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Height-growth response to climatic changes differs among populations of Douglas-fir: a novel analysis of historic data

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Abstract. Projected climate change will affect existing forests, as substantial changes are predicted to occur during their life spans. Species that have ample intraspecific genetic differentiation, such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), are expected to display population-specific growth responses to climate change. Using a mixed-effects modeling approach, we describe three-year height (HT) growth response to changes in climate of interior Douglas-fir populations. We incorporate climate information at the population level, yielding a model that is specific to both species and population. We use data from provenance tests from previous studies that comprised 236 populations from Idaho, Montana, and eastern Washington, USA. The most sensitive indicator of climate was the mean temperature of the coldest month. Population maximum HT and HT growth response to changes in climate were dependent on seed source climate. All populations had optimum HT growth when transferred to climates with warmer winters; those originating in sites with the warmest winters were taller across sites and had highest HT growth at transfer distances closest to zero; those from colder climates were shortest and had optimum HT growth when transferred the farthest. Although this differential response damped the height growth differences among populations, cold-climate populations still achieved their maximum growth at lower temperatures than warm-climate populations. The results highlight the relevance of understanding climate change impacts at the population level, particularly in a species with ample genetic variation among populations.

Key words: climate change response functions; genotype by environment interaction; provenance tests; provenance transfer functions; Pseudotsuga menziesii *var.* glauca.

Introduction

Recent and projected changes in climate have increased interest in the potential growth responses of forest trees to climate change. Forest trees are adapted to their past environments, and their future growth and survival will depend on their ability to modify their phenotype in response to environmental change (Matyas 1996). Some forest species exhibit large intraspecific genetic differentiation, e.g., Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). For these species, the response to climate change may vary among populations. Incorporation of population-specific information may improve models predicting species response to climate change.

Ideally, population-specific responses would be estimated from specifically designed long-term experiments. Practically, the need for answers is immediate. In forestry, provenance tests provide, to a defensible approximation, the long-term data needed (Matyas 1994). In these tests, seeds are collected from a range of known, naturally occurring seed sources and are planted into common gardens. The seed sources, which have adapted to the source area climate, are evaluated in a different climate: that of the test site. The change in climate from source area to test site can be treated as an experimental change in climate. In such tests, provenance generally refers to the location where the seeds were collected, while population refers to the individuals at that location and their descendants derived from intrapopulation pollinations.

Although the original objective of most provenance tests was to identify the best seed sources for the test site area (Matyas 1996), these data can provide insight into climate change effects. Especially when populations within species have been tested in several provenance tests at several sites, growth responses to different growing conditions can be described relative to a range of "climate change" conditions (Matyas 1994, Schmidtling 1994, Carter 1996, Rehfeldt et al. 1999, 2001, 2002). The difference between values of a given climate variable

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at the seed source and at the test site has been termed the *climatic transfer distance* (e.g., Rehfeldt et al. 2003).

Investigating the effect of transfer distances on the expression of genotype by environment interactions began with the innovative analyses of R. K. Campbell (1974), who regressed height growth of populations on geographic transfer distances. The use of transfer distances with the objective of understanding climate change effects on forest growth is more recent (Matyas 1994, 1996, Schmidtling 1994, Carter 1996, Rehfeldt et al. 1999, Wang et al. 2006, Thomson and Parker 2008, Thomson et al. 2009). In some studies, the effect of climate change has been studied using a set of populations to characterize the response of species (e.g., Schmidtling 1994, Carter 1996, Rehfeldt et al. 1999). This approach provides a reasonable set of transfer distances even when test sites number only a few. The model generated has the main advantage of providing information at the species level even when the species has been tested in a few test sites, but it lacks specificity at the population level. Such models also fail to account for the statistical correlation among observations from a given population, thus possibly violating important regression assumptions.

Other studies have taken into account evidence that some populations of some species inhabit suboptimal environments (Namkoong 1969). These studies have used population-level response functions to gain insight on potential intraspecies differences (e.g., Rehfeldt et al. 1999, Wang et al. 2006, Thomson and Parker 2008). These population response models require each population to be tested in many test sites to obtain a reasonable range of transfer distances; the responses, however, support inferences only about the populations being modeled. A recent analysis (Wang et al. 2010) considered the effects of planting-site climate and provenance climate on tree growth in common gardens. The analysis, however, concentrated on the main effects of site and provenance climate, but proved lacking in addressing genotype by environment interactions, which are expected to describe population-specific responses to change (see Matyas and Yeatman 1992, Matyas 1994, Rehfeldt et al. 1999, 2003).

We chose an alternative approach that combines all populations into one model to generate a species-level response, while also incorporating information that characterizes each population to obtain a population-specific response. This improved modeling alternative would be especially advantageous for a variety of a broad-ranging species such as interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco). Genetic variation among interior Douglas-fir populations has been shown to follow geographic clines for traits such as three-year height, time of bud set, and freezing tolerance (Rehfeldt 1989). Genetic differentiation in physiological processes such as photosynthetic rate, stomatal conductance, and carbon isotopic discrimination has also been shown to correlate to geographic clines (Zhang et al. 1993, Zhang and Marshall 1995).

Our specific objective is to model population differences in three-year height (HT, in millimeters) in response to changes in climate transfer distances of interior Douglas-fir populations. We used 236 populations to develop a general, species-level response, while adding climatic information at the population level. This latter approach accounts for population differences in growth response across the geographic window comprised by this study. We did so using a mixed-effects modeling framework that accommodates the hierarchy of the data and helps identify important sources of unexplained variation.

