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ORIGINAL ARTICLE

Ecological impacts and management strategies for western larch in the face of climate-change

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Abstract Approximately 185,000 forest inventory and ecological plots from both USA and Canada were used to predict the contemporary distribution of western larch (*Larix occidentalis* Nutt.) from climate variables. The random forests algorithm, using an 8-variable model, produced an overall error rate of about 2.9 %, nearly all of which consisted of predicting presence at locations where the species was absent. Genetic variation among 143 populations within western larch's natural distribution was predicted from multiple regression models using variables describing the climate of the seed source as predictors and response data from two separate genetic tests: 1) 15-year height at a field site in British Columbia, Canada, and, 2) two principal components of 8 variables describing growth, disease tolerance, and phenology of 6-year-old trees in a test in Idaho, USA. Presence and absence of the species and genetic variation within the species were projected into future climates provided by three General Circulation Models and two scenarios. Although the projections described pronounced impacts on the species and its populations, concurrence among the six projections pinpointed areas where the probability would be high that the future climate would be suitable for western larch. Concurrence among projections also was used to locate those sources of seed that should be best attuned genetically to future climates. The procedures outline a logical approach for developing management strategies for accommodating climate-change while taking into account the variability imposed by the differences among climatic estimates.

Keywords Bioclimate models · Mapped genetic variation · Seed zones · Seed transfer guidelines · Climate responses · Climatic niche

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1 Introduction

Over the last decade, the recognition of anthropogenic induced changes in climate has resulted in a dramatic increase in research focused on documenting and describing biotic responses to a rapidly warming climate (Parmesan 2006). Statistical and mechanistic models have been utilized to describe species' bioclimate relationships and model responses to climate-change in biomes (Prentice et al. 1992; Monserud et al. 1993; Rehfeldt et al. 2008) and ecosystems (Nitschke and Innis 2008), species (e.g. Rehfeldt 2006; McKenney et al. 2007; Tchebakova et al. 2005, 2010; Gómez-Mendoza and Arriaga 2007; and Iverson et al. 2008), and populations (Rehfeldt 2004; Tchebakova et al. 2005; Wang et al. 2006; St Clair and Howe 2007). These models have proven to be effective in describing contemporary distributions and predicting future distributions from climate-change scenarios. Their projections suggest in general that a wholesale geographic redistribution of the vegetation will be required to reestablish a semblance of equilibrium between the vegetation and climate by the end of the century. Yet, one of the weaknesses in much of this work centers on their inability to account effectively for species' intrinsic abilities to respond to climate change (Thuiller et al. 2008); life history characteristics, adaptive strategies, population genetic structure, and patterns of genetic variation are commonly ignored.

Climate is generally recognized as the primary factor controlling plant distributions (e.g., Woodward 1987), largely through edaphoclimatic interactions that function as selection agents to mold systems of genetic variability (White et al. 2007, p. 207). Responses to selection thus determine the adaptive strategy, genetic architecture, and dispersal and establishment rates that interact to control the adjustment and adaptation to a changing climate (Ackerly 2003; Davis and Shaw 2001; Davis et al. 2005; Savolainen et al. 2007; Aitken et al. 2008). Consequently, without basic genetic knowledge, land managers lack science-based information fundamental to making informed decisions. In forestry, for instance, biologically sound conservation programs require an assessment of adaptedness of populations to a changing climate. Managers must also adjust seed transfer guidelines and seed zone boundaries to assure that planting stock remains physiologically suited to the climate of planting sites. Topics dealing with seed zones, seed transfer guidelines, and reforestation are discussed thoroughly elsewhere (e. g., Morgenstern 1996; White et al. 2007). In short, seed zones refer to geographic subdivisions of a species' distribution within which seed is collected and planted; seed transfer refers to the distance that seeds or planting stock is moved from their origin to the planting site. When properly applied, both techniques ensure acceptable growth and adaptation of planted trees.

In this paper, we assess the potential impacts of a changing climate on western larch (*Larix occidentalis* Nutt.), taking into consideration ecologic and genetic responses. The results are used to illustrate management strategies for accommodating a change in climate (see also Rehfeldt 2004). The term 'population' is used to reference the individuals and their descendants growing at a specific geographic location.

Western larch is the most productive of the three *Larix* species native to North America. It is most prominent in the upper Columbia River Basin of southeastern British Columbia (B.C.) and in northwestern Montana and adjacent Idaho but also occurs along the east slopes of the Cascade Range in Washington and Oregon (Fig. 1). This region is characterized by high, rugged mountains and narrow intermountain basins. Even though the distribution of this species is relatively small in comparison to most forest trees (see Little 1971), western larch is an ecologically and commercially important tree species, so much so in fact, that breeding programs have been in place in the USA and B.C. since the early 1980s (Jaquish et al. 1995). Our region of study (Fig. 1) includes the contemporary distribution of western larch plus the region to the north where the future climate may be suitable (see Jump et al. 2009).

In western larch, genetic variation in quantitative traits involving growth (e.g., tree height, annual height increments), phenology (e.g., timing of bud burst and bud set) and adaptation (e.g., tolerance to cold, disease resistance) is abundant among populations, among families within populations, and within families (e.g. Joyce 1985; Rehfeldt 1982, 1992; Zhang and Fins 1993; Zhang et al. 1994; Zhang and Marshall 1994). Populations tend to be differentiated according to the relative mildness of the climate; those native to warm and moist climates tend to have the highest growth potential, highest tolerance to needle diseases, and lowest tolerances to winter cold. Yet, clines in genetic variability (see Morgenstern 1996) are of only modest slope; populations on average must be separated by about 400 m in altitude before genetic differentiation becomes a reasonable possibility. Molecular genetic variation in allozymes (Jaquish and El-Kassaby 1998; Fins and Seeb

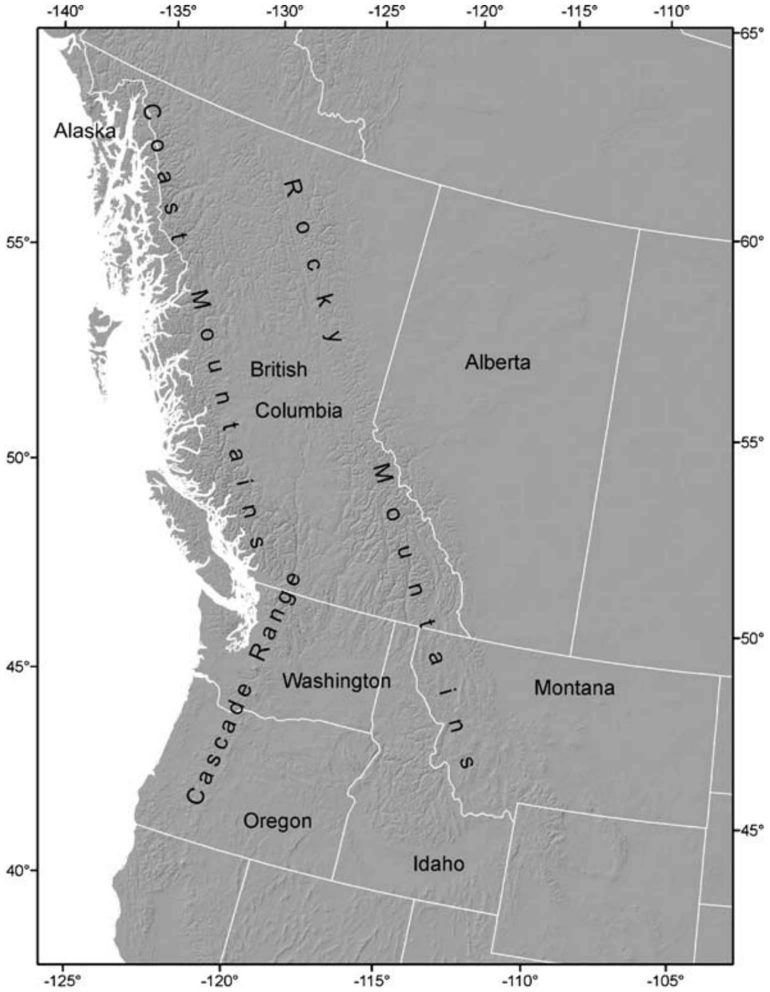

Fig. 1 Geographic region of study

1986) and microsatellites (Khasa et al. 2006) also is abundant and appears to be structured between two climatically disparate regions, also distinguished primarily by the relative mildness of the climate.

