preliminary analyses showed without doubt that using the Weibull as a probability-density function would misrepresent our data by obscuring the underlying variation (Fig. 1*c*). Therefore, the Weibull density function was used as a response function (see Fang and Xu 1987); R-P. Wei (Sino-Forest Corporation, Hong Kong) provided the following conversion of the Weibull response function into a form amenable to nonlinear regressions involving a large number of observations. In this formulation, response, R, is predicted from the difference in climate between the provenance and planting site, X:

$$[5] \qquad R = c(X' - \delta)^{(\alpha - 1)} \exp\left(- \frac{(X' - \delta)^{\alpha}}{\beta} \right),$$

where

$X' = (X - X_{\min})(X_{\max} - X_{\min})^{-1}$
c = performance capacity, > 0
α = shape parameter, > 1
β = scale parameter, > 0
δ = position parameter, $< X'$

Note that climate transfer distances (X) are transformed such that the transformed X' has a relatively small scale, a positive value, and is greater than δ.

[6] $\log R = \log c + (\alpha - 1)\log(X' - \delta) - \frac{(X' - \delta)^{\alpha}}{\beta}$

It follows that :

[7] $R' = c' + a_1 \log(X' - \delta) + a_2 (X' - \delta)^{(a_1 + 1)}$

let $X_1' = \log(X' - \delta)$ and $X_2' = (X' - \delta)$

then

[8] $R' = c' + a_1 X_1' + a_2 X_2'^{(a_1 + 1)}$

where

$c' = \log c,$

$a_1 = \alpha - 1$ which is > -1

$a_2 = -\frac{1}{\beta}$ which is < 0

Regressions were performed iteratively to find a value of (X'-δ) that minimized the residual mean square.

Available for these analyses were 1693 observations for height and 1488 for survival. These large numbers allowed us to design analyses that would reflect the genetic structure of the species. Eurasian populations of the pine, like those of most forest trees, have inherently different growth potentials which have been molded by the climate of the provenance (Iroshnikov 1977; Shutyaev and Giertych 1997, 2000). One can expect, therefore, population responses to climate to be dependent on the general temperature regime of the provenance. In addition, Rehfeldt *et al.* (2002) demonstrate that the colder the provenance, the greater the disparity between the optimal climate and the inhabited climate. Under this eventuality, the optimal transfer distance will vary among populations.

To accommodate these possibilities, populations were grouped into 10 classes (Table 1) based on degree-days>5°C of the provenance. Boundaries of the classes were chosen to balance degree-day differences between classes with the number of observations. This meant that the number of observations within classes and the intervals separating the classes were both unequal. The Weibull function was then fit for each class. Note that because of the climate patterns across Eurasia, these classes are as much or more a reflection of longitude as they are of latitude (Table 1).

Because provenance tests are costly, they are rarely established in ecologically marginal climates where growth and survival are expected to be poor. To assure that the Weibull functions would be asymptotic to zero for large absolute values of climate transfer, two locations were selected that were beyond the species' climatic distribution, one on the steppe in European Russia and the second in the tundra of Siberia. Transfer

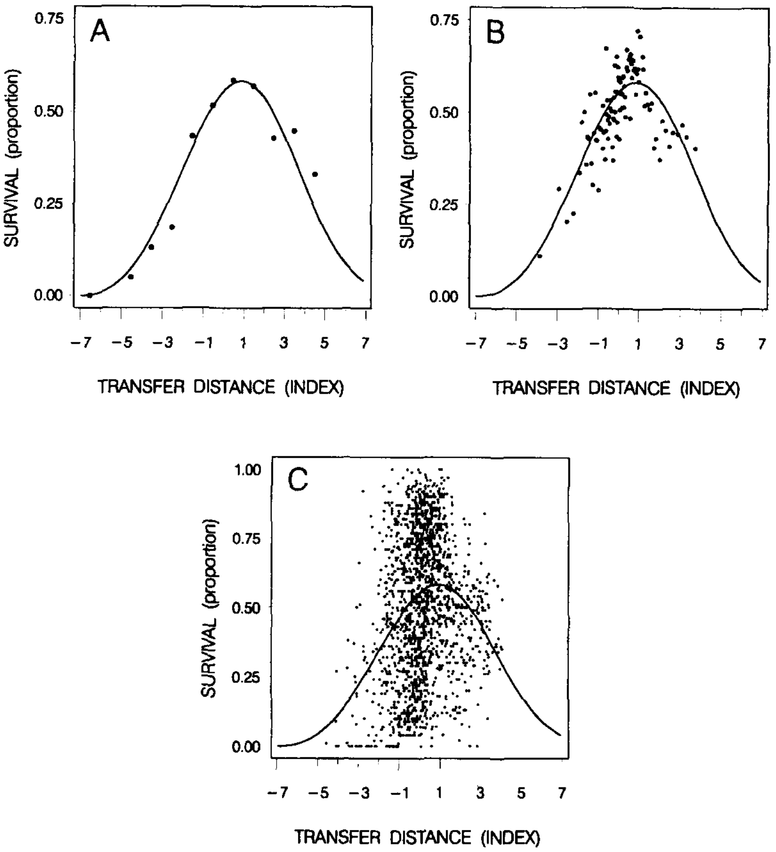

Fig. 1. Weibull models and observed survival of Scots pine populations plotted against transfer distance (planting site climate minus provenance climate) for the annual moisture index. A: observed data plotted as class means with each class occupying 1 unit of the moisture index. B: observed data plotted as means for 100 classes with an equal number of observations in each class. C: observed data plotted in their natural state.

Table 1. Climate, location, and composition of ten Scots pine classes based on degree-days>5°C of the provenance.

class	range in degree-days>5°C	number of populations	average latitude (°N)	average longitude (°E)	moisture index	continentality index	degree-days<0 °C	annual temperature (°C)
1	625 - 1000	159	59.64	79.41	1.65	48.8	-2355	-2.01
2	1001 - 1158	182	58.76	87.76	2.37	61.2	-2892	-2.85
3	1159 - 1238	149	56.6	78.09	2.25	53.6	-2189	-0.48
4	1239 - 1329	175	55.96	82.36	2.63	58.1	-2387	-0.75
5	1330 - 1400	192	56.34	62.45	2.33	48.4	-1697	1.49
6	1401 - 1490	189	54.00	69.84	2.79	51.6	-1795	1.51
7	1491 - 1624	194	54.88	56.39	2.60	47.7	-1560	2.44
8	1625 - 1764	182	52.78	46.61	3.32	43.9	-1167	4.14
9	1765 - 2009	177	52.00	45.22	3.15	45.1	-1125	4.65
10	2010 - 2800	94	51.29	44.72	4.24	47.0	-1040	5.55

distances to these fictitious sites were calculated, and the maximum and minimum values for each class were included in the analyses as dummy observations with height and survival of zero. Each regression, therefore, included two dummy variables that were specific to each temperature class.