Methods

Data

Wind-pollinated cones were collected from natural populations of Douglas-fir occurring through northern Idaho and northeastern Washington (region 1), western Montana (region 2), central Idaho (region 3), and Montana and Idaho near the Continental Divide (region 4). Seedlings obtained from these cones have been compared in four previous studies (Rehfeldt 1979, 1982, 1983, 1988). In total, seeds had been collected from a total of 236 seed sources (hereafter *populations*) that were chosen to represent the distribution of the interior variety in the Inland Northwest (between latitudes 43° and 49° N, longitude 118° to 110° W, and comprising an elevation range of 680–2500 m; Fig. 1). Within each study, the seedlings from each population were grown in three to four common-field plantings, the location of which differed in latitude, longitude, and elevation (Table 1). The studies were conducted in different years, and they tested a different set of populations, except for 16 populations planted in more than one study. Within each test location, plantings had been established with and without additional treatments (e.g., shade, moisture, competition), but for this analysis we used only those without treatments, reducing the number of plantings per test location to one or two. Within each planting, seedlings representing the populations were planted in row plots (10–12 seedlings) in each of two or three blocks (depending on the study) in a completely randomized block design. Only the mean height of seedlings within plots was available for this analysis. This study focuses on the three-year height growth (HT, in millimeters). The data are summarized in Table 1 and Fig. 1.

Climate normals for the period 1961 to 1990 were calculated for each seed source and for each of the test locations using the thin-plate spline surfaces developed for the western USA by Rehfeldt (2006). This model uses Hutchinson's (2000) thin-plate splines upon records from >2700 weather stations to estimate climate for specific locations for which latitude, longitude, and elevation are known. All 17 climate variables provided by the model were used in this analysis (Appendix A and

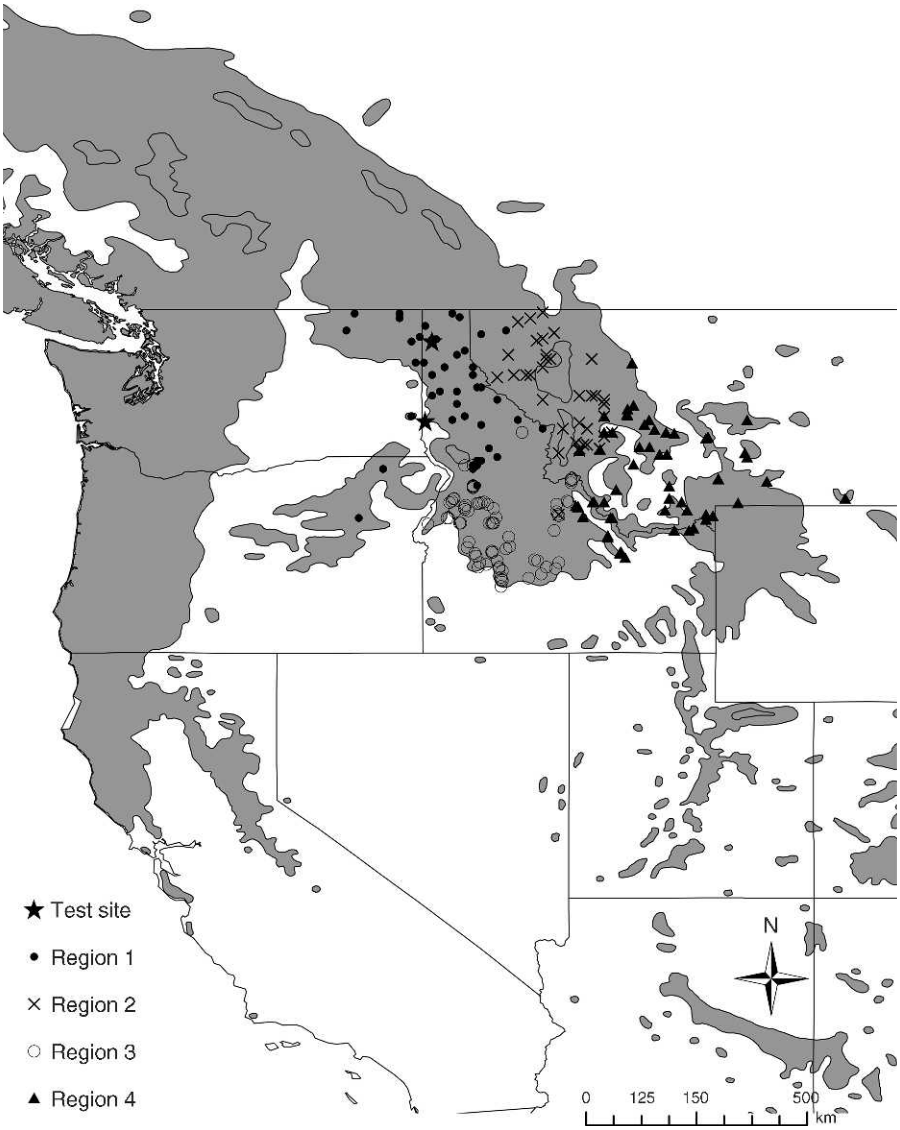


FIG. 1. Geographical location of the Douglas-fir populations from Idaho, Montana, and eastern Washington, USA, included in this study, grouped by region, and geographical location of the test sites. Little's (1971) map of the Douglas-fir distribution is shown in gray. Note that four of the test sites differed in elevation (see Table 1).

Rehfeldt 2006). These variables were derived from normalized monthly means and attempted to provide biologically relevant climate descriptions based on various means of weighting and summarizing raw climate data.

Analysis

We develop a conceptual diagram (Fig. 2) using as a foundation the diagram by Monserud and Rehfeldt (1990: Fig. 3). Monserud and Rehfeldt (1990) illustrate how phenotype is determined by genetic and environmental effects. The long-term environment shapes the genetics of trees and populations. In turn, genetics, the short-term environment, and their interaction determine the phenotype, which in this study is expressed as the realized HT. They also point to the relationship between short-term environment and long-term environment, recognizing that as short-term environment changes, so does the long-term environment. In well-adapted populations, the maximum realized growth occurs when the short-term climate is similar to the long-term climate.