The availability of comprehensive data sets, superb statistical software, and modern computers now makes possible analyses of scope not addressable until recently. Our analyses concern ecologic and genetic responses to climate of western larch, taking into consideration output from General Circulation Models (GCM) in order to develop management strategies applicable to the species' entire botanical distribution. Our specific objectives are to: (1) define the climate profile (sensu Rehfeldt et al. 2006) with a bioclimatic model that predicts presence or absence from climate variables, (2) develop models of genetic variation that predict genetic differences among populations from the inhabited climate, (3) develop and map seed zones within the climate profile for present climates and project their future distributions, (4) identify populations that are likely to become threatened and identify appropriate conservation strategies, and (5) develop management strategies for the transfer of the seeds from their source to the future location of suitable climates, taking into consideration future distributions, adaptation of populations, and variability in the output of disparate GCM.

2 Methods

2.1 Climate estimates

We used the climate surfaces of Rehfeldt (2006), available at URL: http://forest.moscowfsl.wsu.edu/climate/, to provide estimates of normalized (1961–1990) monthly means of total precipitation and average, maximum, and minimum temperature. These surfaces, constructed with the software of Hutchinson (1991, 2000), provided climate predictions from geographic input, latitude, longitude, and elevation. Our analyses employed 34 variables, 18 of which were derived directly from monthly climate estimates (see Rehfeldt 2006). This set of derived variables included simple expressions of average temperature and precipitation (e.g., mean annual temperature, mean annual precipitation), temperature sums (e.g., degree-days>5° C, degree-days<0° C), freezing dates (e.g., date of the last freeze of spring), and expressions of the balance between temperature and precipitation (e.g., the ratio of degree-days>5° C to mean annual precipitation). The remaining variables were interactions among these eighteen. Definition and acronyms for several of the climate variables relevant to our results are presented in Table 1.

2.2 Bioclimate models

2.2.1 Data

We used data primarily from three sources: (1) ca. 120,000 permanent sample plots of Forest Inventory and Analysis, U. S. Forest Service, for western United States (see Alerich et al. 2004; Bechtold and Patterson 2005), (2) 719 plots established for ecological analyses of USA's northern Rocky Mountain forests (Cooper et al. 1991), and (3) ca. 25,000 ecological plots of the B.C. Ministry of Forest and Range (2009), which form the basis of a biogeoclimatic ecosystem classification (Pojar et al. 1987). In B.C., ecological plots were systematically located to represent the range of forested and non-forested ecosystems that occur on different site types in landscapes of each of several regional climates. The U.S.

Table 1 Acronyms and derivation of relevant climate variables. Importance rankings pertain to predictor variables for the climate profile. Bold face type indicate predictors of genetic effects

Acronym	Definition	Importance ranking
DD5	degree-days>5 ° C	–
MAP	mean annual precipitation	–
MMAX	mean maximum temperature in warmest month	5[a]
GSP	April–September precipitation	–
MTCM	mean temperature in coldest month	–
GSPDD5	(GSP * DD5) / 1000	–[c]
FDAY	Julian date of first freeze in autumn	6
GSDD5	degree-days>5° summed between the last freeze of springand FDAY	–
MINDD0	Degree-days<0 ° C based on the minimum temperature	4
MTWM	mean temperature in warmest month	–
MMIN	mean minimum temperature in coldest month	8
TDIFF	summer–winter temperature differential: MTWM-MTCM	–
PRATIO	GSP / MAP	2
SDI	summer dryness index: $(GSDD5)^{0.5}$ / GSP	–
SDIMINDD0	SDI * MINDD0	1
ADI	annual dryness index: $(DD5)^{0.5}$ / MAP	–
ADIMINDD0	ADI * MINDD0	–[a]
DD5MTCM	(DD5 * MTCM) / 1000	3
GSPTD	(GSP * TDIFF) / 100	7
MTCMMAP	MTCM/MAP	–
MAPDD5	(MAP*DD5)/1000	–[b]

[a] most important variable for predicting the first principal component from Idaho tests

[b] most important variable for predicting the second principal component from Idaho tests

[c] most important variable for predicting 15-year height in British Columbia tests

Forest Inventory and Analysis plots were systematically located to sample the vegetation on forested and non-forested lands. Plots ordinarily were established with four subplots, but for our analyses, data from subplots were combined.

Because plots established for forestry purposes tend to emphasize forested lands, we assembled data sampling the treeless lands of North America to assure adequate representation in our analyses the non forested lands, particularly those from the alpine tundra. This sample consisted of data points from treeless biomes of Brown et al. (1998) that were employed by Rehfeldt et al. (2006) in their analyses of vegetation distributions of western USA. This supplemental dataset contained about 28,000 observations for western USA and 12,500 for B. C.

The database available for our analyses consisted in total of about 185,000 observations, 2.5 % (4548 observations) of which contained western larch.

2.2.2 Statistical procedures

Our statistical models were built on the framework of Iverson and Prassad (1998), closely paralleled those of Rehfeldt et al. (2006), and essentially duplicated those of Rehfeldt et al. (2009). We used the Random Forests classification tree (Breiman 2001), available in R

(Development Core Team 2004; Liaw and Wiener 2002) to predict the presence-absence of western larch from climate variables. The model thus predicted the realized niche for the contemporary climate, which we call the climate profile (see Rehfeldt et al. 2006). The Random Forests algorithm constructs a set of trees from an input data set which in their aggregate is called a forest. In making predictions, each tree of each forest provides a 'vote' concerning the classification of an observation. Our analyses consisted of 100 trees in each of 10 forests.

For classification trees, Breiman (2001) recommended that the number of observations within classes be approximately equal. Because western larch occurs in only 2.5 % of our observations, we used the sampling protocol of Rehfeldt et al. (2009) to draw from our database10 samples, each of which was used to construct a forest. According to this protocol, all observations with western larch are used in each sample, with the remainder of the sample concentrated in those climates for which separating presence from absence would be the most difficult, but still encompassed the full range of climatic variation among the observations. The protocol was applied in three steps:

1. Select all of the 4,548 observations with western larch, weight them by a factor of 2 (e.g., duplicate them), and fix their proportion in the sample at 40 % of the total. This meant that each sample would contain ca. 22,750 observations. Weighting permitted a higher proportion of the total observations to be used in each forest which acted to minimize the errors of omission, that is, predicting absence when larch was present.

2. Construct from the set of 18 derived variables a multivariate hypervolume (sensu Hutchinson 1958), each dimension of which was an estimate of climatic limits of western larch expanded by ± 1 s.d. This expansion factor produced a hypervolume containing ca. 70,000 observations without larch from which ca. 10,000 (40 % of the total number in the sample) were drawn at random for each sample. Using 10 forests increased the probability that each observation within the hypervolume would be used in at least one forest.

3. Calculate the first and second principal components of the 18 derived variables using the entire database of ca. 185,000 observations. For each sample, make a random drawing of 250 observations (1% of the total number in the sample) from each of 10 uniform classes subtending each of the first and second principal components.

For each forest, a stepwise procedure was used to cull predictors, starting with a full complement of the 34 climate variables. At each step, variable importance was judged according to the mean decrease in accuracy, a statistic calculated for each tree by permuting predictor variables. Variables were culled according to an average of importance values for the 10 forests. Predictors for the final model were chosen according to the errors of prediction (out-of-bag errors): when errors began increasing exponentially, we assumed that the corresponding model was of reasonable parsimony.

2.3 Climatic predictors of genetic variation

We analyzed measurements made on seedling populations of western larch growing in common gardens at two locations. One was at Lamb Creek, a site at 1035 m elevation in southeastern B.C., from which measurements of 15-year height were available. A second was at the Priest River Experimental Forest in northern Idaho where 4-year data were available for a re-analysis from tests established at 720 m. Tests at both locations were established with many the same populations, representing in their aggregate much of the botanic distribution of the species.

The B.C. test was established with 128 populations, each represented by 7 seedlings planted in row plots within 5 blocks of a randomized complete block design. Trees were planted in 1991 on a 2×2 m grid and maintenance consisted of the control of in-growth. Although trees were measured periodically, we analyzed only the 15-year height.

The Idaho tests were short-term studies lasting 4 years. Previous analyses (see Rehfeldt 1995) dealt with 8 variables describing the phenology of shoot growth, growth potential, and impacts of *Meria* needle cast of 143 populations. For this paper, we conducted principal component analysis to reduce the dimensions of the data.

Data from both tests were subjected to an analysis of variance for assessing the degree of differentiation among populations for the genetic attributes, 15-year height and principal component scores. Multiple regression analyses were then used to relate genetic variation among populations to the climate of the seed source. The underlying assumption for these analyses is that genetic differences are related to the climate where the seeds were produced and arise through natural selection by climate (see Morgenstern 1996).

