Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Clines in growth potential

Gerald E. Rehfeldt [a,*], Laura P. Leites [b], J. Bradley St Clair [c], Barry C. Jaquish [d], Cuauhtémoc Sáenz-Romero [e], Javier López-Upton [f], Dennis G. Joyce [g]

[a] USDA Forest Service, Rocky Mountain Research Station, Forestry Sciences Laboratory, 1221 S. Main, Moscow, ID 83843, USA
[b] Department of Ecosystem Science and Management, Pennsylvania State University, University Park, PA 16802, USA
[c] USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331-4401, USA
[d] Research Branch, B.C. Ministry of Forests, Lands and Natural Resource Operations, Kalamalka Forestry Centre, 3401 Reservoir Rd, Vernon, BC V1B 2C7, Canada
[e] Instituto de Investigaciones Agropecuarias y Forestales, Universidad Michoacana de San Nicolás de Hidalgo (IIAF-UMSNH), Km 9.5 Carretera Morelia-Zinapécuaro, Tarímbaro, Michoacán 58880, Mexico
[f] Colegio de Postgraduados, Km 35.5 Carretera México-Texcoco, Montecillo, México C.P. 56230, Mexico
[g] Independent Contractor, 449 Walls Road, Sault Ste. Marie, Ontario P6A 6K4, Canada

ARTICLE INFO

ABSTRACT

Height growth data were assembled from 10 *Pinus ponderosa* and 17 *Pseudotsuga menziesii* provenance tests. Data from the disparate studies were scaled according to climate similarities of the provenances to provide single datasets for 781 *P. ponderosa* and 1193 *P. menziesii* populations. Mixed effects models were used for two sub-specific varieties of each species to describe clines in growth potential associated with provenance climate while accounting for study effects not eliminated by scaling. Variables related to winter temperatures controlled genetic variation within the varieties of both species. Clines were converted to climatypes by classifying genetic variation, using variation within provenances in relation to the slope of the cline to determine climatype breadth. Climatypes were broader in varieties of *P. ponderosa* than in *P. menziesii* and were broader for varieties inhabiting coastal regions of both species than for varieties from interior regions. Projected impacts of climate change on adaptedness used output from an ensemble of 17 general circulation models. Impacts were dependent on cline steepness and climatype breadth but implied that maintaining adaptedness of populations to future climates will require a redistribution of genotypes across forested landscapes.

Published by Elsevier B.V.

1. Introduction

From the earliest (e.g., Kempff, 1928; Munger and Morris, 1936) to more recent (Burdon and Low, 1991, St Clair et al., 2005), provenance tests have demonstrated extensive genetic differentiation among populations of *Pinus ponderosa* and *Pseudotsuga menziesii*. The oldest of these tests broadly sampled range-wide distributions, and while supporting the sub-specific taxonomic varieties, *P. p.* var. *ponderosa* and var. *scopulorum* and *P. m.* var. *menziesii* and var. *glauca* (Fig. 1), also documented genetic differences among populations in numerous traits related to growth, development and morphology (e.g., Squillace and Silen, 1962; Hanover, 1963; Haddock

et al., 1967). Subsequent tests, addressing regional genetic effects within varieties, repeatedly illustrated genetic differences among populations for traits controlling growth, phenology, cold hardiness (e.g., Callaham and Liddicoet, 1961; Wells, 1964; Campbell, 1979) and tolerances to pests (e. g., Burdon and Low, 1991; Stephan, 1980; McDermott and Robinson, 1989). In this paper, the term *population* is used to reference the individuals and their inter-pollinated descendants native to a specific geographic location, the *provenance*.

At regional scales, genetic variation among populations of *P. ponderosa* and *P. menziesii* invariably revealed geographic patterns of genetic variation that were related clinally to the environment of the provenance (see Langlet, 1936) and, therefore, were consistent with presumed effects of natural selection (see Morgenstern, 1996). The clines most frequently were related to provenance elevation, a surrogate for temperature (Campbell, 1979, 1986; Rehfeldt, 1979, 1986a,b; Sorensen, 1994), and, therefore, are
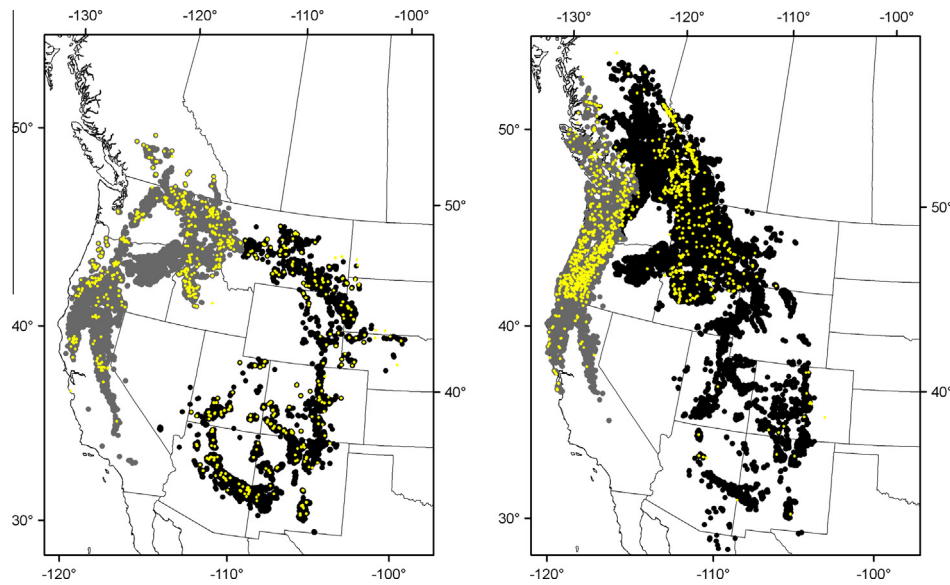
Fig. 1. Location of ground plots containing *Pinus ponderosa* (left) var. *ponderosa* (gray) and var. *scopulorum* (black) and *Pseudotsuga menziesii* (right) var. *menziesii* (gray), and var. *glauca* (black) used to construct the climate profiles of PART 1. Yellow dots locate the populations contributing data for the genecology models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

interpreted as responses to selection along temperature gradients. Populations of both species occupying warm, mild environments tend to have high growth potential but low cold tolerance while those from cold environments tend to have low growth potential and high cold hardiness. As a result, adaptation to heterogeneous environments can be viewed simplistically as a trade-off between selection for high growth in mild climates and selection for cold hardiness in severe climates (see Rehfeldt, 1988, 1989, 1991, 1994a, 2004). With adaptation of populations to the climate being unequivocal (see St Clair et al., 2005), a change in climate will have an effect on the growth and survival of individuals and populations.