In the context of global climate change, predictions suggest that the short-term environment may depart substantially from the long-term environment that has shaped the genetics. We argue that the magnitude of this departure will be an important determinant of the realized growth (Fig. 2). We hypothesize that changes in realized growth due to this departure can be quantified by the difference between short- and long-term climates. We use climate normals at seed source as a proxy for

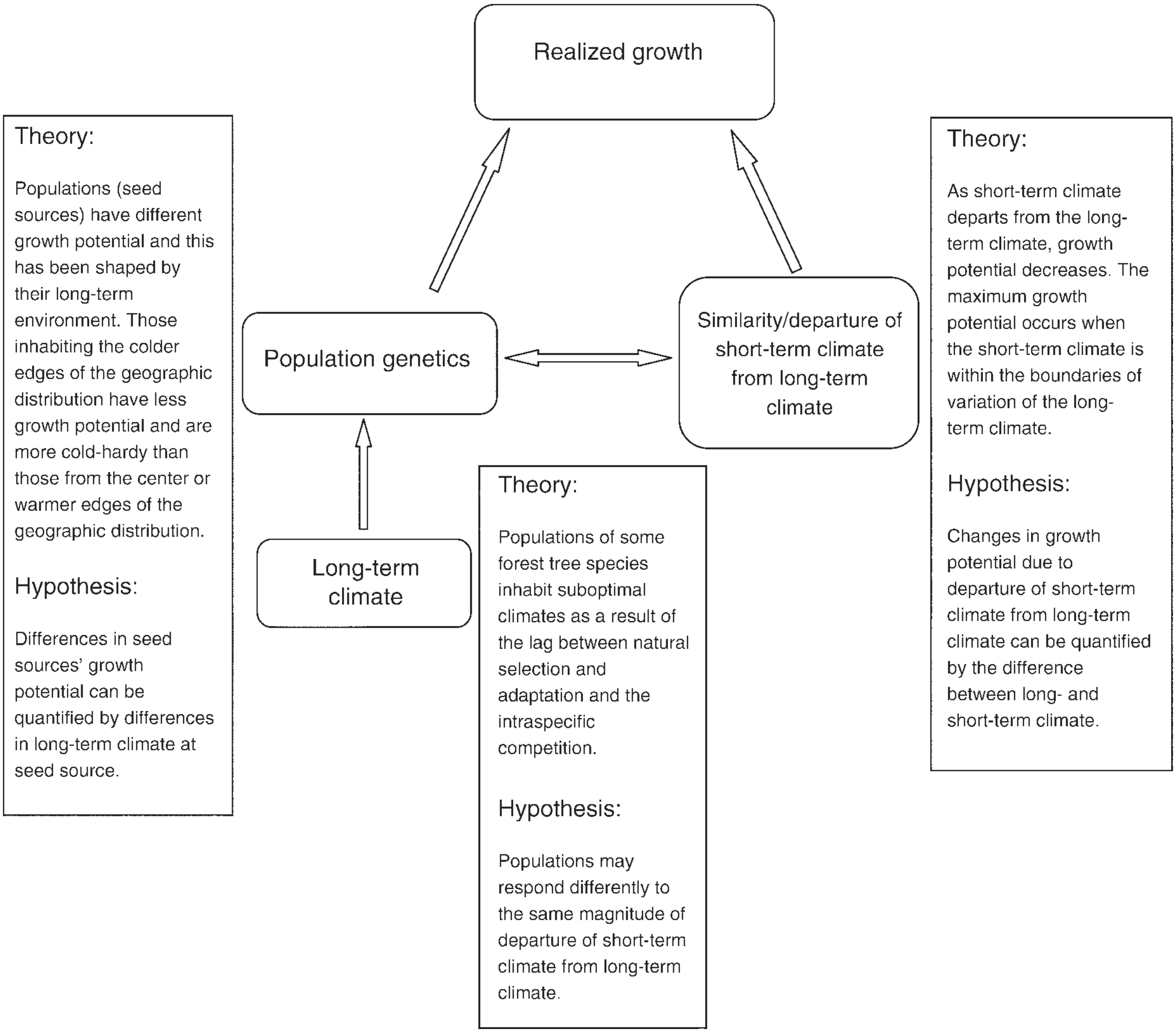
TABLE 1. Summary of the provenance test data used in the studies.

					Region‡				HT (mm)	
Study†	Test locations (longitude and latitude; elevation)	No. plantings	No. blocks	No. seed sources	1	2	3	4	Mean	SD
1	Moscow (116.97° W; 46.73° N; 811 m)	1	2	50	X				219.5	33.7
1	PREF (116.83° W; 48.35° N; 726 m)	1	2	50	X				193.6	36.7
1	TARLAC (116.83° W; 48.35° N; 1450 m)	2	2	50	X				130.9	36.1
2	M2 (116.83° W; 48.35° N; 1150 m)	1	2	54	X	X	X	X	116.7	23.4
2	RESERV (116.83° W; 48.35° N; 800 m)	1	2	54	X	X	X	X	154.1	36.0
2	PREF (116.83° W; 48.35° N; 726 m)	1	2	54	X	X	X	X	171.6	40.9
2	TARLAC (116.83° W; 48.35° N; 1450 m)	2	2	54	X	X	X	X	116.6	23.0
3	Moscow (116.97° W; 46.73° N; 811 m)	1	2	74	X		X		162.1	61.7
3	PREF (116.83° W; 48.35° N; 726 m)	1	3	74	X		X		172.7	55.0
3	TARLAC (116.83° W; 48.35° N; 1450 m)	1	3	74	X		X		133.3	22.9
4	Moscow (116.97° W; 46.73° N; 811 m)	1	3	77	X	X	X	X	160.9	69.9
4	PREF (116.83° W; 48.35° N; 726 m)	1	3	77	X	X	X	X	202.5	49.9
4	TARLAC (116.83° W; 48.35° N; 1450 m)	1	3	77	X	X	X	X	108.4	27.1

Notes: Data include test locations, number of plantings within test location, number of blocks within planting within test location, number of populations (seed sources) evaluated, regions tested in each study, and three-year height (HT) for the populations in this study.

† Study: 1, Rehfeldt (1979); 2, Rehfeldt (1982); 3, Rehfeldt (1983); 4, Rehfeldt (1988).