In using output from statistical analyses to develop management strategies, a useful statistic addresses the probability that differences among populations were real. For this statistic, we used the confidence interval that surrounds an observed mean (see for instance, Rehfeldt 1982), calculated as $\pm s_{\bar{x}} \cdot t_{0.2}$, where $s_{\bar{x}}$ is the standard error of the mean calculated from the population error in the analysis of variance, and $t_{0.2}$ is a value of t for a probability of 0.2. A relatively high level of probability was used for the value of t to assuage the impact of type II errors, the prediction of no difference when differences are real; errors of this type are of highest potential negative consequences for managers. The breadth of these confidence intervals is used to develop (1) seed zones for the contemporary climate, and (2) seed transfer guidelines (see Morgenstern 1996).

2.4 Mapping bioclimate profiles and genetic attributes

Approximately 9.5 million pixels of 0.0083° resolution comprise the terrestrial portion of our geographic window (Fig. 1). Climate estimates for each of these pixels have been developed (see Rehfeldt et al. 2006) using the digitized elevations of GLOBE (1999) for generating climate grids from the spline surfaces of Rehfeldt (2006). These grids, available at http://forest.moscowfsl.wsu.edu/climate/, were run through the bioclimate model and the models of genetic variation. In the former, each tree of each forest provided a vote as to whether a pixel fell within the climate profile of western larch; a pixel was assumed to have a suitable climate when receiving a majority of favorable votes (see Rehfeldt et al. 2006). For the latter, the regression models were used to predict a genetic attribute, either 15-year height or a principal component score (see Rehfeldt 2004).

Projections of the climate profile and genetic attributes into future climate space were made for three GCMs and two emissions scenarios (SRES) described in detail at the International Panel on Climate Change Data Distribution Center (http://www.ipcc-data.org/): (1) Canadian Center for Climate Modelling and Analysis (CCCMA), using the CGCM3 (T63 resolution) model, SRES A2 and B1 scenarios; (2) Met Office, Hadley Centre (UKMO), using the HadCM3 model, SRES A2 and B2 scenarios; and (3) Geophysical Fluid Dynamics Laboratory (GFDL), using the CM2.1 model, SRES A2 and B1 scenarios. In general, the SRES A2 scenario reflects unrestrained carbon emissions while the B1 and B2 scenarios incorporate social and economic restraints. These scenarios should begin diverging by 2030.

Our studies use the climate grids (1 km^2 resolution) available at http://forest.moscowfsl.wsu.edu/climate/, which are described in detail elsewhere (Rehfeldt et al. 2006; Saenz-Romero et al. 2010). To produce these grids, GCM output was used to calculate the monthly change in climate between the normalization period and the decades surrounding

2030, 2060, and 2090 for each weather station used in developing the climate surfaces of Rehfeldt (2006). Downscaling from the relatively coarse grids of the GCMs to the point locations of the weather stations used a weighted average of the monthly change in climate calculated for the GCM cell centers lying within 400 km of a station. The inverse of the square of the distance from the station to the cell center was used for weighting. Monthly climate surfaces for average, minimum, and maximum temperature and precipitation were then fit anew for each GCM and each scenario. Updating weather records from existing stations circumvents downscaling issues dealing with adjusting the 2-dimensional grids of coarse resolution from GCM output to the complex 3-dimensional topographic surfaces of western North America (see Saenz-Romero et al. 2010).

The new monthly climate surfaces were used to project the set of derived variables for the future climate of each pixel in our geographic window. Gridded estimates of future climates (available at http://forest.moscowfsl.wsu.edu/climate/) were run through the bioclimate profile and models of genetic variation. Votes generated by the bioclimate model were used to assess for each pixel the suitability of the future climate for western larch. If suitable, the genetic attributes of a population expected to be genetically suited to that climate were estimated from the models of genetic variation. All mapping was done with the ARCMAP software.

3 Results and discussion

3.1 Bioclimatic model

Errors of prediction averaged across the 10 forests for each step in the stepwise process fluctuated between 2.85% and 2.94% until five variables remained. Error rates for the 5-variable model averaged 3.1% and increased for subsequent models to 3.7% for four predictors, 5.3% for three, 8.0 for two, and 11.8% for a single variable. We chose an 8-variable model for describing the climate profile largely because eight predictors tend to buffer projections against vagaries of single variables (see Rehfeldt et al. 2006, 2009). This model had an out of bag error of 2.9%, for which the errors of commission and errors of omission averaged 4.9% and 0.05%, respectively. Indeed, only 5 observations with western larch were misclassified.

According to the mean decrease in accuracy, the most important variable (Table 1), judged from the last remaining variable in the stepwise elimination procedure, was an interaction of the summer dryness index and winter temperatures (SDIMINDD0). Next was the ratio of summer to total precipitation (PRATIO), followed by the interaction of degree-days>5°C and the mean temperature in the coldest month (DD5MTCM). Additional variables appearing in the eight-variable model included two describing the amount of winter cold, two pertaining to summer warmth, and an additional variable describing an interaction of summer precipitation and the annual temperature regime. The fit of this model and the predictor variables are essentially the same as those of Rehfeldt et al. (2006) whose analysis dealt with only the USA portion of the larch distribution.

Histograms for the three most important variables in the climate profile (Fig. 2) show the frequency of occurrence of western larch in relation to that of 12 common associates (*Pseudosuga menziesii*, *Pinus ponderosa*, *Abies grandis*, *Pinus monticola*, *Thuja plicata*, *Tsuga heterophylla*, *Picea engelmannii*, *Picea glauca*, *Pinus contorta*, *Abies lasiocarpa*, *Populus tremuloides*, *Tsuga mertensiana*) and for all lands in Forest Inventory's database for western USA. This figure quantifies the relatively narrow range of climates in which

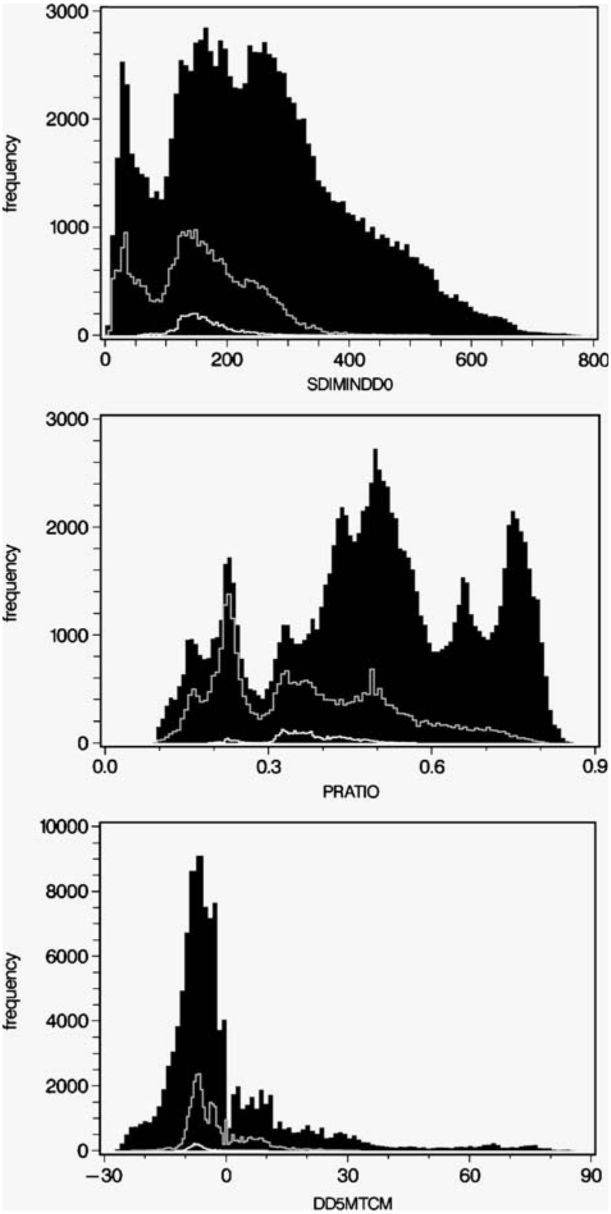

Fig. 2 Frequency of plots within the Forest Inventory Database for western USA plotted for 100 classes of the three most important predictors (top to bottom) of western larch's climate profile (Table 1) for all plots (*black*), those of 12 species with which western larch co-occurs (*gray*), and those with western larch (*white*)

western larch occurs compared to its common associates and compared to forested and non-forested lands in general: for SDIMINDD0 where winters are cool but not severely cold, with the impact of negative temperatures weighted by summer precipitation; for PRATIO where the balance between summer temperature and precipitation is such that moisture stresses are generally minimized; and for DD5MTCM where both winter and summer temperatures generally are not extreme. Yet, the relatively low frequency of western larch within the range of suitable climates demonstrates the need for multivariate models to predict occurrence. The low frequencies also reflect the importance of non-climatic factors (e. g., succession, disturbance, substrate) in determining presence and absence.