Yet, for provenance test results to be useful in assessing potential impacts of climate change (see Mátýas, 1994), geographic descriptors of clinal variation must be replaced by climatic descriptors (see St Clair et al., 2005; Rehfeldt and Jaquish, 2010; Joyce and Rehfeldt, 2013). The primary goal of the present study is to synthesize disparate provenance test data so that range-wide, climate-based clines in the sub-specific varieties of *P. ponderosa* and *P. menziesii* can be described statistically. Our second objective is to map the clines for contemporary and future climates so that impacts of a changing climate on the adaptedness of populations can be assessed.

These objectives are genecological, aimed at understanding the ecological basis for genetic differences among populations. Because genetic effects control adaptation, population performance in provenance tests is dependent on genotype by environment interactions, that is, expression of the clines is dependent on the climate at the test site (e.g., Campbell and Sorensen, 1978; Rehfeldt 1979, 1993). While algorithms have been developed for predicting performance (e.g., Wang et al., 2006; Leites et al., 2012a,b), our focus is on the abstract concept of *growth potential* (see Rehfeldt, 1990), the inherent capacity for growth when environmental conditions are optimal. Height growth can act as a surrogate for growth potential when provenance tests are located in mild, relatively stress-free environments (e.g., Rehfeldt et al., 1999; Leites et al., 2012a,b; Joyce and Rehfeldt, 2013). Variables reflecting growth potential have been shown repeatedly to integrate a variety of adaptive responses and to be among those with greatest genetic variances and steepest clines. Growth potential, therefore, is highly suited for our objectives.

This paper is the second of a series dealing with responses of *P. ponderosa* and *P. menziesii* to climate. The first of the series (PART 1, Rehfeldt et al., 2014a) defined the climatic niche of the sub-specific varieties of these species within which reside the clines of genetic variability that convey adaptation of populations to heterogeneous environments. The climatic clines derived herein are mapped within the climatic niche (PART 1) to produce a foundation suited to developing conservation, reforestation, and management options for a changing climate, the subject of the third paper of the series (PART 3, Rehfeldt et al., 2014b). In the present paper, the unnamed Mexican variety of *P. menziesii* was not considered because of lack of provenance test data.

Climate estimates for the contemporary period are from thin plate spline surfaces, and estimates for the future climates are from an ensemble of 17 General Circulation Models (GCM) using the RCP6.0 scenario for the decade surrounding 2060 (see PART 1).

2. Methods

2.1. Provenance test data

Height growth data were obtained for 10 *P. ponderosa* and 17 *P. menziesii* studies of regional scope (Tables 1 and 2), all of which had been conducted with a randomized block design. For studies with multiple test sites, we used data from the climatically benign sites which presumably allowed genotypes to express their growth potential. Provenance means were available for multiple blocks for all but the Nebraska study of *P. ponderosa* and the New Zealand studies of both species. For *P. ponderosa* in the latter, population mean heights from two test sites were treated as blocks of a randomized complete block experiment. Data were scaled (see Section 2.1.2) between the sites according to the performance of 22 provenances in common between the two tests. For *P. menziesii*, population means from five test sites were scaled according to the performance of 32-44 populations in common with the test at Rankleburn.

Compared to the other studies, the tests conducted in New Zealand appear anomalous (Tables 1 and 2), not necessarily because of being conducted in the Southern Hemisphere, but mostly because of their age. After 22 years, stand dynamics undoubtedly would be influencing the expression of innate growth potential. These

Table 1
General attributes of the studies contributing to the *Pinus ponderosa* analysis of growth potential, including the number of populations tested and the number used in scaling and merging the datasets.

Study	Test site location	Age	Blocks	Populations		Reference
				Total	Used for scaling[a]	
1	Priest River, Idaho	3	3	138	–	Rehfeldt (1986b)
2	Priest River, Idaho	3	5	64	12 (14)	Rehfeldt (1986a)
3	Priest River, Idaho	3	3	70	5 (14)	RMRS (unpublished)
4	Halsey, Nebraska	3	1[b]	78	34 (74)	Read (1980)
5	Moscow, Idaho	2	3	51	29 (71)	RMRS (unpublished)
6	Priest River, Idaho	3	3	63	10 (14)	Rehfeldt (1990)
7	Ft. Bayard, New Mexico	3	4	93	27 (57)	Rehfeldt (1993)
8	Skimikin, BC	8	8	71	46 (115)	BCMF (unpublished)
9	New Zealand	22	2[c]	38	2 (5)	Burdon and Low (1991)
10	Corvallis, Oregon	3	5	115	26 (32)	PNW (unpublished)

Note: PNW, Pacific Northwest Experiment Station, U.S. Forest Service; RMRS, Rocky Mountain Experiment Station, U.S. Forest Service; FRI, Forest Research Institute, New Zealand Forest Service; BC, British Columbia; BCMF, British Columbia Ministry of Forests.
[a] Number of climatically similar provenances and number of population pairs (in parentheses) used to calculate scaling factors.
[b] Population mean heights from three blocks at a single planting site.
[c] Population mean heights from two test sites (Hanmer and Whaka) treated herein as blocks of a randomized complete block design.

Table 2
General attributes of the studies contributing to the *Pseudotsuga menziesii* analysis of growth potential, including the number of populations tested and the number used in scaling and merging the datasets.