‡ An X indicates that the study tested one or more populations of the following regions: 1, North Idaho and northeast Washington; 2, western Montana; 3, central Idaho; 4, Montana and Idaho near the Continental Divide.



Theory:

Populations (seed sources) have different growth potential and this has been shaped by their long-term environment. Those inhabiting the colder edges of the geographic distribution have less growth potential and are more cold-hardy than those from the center or warmer edges of the geographic distribution.

Hypothesis:

Differences in seed sources' growth potential can be quantified by differences in long-term climate at seed source.

Theory:

Populations of some forest tree species inhabit suboptimal climates as a result of the lag between natural selection and adaptation and the intraspecific competition.

Hypothesis:

Populations may respond differently to the same magnitude of departure of short-term climate from long-term climate.

Theory:

As short-term climate departs from the long-term climate, growth potential decreases. The maximum growth potential occurs when the short-term climate is within the boundaries of variation of the long-term climate.

Hypothesis:

Changes in growth potential due to departure of short-term climate from long-term climate can be quantified by the difference between long- and short-term climate.

FIG. 2. The conceptual framework used for model development.

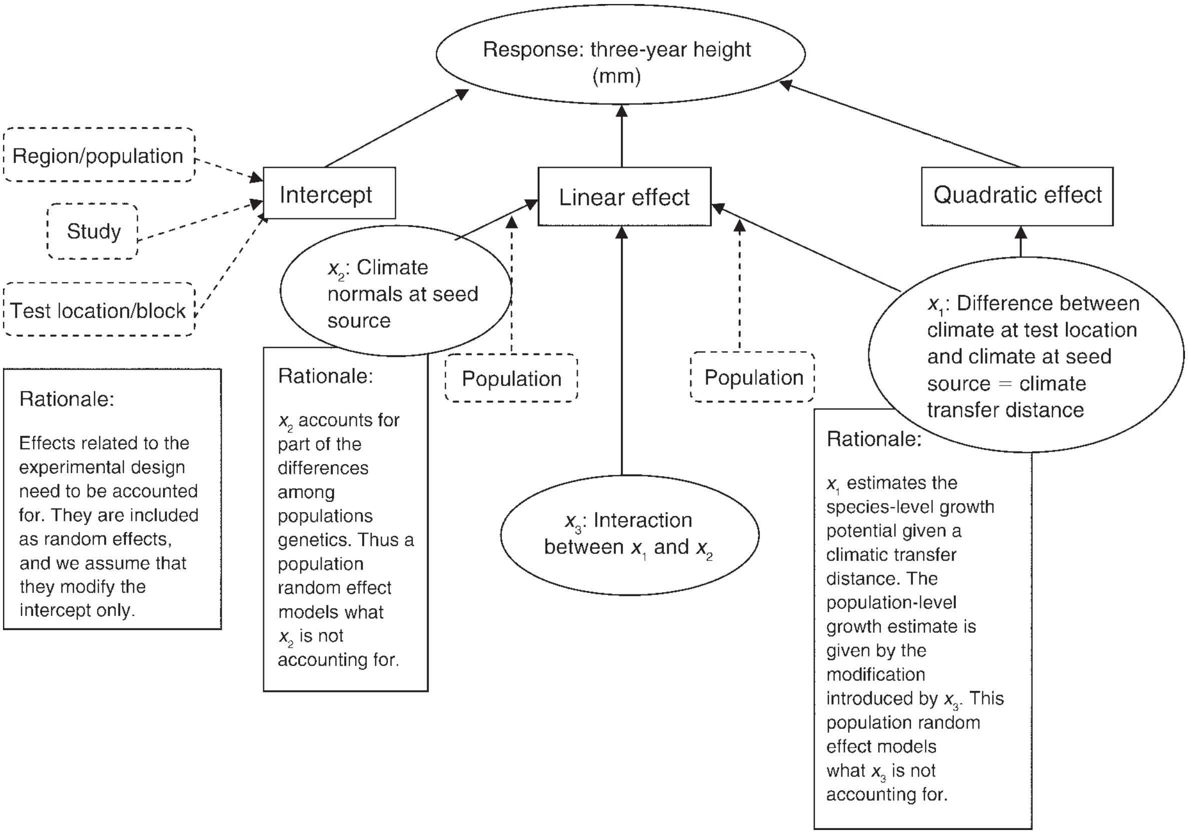


FIG. 3. Graphical summary of the fitted linear mixed-effects quadratic model. Oval shapes indicate fixed effects, and rectangular shapes indicate random effects. Climate variables x_1, x_2, and x_3 are described in *Methods: Analysis*, Eq. 1.

long-term climate, and climate normals at the test location as a proxy for short-term climate. We calculate transfer distance as the difference between a given climate variable at the test location and that at each population's point of origin.

Inland Douglas-fir populations have been shown to differ in their growth ability. When grown in common gardens, those inhabiting the colder parts of the geographic distribution grow less and are more cold-hardy than those from the center or warmer portions of the geographic distribution (Rehfeldt 1989). We hypothesize that those differences can be reasonably quantified by differences in climate at the seed source, and thus we use climate at seed source to incorporate population-level specificity into the model.

Given evidence regarding populations of some forest tree species inhabiting suboptimal climates (e.g., Namkoong 1969), we hypothesize that populations may respond differently to the same magnitude of departure of short-term climate from long-term climate. We account for this population difference by including an interaction between populations and the climatic departure.

We model population HT as a function of climatic transfer distance, climate at seed source, and their interaction using a linear mixed-effect model of quadratic form. We considered a mixed-effects modeling approach to be optimal in this situation because by combining fixed and random effects, we were able to attain our model objectives while accommodating the complex structure of the data. We defined the fixed effects as those with well-defined and measurable levels that were of interest when explaining variation of the response variable; i.e., climate transfer distance, climate at seed source, and their interaction.