Weibull models were validated with data from three sets of provenance tests established in North America: (1) the transcontinental test of 80 provenances, (2) the North Dakota test of 49 provenances, and (3) the Quebec tests of 22 provenances. Besides correlating the observed height and survival with the predicted for each of five univariate models, we also correlated the observed with (1) the mean of the five univariate predictions, and (2) the minimum of the univariate predictions.

Statistical analyses – larch

Height measurements at multiple ages were available for only three sites, all of which were within the distribution of L. sibirica. Measurements at these sites had been made at seven- or eight-year intervals between the ages of 3 and 12. Adjusting population heights for a standard age was done by first regressing population mean heights at each of the sites on age with a linear model:

$$[9] \quad Y_{ij} = a + bX_j$$

where Y is the mean height of population i at age j, X is the age j of the trees at the time of measurement, and a and b are regression coefficients.

These procedures thus produced three regression models of height on age. As detailed in [3], each model was forced through an observed plantation mean to predict a mean height for a standard age of 12. The average of these three predictions was then accepted as the adjusted 12-year height for the plantation. Provenance variation was introduced about this mean according to [4].

Effectiveness of the procedure was judged according to errors of estimate between observed and adjusted heights for two sets of independent data. One of these sets, Bronnitsky, was from a provenance test in European Russia where measurements of 19 provenances had been made at ages 11 and 12 (Dementiev 1969). The second involved the 7- and 15-yr heights of 28 provenances tested at Footner Lake, Alberta, Canada (unpublished data of Dr. N. K. Dhir, Alberta Sustainable Resource Management, Edmonton, Alberta, Canada).

The Weibull function [8] was used to fit the five climate variables to adjusted heights and survivals for each of the larch species. For *L. sibirica*, 145 observations were available for analyses of height, and 111 were available for survival; for *L. gmelinii*, 61 and 44 were available, respectively; and for *L. sukaczewii*, 44 and 22. Dummy observations were included for each species as described above.

Weibull models were validated by correlating actual with predicted 15-yr heights and survivals of provenances at three sites in Alberta, Canada (see Rehfeldt *et al*, 1999*a*). Twenty-one observations were available for these correlations.

Response to a changing climate

Predictions from a GCM of the Hadley Centre, HadCM3GGa1 (Gordon *et al.* 2000) were used to assess the impact of a change in climate on genetic responses of populations at several locations spread across the pine and larch forests of Eurasia. This model projects for Eurasia changes in winter temperatures of +3°C to +9°C, in summer temperature +4°C to +6°C, and in annual precipitation of –4% to +9% by the end of the current Century (see Rehfeldt *et al.* 2002).

The Hadley predictions were used to calculate for eight pine locations and nine larch locations the change in monthly temperature and precipitation between 1961-1990, the period of normalization, and three future decades (2030 to 2039, 2060 to 2069, and 2090 to 2099). These monthly means were converted to the variables driving our response functions according to the linear regressions of Rehfeldt *et al.* (2002). Differences between the contemporary and future climates were then used as independent variables in the Weibull transfer functions to estimate the response of contemporary populations as the climate changes (see Rehfeldt *et al.* 2002). By calculating the expected responses of each population in our database, we could also select the population expected to have the greatest growth and survival in the climate of 2090.

The procedure produced for each population of each species five estimates of height and survival for each of three future decades. In accord with the concept of limiting factors, the smallest of the five was considered to be the best estimate. In predicting future responses, we assume that climatic limits of distribution in the future will be the same as the contemporary limits. These limits were inferred from the provenances in our databases. Predicted heights were equated to zero for future climates lying beyond these limits. Results are presented as (1) short-term plastic responses of the contemporary population to the climate as it changes, and (2) long-term evolutionary responses that in time will produce for the novel climates the best suited genotypes (see Rehfeldt *et al.* 2001, 2002).

Results

Adjustments for age

Procedures by which heights were standardized for a common age were evaluated according to the percent error of adjusted to observed heights. For Scots pine, the validations were preformed by Rehfeldt *et al.* (2002) and showed that as long as the age of the observed height did not differ greatly from the age to which heights were being adjusted, errors of estimate should be less than 10%. Verification of the approach for the species of larch produced similar results: 11-yr heights at Bronnitsky averaged 458 cm while heights adjusted from age 10 were 423 cm, an error 7.7%. For data from Footner Lake, 15 yr heights averaged 432 cm, and heights adjusted from age 7 were 420 cm; the error, therefore, was 2.8%. As concluded by Rehfeldt *et al.* (2002), the errors of estimate thus seem to be within acceptable limits. It is important to realize, however, that without such adjustments, analyses such as ours would not be possible. The approach is, therefore, a reasonable means of assembling heterogeneous data into a form suitable for analysis.

Weibull regression models

All Scots pine regression models were statistically significant ($p < 0.01$). Height models driven by transfer distance in degree-days>5°C (Fig. 2) produced the smallest residual mean square for six of the 10 classes, five of which were for the coldest provenances (Table 2). Fig. 2*a* illustrates response functions for each of the 10 classes, and Fig. 2*b* shows the fit for two classes. The proportion of the variance explained by these regressions was about 0.20 for the model driven by transfers in degree-days>5°C; 0.16 for those driven by transfer distance in degree-days<0°C, mean annual temperature, and the continentality index; and 0.10 for those driven by transfers in the annual moisture index. For survival, the model driven by transfers in the annual moisture index (Fig. 1*c*) produced the lowest residual mean square while accounting for about 11% of the total variance.