Study	Test site location	Age	Blocks	Populations		Reference
				Total tested	Used for scaling[a]	
1	Priest River, Idaho	3	4	50	–	Rehfeldt (1979)
2	Priest River, Idaho	3	4	54	5 (9)	Rehfeldt (1982)
3	Priest River, Idaho	3	5	74	10 (13)	Rehfeldt (1983)
4	Priest River, Idaho	3	6	77	22 (35)	Rehfeldt (1988)
5	Trinity Valley, interior BC	10	3	61	4 (6)	BCMF (unpublished)
6	Lillooet River, coastal BC	10	7	39	20 (21)	Krakowski and Stoehr (2011)
7	Skimikin, interior BC	10	8[b,c]	30	3 (6)	BCMF (unpublished)
8	Haney, coastal BC	20	4	16	3 (4)	Ching and Hinz (1978)
9	Sooke (low), coastal BC	10	4	77	7 (9)	Stoehr (unpublished)
10	Lumberton, interior BC	10	8[b,c]	53	3 (11)	BCMF (unpublished)
11	Gold Hill, interior BC	10	8[b,c]	49	17 (25)	BCMF (unpublished)
12	Duncan Lake, interior BC	10	8[b,c]	59	3 (3)	BCMF (unpublished)
13	Valemont, interior BC	10	8[b,c]	43	10 (13)	BCMF (unpublished)
14	New Zealand[d]	15	6	44	3 (3)	FRI (unpublished)
15	Corvallis, coastal Oregon	2	4[b]	184	18 (19)	St Clair et al. (2005)
16	Corvallis, coastal Oregon	2	4[b]	164	26 (26)	St Clair et al. (2005)
17	Corvallis, coastal Oregon	2	4[b]	119	34 (34)	St Clair et al. (2005)

Note: FRI, Forest Research Institute, New Zealand Forest Service; BC, British Columbia; BCMF, British Columbia Ministry of Forests.
[a] Number of climatically similar provenances and number of population pairs (in parentheses) used to calculate scaling factors.
[b] Single tree collections grouped into populations.
[c] Progeny test site.
[d] Population mean heights from six test sites (Rapanui, Kaingaroa, Gwavas, Golden Downs, Hanmer, and Rankleburn) treated herein as blocks of a randomized complete block design.

tests, however, provided 24 of the 48 *P. p.* var. *ponderosa* provenances and 20 of the 38 *P. m.* var. *menziesii* provenances from south of 42°N., that is, from California where growth potentials tend to be high. Data from the New Zealand tests, therefore, were an important cog in range-wide analyses and interpretations. Because the sites on which they were tested were of high quality, the advantages of including them seemingly outweighed the potential disadvantages.

2.2. Scaling and merging datasets

Because the studies (Tables 1 and 2) were largely regional in scope, geographically-based genetic effects would be confounded with effects of studies. This confounding would obscure clinal pattern of genetic variation and, therefore, needed to be addressed. To produce datasets suitable for analysis, data from the disparate regional studies needed to be merged such that variation among populations would be preserved and clines in genetic variability would remain intact. Merging procedures were handicapped,

however, by a low number of populations in common between the studies. Although genecology studies conducted by the same personnel (Tables 1 and 2) contained a nominal number of provenances in common, most studies, particularly those designed to support local tree improvement programs, contained a unique assortment of provenances. Our approach was to merge height measurements from the disparate studies according to the principle that populations occupying the same or similar climates should have the same growth potential as a result of parallel selection along similar climate gradients. To do this, we used a series of steps to calculate scaling factors that would allow the disparate datasets to be merged such that discrepancies in age and site productivity would be largely removed. The fallacy in this assumption would arise if natural selection had not yet optimized genetic variability within populations, as, for instance, would occur with adaptation lags or founder effects. For this reason, it was desirable to base scaling factors on as many populations as reasonably possible.

The first step in calculating the scaling factors was to find for each population in all studies the Euclidean distance in climate

space to all populations in all studies. For this step, we used 'yalmpute' (Crookston and Finley, 2008), a package in R, and 11 climate variables. Of the 34 climate variables at our disposal (see PART 1), these 11 were relatively independent, that is, the absolute value of a Pearsonian correlation coefficient (r) between any two variables was <0.7.

The second step was to infer from the array of Euclidean distances a threshold value below which two populations could be considered as originating from climatically similar provenances and, therefore, should have the similar growth potentials. This threshold was obtained from the maximum climate distance in an array of 187 pairs of *P. menziesii* populations located within 1 km and 50 m elevation of each other, and 177 pairs *P. ponderosa* populations located within 1 km and 100 m elevation of each other. These geographic limits were chosen primarily to be consistent with results of the individual studies but still provide a suitable number of observations for scaling individual datasets. Using a different limit for the species is consistent with results demonstrating clines of different steepness in the two species (Rehfeldt, 1994b; Sorensen and Weber, 1994). We assume that populations within these limits would be occupying similar climates, and, therefore, the maximum climate distance within the array could be used as a threshold for inferring genetic similarity; that is, any two populations with climate distances less than this threshold would have the same growth potential.

In the third step, pairs of populations from different studies were identified that, according to our criterion, should have similar growth potentials. To do this, a study was designated as the base study, that is, study 1 in Tables 1 and 2, chosen largely because of its geographically central location. A second study was selected that contained either or both identical and geographically proximal populations to those in study 1, that is, study 2 in these tables. The pairs of populations expected to be genetically similar were selected from the array of Euclidean distances. Because a single population tested in study 2 may have been climatically similar to more than one population of study 1, the tables list both the number of populations and number of population pairs used for scaling. For the array of pairs with Euclidian distances less than the threshold, a weighted mean was calculated for the ratio of height in study 2 to that in study 1. Weights were based on the climate distance (d) between pairs of populations such that a distance of zero was given a weight of 3 and a distance approaching the distance threshold (max) was given a weight of 1: $w = 3-((d \times 2)/max)$. The weighted mean was then used as a scaling factor by which all observations in study 2 were multiplied. The weight was chosen subjectively after a period of trial and error.