We incorporated random effects in two ways: (1) to provide structure for potential sources of variation not explained by the fixed effects, and (2) to account for the structure of the data related to the experimental design. An example of the former case is the inclusion of a population random effect to affect the fixed-effect climate at seed source. The two effects jointly account for differences among populations. The fixed effect provides an observed difference between the populations, and it likely accounts for part of the genetic differences among populations (Fig. 2). By including a population-level random effect, we provide structure for population-level variation that is not explained by the climate at seed source fixed-effect variable. The omission of the random effect would lead to unacceptable within-population correlation, which violates important regression assumptions. The same rationale was used to include a population-level random effect affecting the climatic transfer distance.

Table 1 presents a summary of the structure of the data resulting from collating data from different studies and each study's experimental design. Random effects accounting for this structure were incorporated as follows. Each study was conducted during a different period of time, but within the time period for the calculated climatic normals. This suggested that a random effect at the study level was necessary. Random effects for test location, planting within test location, and block within planting within test location were included to account for hierarchical within-group correlation. Because some of the test locations were included in multiple studies, the test location random effect was crossed with the study random effect. To accommodate the fact that each study tested a set of populations originally from the same geographic region, and a few that were from other regions and planted in more than one study, we included a random effect at the region level crossed with the study random effect. Finally, a population-level random effect was nested within region. A graphical summary of the fitted linear mixed-effects model is presented in Fig. 3. The model form was

$$\begin{aligned} y_{i(j(k(lmn(q))))} = {} & (b_0 + u_{1m} + u_{2n(q)} + u_{3j(k(lm))} + u_{4k(lm)} \\ & + u_{5l} + u_{6q}) + (b_1 + u_{7n})x_{1nl} + b_2 x_{1nl}^2 \\ & + (b_3 + u_{8n})x_{2n} + b_4(x_{1nl} \times x_{2n}) \\ & + \varepsilon_{i(j(k(lmn(q))))} \end{aligned} \qquad (1)$$

where y = three-year height for the ith observation in the jth block in the kth planting in the lth test location and the mth study and of the nth population in the qth geographic region; x_{1nl} = climate transfer distance for the nth population at the lth test location; x_2 = climate at seed source for the nth population; j = block index; n = population index; k = planting index; l = test location index; m = study index; q = geographic region index; $b_0 - b_4$ are fixed-effects parameters; $u_1 - u_8$ are random effects.

The process used to select variables and identify candidate models proceeded as follows and is summarized in Fig. 4. Seventeen climate transfer distance variables were screened to identify those with the strongest quadratic response between HT and the climate transfer variable (Appendix A and Rehfeldt 2006). Quadratic functions have been used in previous studies for representing growth responses to climate transfer distances (Schmidtling 1994, Carter 1996, Rehfeldt et al. 1999, Wang et al. 2006). Because the original objectives of these common garden tests were to understand genetic differences among populations, test locations were not established in harsh sites. For this reason, a limitation in these data is lack of information for transfer distances where height is close to or equal to zero (roots of the quadratic function). An additional limitation was that the three-year-old trees were under snow for much of the winter at the coldest test sites and, therefore, were not exposed to the full vicissitudes of the high-elevation climate. The screening process allowed identification of the variables for which the range of transfer distances comprised enough information to allow the fitting of the quadratic response of HT to the climate transfer distance variable. Variables were evaluated with a simple linear model of quadratic form. We chose the eight with the lowest P value in the significance test for their quadratic term (t test, $P < 0.0001$ for the five cases). We did not explore combinations of two or more variables for two reasons: (1) most of these 17 variables are highly correlated (results not shown), and (2) the structure of the data was accommodated by including several random effects with the consequent large number of parameters in the model.

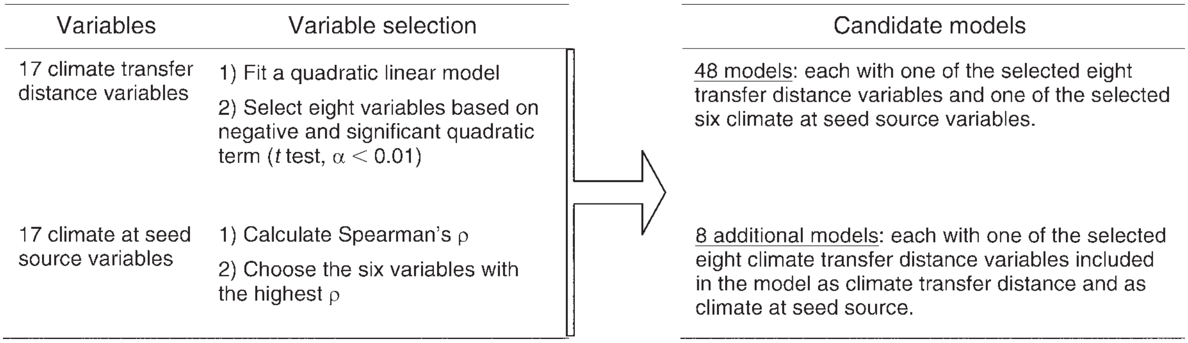
To identify the climate variable at seed source that best described differences among populations, we calculated correlations between each climate variable at seed source and the mean HT of populations across test locations. In other words, we looked for the climate variable of the seed source that best explained the overall performance of the populations. We used Spearman's rank correlation to select the six variables that presented the highest correlation between HT and climate.

In total 56 different models were evaluated. The competing model versions were compared using Akaike's information criterion (AIC [Akaike 1973]). For the selected model, the statistical significance of the random effects was assessed using likelihood ratio tests. The statistical significance of the fixed effects in the selected model was assessed by calculating 95% nonparametric bootstrap confidence intervals for the parameter estimates using 1000 bootstrap replications. The bootstrap intervals were based on resampling the populations, rather than the plots. All the models were fitted with the R package lme4 (Bates and Maechler 2009).

Finally, the best model was evaluated by estimating the root mean squared predicted error (RMSPE) within climate transfer distance classes using the 0.632 bootstrap (Efron and Tibshirani 1997). The 0.632 bootstrap is an efficient version of cross validation, as the RMSPE estimate is taken as the weighted average of the RMSPE calculated on the full data set (analogous to the fitting data set in cross validation) and the RMSPE calculated on the leave-one-out data (analogous to the testing data set in cross validation). All analyses were performed in the statistical environment R (R Development Core Team 2008).