For larch, all Weibull regressions were statistically significant ($p < 0.01$). Models driven by transfer distance in the annual moisture index produced the lowest residual mean squares for both height (Fig. 3) and survival of *L. gmelinii* and *L. sibirica* (Table 2). For height and survival of *L. sukaczewii*, models driven by

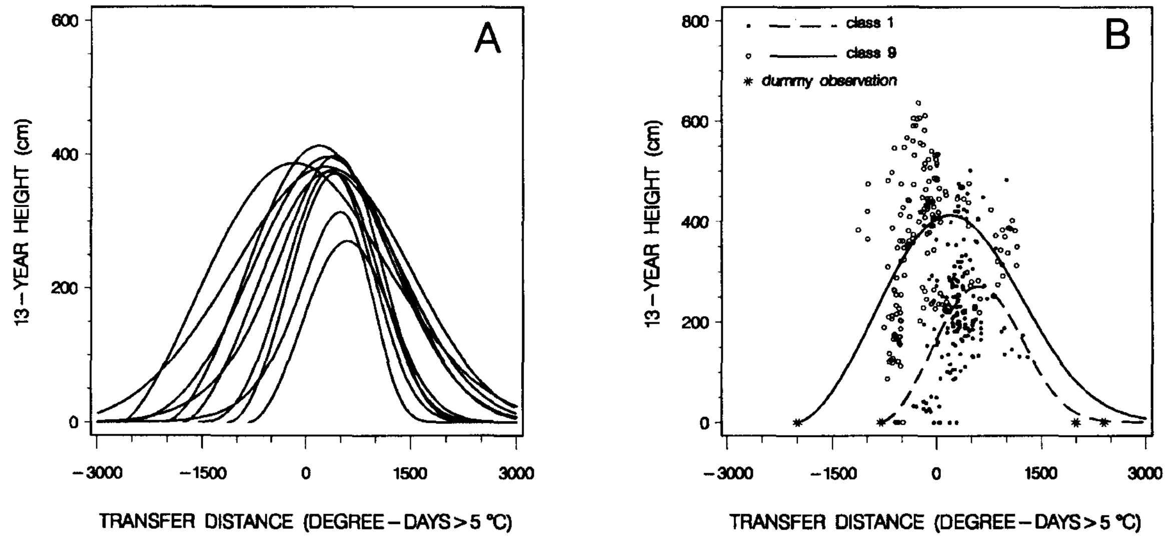

Fig. 2. Weibull regression models of 13-year height of Scots pine populations on provenance transfer distance (planting site climate minus provenance climate) in units of degree-days>5°C. A: functions for 10 groups of provenances classified according to summer temperature of the provenance (Table 1). B: plots of observed data against modeled responses for populations in class 9, the provenances with the highest growth potential, and class 1, the group with the lowest growth potential. Dummy observations are located with asterisks.

transfers in units of mean annual temperature were the best fitting (Table 2). For all species together, models driven by transfers in the annual moisture index (Fig. 3) accounted for about 25% of the variance in height; those driven by transfers in degree-days>5°C, degree-days<0°C, and mean annual temperature (Fig. 4*b*) accounted for about 20%; and those driven by transfers in the continentality index (Fig. 4*a*) accounted for 10%. For survival, models driven by transfers in the annual moisture index accounted for 31% of the variance while those driven by the other independent variables accounted for about 20%.

Validation of the Scots pine height models was strongly supportive (Table 3). Simple correlations between observed heights and those predicted by the models were statistically significant ($p < 0.01$) for all three sets of independent data, but the model driven by transfer distance in degree-days>5°C received by far the strongest validation. Correlations of the observed height with the mean of the five predicted values were all statistically significant ($p < 0.01$), with coefficients (r) ranging from 0.61 for the trans-North America data (Fig. 5*a*) to 0.55 from the Quebec data. The correlation of the minimum of the predicted values with the observed was about 0.57 ($p < 0.01$) in each of the comparisons.

None of the Scots pine survival functions received validation from the trans-North America tests when all plantings were included in a single analysis (Table 3). These tests, however, involved seven planting sites that ranged from maritime to continental. Across such an environmental range, different climatic factors undoubtedly control survival. When the correlations between observed and predicted survivals were calculated separately for each site, significant simple correlations were obtained for three of the seven sites. At two, the model driven by transfers in units of mean annual temperature produced a significant simple correlation ($r = 0.41$ and $p = 0.04$), and at the third, the model driven by transfer distance in the annual moisture index produced a simple correlation of $r = 0.37$ ($p < 0.01$).

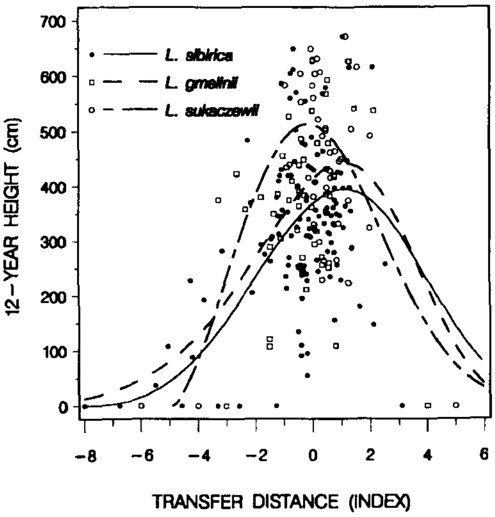

Fig. 3. Plots of observed data and Weibull models of 12-yr height in three species of larch on transfer distance (planting site climate minus provenance climate) in units of the annual moisture index.

Table 2. Error mean squares (x 10^{-4} for height; x 10^{2} for survival) for Weibull regressions of height (cm) and survival (proportions) on climate differences between planting site and provenance. Boldface type marks the smallest residual for each dependent variable.

	climate transfer variable				
dependent variable	moisture index	contentality index	degree-days<0°C	degree-days>5°C	mean annual temperature
pine height					
class 1	1.33	1.30	1.29	**1.11**	1.31
class 2	1.26	1.12	1.15	**1.11**	1.21
class 3	1.79	1.55	1.57	**1.22**	1.55
class 4	1.62	1.56	1.59	**1.38**	1.56
class 5	2.03	1.82	1.70	**1.59**	1.70
class 6	1.75	1.63	1.51	1.55	**1.48**
class 7	1.97	1.83	1.87	**1.77**	1.79
class 8	**1.75**	1.85	1.87	1.98	1.91
class 9	1.75	1.64	1.60	1.69	**1.58**
class 10	**1.29**	1.43	1.39	1.34	1.39
pine survival	**5.98**	6.36	6.23	6.11	6.11
larch height					
L. gmelinii	**2.33**	2.82	2.55	2.96	2.79
L. sibirica	**2.32**	3.05	2.57	2.33	2.52
L. sukaczewii	1.44	1.55	1.51	1.38	**1.29**
larch survival					
L. gmelinii	**2.69**	2.79	2.99	3.22	3.20
L. sibirica	**2.84**	4.08	4.10	3.84	4.12
L. sukaczewii	1.68	1.83	1.56	1.68	**1.44**