Mapped predictions of the geographic distribution of the climate profile (Fig. 3) are color-coded according to the proportion of the total votes cast in favor of the climate of a pixel being within the profile. Comparing the distribution of pixels predicted to have a suitable climate to Little's (1971) range map provides a visual corroboration of the fit of the model; the correspondence between the predictions and range map indeed is strong. Yet, as shown previously (Rehfeldt et al. 2006) for western larch, areas exist where discrepancies between the range map and predictions from the bioclimatic model are obvious (Fig. 3). As demonstrated with analyses of aspen (*Populus tremuloides*) (Rehfeldt et al. 2009), bioclimate models using inventory data and the Random Forests algorithm provide a more accurate portrayal of the species' distribution than range maps, can reflect abundance where range maps cannot, and can pinpoint areas where the climate should be suitable but where the species is absent. In the remainder of this paper, the bioclimate model is used in place of the range map to represent contemporary distributions.

3.2 Climate profile projections

Projections of the contemporary climate profile into the climates of the future portray different impacts on western larch (Table 2, Fig. 4). By the end of the century, the contemporary climate profile would all but disappear according to UKMO, especially in USA; would be reduced by about 70% according to GFDL; and would remain of relatively constant area according to CCCMA. All projections, however, agree that much of the future distribution of climates suitable for western larch would be on lands currently not inhabited by the species today (Table 2). In fact, the impacts of a changing climate portrayed by these disparate projections are so pronounced that the similarities tend to be obscured.

Agreement among mapped projections can be examined by superimposing them and viewing the result as a probability that the future climate would be suitable (see Rehfeldt et al. 2009). For example, the six projections (Fig. 5) that we use agree that the 2030 climates suitable for western larch should be concentrated in four geographic regions, one of which (insert D in the B.C. Coast Mountains) is largely beyond the distribution of today. By 2060, the concurrence would be greatly reduced, with the only areas of unanimity restricted to a few valley locations in the Coast Mountains. For making comparisons, note that the geographic position of the inserts are the same in the 2030 and 2060 panels. Because western larch rotations usually are longer than 50 years, these maps suggest that the speed of climate-change may force managers to compromise growth and adaptedness in the short term in order to secure survival over the long term. Maps such as Fig. 5 are tools ideal for prioritizing larch management.

3.3 Models of genetic variation

Analyses of variance detected statistically significant ($p<0.0001$) differences among populations for 15-year height at Lamb Creek and for three of the principal components of 4-year data in Idaho plantings. These three principal components accounted for 37 %, 19 % and 15 % of the variation in seedling measurements, respectively. Of these, the first eigenvector was controlled primarily by traits conveying a high growth potential (4-year

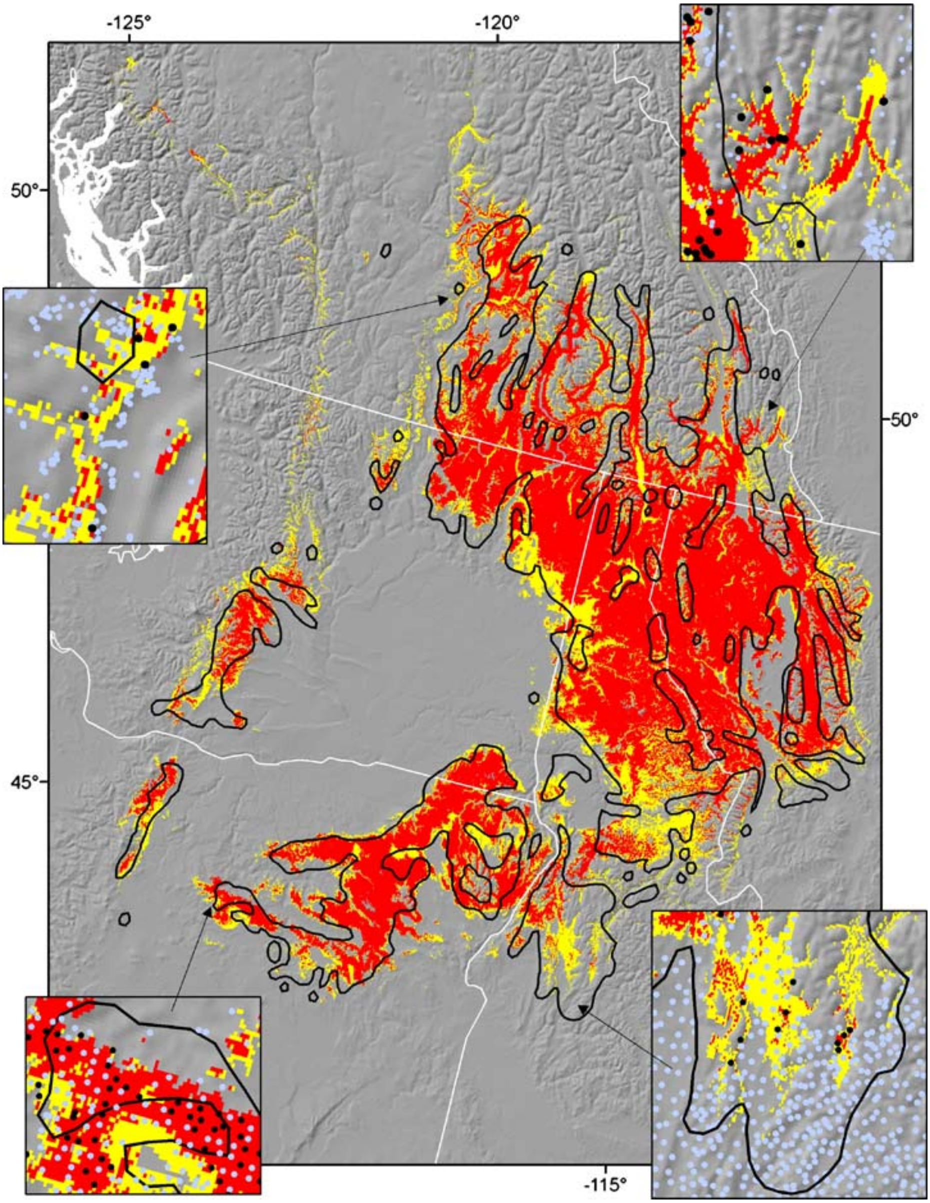

Fig. 3 Mapped climate profile (yellow and red pixels) of *Larix occidentalis* in relation to Little's (1971) digitized range map (lines). Yellow, 50–75 % of the votes; red, 75–100 % of the votes. Dots within the inserts are approximate locations of data points, black containing *L. occidentalis*, light blue without *L. occidentalis*

height, cessation of shoot elongation, and absence of needle cast); and the second largely by mortality from the needle cast, the impact of which was lessened in trees that began shoot elongation late and also ceased late. Control of the third eigenvector was much more complex and not readily interpreted. Although subsequent analyses were carried out with the three eigenvectors, results for the third were inconsequential and are not presented.

Table 2 Ratio of future area projected to be within the contemporary climate profile of *Larix occidentalis* to the contemporary area of the profile according to three general circulation models, two scenarios, and three time periods. In parentheses is the proportion of the future area expected to coincide with the contemporary area

Circulation Model	Period[a]		
	2030	2060	2090
CCCMA_A2	1.02 (0.62)	1.33 (0.26)	0.99 (0.11)
GFDL_A2	0.44 (0.13)	0.60 (0.05)	0.39 (0.00)
UKMO_A2	0.67 (0.45)	0.07 (0.01)	0.03 (0.00)
CCCMA_B1	1.04 (0.55)	1.03 (0.32)	0.91 (0.24)
GFDL_B1	1.20 (0.55)	0.79 (0.25)	0.28 (0.05)
UKMO_B2	0.51 (0.33)	0.03 (0.00)	0.01 (0.00)

[a] decade surrounding the date, e.g., 2026–2035

CCCMA, Canadian Center for Climate and Modeling

GFDL, Geophysical Fluid Dynamics Laboratory

UKMO, Met Office Hadley Centre

Mean squares from the analysis of variance produced confidence intervals (alpha≈0.2) surrounding an observation of ±0.76 and ±0.68 for the first and second principal components, respectively, and ±82 cm for 15-year height.

Stepwise multiple regression analyses for predicting genetic variation among populations from climate variables of the seed source were statistically significant ($p<0.0001$) but, as in other analyses of population differentiation in western larch (Rehfeldt 1982, 1995), showed that clines among populations were relatively flat. Regression models accounted for only 13 % of the variance among populations for 15-year height with a two-variable model, 29 % for the first principal component with a four-variable model, and 28 % for the second component with a two-variable model.