RESULTS

The climate at the seed source was correlated with three-year height. Climate variables that presented the highest Spearman rank correlation with HT were Julian date of the last spring freeze (SDAY, $\rho = -0.32$), degree days <0°C calculated with daily minimum temperatures



Variables	Variable selection
17 climate transfer distance variables	1) Fit a quadratic linear model 2) Select eight variables based on negative and significant quadratic term (*t* test, $\alpha < 0.01$)
17 climate at seed source variables	1) Calculate Spearman's ρ 2) Choose the six variables with the highest ρ

Candidate models

48 models: each with one of the selected eight transfer distance variables and one of the selected six climate at seed source variables.

8 additional models: each with one of the selected eight climate transfer distance variables included in the model as climate transfer distance and as climate at seed source.

FIG. 4. Diagram of the variable selection process and the resulting candidate models.

(MINDD0, $\rho = -0.306$), Julian date when the sum of degree-days >5°C reaches 100 (D100, $\rho = -0.314$), mean annual temperature (MAT, $\rho = 0.308$), frost-free period in number of days (FFP, $\rho = 0.308$), and sum of degree-days >5°C during the growing season (GSDD5, $\rho = 0.310$). By all of these measures, populations from colder climates grew less than those from warmer climates.

Early height growth was influenced by changes in climate transfer distance. When these variables were related to HT using quadratic functions, the variables with the highest significance of the quadratic term (*t* test, $\alpha = 0.0001$) were all related to temperature.

Of the 56 evaluated models (Eq. 1), the two models that best fit the data (using AIC as selection criterion) included as predictor variables (1) the minimum temperature of the coldest month (MMIN) as transfer distance and minimum temperature of the coldest month at seed source (AIC = 20 603); and (2) the mean temperature of the coldest month (MTCM) as transfer distance and mean temperature of the coldest month at seed source (AIC = 20 647).

In both models, the interaction between the climate transfer distance and the climate at seed source variable was statistically significant (i.e., confidence interval for this parameter entirely below zero, $\alpha < 0.05$), which suggests a population-specific response. Fixed effects of both models indicate that populations from warmer climates have maximum growth when transfer distance is positive (i.e., moved to warmer winters) and close to zero, whereas populations from colder climates have maximum growth when transfer distance is positive by several degrees. The fixed effects of the model including MMIN, however, predicted zero height for a transfer distance of zero for populations with MMIN at seed source lower than the data set's average MMIN. This implausible result stems from the lack of significance and high standard error for the linear transfer distance term, both of which add uncertainty to the predictions of where along the *x*-axis a population should attain maximum growth. Also, the standard deviation of the population-level random effect on the linear transfer distance was high; we speculate that this also contributed to this model's poor behavior. Therefore, we focus our discussion on the model incorporating MTCM, but nonetheless present model parameters and their corresponding 95% bootstrap confidence intervals for the model incorporating MMIN in Appendix B.

Parameter estimates for the model using MTCM as a transfer distance and as an effect of the seed source and their 95% bootstrap confidence intervals are presented in Table 2. In this model a random effect for the test location was not necessary according to the likelihood ratio test ($\alpha = 0.05$). Diagnostic plots and the R script for this model are presented in Appendix C.

We used all data within our geographic window from the Forest Inventory Analysis Program (Alerich et al. 2004, Bechtold and Patterson 2005) plots containing Douglas-fir trees (6367 plots) to assess how well the populations in the fitting data set represented the natural geographic distribution in terms of MTCM, latitude, longitude, and elevation range. According to the chosen variables, the fitting data set is an adequate representation of the occurrence of Douglas-fir in our area of study. The average MTCM is very similar for both data sets (−6.9°C and −6.3°C for fitting and FIA data sets, respectively), and much of the range in MTCM is also represented in the fitting data set.

Fixed-effects responses for a set of five hypothetical populations (Fig. 5) show that maximum growth occurs at positive MTCM transfer distances. That is, maximum growth occurs when populations are transferred to climates with warmer winters than that of the seed source. The populations differ, however, for the transfer distance at which maximum HT occurs. For populations originating in locations with warm winters (e.g., MTCM = −1°C), maximum HT occurs close to transfer distance zero. For populations from locations with the coldest winters (e.g., MTCM = −9°C), however, maximum HT occurs at larger positive transfer distances. This figure illustrates the interaction of genotype and environment that could be used to describe and predict differential adaptive responses of plants to a change in climate.

Random effects in our model included study, region, population, planting, and block. As indicated by their high standard deviations, these effects captured a portion of the variation in three-year height. (See the

TABLE 2. Parameter estimates, 95% approximate confidence intervals, and correlation information for the chosen model (see *Methods: Analysis*, Eq. 1).

Parameter	Parameter estimate	Confidence intervals ($\alpha = 0.95$)	
		Lower	Upper
*b*0 (intercept)	373.97	320.8	415.6
*b*1 (MTCM.trds)†	6.799	3.256	11.49
*b*2 (MTCM.trds^2)†	−3.726	−4.759	−2.355
*b*3 (MTCM)	38.52	31.37	43.55
*b*4 (MTCM.trds × MTCM)†	−3.602	−4.744	−2.073
SD (*u*1, study)	46.67		
SD (*u*2, population)	45.30		
SD (*u*3, block)	8.87		
SD (*u*4, planting)	17.46		
SD (*u*6, region)	26.26		
SD (*u*7, population linear-MTCM.trds)	5.99		
SD (*u*8, population linear-MTCM)	5.51		
SD (ε)‡	21.01		
Cor(*u*2, *u*7)	0.89		
Cor(*u*2, *u*8)	0.99		
Cor(*u*7, *u*8)	0.83		

Notes: Given the selection of a fixed number of the possible variables at each of the two stages of model development, not all possible models resulting from all possible variable combinations were evaluated. This may potentially result in the confidence intervals for the parameter estimates being at a lower confidence level than $\alpha = 0.05$.