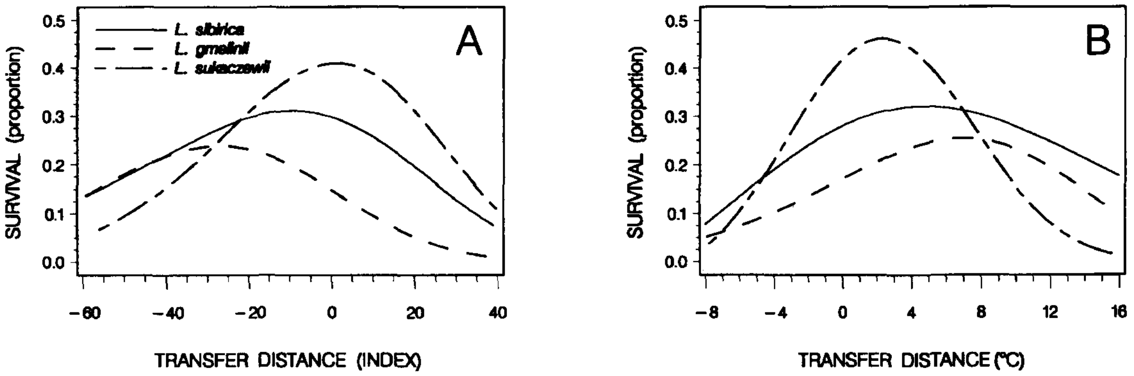

Fig. 4. Weibull models of survival for three species of larch in relation to transfer distance (planting site climate minus provenance climate) for: (A) the continentality index (function of the summer-winter temperature differential and latitude), and (A) mean annual temperature.

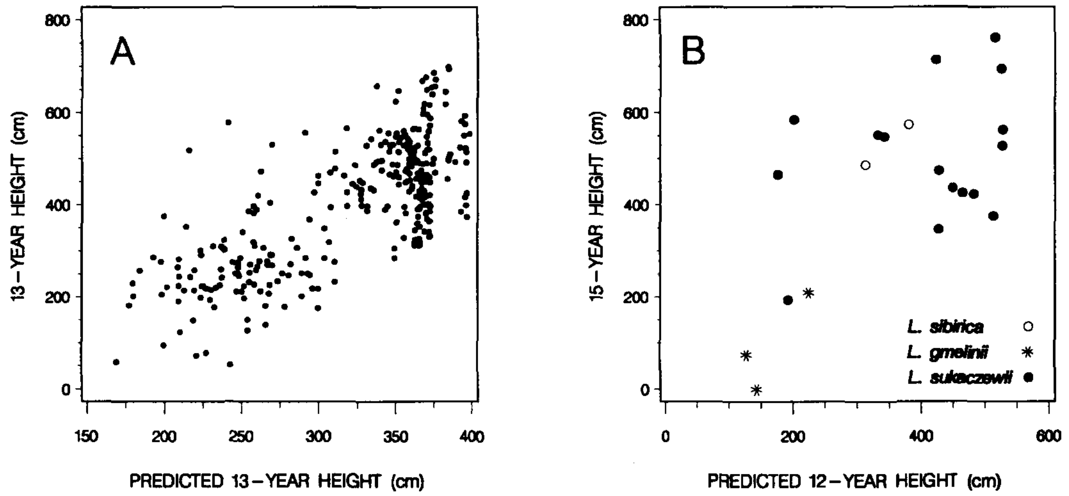

Fig. 5. Plots of population height predicted by Weibull models in relation to the observed: (A) for the trans-North American provenance trials of *Pinus sylvestris*, and (B) for populations of three larch species growing in Alberta.

Table 3. Simple correlations of heights predicted by the Weibull models with independent data.

	independent variable of climate transfer model				
test locations supplying independent data	moisture index	contentality index	degree-days<0°C	degree-days>5°C	mean annual temperature
pine					
height in trans-North America[a]	0.48**	0.52**	0.40**	0.75**	0.52**
height in North Dakota[b]	0.38**	0.54**	0.55**	0.46**	0.54**
height in Quebec[c]	0.23**	0.27**	0.49**	0.57**	0.27**
survival in trans-North America[a]	0.07 †	0.09 †	0.07 †	-0.18 †	-0.02 †
larch					
height in Alberta[d]	0.62**	0.56**	0.63**	0.36 †	0.55**
survival in Alberta[d]	0.37 †	0.58**	0.59**	-0.07 †	0.46*

[a] 313 observations
[b] 49 observations
[c] 1360 observations
[d] 21 observations

† not statistically significant
* statistically significant at $0.05 > p > 0.01$
** statistically significant at $p < 0.01$

Validation of the larch models were supportive even though based on only 21 observations (Table 3). All height models received validation except that driven by transfer distance in degree-days>5°C. The strongest validations were for the height models driven by transfers in units of the annual moisture index and degree-days<0°C. A correlation coefficient of $r = 0.72$ ($p < 0.01$) was produced when the average of the five predicted values was correlated with the observed height (Fig. 5*b*), while that of $r = 0.73$ ($p < 0.01$) related the minimum of the predicted values to the observed. Predictions of survival made from models driven by transfer distances in the continentality index, degree-days<0°C, and the mean annual temperature produced the strongest correlations with observed survival (Table 3). The simple correlation between the observed and the mean of the five predicted values was 0.67 while that with the minimum of the predicted values was 0.54, both of which were significant at $p < 0.01$.

Interpretation of regression models

The *x*- and *y*-axis coordinates of the vertex of the transfer function define the optimal transfer distance, X_{opt}, and the optimum performance, Y_{max}, respectively. These values are presented in Tables 4 to 7 along with two other statistics that pertain to confidence limits about Y_{max}. As illustrated by Rehfeldt *et al.* (1999*a*), the lower of these confidence limits intersects with the regression line at two points, the *x*-axis coordinates of which are labeled in the Tables as X_1 for the smallest value and X_2 for the larger. When the interval between X_1 and X_2 includes zero, the optimum climate does not differ statistically from a transfer distance of zero, which is the climate of the provenance. For our analyses, we use $\alpha = 0.2$ for the confidence intervals. This relatively high level of probability limits type II errors (accepting no differences when they are real) which are of the greatest consequence when models are applied to practical problems.