Regression equations for predicting genetic effects are:

$$\mathrm{PC1} = -7.5939 - 204.4423\,\mathrm{MTCMMAP} - 0.0378\,\mathrm{ADIMINDD0} + 0.3625\,\mathrm{MMAX} \quad (1)$$

$$\mathrm{PC2} = 2.1821 - 0.0012\,\mathrm{MAPDD5} - 0.0028\,\mathrm{GSPDD5} \quad (2)$$

$$\mathrm{H15} = -536.979 + 0.394\,\mathrm{GSPDD5} - 0.069\,\mathrm{MAPDD5} \quad (3)$$

where PC1 and PC2 are the first and second principal components for traits measured at Priest River, Idaho, and H15 is 15-year height measured at Lamb Creek, B.C. Independent variables are defined in Table 1. The stepwise elimination procedure indicated that the most important predictors were MTCMMAP for PC1, MAPDD5 for PC2, and GSPDD5 for H15. Perhaps noteworthy is that predictors of PC2 and H15 are identical, although their coefficients are much different.

Mapped patterns of genetic variation for the three attributes are shown in Fig. 6 for pixels lying within the climate profile (Fig. 3). This figure shows in general that 15-year height of populations at Lamb Creek. was greatest for populations from the valleys in south-central B. C., near the northernmost limits of the contemporary distribution; the

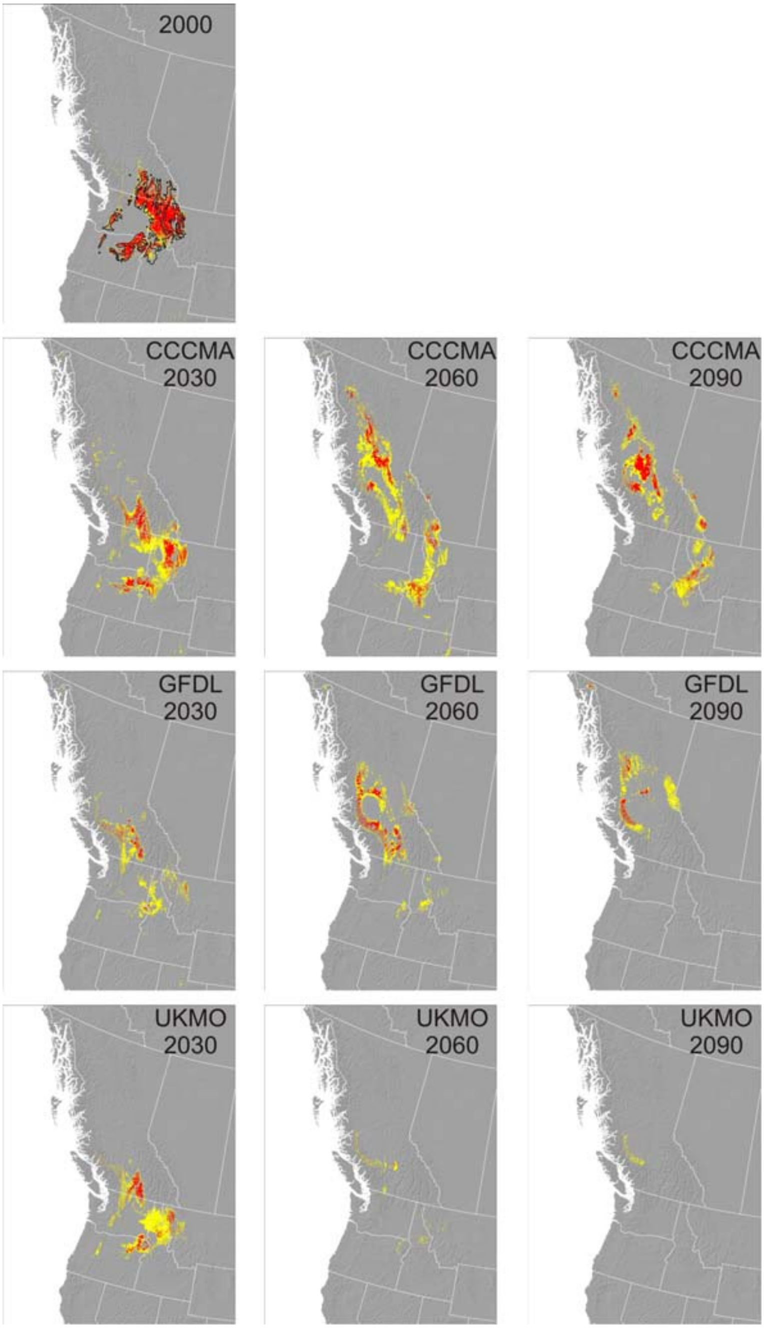

Fig. 4 Mapped climate profile of *Larix occidentalis* for the contemporary climate (*upper left*) and for future climates as depicted for the SRES A2 scenarios and three GCMs for decades centered on 2030, 2060, and 2090. CCCMA, Canadian Center for Climate Modelling; GFDL, Geophysical Fluid Dynamics Laboratory; UKMO, Met Office, Hadley Centre

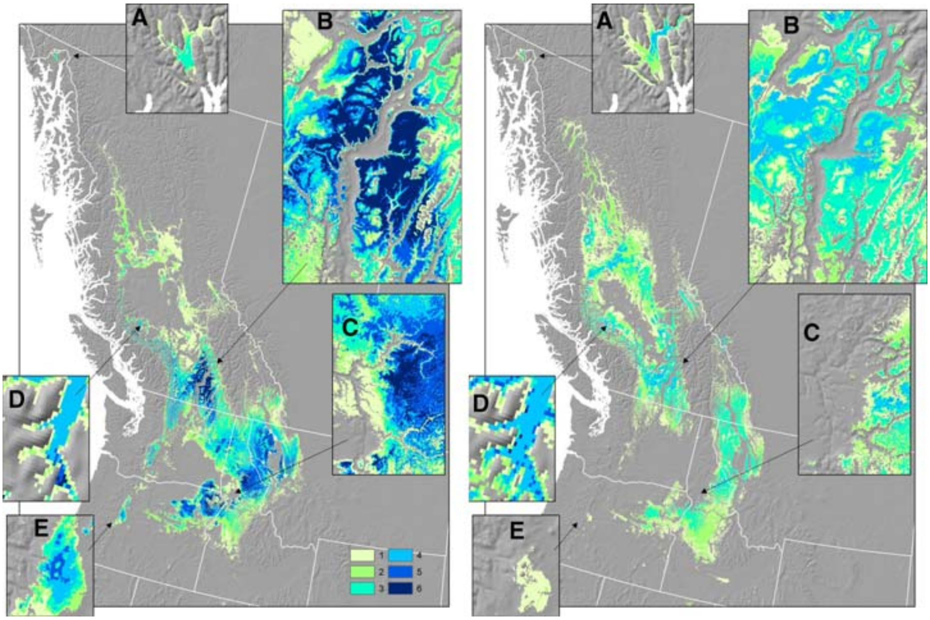

Fig. 5 Mapped climate profile of *Larix occidentalis* projected for the decade surrounding 2030 (*left*) and 2060 (*right*) superimposed for three GCMs and two scenarios. Coloring codes the number of projections agreeing that the climate should be suitable

smallest trees tended to come from seed sources in the Blue Mountains of northeastern Oregon and Cascade Range of western Oregon and Washington (see Fig. 1). Trees of highest growth potential and highest tolerance to *Meria* needle cast (PC-1) tended to originate from seed sources from the valleys of northern Idaho and adjacent British Columbia, while those with the lowest values of these traits came from the relatively high elevations in Montana, northeastern Oregon and the Washington Cascades (Fig. 6, middle). Geographic patterns of variation for PC-2 (Fig. 6, right) suggested that when tested in Idaho, trees originating particularly from the valleys of northern Idaho had the lowest mortality (light brown) from the needle cast while seed sources from the highest elevations had the highest (darkest brown).

3.4 Seed transfer guidelines and seed zones

3.4.1 Transfer guidelines

Location-specific seed transfer guidelines can be constructed by searching for all pixels with predictions of our three genetic attributes (H15, PC-1, and PC-2) lying within the breadth of the confidence intervals surrounding predicted values for that location. Figure 7 is illustrative for two hypothetical locations currently lying within the contemporary climate profile. In Fig. 7a and c, sources of seed genetically compatible with the climate of a targeted location are colored a bright pink and are set within the contemporary climate profile (black) of Fig. 3. If the hypothetical points were seed sources, the pink pixels would represent the array of sites for which seeds from the source would make suitable planting stock.