† MTCM.trds is mean temperature (°C) of the coldest month transfer distance; MTCM is mean temperature (°C) of the coldest month at seed source location.

‡ The parameter ε is the error or innermost residuals.

SD estimates in Table 2.) Random effects of a given grouping level (e.g., study) are adjustments around a parameter estimate of a fixed effect that improve the prediction for the observations within the grouping level. They are also unobservable variables; i.e., we cannot estimate or measure their magnitude in a new subject (e.g., the "study" effect of a new study). When a random effect in the model is needed we have identified

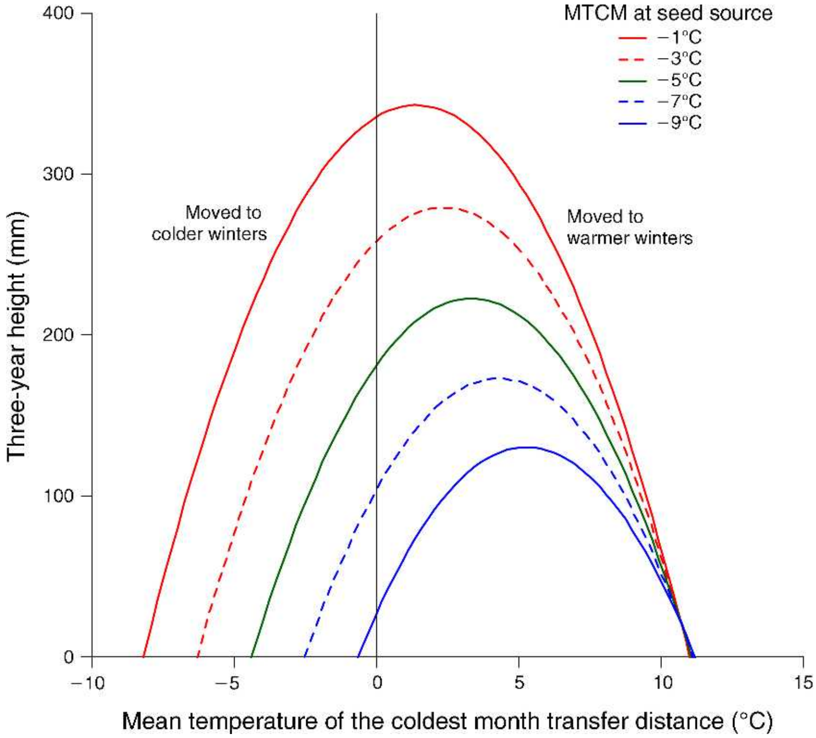


FIG. 5. Illustration of the model's fixed-effects predictions for a set of five values of mean temperature of the coldest month (MTCM) at seed source.

TABLE 3. Root mean-square prediction error (RMSPE [mm]) and mean height (mm) by mean temperature of the coldest month transfer distance (MTCM.trds) class for the best model (Table 2).

MTCM.trds class (°C)	N†	Mean height (mm)	RMSPE (mm)	RMSPE (%)
−7 to −5	4	145.3	48.33	33.26
−5 to −3	47	147.9	40.51	27.39
−3 to −1	213	135.8	36.29	26.72
−1 to 1	471	146.2	38.55	26.37
1 to 3	585	157.5	39.86	25.31
3 to 5	493	164.1	47.40	28.89
5 to 7	283	167.5	66.77	39.86
>7.1	126	121.3	57.18	47.14

† N = number of observations.

a source of variation, for example the "study" effect, but we do not know which attributes of that effect are responsible for that variation. For example, the "study" effect could have arisen because of different test years or differences of planting management. For predictions in new observations only the fixed effects are used.

In this model, the Pearson correlation coefficient between fixed-effects predictions and observations was 0.59 ($\alpha = 0.05$), while the correlation coefficient between the model's prediction using fixed and random effects and the observations was 0.93 ($\alpha = 0.05$). The difference between those illustrates that part of the variation was captured by the random effects. The SD of the random effects indicates the magnitude of the effect on the fixed effect they adjust. The larger the SD, the larger the variation explained by the random effect; the smaller the SD, the better the fixed-effect parameter estimates represent all populations. The models with the best prediction ability are those with the smallest SD of the random effects.

For explanatory purposes the random effects help identify important sources of variation that need further exploration to fully understand the response. The three population-level random effects were significant, and the population random effect affecting the intercept (Fig. 3, Table 2) was the second largest in terms of SD (the largest was the study random effect). Therefore, quantifying the differences among the genetics of populations is relevant to understanding the HT response to changes in climate.

To evaluate our model's predictive ability, we calculated RMSPE by MTCM transfer distance classes and present the RMSPE in the observed units (millimeters) as well as expressed as the percentage of the mean HT for each of the MTCM transfer distance classes (Table 3). The RMSPE was between 25% and 27% of mean HT for transfer distances between −3°C and 3°C, and increased as the absolute value of the transfer distances increased.

DISCUSSION

The HT-growth responses to changes in MTCM were population-specific because the interaction between MTCM transfer distance and MTCM at seed source was statistically significant ($b4$; Table 2). Optimum transfer distance differed depending on the MTCM at seed source of the population. According to our model, Douglas-fir populations originating at the average MTCM for our geographic window (−6.3°C) had optimum growth at MTCM transfer distance equal to 4.0°C. Those from warmer climates had optimum growth closer to transfer distance zero. For example, maximum HT of a population from a location with a MTCM of −1°C occurs at a transfer distance equal to 1.4°C. Populations from colder climates had optimum growth when moved into climates that had warmer winters by several degrees Celsius (e.g., maximum HT of a population from a location with a MTCM equal to −9°C occurs at −3.7°C, 5.3°C warmer than the source climate). All populations, therefore, inhabit suboptimal climates, but cold populations especially so. Note that we define suboptimal here relative to the climate at which a particular population would grow best; other definitions can be conceived.