Table 1 shows, for instance, that the scaling factor used for adjusting study 2 data was based on 12 populations that had climate distances to populations in study 1 that were less than the threshold. These 12 populations comprised 14 pairs that were used to calculate the scaling factor. Of the 14, there was one identical population, for which the ratio of height measurements in the two studies was 0.91; this ratio received a weight of 3. The populations forming the pair of largest climate distance but still within the threshold were separated by 200 k and 200 m elevation; the ratio was 1.12 and received a weight of 1.04. For the 14, ratios ranged from 0.90 to 1.16, and the weighted average was 0.99. This latter mean was used to scale all observations in study 2 to those in study 1.

The process was repeated to scale data from study 3 to those in studies 1 plus 2 and was terminated when data from all studies had been scaled and merged into a single dataset for each species. The order by which studies were entered into the scaling process depended on the number of populations climatically similar to those already scaled. Although the scaled dataset would take on the units of measurements in study 1, scaled growth potential is treated as an index.

2.3. Genetic responses to climate

Linear mixed effects models (SAS Institute, 2008) were used to describe clinal variation in growth potential of populations within the varieties of these two species (hereafter, genecology models). Climate variables were specified as fixed effects and studies, blocks within studies, and populations within studies as random effects. The random effects accommodated the data hierarchy and the likelihood that the scaling procedures had not removed all bias attributable to the disparate studies. With regional studies, remaining bias could dampen clinal effects. Analyses were performed separately for each variety, the delineation of which is described in PART 1. The best model was chosen according to the lowest value of AIC, significance of the fixed effects, and a lack of colinearity among predictors, that is, $|r| < 0.7$

Residuals from the 'best' models were used to calculate a confidence interval ($\alpha = 0.2$) about a population mean, a statistic useful for defining the amount of difference that must separate populations before being reasonably assured that the differences are real. Genetic variation could then be classified into climatypes (sensu Turesson, 1925, but see also Tchebakova et al., 2003, Rehfeldt, 2004), using the confidence interval for determining climatype breadth.

Predictions made from the genecological models use only the fixed effects. Geographic patterns of genetic variation were mapped for each variety within their climate niche (PART 1) for 1961–1990 and 2060 climates.

3. Results

3.1. Genecological analyses

To illustrate the results of the scaling procedures, population mean growth potentials are plotted against the provenance climate variable of largest Pearsonian correlation (Fig. 2) with growth potential. While showing no obvious bias attributable to the disparate studies, the scatter of data points in this figure illustrates declining growth potential with increasing severity of provenance winters. Populations originating where winters are mild tend to have the highest growth potentials, a relationship well established within the varieties of these species.

In the mixed effects analysis, the random effects attributable to studies accounted for considerable variance (Table 3), a result suggesting that scaling and merging of the disparate data sets left behind variance that could be influencing the scatter in Fig. 2. As a result, the most important fixed effects were different from those of Fig. 2, although all results pointed to the importance of winter cold in controlling genetic differentiation among populations and in shaping the clines. Notice that for the two *P. menziesii* models, the most influential climate variable, negative degree-days calculated from minimum temperatures, has been transformed to accommodate a non-linear relationship (Table 3, and Fig. 2).

Fig. 3 shows for population means the relationship between observed and predicted growth potentials. While Pearsonian correlations between observed and predicted growth potentials are statistically significant for all varieties, those for the species as a whole were slightly greater than 0.9.

3.2. Mapped genetic variation

In Figs. 4 and 5, genetic variation in growth potential is mapped within the contemporary climate niche (see Figs. 2 and 3 in PART 1) and for the climate niche projected for the decade surrounding 2060 (see Figs. 5 and 6 in PART 1). To better visualize and interpret geographic patterns, continuous genetic variation has been

Table 3
Summary statistics of genecology analyses of growth potential using mixed effects models for two varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*. Bold face type indicates climate variables of greatest importance.

Parameter	Pinus ponderosa		Pseudotsuga menziesii	
	var. ponderosa	var. scopulorum	var. menziesii	var. glauca
Random effects (variances)				
Studies	68.	313.	1558.	2985.
Populations in studies	1191.	838.	988.	677.
Blocks in studies	1469.	217.	1541.	399.
Residual	1963.	842.	1921.	542.
Fixed effects (parameter estimates)				
Intercept	492.49	641.71	418.07	444.83
MINDD0[a]			**−0.418****	**−0.425****
PRATIO		−120.66**	151.70**	−63.307**
SDI	168.28**			−472.97**
TDIFF				2.921**
SPRP		−0.552**		−0.186*
DD0	**−0.157****			
SUMP	.647**	0.546**		
D100	**−1.804****			

Note: MINDD0, degree-days < 0C based on the minimum daily temperature; PRATIO, ratio of April–September precipitation to mean annual precipitation; SDI, ratio of the square root degree-days > 5C accumulating in the frost free season to annual precipitation; TDIFF, the difference between the mean temperature in the warmest and coldest months; SPRP, April–May precipitation; DD0, degree-days < 0C based on the mean daily temperature; SUMP, July–August precipitation; D100, date the sum of degree-days above 5 °C reaches 100.