Table 4 shows, for instance, that the model describing the height of pine populations from the coolest provenances (class 1) peaks at a transfer distance of +592 degree-days>5°C where 13-year height is expected to be 270 cm. The 80% confidence interval about Y_{max} intercepts the regression line at $X_1 = 352$ and $X_2 = 832$ degree-days>5°C. Because the interval between X_1 and X_2 does not include zero, the optimal climate for this group of populations differs significantly ($p \cong 0.2$) from the climate of the provenance. Indeed, populations in the six coldest classes would all grow significantly better in climates that are warmer than that of their provenance.

Table 4 also illustrates (1) the well-known positive relationship between the warmth of the provenance and the growth potential (Y_{max}) of the population; (2) a negative relationship between the warmth of the growing season and X_{opt}, the optimal transfer distance; and (3) a negative relationship between growth potential and optimal transfer distance. While populations from climates with degree-days>5°C of about 1800 (class 9) tend to inhabit their ecological optima, the optimal transfer distance increases as the climate becomes increasingly severe. Most populations, therefore, inhabit climates that are colder than their optima and, therefore, benefit from a transfer to a warmer climate. Populations that inhabit the coldest climates thus occur under conditions that are the most suboptimal and, therefore, have the largest transfer distances to their climatic optima. Those populations from the warmest climates in the forest-steppe ecotone (class 10) comprised the only group expected to benefit from a transfer into climates cooler than their provenance.

Table 4. Parameters characterizing transfer functions developed from Weibull regressions of height of Scots pine populations on the difference in degree-days>5°C between the provenance and planting site. Statistics are presented for each of the temperature classes of Table 1. Y_{max} is the value (cm) of Y at the vertex of the function, and X_{opt} is the X-axis coordinate of Y_{max}. X_1 and X_2 are the x-axis coordinates of the points of intersection of the Weibull function with the lower confidence interval ($\alpha = 0.2$) of Y_{max}. Bold face type marks those functions for which the interval between X_1 and X_2 does not include zero.

provenance temperature classes	Y_{max}	X_{opt}	X_1	X_2	interval size ($X_2 - X_1$)
class 1	270	592	**352**	**832**	480
class 2	313	485	**265**	**688**	423
class 3	371	400	**176**	**642**	465
class 4	375	340	**112**	**568**	455
class 5	397	404	**155**	**652**	497
class 6	373	340	**14**	**684**	670
class 7	396	293	-34	642	676
class 8	381	275	-155	706	861
class 9	412	180	-140	520	660
class 10	386	-180	-600	260	860

Table 5. Parameters characterizing five transfer functions developed from Weibull regressions of population height and survival for Scots pine on transfer distance. Responses are presented as means for the temperature classes of (Table 1). Y_{max} is the Y-axis coordinate of the vertex, and X_{opt} is the X-axis coordinate of Y_{max}. X_1 and X_2 are the x-axis coordinates of the points of intersection of the Weibull function with the lower confidence interval (α= 0.2) of Y_{max}. Bold face type marks those functions for which the interval between X_1 and X_2 does not include zero.

climate transfer function	Y_{max}	X_{opt}	X_1	X_2	$(X_2 - X_1)$
height at age 13					
moisture index	335	0.75	-0.60	2.02	2.61
continentality index	341	1.20	-8.59	11.10	19.69
degree-days<0°C	341	220	-434	871	1306
degree-days>5°C	368	313	**15**	**619**	604
mean annual temperature	342	1.30	-1.22	3.87	5.09
survival					
moisture index	0.58	0.88	**0.34**	**1.52**	1.18
continentality index	0.55	1.27	-7.50	9.38	16.88
degree-days<0°C	0.56	450	-150	1000	1150
degree-days>5°C	0.59	460	**220**	**700**	480
mean annual temperature	0.57	2.68	**0.75**	**4.95**	4.20

note: units for the Y-axis coordinates are cm for height and proportions for survival; for X-axis coordinates are °C except for functions driven by the moisture index (degree-days>5°C per mm annual precipitation) and the continentality index (without units)

Table 6. Parameters characterizing five transfer functions developed from Weibull regressions of population height for three species of larch on transfer distance. Y_{max} is the Y-axis coordinate of the vertex, and X_{opt} is the X-axis coordinate of Y_{max}. X_1 and X_2 are the x-axis coordinates of the points of intersection of the Weibull function with the lower confidence interval (α= 0.2) of Y_{max}. Bold face type marks those functions for which the interval between X_1 and X_2 does not include zero.

climate transfer variable	Y_{max}	X_{opt}	X_1	X_2	$(X_2 - X_1)$
L. sukaczewii					
moisture index	513	-0.13	-1.12	0.86	1.98
continentality index	501	-3.20	-15.20	8.00	23.20
degree-days<0°C	529	55	-660	770	1430
degree-days>5°C	529	156	-113	426	539
mean annual temperature	544	0.56	-1.86	2.76	4.62
L. sibirica					
moisture index	394	1.10	-0.07	2.14	2.21
continentality index	362	-3.00	-33.80	27.80	61.60
degree-days<0°C	396	1490	**320**	**2660**	2340
degree-days>5°C	406	432	**112**	**784**	672
mean annual temperature	419	5.50	**2.50**	**8.25**	5.75
L. gmelinii					
moisture index	443	1.10	-0.20	2.20	2.40
continentality index	437	-0.60	-19.00	20.10	39.10
degree-days<0°C	428	475	-800	1675	2475
degree-days>5°C	383	161	-433	701	1134
mean annual temperature	416	1.20	-3.84	6.00	9.84

note: units for the Y-axis coordinates are cm for height and proportions for survival; for X-axis coordinates are °C except for functions driven by the moisture index (degree-days>5°C per mm annual precipitation) and the continentality index (without units)

Table 5 presents the transfer statistics of Table 4 as means for the 10 classes and shows that the interval between X_1 and X_2 fails to include zero for only degree-days>5°C. On average, therefore, height growth of Scots pine provenances is enhanced when populations grow in climates warmer than their provenance. Similar statistics for the survival functions (Table 5) likewise suggest that survival is increased slightly when populations are transferred into climates that are warmer and, therefore, have a higher moisture index (more heat per unit precipitation) than their provenance.