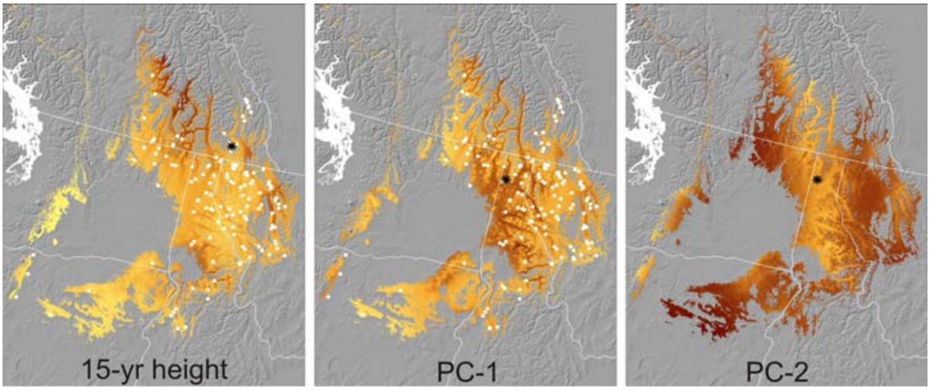

Fig. 6 Mapped genetic variation predicted from regression models for three attributes: A, 15 year height of trees growing at Lamb Creek, British Columbia (asterisk); B, first principal component of 8 traits measured on 4-year seedlings at Priest River, Idaho (asterisk), and C, second principal component of traits measured in Idaho. White dots in A and B locate seed sources included in the tests. Shading indicates predicted performance of populations within the contemporary climate profile (Fig. 3), dark for high values and light for low values

To find sources of seed suitable for future climates, the exercise was repeated for the two hypothetical locations using instead the climate of 2030 as the target climate. In doing this, each of the six scenarios we use provided an estimate. In Fig. 7b and d, the six estimates are summarized according to their concurrence: lightest shades of pink code agreement of three scenarios while darkest shades code agreement of all six. The implication is that sources of seeds from localities colored purple will have the highest probability of being suited to the 2030 climates.

In Figure 8, the same approach to seed transfer is illustrated for two more hypothetical planting sites that today are north of the distribution of western larch. In this example, managers contemplating western larch introductions at an elevation of 960 m near Gavin Lake, B. C. are given an array of suitable locations (Fig. 8, left) from which seeds could be used to target the 2030 climate. In Fig. 8, right, managers of a site near Mahood Lake, only 110 km distant from Gavin Lake but 160 m lower in elevation, can also choose from an array that is considerably different from those suited for Gavin Lake. The differences largely reflect elevation: on average, the site at Mahood Lake should be 0.7°C warmer than Gavin Lake in mean annual temperature in 2030 while precipitation at both sites would remain about the same as today (630 mm).

To be developed into a tool suitable for managers, the procedural steps taken to develop the maps of Fig. 7 and 8 need to be housed in a web-based system where managers could enter the geographic coordinates (latitude, longitude and elevation) of a planting site and receive a map that would show suitable sources of seeds for targeting future climates. Yet, the future period to be targeted should be carefully selected such that adaptedness in neither the short term nor the long term is compromised (see Rehfeldt et al. 2001; Aitken et al. 2008).

3.4.2 Discrete seed zones

The range of predicted values for the populations of Fig. 6 was 317 cm for H15 and 3.38 and 1.87 standardized normal deviates for PC-1 and PC-2, respectively. The breadth

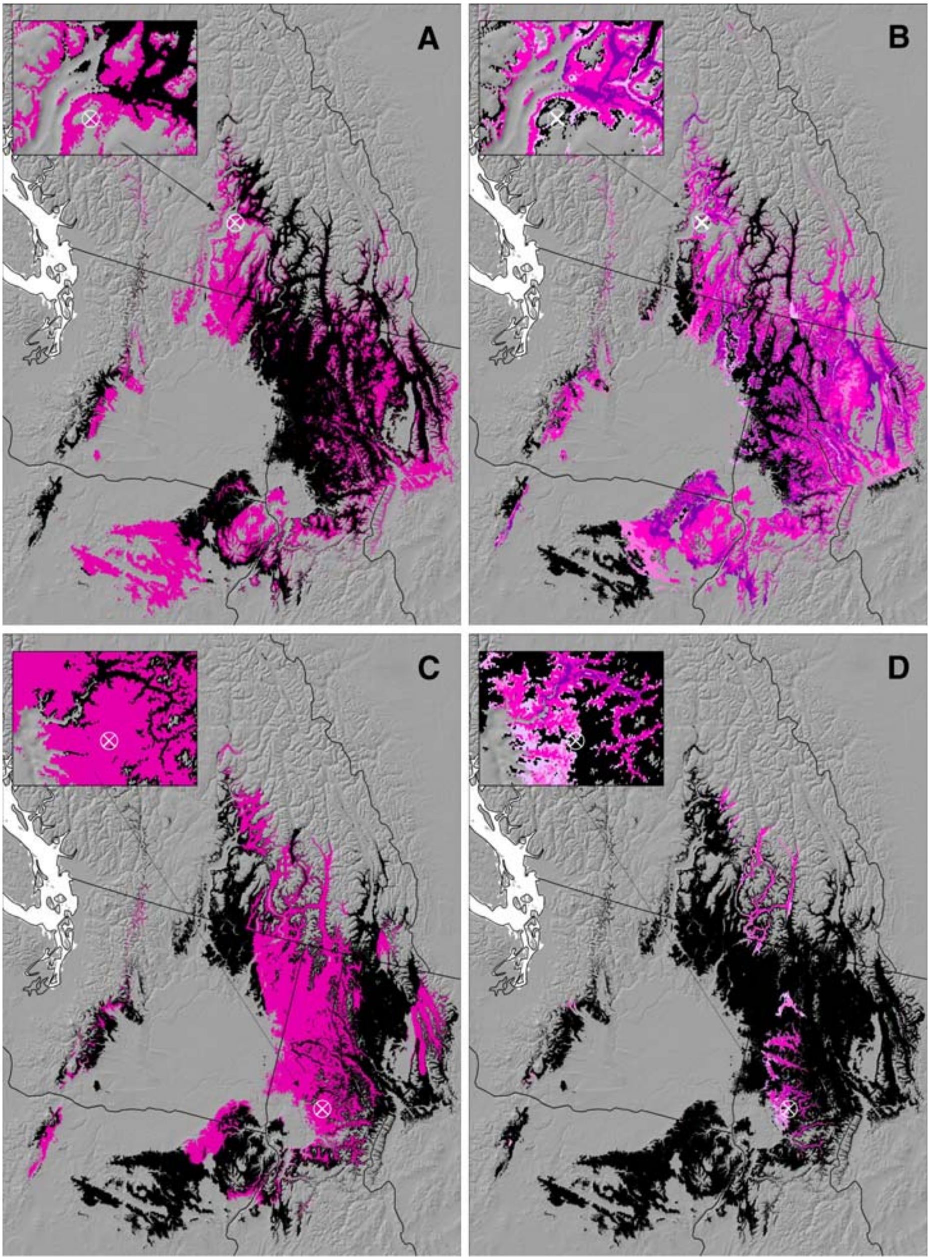

Fig. 7 Mapped seed transfer guidelines for obtaining sources of seeds (*bright pink*) genetically compatible with the climate of a targeted locality (*symbol*) within the contemporary distribution (*black*) for the current climate (A and C) and for the climate surrounding the decade of 2030 (**b** and **d**). Four colors, light pink to purple, in B and D code agreement among projections from three General Circulation Models and two scenarios, with the lightest shade representing agreement for 3 predictions and the darkest for six