[a] Transformed to $(MINDD0)^{0.8}$.
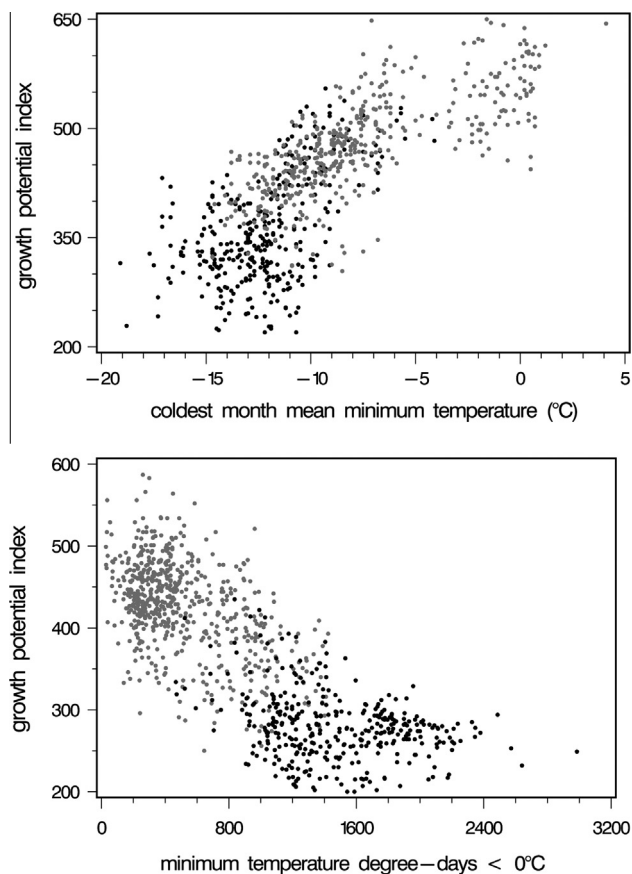** $p < .01$.
* $p = .02$.

Fig. 2. Scaled growth potential of *Pinus ponderosa* populations plotted against the mean minimum temperature of the coldest month of their provenance (top) and that of *Pseudotsuga menziesii* populations plotted against provenance negative degree-days based on minimum temperatures. Top: *P. p.* var. *ponderosa*, gray; *P. p.* var. *scopulorum* (black). Bottom: *P. m.* var. *menziesii*, gray; *P. m.* var. *glauca* (black).

assorted into classes. Maximum breadth of a class was determined by the confidence interval about a population mean: 70 and 50 units of growth potential for *P. p.* vars. *ponderosa* and *scopulorum*, respectively, and 52 and 26 units for *P. m.* vars. *menziesii* and *glauca*, respectively. The classes used for Figs. 4 and 5 are of breadth equal to ½ the confidence interval to make genetic variation more obvious. A climatype, therefore, would consist of any two adjacent classes. Mapped growth potentials for *P. m.* var. *glauca* south of 42° are largely extrapolations, as few populations were located in that area (Fig. 1).

Because genetic variation in the varieties of both species is under the primary control of winter temperatures (Table 3), geographic patterns of variation depicted in the left panels of Figs. 4 and 5 are similar. Growth potential is highest for climatypes inhabiting the warmest winters: the low elevations of California and Oregon for *P. p.* var. *ponderosa* and *P. m.* var. *menziesii*; the low elevations in the mountains of Arizona for *P. p.* var. *scopulorum*; and in the transition zone of British Columbia for *P. m.* var. *glauca*. The climatypes with the lowest growth potential are at the high elevations in the coldest portion of the climate niche: the Salmon River Mountains of central Idaho and the Black Hills of South Dakota for *P. p.* vars. *ponderosa* and *scopulorum*, respectively; the high elevations of the North Cascades and Sierra Nevada for *P. m.* var. *menziesii*; and the mountains of eastern Idaho and western Wyoming for *P. m.* var. *glauca*.

The climatic clines of Figs. 4 and 5 thus corroborate the geographic patterns of genetic variation that are well established historically: strong relationships to elevation everywhere; patterns paralleling longitude, following the westerly flow of air masses from the Pacific that cross two mountain ranges before merging into the continental climates to the east; and a weak relationship with latitude, most noticeable in *P. ponderosa* in the interior West.

3.3. Projections

The 2060 projections of classified genetic variation (right panels, Figs. 4 and 5) show a general northward and upward shift in climatype niche. For *P. p.* var. *ponderosa* and *P. m.* var. *menziesii* that
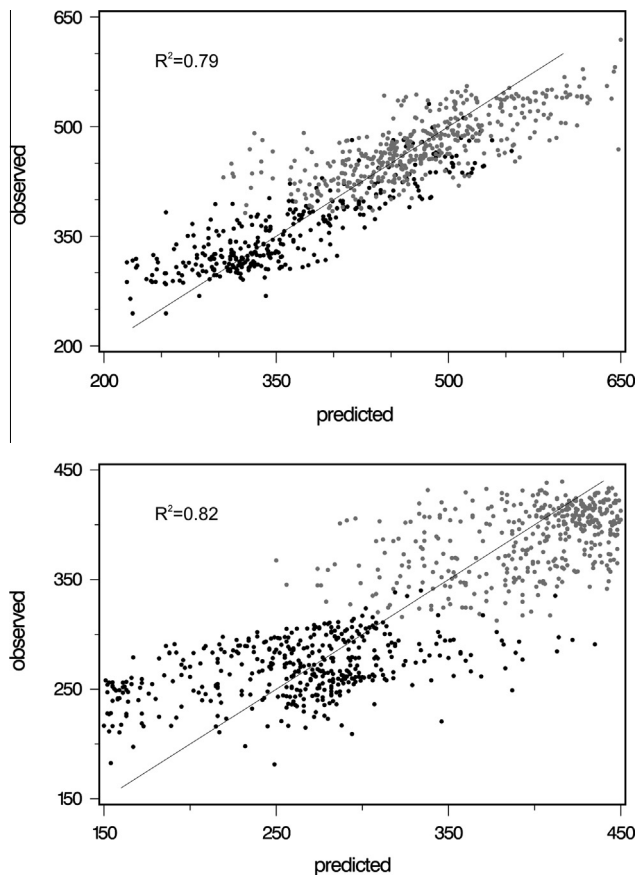
Fig. 3. Scaled growth potential of populations of two varieties of *Pinus ponderosa* (top) and that of populations of two varieties of *Pseudotsuga menziesii* (bottom) plotted against values predicted from the fixed effects in a mixed model analysis. Top: *P. p.* var. *ponderosa,* gray; *P. p.* var. *scopulorum* (black). Bottom: *P. m.* var. *menziesii*, gray; *P. m.* var. *glauca* (black).

inhabit coastal regions, the biggest increases in areas with suitable climate would be for climatypes of highest growth potential, an effect particularly striking for *P. m.* var. *menziesii*. While suitable habitat for no climatypes of either variety is projected to disappear, that for climatypes currently occupying the highest elevations, particularly in the Sierra Nevada, would become scarce.