The larch transfer functions suggest, first, that *L. sukaczewii*, which occupies the least severe climates of the three species, achieves optimal height with a transfer distance of zero (Table 6, Fig. 3) but that its survival is enhanced somewhat when populations are transferred into climates with summers slightly warmer than their provenance (Table 7, Fig 4*b*). For *L. sibirica* populations native to the continental climates of western and central Siberia, growth and survival is enhanced with transfers into climates that have warmer temperatures, higher moisture indices, and lower continentality indices than those of their provenance (Table 6; Figs. 3 and 4). And, for *L. gmelinii* which inhabits the severe continental climates of eastern Siberia and the Far East, survival in particular is enhanced in climates that are somewhat warmer (Fig. 4*b*) but much less continental (Fig. 4*a*) than those of their provenance. Note, however, for height functions of L. gmelinii (Table 6), the intervals between X1 and X2 include zero but nonetheless are skewed about Xopt toward positive values which would lead toward the conclusion that performance would be enhanced with transfers to warmer climates.

Response to climate-change

Our Weibull response functions are driven solely by climate. In using these functions to predict responses to a change in climate (Tables 8 and 9), we readily acknowledge that ecologic factors other than climate (e. g., soils, insects, diseases, topography) also interact to determine responses. However, under the view that climate is the primary factor controlling the distribution of organisms, a model driven by climate becomes the solid footing on which effects of additional ecological factors are superimposed.

For Scots pine, global warming according to the Hadley greenhouse gas scenario should produce short-term plastic responses in contemporary populations that include (1) large losses in growth and productivity in the central and southern portions of eastern Europe, (2) modest losses in growth and productivity along the southern periphery of the species distribution in Asia, and (3) gains in productivity elsewhere but particularly in the north and east (Table 8). Long-term evolutionary impacts would include large gains in growth and productivity throughout Siberia and also in the north of European Russia. Permanent shifts in distribution

Table 7. Parameters characterizing five transfer functions developed from Weibull regressions of population survival for three species of larch on transfer distance. Y_{max} is the Y-axis coordinate of the vertex, and X_{opt} is the X-axis coordinate of Y_{max}. X_1 and X_2 are the x-axis coordinates of the points of intersection of the Weibull function with the lower confidence interval (α= 0.2) of Y_{max}. Bold face type marks those functions for which the interval between X_1 and X_2 does not include zero.

climate transfer variable	Y_{max}	X_{opt}	X_1	X_2	$(X_2 - X_1)$
L. sukaczewii					
moisture index	0.41	0.68	-0.76	2.12	2.88
continentality index	0.41	1.60	-13.6	15.2	28.8
degree-days<0°C	0.42	705	-400	1615	2015
degree-days>5°C	0.46	426	**132**	**720**	588
mean annual temperature	0.46	2.32	-0.32	4.96	5.28
L. sibirica					
moisture index	0.44	1.10	**0.58**	**1.62**	1.04
continentality index	0.31	-10.00	-28.2	6.8	35
degree-days<0°C	0.31	500	-1210	2210	3420
degree-days>5°C	0.34	560	**80**	**1104**	1024
mean annual temperature	0.32	4.75	0.00	10.00	10.00
L. gmelinii					
moisture index	0.32	1.00	-0.40	2.20	2.60
continentality index	0.24	-27.05	**-48.90**	**-7.50**	41.40
degree-days<0°C	0.27	1975	**925**	**2875**	1950
degree-days>5°C	0.25	323	-406	1052	1458
mean annual temperature	0.26	6.96	**1.44**	**12.00**	10.56

note: units for the Y-axis coordinates are cm for height and proportions for survival; for X-axis coordinates are °C except for functions driven by the moisture index (degree-days>5°C per mm annual precipitation) and the continentality index (without units)

Table 8. Short-term plastic and long-term evolutionary responses to global warming predicted by transfer functions for populations of Scots pine. Responses are expressed as percent changes in height relative to the contemporary population at eight geographic locations within the contemporary distribution. Plastic responses are made for three decades beginning on 2030, 2060, and 2090.

contemporary population		plastic response			evolutionary response (%)
location	13-yr height (cm)	2030 (%)	2060 (%)	2090 (%)	
Belorussia	372	-1.8	-3.5	-14.0	-4.9
southern European Russia	371	-8.9	-21.2	-39.9	-
northeast European Russia	166	36.4	35.7	28.6	138.9
northeast Kazakstan	372	-4.1	-8.0	-14.0	-0.3
western Siberia	166	35.4	33.8	25.7	118.0
northern Siberia	166	30.1	30.9	21.9	88.1
southern Siberia	336	0.6	0.5	-0.1	13.8
northeast Siberia	221	3.0	0.8	-1.8	48.3

Table 9. Short-term plastic and long-term evolutionary responses to global warming predicted by transfer functions for three species of larch. Responses are presented as percent changes in height relative to the contemporary population at nine geographic locations within the contemporary distribution. Plastic responses are made for three decades beginning on 2030, 2060, and 2090.

contemporary population			plastic response			evolutionary response	
location	species	12-yr height (cm)	2030 (%)	2060 (%)	2090 (%)	species	(%)
south-central Ukraine	*sukaczewii*	497	-7.8	-12.0	-42.0	-	-
west-central European Russia	*sukaczewii*	497	-0.9	-7.3	-37.0	-	-
east-central European Russia	*sukaczewii*	497	0.8	-3.0	-21.0	*sukaczewii*	0.2
west-central Siberia	*sibirica*	335	8.1	8.0	7.9	-	-
southwest Siberia	*sibirica*	335	8.1	8.0	8.0	-	-
north-central Siberia	*sibirica*	335	8.0	7.9	7.5	*sibirica*	7.8
southeast Siberia	*gmelinii*	379	0.9	-0.3	-2.5	*gmelinii*	0.7
southwest Far East	*gmelinii*	379	0.3	-4.9	-10.0	*sibirica*	5.3
northwest Far East	*gmelinii*	379	0.7	0.9	0.7	*gmelinii*	0.9

should occur in the southwest and western portions of Eastern Europe as the climate becomes hotter and drier than any climates inhabited contemporarily by our sample of populations. Whether populations not sampled in our studies exist today in western Europe that are suitable for such climates is not known.