The fact that populations inhabit suboptimal environments has been previously noted by Namkoong (1969) and documented for species such as *Pinus banksiana* Lamb. (Matyas and Yeatman 1992, Thomson and Parker 2008); *Abies balsamea* L. and *Acer rubrum* L. (Carter 1996); *Pinus contorta* Dougl. ex Loud. (Rehfeldt et al. 1999, 2001); and *Pinus sylvestris* (Rehfeldt et al. 2003). Our analysis suggests that during early growth of interior Douglas-fir populations, there is also a differential response depending on the direction of the transfer. Including information at the population level in the species-level response enabled the detection of such differences and highlights the need for population-specific responses when predicting early growth under climate change of a variety such as interior Douglas-fir.

Across test locations, populations from climates with lower winter temperatures (lower MINDD0) and shorter growing seasons (larger D100, larger SDAY and shorter FFP) grew less than did those from warmer climates. The correlation between climate at seed source and population HT confirms the well-documented trade-off between cold tolerance and growth rates in Douglas-fir (Rehfeldt 1989, Howe et al. 2003, St. Clair 2006). Populations with high growth potential usually originate in milder climates but have lower freezing tolerance, whereas those originating from colder environments grow less and are more frost tolerant (Rehfeldt 1991).

In the final model, a proportion of variation was accounted for by the random effects and therefore remains unexplained (Tables 2 and 3). This was expected because data from disparate studies were combined, and information detailing any differences in test installation and management were not available, and, therefore, could not be included as fixed effects. Standard deviations of the random effects on the intercept were largest for study and population. The former may be explained by weather differences during the study years. This suggests that a temporal resolution of climate finer than the one used in this analysis may improve characterization of climate transfer distances and thus improve the model's predictive ability. The large SD of the population random effects indicates that the MTCM at seed source needs to be supplemented with additional population-level information to better capture the populations' genetic differences (Figs. 2 and 3, Table 2). The population-level fixed (MTCM at seed source and interaction) and random effects highlight the importance of population differences in understanding the HT response to climate changes. Including such information as fixed effects in future work will improve predictions of climate change effects.

Our modeling approach provides several innovations for elucidating genetic responses of forest trees to climate. First, the use of mixed-effects models made possible the use of historic data because it allowed accounting for the within-group (i.e., study, region, etc.) correlations that were part of the original design and that were generated by combining studies. Second, each population was tested in only three to four locations; this would make it unreliable to fit a response for each population. By using a mixed-effects model, we were able to draw from the information in all populations, and thereby generate a broad range of transfer distances, to describe the overall species-level HT response. This was attained without losing population-level specificity because climate at seed source was included as a fixed effect. The result was a model capable of explaining the different populations' HT response to changes in climate as measured by MTCM transfer distances. With this approach, the population-level information is incorporated directly into the species-level response function, and can thus be readily applied to other localities within our geographic window.

We note that our model does not account for the effects of potential changes in precipitation. None of the precipitation-related variables were among the variables most strongly related to HT in this study. We note that even though all plantings were irrigated once or twice in August when the seedlings showed signs of moisture stress, the plantings used in this study were not continuously irrigated. We argue that it is unlikely that these August irrigations completely explain the lack of correlation between HT and the precipitation-related variables. According to Matyas (1996), precipitation seems to be a minor factor in shaping intraspecific adaptation to climate. This does not imply that precipitation is unimportant at the species level. To the contrary, studies of species–climate relations suggest (e.g., Stephenson 1990, Rehfeldt et al. 2006) that the combination of temperature and moisture seems to determine whether a species occurs in a given environment. Consequently, our model is conditioned in its application by the climate being suitable for interior Douglas-fir in terms of temperature and moisture. We also note that empirical analyses such as ours tacitly ignore potential impacts on growth of changes in atmospheric CO_2 concentrations accompanying climate change. Lastly, we note that the use of a quadratic function imposes symmetry about the optimum transfer distance that may not describe accurately responses of all populations. The use of nonsymmetrical functions may be worth exploring in data sets with a less complex structure (see Rehfeldt et al. 2003).

Our model provides useful information on the impacts of a climate change on the growth of existing forests. The concept of assisted migration (e.g., McLachlan et al. 2007) is being discussed as a management option for establishing subsequent generations genetically suited to climates of the future. While response functions have been viewed as a tool to select populations better suited for future climates, we note that models such as ours may provide useful insights on the effects of changes in climate on early growth and hence on regeneration and survival. However, considerable additional information on ecologic adaptation of populations is required before implementing programs of assisted migration.

Conclusions

The model showed a population-specific response of early growth (three-year height) to changes in climate. Optimum transfer distance differed depending on the MTCM at seed source of the population. Seed sources from warmer climates had optimum growth at transfer distances close to zero, whereas populations from colder climates had optimum growth when moved into much warmer climates. Nonetheless, seed sources from colder climates still have colder temperature optima for height growth than do seed sources from warmer climates. Including climate at seed source is a key to understanding climate change impacts. Winter temperatures, as reflected in the population-specific MTCM transfer distance at which the optimum three-year height occurred, strongly influence the differential responses of inland Douglas-fir populations to a change in climate. The analysis of data from provenance tests provides preliminary information regarding the effects of climate change on currently growing forests. However, because most provenance tests were established with objectives other than eliciting responses to climate, they have limitations, the greatest of which are the relatively narrow range of transfer distances present in a given test site, and the lack of tests located at either the thermal or xeric limits of the species geographic distribution.

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SUPPLEMENTAL MATERIAL

Appendix A

A list of climate variables calculated by the Rehfeldt climate model (*Ecological Archives* A022-009-A1).

Appendix B

Parameter estimates, 95% approximate confidence intervals, and correlation information for the model including minimum temperature of the coldest month as the transfer distance variable and as the climate-at-seed-source variable (*Ecological Archives* A022-009-A2).

Appendix C

Diagnostic plots and R script for the selected model (Eq. 1 and Table 2 of the article) (*Ecological Archives* A022-009-A3).