Projections for varieties of the interior portray much different effects than those for coastal varieties. The projection for *P. p.* var. *scopulorum* readily illustrates the loss of niche space (Fig. 4) for the variety as a whole (PART 1). The array of 2060 climates is expected to include niche space for each climatype of today, but for some climatypes, such that encompassing the southernmost populations of highest growth potential, a loss of suitable climate suggests that their persistence may be precarious. For *P. m.* var. *glauca*, the area suited to the climatypes most tolerant of the cold would decline as it is pushed upwards, an effect that would make space available, for instance, in northern Idaho and south-central British Columbia for genotypes of higher growth potential than occur there now. Yet, climates suited to the fast-growing genotypes of the varietal transition would migrate very little to the east.

4. Discussion

In our analyses, variables describing winter cold were found to be the best predictors of population growth potential for both varieties of *P. ponderosa* and *P. menziesii*. These results concur with regional studies of *P. m.* var. *menziesii* (St Clair et al., 2005) and *P. p.* var. *ponderosa* (Sorensen et al., 2001) which also identified expressions of winter cold as drivers of genetic variation. Our results together with those of *Picea engelmannii* (Rehfeldt, 2004) and *Larix occidentalis* (Rehfeldt and Jaquish, 2010) further implicate winter cold as a primary agent of selection in molding the clinal variation within conifers of western North America. The many studies showing strong relationships between provenance elevation and genetic variation provide additional indirect support (e.g., Sorensen, 1994). In *Pinus strobus* of eastern North America, moreover, growth
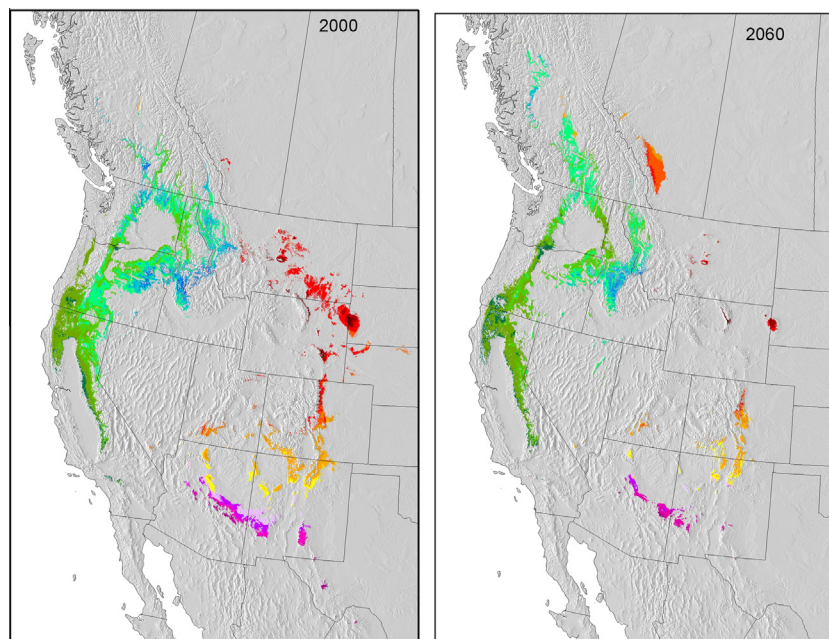

Fig. 4. Mapped genetic variation in growth potential in *Pinus ponderosa* predicted by the genecology model for the 1961–1990 climate (left) and climate for the decade surrounding 2060 (right). Genetic variation is assorted into classes of breadth equal to one-half the confidence interval surrounding a population mean. Climate of 2060 is from an ensemble of 17 general circulation models. Colorpaths of decreasing growth potential for var. *ponderosa*: dark green, light green, light blue, dark blue; for var. *scopulorum*: magenta, purple, yellow, light orange, dark orange, bright red, dark red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
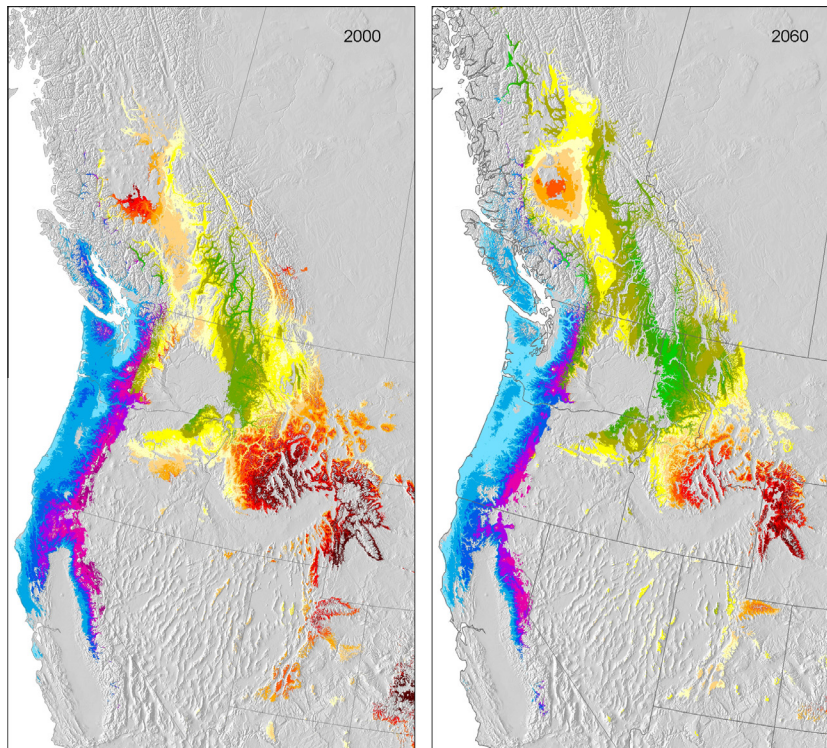
Fig. 5. Mapped genetic variation in growth potential in *Pseudotsuga menziesii* predicted by the genecology model for the 1961–1990 climate (left) and climate for the decade surrounding 2060 (right). Genetic variation is assorted into classes of breadth equal to one-half the confidence interval surrounding a population mean. Climate of 2060 is from an ensemble of 17 general circulation models. Colorpaths of decreasing growth potential for var. *menziesii*: light blue, dark blue, purple, magenta; for var. *glauca*: dark green, bright green, olive, olive-yellow, bright yellow, light yellow, light orange, dark orange, orange-red, dark red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

potential of populations was most closely related to the sum of degree-days > 5 °C, a variable so closely correlated with negative degree-days in eastern North America that whether genetic variation is best related to summer warmth or winter cold becomes moot (Joyce and Rehfeldt, 2013).