The pine survival functions suggest that survival in the short term should change little, from +3% in Belorussia to –8% in both eastern Siberia and in the southern portions of European Russia. Estimates of long-term effects also suggest little change in survival except, of course, where distributions shift.

For larch, short-term responses to global warming should include large-scale reductions in growth for *L. sukaczewii* throughout its distribution in eastern Europe (Table 9). For *L. sibirica* and *L. gmelinii*, however, losses in growth are expected only along the southern boundary of their distributions; gains in height of as much as 8% are projected for elsewhere. Long-term evolutionary responses purport modest gains in growth up to 10% that would accrue in those populations best suited to the climates of the future.

Table 9 also indicates that by far the most prominent effects of global warming on larch should be extirpation and immigration. For *L. sukaczewii*, future climates that are hotter in both the summer and winter than those currently inhabited by contemporary populations are expected for all but in the northernmost of its distribution. Extirpation for similar reasons is expected for populations of *L. sibirica* in western Siberia and *L. gmelinii* in eastern Siberia and the western portions of the Far East. One can visualize, therefore, an orderly shift in the distribution of all three species toward the east and north, with the contemporary forest species of western Europe replacing *L. sukaczewii* in European Russia; *L. sukaczewii* replacing *L. sibirica* in western Siberia; *L. sibirica* replacing *L. gmelinii* in eastern Siberia; and *L. gmelinii* expanding its range in the north of the Far East. Yet, the Hadley projections suggest that such a view is an oversimplification. For instance, temperatures at sites in the Ural Mountains (eastern portions of European Russia in Table 9) should be suitable for *L. sukaczewii* in 2090. But, immediately across these mountains in western Siberia where *L. sibirica* exists today, future climates are projected to have summer and winter temperatures that are warmer than either *L. sukaczewii* or *L. sibirica* inhabit today. Consequently, with an eastward expansion limited to the Ural Mountains, *L. sukaczewii* would not be a logical replacement for *L. sibirica* in western Siberia.

Larch survival functions project modest short-term increases (4% to 6%) in survival throughout Eurasia as the climate warms. Except for those areas where the distribution of species is under change, long-term effects on survival are expected to range from modest increases to as much as 15% increases in the southern portions of eastern Siberia

Discussion

For both the pine and the larch species, Weibull regressions of height and survival on climate-transfer distances were statistically sound; validation tests were strongly supportive, particularly for models of height; and interpretations were biologically sensible. Nevertheless, underlying these regressions were distributions that were extremely noisy (Fig. 1*c*). Some of this noise undoubtedly accumulated from our use of univariate models: transfer distances conceivably could be small for some variables while being large for others. While multivariate approaches may be feasible, univariate models nonetheless are a first step in understanding the process by which climate controls response. Still, even though statistically sound, the regressions models left much of the variance unexplained. For this reason, validations with independent data were mandatory before confidence could be placed in the predictions made by these models.

In interpreting the results of the validation analyses (Table 3 and Fig. 4), it is pertinent to realize that the data used for validation were from North American plantings established in foreign climates geographically far removed from the natural distribution of the species and populations under study. Indeed, one can readily envision a failure to achieve validation arising from ecological effects other than climate (e. g., soils, pests) that were not considered by our models. Yet, the validation tests were statistical significant, and this fact alone underscores the dependence of performance on the adaptation of populations to climate. The results, therefore, are consistent with and offer support for the view that climate is the primary factor controlling adaptedness in living organisms.

Genecology

It is well known for forest trees in general and for Scots pine in particular (Langlet 1936; Giertych 1991) that populations from mild climates tend to have higher growth potentials than populations from severe climates. Not surprisingly, therefore, the transfer functions of Fig. 2*a* and Table 4 show growth potential to be directly related to the summer temperature (degree-days>5°C) of the provenance. The same functions demonstrate further that most populations occupy suboptimal climates, with the degree by which the inhabited climate is suboptimal being directly related to the severity of the climate. As a result, populations from the coldest climates not only have the lowest growth potentials but also tend to occur in climates that are much colder than their ecologic optima. These results are precisely the same as those obtained from population-specific response functions of Scots pine (Rehfeldt *et al.* 2002) that used much the same data. They also mirror results with lodgepole pine (Rehfeldt *et al.* 1999*b*).

Transfer functions describing the survival of Scots pine populations were statistically significant but were poorly validated. True, survival is controlled by many factors other than adaptation to the climate, and the effects of these other factors would contribute error. Indeed, in using results of provenance tests to model survival, adverse effects typically occurring during the first two years which are critical for establishment have been circumvented by planting and, therefore, would be ignored by our models. Likewise, our analyses considered survival up to an age of 20 and therefore would ignore effects such as insects and diseases which frequently accrue at advanced ages. Validation of a model driven by climate also will depend on the climate at the site from which independent data are derived. Of our models, the function driven by the moisture index was the best fitting statistically (Table 2). Yet, none of the test sites providing data suitable for validation had moisture indices greater than 3.5, a value approaching the optimum for the populations under test (see Fig. 6, Rehfeldt *et al.*, 2002). Without warm and dry (high moisture index) test sites to induce mortality, attempts to validate survival functions driven by transfers in units of the moisture index would be doomed at the outset. It should not be surprising, perhaps, that validation of the survival models was, first, weak and, second, dependent on statistical tests being conducted for individual planting sites.

For all of the larch species, the number of observations was too few to allow analyses to account for genetic structure. Population effects, therefore, appear as errors about the regressions. Perhaps more importantly, predictions made by our functions apply to the species as a whole despite the fact that genetic variation within species is well documented (Abaimov *et al.* 1998). Nonetheless, when viewed collectively, results for the species of larch parallel those for both Scots and lodgepole pines: *L. sukaczewii*, a species occurying the least severe climates, occurs at or near its ecologic optima, but both *L. sibirica* and *L. gmelinii* respond to warmer climates with either or both increased growth and survival. As a result, optimal performance of *L. gmelinii* populations should occur in climates typically inhabited by *L. sibirica*; and that of *L. sibirica* populations in those typically inhabited by *L. sukaczewii*.