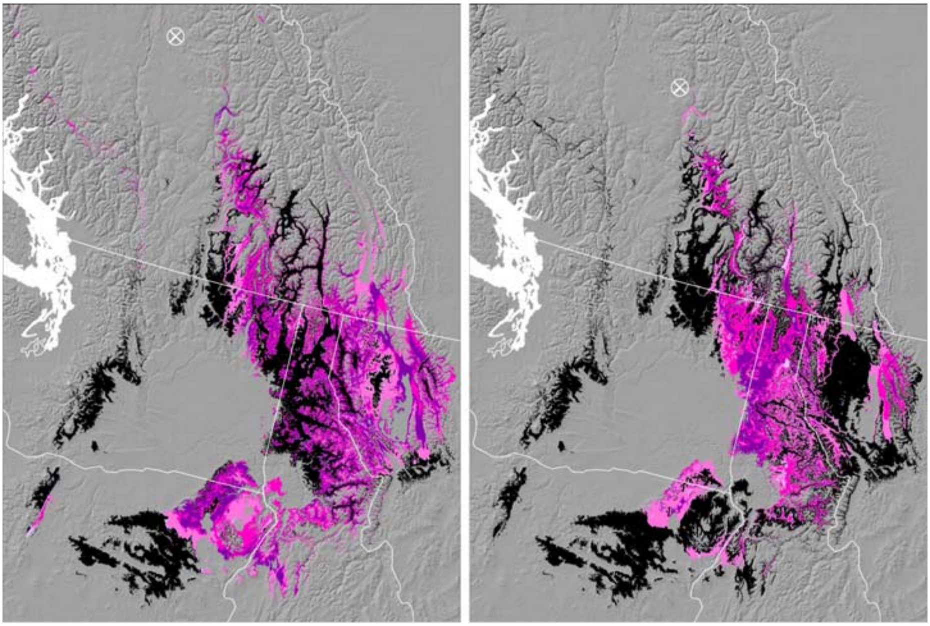

Fig. 8 Mapped seed transfer guidelines for obtaining sources of seeds (bright purple) to target the climate of 2030 for two British Columbia locations currently north of the *L. occidentalis* distribution, Gavin Lake (*left*) and Mahood Lake (*right*). Four colors, light pink to purple, in B and D code agreement among projections from three General Circulation Models and two scenarios, with the lightest shade representing agreement for three predictions and the darkest for six

of the confidence interval (i.e., 2 times the interval) surrounding population means for these variables suggests that seed zones should be constructed such that the populations comprising a zone would not differ by more than 164 cm in 15-year height and 1.52 and 1.36 standardized normal deviates for the two principal components. This means that two classes would be sufficient for classifying the genetic variation in each of the three attributes into groups within which genetic differences were slight. The resulting six classes could then be assorted into climatic ecotypes (sensu Turesson 1925), each of which would contain one class for each of the three attributes to produce the eight ecotypes of Table 3. In theory, each of these ecotypes should be represented by a seed zone.

Because the ecotypes, and, therefore, the seed zones, are a qualitative subdivision of continuous variation, the delineation of zoneal boundaries can be somewhat subjective. Our approach was to use histograms produced by ARCMAP software to view the frequency of observations for an array of classes. From these histograms, natural breaks in the continuous distributions of predicted values could be identified readily for each of the three attributes. The points at which the breaks occurred were then used to classify genetic variation in each attribute into the two groups such that variation within groups remained less than the breadth of the confidence interval. The resulting six classes were assorted into eight seed zones by the software (Table 3). Note that script can be written to assort data points into these seed zones.

Table 3 Size, proportion of total area, and assortment into seed zones of 8 climatic ecotypes composed of genetic variation classified into one of two groupings for each of three attributes describing genetic variation among populations of *Larix occidentalis*

Ecotypes			Seed zones	
Composition[a]	Pixels	Proportion	Number code	Color
1,1,1	123,243	0.433	1	Yellow
1,1,2	8,638	0.030	2	Blue
1,2,1	57,306	0.202	3	Brown
1,2,2	21,602	0.076	4	Red
2,1,1	65,816	0.232	2	Blue
2,1,2	512	0.001	4	Red
2,2,1	4,394	0.015	5	Green
2,2,2	2,733	0.010	5	Green

[a] classification group numbers (1 or 2) for 15-year height and two principal components, respectively

Color of seed zones linked to Fig. 9

The original maps of the eight zones showed that three of the zones together accounted <5 % of the total area of the climate profile (Table 3), one of which occupied only 512 pixels. The three all were within the Cascade Range (Fig. 1) where few data points existed (Fig. 6), and, therefore, the possibilities of spurious results arising from extrapolating genetic models become likely. Consequently, these five zones were combined either with each other or with a climatically similar group (Table 3) without greatly compromising our rules for classifying genetic variation. The result (Table 3) was the five seed zones of Fig. 9 (upper left).

Consistent with patterns of genetic variation described by geographic variables (Rehfeldt 1982, 1995), these five seed zones (Fig. 9, upper left panel) tend to be stratified by elevation. In northeast Oregon and adjacent Idaho (inserts A and D), for instance, the altitudinal range of these zones is ca. 800–1100 m for the blue, 1000–1300 m for the brown, 1200–1500 m for the yellow, and 1600–2000 m for the red. In the Cascade Range (insert C), the green zone tends to occur between 900 and 1500 m, an altitudinal range that places it between the blue zone at somewhat lower elevations and the red zone at higher elevations. The breadth of these seed zones is also consistent with previous work which suggested limits of transfer of about ±200 m (Rehfeldt 1982).

Projecting the seed zones into the 2030 climates generated for the A2 scenarios of the three GCMs produced the widely disparate results of Fig. 9. Figure 10 synthesizes the disparate results in a map showing the five seed zones in the same base colors used in Fig. 9, with color intensity denoting concurrence among the projections. In mapping the zones (Fig. 10), conflicts in assigning a zone to a pixel were numerous, but by considering only those pixels for which the 2030 climate was predicted to be suited for larch by three or more of our projections (Fig. 5, left), conflicts became trivial.

Maps like those in Fig. 10 provide land managers with information basic for making informed decisions. From the maps, managers could decide for the 2030 climate which locations would have the highest probability of being suited to western larch, and for them, select contemporary sources of seeds with the highest probability of being genetically compatible with the future climate.

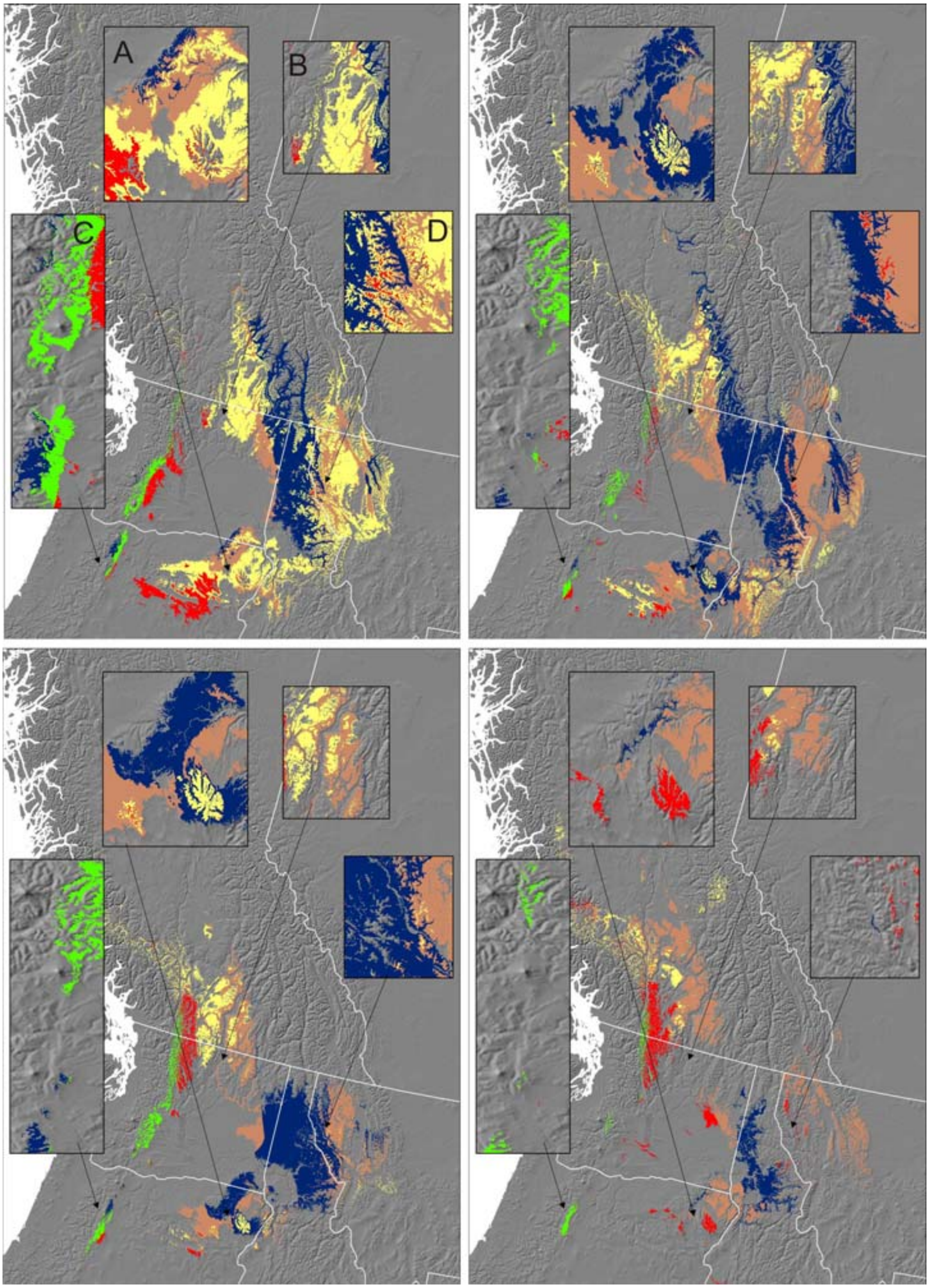

Fig. 9 Map of five seed zones (*upper left*) and their 2030 projections according to the A2 scenarios of CCCMA (*upper right*), GFDL (*lower left*), and UKMO (*lower right*). Geographic extent shown in inserts A–E (*upper left*) is repeated in all panels