In addition, the results of this study, along with those of PART 1, illustrate that the distribution of species and their varieties are described by a different set of climate variables than drive intraspecific clines. While temperature tends to drive genetic variation within the varieties of *P. ponderosa* and *P. menziesii*, the occurrence of the species themselves is predicted from a combination of precipitation and temperature variables (PART 1, but also Rehfeldt et al., 2006; Hamann and Wang, 2006; Gray and Hamann, 2013). Responses to climate, therefore, will occur at both the specific and intraspecific levels (see also, for example, Rehfeldt et al., 2006; Leites et al., 2012a,b). While temperature–precipitation interactions tend to set the limits where species can successfully compete, temperature alone seems primarily responsible for adaptation of populations within those limits.

4.1. Clines in growth potential

Because the clines described by the genecology models are driven by different climate variables, comparing rates of genetic change in response to environmental selection is not straightforward. For doing this, an instructive approach is to relate growth potential to elevation. The regression statistics of Table 4 were calculated from a linear regression of growth potential predicted from the genecological models (Table 3) on elevation of ground plots inhabited by either *P. ponderosa* or *P. menziesii*. The ground plot data were used originally for developing climate profiles of PART 1. Statistics are presented for several geographic regions because

the same elevations in disparate regions will have different climates. Climatype breadth, the ratio of the confidence interval surrounding a population's growth potential to the regression coefficient, represents an approximate difference in elevation by which two populations must be separated before differences in growth potential become statistically valid. The values in this table are somewhat larger than those of Rehfeldt (1994b) because the current assessment uses confidence intervals while the latter used the least significant difference among population means, two statistics differing by the square root of 2.

Table 4 shows broader climatypes for (1) varieties inhabiting coastal regions than for those from interior regions; (2) varieties of *P. ponderosa* than for those of *P. menziesii* inhabiting the same regions; and, therefore, and (3) *P. ponderosa* than for *P. menziesii*. There's little doubt, however, that our cline for growth potential in *P. m.* var. *menziesii* (Fig. 2) is not as closely related to winter temperatures as reported by St Clair et al. (2005) for a principal component reflecting growth potential. While our analyses considered only 3 yr height, their synthetic variable included seedling dry weight, a variable more closely correlated with climate than height alone. Although our scaled data of growth potential may underestimate the steepness of the *P. menziesii* cline in coastal climates, our results support those of earlier work in demonstrating steeper clines for inland populations than for coastal populations of both species (Sorensen and Weber, 1994) and in *P. menziesii* than in *P. ponderosa* (Sorensen and Weber, 1994; Rehfeldt, 1994b). The relatively steep cline for *P. p.* var. *scopulorum* in southwestern USA (see also Rehfeldt, 1993), is inconsistent with the northern distribution of that variety and is, therefore, intriguing but not readily explained.

Table 4 also shows that the absolute size of the regression coefficient of growth potential on population altitude varies little

Table 4

Numeric basis and summary statistics for linear regressions of predicted growth potential on elevation, using ground plot observations of presence for various geographic regions for two varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*. Climatype breadth is the altitudinal interval separating two populations that differ genetically with a reasonable likelihood.

Taxon	Region	Number of observations	Coefficient of determination (R^2)	Regression coefficient (b)	Climatype breadth[a] (m)
Pseudotsuga menziesii					
var. *menziesii*	Southern coastal	1367	0.70	−0.054	956
var. *menziesii*	Northern coastal	7410	0.78	−0.064	816
var. *glauca*	Canadian interior	4247	0.41	−0.051	509
var. *glauca*	USA western interior	3282	0.55	−0.051	512
var. *glauca*	USA eastern interior	5180	0.70	−0.059	436
Pinus ponderosa					
var. *ponderosa*	Southern coastal	2808	0.43	−0.042	1662
var. *ponderosa*	Northwest coastal	2156	0.74	−0.063	1105
var. *ponderosa*	Western interior	2054	0.74	−0.082	857
var. *scopulorum*	Northern interior	1120	0.60	−0.036	1400
var. *scopulorum*	Southern interior	2080	0.44	−0.118	424

[a] Ratio of the confidence interval surrounding a population mean growth potential to the regression coefficient.

between regions within varieties, varieties within species, and species. This means that the differing breadth of climatypes is due largely to the size of the residual variation in the genecology models (Table 4). In analyses not designed to assess genetic effects within populations, the residual contains genetic variances among trees within populations and among individuals from the same mother tree, as well as experimental errors. In carefully maintained studies in which experimental errors are controlled, large residuals would reflect high genetic variability within individuals and populations: the weaker the environmental selection, the greater the genetic variances within populations, the larger the residuals, the broader the climatypes, the flatter the clines. Sorensen et al. (2001) further discuss the possibility that relatively flat clines of *P. ponderosa* might reflect contingencies of evolutionary history (e.g., founder effects, genetic bottlenecks, genetic drift) as much as selection along climate gradients.

The clines we describe are based solely on growth potential. Yet, research has shown repeatedly that populations of these two species differ for additional adaptive traits, which, in fact, may have different responses to climate (see St Clair et al., 2005). To be sure, growth potential integrates many adaptive responses by means of strong negative correlations with cold hardiness and positive correlations with developmental events (e.g., Rehfeldt 1989, 1991; Rehfeldt et al., 2004). In addition, the traits integrated by growth potential frequently are those with the strongest responses to climate (e.g., St Clair et al., 2005). Nonetheless, reliance on growth potential alone to describe adaptive response undoubtedly will underestimate differentiation. Application of these results in forest management must take this into consideration. This topic is addressed further in PART 3.