Parallel results in five conifer species thus suggest that the same principles are governing the distribution of genotypes in the boreal forests of the Northern Hemisphere. Populations on average inhabit climates that are colder than their ecological optima and, therefore, respond in a positive manner when transferred to climates warmer than their provenance. As viewed by Rehfeldt *et al.* (1999*b*), genotypes tend to occur in those climates for which their adaptedness is adequate but in which they can be competitively exclusive. While genotypes with the highest growth potentials tend to inhabit their ecologic optima, competition for resources and its associated density-dependent selection tend to relegate most genotypes and, therefore, most populations to suboptimal climates. Although factors such as natural sampling errors, lags in adaptation from historical events (*e. g.* the Little Ice Age), or short term warming periods such as occurred in the 20th Century may be influential, the primary force driving populations into suboptimal environments appears to be competitive exclusion. The system seems to be perpetuated by high rates of gene flow that in each generation provide the fuel for the density-dependent selection that ultimately prevent most genotypes from inhabiting their optimum Rehfeldt *et al.* (1999*b*).

Seed zones and climatypes

Forest managers throughout the world are well aware that success in reforestation requires planted trees to be physiologically suited to the climate at a planting site. To help assure adaptedness in planted trees, managers limit the distance that seeds are transferred between their provenance and the planting site._In Russia, seed transfer guidelines are based on climatypes (Turesson 1925), groups of populations adapted to similar climates. The concept deals with the adaptation of trees to climate, and, consequently, our results are suitable for defining the breadth of a climatype.

In applying our results to practical problems, one should recognize that density-dependent selection and competitive exclusion have been primarily responsible for the fact that most populations occupy suboptimal climates. Nonetheless, as discussed thoroughly by Rehfeldt et al. (1999b), optimizing productivity in reforestation does not mean that populations should be transferred to climates warmer than their provenance. A local population, in fact, has been excluded from its optimum by genotypes that have higher growth potentials. Populations, therefore, should be grown in the climate where they are competitively exclusive. On average, this climate is defined by a climate-transfer distance of zero, the climate in which a population occurs naturally.

In Tables 5, 6, and 7, the difference between X_1 and X_2 quantifies a climatic interval within which the performance of a population does not differ (80% level of probability) from its optimum. Our functions suggest, therefore, that the climatic breadth of a Scots pine climatype should be about 1.2 units of the moisture index, 500 degree-days>5°C, 4°C in mean annual temperature, or 1200 degree-days<0°C (Table 5). Climatypes of *L. sibirica* and *L. sukaczewii* should encompass no more than 1 unit of the moisture index and 600 degree-days>5°C; while those for *L. gmelinii* should be about 2 units of the moisture index and 1100 degree-days<°C (Tables 6 and 7). A next step would be to use these intervals to map geographic zones on climate surfaces.

Climate-change

A comparison of Tables 8 and 9 suggests that the impact of global warming should be much different for Scots pine than for the species of larch. These differences stem largely from the fact that in Eurasia, much the same climatic gradient occupied by a single species of pine is occupied by three species of larch. It should not be surprising, therefore, that the primary impact of global warming is expected to reflect extirpation and immigration for the larch species but redistribution of genotypes in the pine.

On the short term, our models of both the pine and the larch species describe similar transient effects that are highly negative in the least severe climates but strongly positive in the most severe. While these effects tend to be offsetting, it is unlikely that positive effects on genotypes that are of innately low growth potential in contemporary climates can offset a highly negative impact on genotypes with the highest growth potentials. Consequently, the overall species-wide, short-term impacts should be largely negative in all of these species, a conclusion quite similar to those reached for lodgepole (Rehfeldt *et al.* 2001) and Scots pines (Rehfeldt *et al.* 2002) by a much different route.

Long-term evolutionary impacts of global warming described by the pine transfer functions also are essentially the same as those derived from population-specific response functions for lodgepole (Rehfeldt *et al.* 2001) and Scots pines (Rehfeldt *et al.* 2002): shifts in distributions at the margins accompanied by large gains in growth and productivity elsewhere. These gains, however, would be dependent on the presence in the novel climates of those genotypes that are the best suited. Realizing the gains, therefore, will require a redistribution of genotypes across the landscape, a process that may require more than 1000 years (Rehfeldt et al. 2002) in natural ecologic systems.

Long-term effects predicted for the species of larch primarily reflect shifts in distribution with only modest gains in growth and survival. Without being able to subdivide populations into groups of innately different growth potential, however, we are unable to assess the intraspecific adjustments necessary for adaptedness to be maintained in future climates.

Climate-transfer vs. population-specific response functions

The present results join with those of Rehfeldt *et al.* (2002) to present two very different analyses of response to climate in Scots pine. While the present analyses deal with response functions driven by climate-transfer distances, the previous were concerned with population-specific functions driven directly by climate variables. Both relate genetic responses to climate, and both led toward the same conclusions. The approaches, however, have respective strengths and weaknesses. On the one hand, response functions driven directly by climate variables provide predictions that are either or both site-specific and population-specific. Yet, their formulation requires that (1) each population is tested on many sites, and (2) the test sites are sufficiently diverse climatically to elicit highly disparate responses. Because provenance tests are costly, rarely are tests established on severe sites (cold or hot-dry) where survival would be low. Few, moreover, are established on enough sites to permit population-specific analyses. As a result, there are few species for which population-specific response functions can be contemplated.

Climate-transfer functions, therefore, appear as a reasonable alternative. As the present paper has shown, by using such functions, a chaotic assemblage of data can be brought into an order capable of yielding practical solutions to otherwise intractable problems. Their main advantage is that performance data are useful even if populations have been planted on only one site; suitable data, therefore, can come from an extremely heterogeneous mixture of provenance tests. Transfer functions, however, have weaknesses that can greatly limit their applications. First, even if the number of observations is sufficient to take into account population effects, predictions are not site-specific. Table 8 shows, for example, that predicted 13-yr heights of Scots pine populations in class 1 are the same (166 cm) for sites as diverse climatically as those in the north of European Russia, the west of central Siberia, and the north of central Siberia. Second, if population effects cannot be taken into consideration, then predictions are neither site- nor population-specific. Thus, all populations of *L. sibirica* have the same predicted height for the contemporary climate at all locations (Table 9). Although it is conceivable that problems such as these could be circumvented by working with percent change from a known starting point (*e.g.*, site index), it nonetheless seems obvious that if sufficient data are available, population-specific response functions driven directly by climate variables are superior.

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