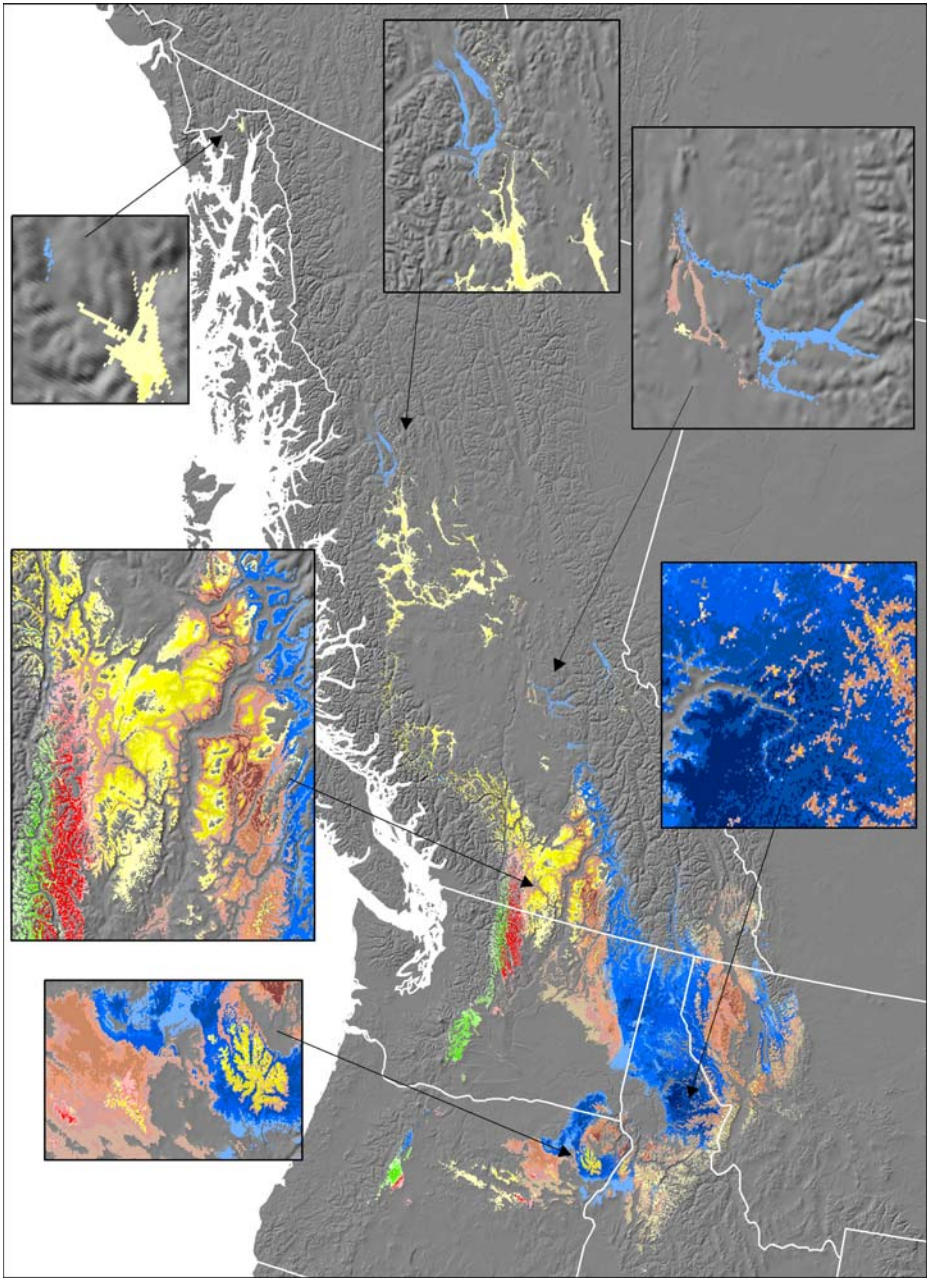

Fig. 10 Concurrence among three GCMs and two scenarios for the 2030 location of five seed zones. Zones are coded by the color paths of in Fig. 9, blue, yellow, brown, green and red, with the lightest shades denoting agreement among 3 projections and the darkest, agreement among 6 projections

Table 4 Percent change in pixels of 5 seed zones between the contemporary and future climates of the decades surrounding 2030, 2060, and 2090 averaged for three GCMs and two scenarios

Seed zone	Period[a]		
	2030	2060	2090
1 (yellow)	−56.5	−51.1	−72.7
2 (blue)	+18.2	+6.1	−17.8
3 (brown)	+46.5	−21.3	−40.7
4 (red)	−59.8	−85.7	−94.6
5 (green)	−12.1	−78.0	−92.2

[a] decade surrounding the date, e.g., 2026–2035

Colors of seed zones are linked to Fig. 9

3.5 Conservation of genetic resources

As illustrated for populations of *Picea* (Rehfeldt 2004; Ledig et al. 2010), bioclimate profiles projected in time can provide land managers with tools suitable for developing conservation programs. Table 4, for instance, shows an average percent change in area of five western larch seed zones (Fig. 9, upper left) expected in three future decades. These statistics suggest that by the end of the century, the area occupied by the western larch climate profile should be best suited to genotypes within the blue seed zone of today (Fig. 9). This blue zone therefore would have the least decline in area, ca. 17 %.

Even though variation according to the GCMs and scenarios is large, all projections agree that the area suited to genotypes from two of the zones, the green and red (Fig. 9), should rapidly and largely disappear during the course of the century, as the area suitable for genotypes of these two zones shifts rapidly toward higher altitudes and latitudes. Today, the green zone occurs exclusively in the Cascade Range while the red zone is typical of the high and dry climates common in eastern Oregon and central Washington. The results suggest, therefore, that genotypes from both zones may be worthy targets of conservation.

Concurrence maps for climate profiles (Fig. 5) and seed zones (Fig 10) also have utility in evaluating the long-term safety of existing in situ conservation reserves and in the planning and establishment of new reserves. Existing in situ reserves located in regions of high, medium and low levels of climate concurrence possess high, medium and low probabilities of long-term success, respectively. Similarly, agencies attempting to establish new ex situ reserves for long-term conservation should consider locating reserves in regions of high concurrence.

4 Conclusions

These results for western larch join those of Tchebakova et al. (2005, 2010) and Rehfeldt et al. (2004) to demonstrate that climate change will disrupt the adaptedness of populations and ultimately force the realignment of species distributions. They also demonstrate that bioclimate models for western larch can be used in conjunction with modeled geographic patterns of genetic variation to develop and map for the contemporary climate the seed zones and seed transfer guidelines needed for reforestation. Because the models are driven by climate, both can be projected into the climate space generated by various GCMs and IPCC scenarios. Variation among mapped projections resulting from disparate climate models can be viewed as a probability to provide managers proactive options that would have the highest probability of success within the framework of current projections of future climates.

Management of western larch forests is predicated on natural cycles of succession, maturity, demise, wildfire and regeneration. Climate-change will impact each process, starting with the demise that occurs as plants become more and more poorly adapted to the climate at the site where they are growing (see Rehfeldt et al. 1999, 2001, 2002; Aitken et al. 2008). This demise, when coupled with a climate becoming warmer and drier, will provide the fuel for wildfire of increased frequency and severity (see Tchebakova et al. 2005). The wildfire then provides conditions suitable for regeneration of seral species such as western larch. At this stage, our methods provide a framework for assuring that the appropriate seed sources of the best suited species are planted in proper climates.

An additional practical lesson learned from this work is that comprehensive programs of conservation or management will either require or benefit from cooperation across national boundaries. Our figures demonstrate unequivocally that climatic ecotypes transcend political boundaries. Consequently, programs involving seed procurement and deployment, tree breeding and maintenance of breeding populations, and accrual of genetic gains in commercially important traits will be most efficient through transboundary cooperation. Threatened populations in particular may require conservation plantings in ex situ reserves outside political jurisdictions where future climates are amenable to the species.

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