4.2. Climate change impacts

Climate change impacts arising from populations no longer being suited to the climate they inhabit are more subtle to witness and more difficult to demonstrate than the species-level impacts at the trailing and leading edges (see Figs. 5–7 of PART 1). Yet, the intraspecific impacts are of greater potential disruption of native ecosystems than the displacement of species. This is because many locations expected to remain suitable throughout the century for a species are, in fact, inhabited today by genotypes that are destined to be poorly suited to the future climate (Rehfeldt et al., 1999, St Clair and Howe, 2007, Alberto et al., 2013). From Figs. 4 and 5, for instance, statistics can be generated to estimate the proportion of future grid cells for which the future climate should remain

suitable for both the variety and the climatype suitable for that site today. We find these statistics to be astounding: 57% and 0.7% for *P. m.* var. *menziesii* and var. *glauca*, respectively, and 25% and 8% for *P. p.* var. *ponderosa* and var. *scopulorum*, respectively. Managerial implications are considered in depth in PART 3.

Provenance test results unequivocally demonstrate that as the climate changes, trees eventually will become less suited genetically to the environment in which they currently grow (Rehfeldt et al., 1999, 2002, 2004; Wang et al., 2006; St Clair and Howe, 2007; Leites et al., 2012a,b). Maladaptation, therefore, will become widespread. Although rates of demise associated with maladaptation will be linked to the speed of climate change and plasticity of individuals, little is known quantitatively about the lag between cause and effect. Provenance testing, however, has repeatedly demonstrated the process: loss of productivity, increased environmental stress, loss of vigor, and mortality from numerous potential agents (e.g., Worrall et al., 2013).

While clines in adaptive traits will determine the onset of maladaptive effects as the climate changes, the clines also provide an avenue from which management strategies can be developed. The premise for such strategies is preadaptation, that is, populations exist today that are expected to be genetically suited to climates of the future. Techniques for formulating and implementing strategies designed to maintain adaptedness in future generations are addressed in PART 3.

References

Alberto, F.J., Aitken, S.N., Ali'A, R., Gonzá Lez-MartíNez, S.C., Hänninen, H., Kremer, A., Lefèvre, F., Lenormand, T., Yeaman, S., Whetten, R., Savolainen, O., 2013. Potential for evolutionary responses to climate change – evidence from tree populations. Glob. Change Biol. 19, 1645–1661.

Burdon, R.D., Low, C.B., 1991. Performance of *Pinus ponderosa* and *Pinus jeffreyi* provenances in New Zealand. Can. J. Forest Res. 21, 1401–1414.

Callaham, R.Z., Liddicoet, A.E., 1961. Altitudinal variation at 20 years in ponderosa and Jeffery pines. J. Forest 59, 814–820.

Campbell, R.K., 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. Ecology 60, 1036–1050.

Campbell, R.K., 1986. Mapped genetic variation of Douglas fir to guide seed transfer in southwest Oregon. Silvae Genet. 35, 85–96.

Campbell, R.K., Sorensen, F.C., 1978. Effect of test environment on expression of clines and delimitation of seed zones in Douglas-fir. Theor. Appl. Genet. 51, 233–246.

Ching, K.K., Hinz, P.N., 1978. Provenance study of Douglas-fir in the Pacific Northwest Region. III. Field performance at age twenty years. Silvae Genet. 27, 229–233.

Crookston, N.L., Finley, A.O., 2008. yaImpute: an R package for kNN imputation. J. Stat. Softw. 23, 16.

Gray, L.K., Hamann, A., 2013. Tracking suitable habitat for tree populations under climate change in western North America. Clim. Change 117, 289–303.

Haddock, P.G., Walters, J., Kozak, A., 1967. Growth of coastal and interior provenances of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) at Vancouver and Haney in British Columbia. In: Faculty of Forestry Research Paper No. 79, University of British Columbia, Vancouver.

Hamann, A., Wang, T., 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87, 2773–2786.

Hanover, J.W., 1963. Geographic variation in ponderosa pine leader growth. Forest Sci. 9, 86–95.

Joyce, D.G., Rehfeldt, G.E., 2013. Climatic niche, ecological genetics, and impact of climate change on eastern white pine (*Pinus strobus* L.): guidelines for land managers. Forest Ecol. Manage. 295, 173–192.

Kempff, G., 1928. Non-indigenous western yellow pine plantations in northern Idaho. Northwest Sci. 2, 54–58.

Krakowski, J., Stoehr, M.U., 2011. Douglas-fir provenance survival and growth in the British Columbia south submaritime seed planning zone. Know. Manage. Br. Nat. Resource Sec., Victoria, BC Extension Note 105.

Langlet, O., 1936. Studier över tallens fysiologiska variabilitet och dess samband med klimatet. Meddelelser Statens Skogsförsöksanstalt 29, 219–470.

Leites, L.P., Rehfeldt, G.E., Robinson, A.P., Crookston, N.L., Jaquish, B.C., 2012a. Possibilities and limitations of using historic provenance tests to infer forest species growth responses to climate change. Nat. Resour. Model. 25, 409–433.

Leites, L.P., Robinson, A.P., Rehfeldt, G.E., Marshall, J.D., 2012b. Height-growth response to climate changesdiffers among populations of Douglas-fir: a novel analysis of historic data. Ecol. Appl. 22, 199–206.

McDermott, J.M., Robinson, R.A., 1989. Provenance variation for disease resistance in *Pseudotsuga menziesii* to the Swiss needle-cast pathogen, *Phaeocryptopus gaeumannii*. Can. J. Forest Res. 19, 244–246.

Mátýas, C., 1994. Modeling climate change effects with provenance test data. Tree Physiol. 14, 797–804.

Morgenstern, E.K., 1996. Geographic Variation in Forest Trees. UBC Press, Vancouver, BC.

Munger, T.T., Morris, W.G., 1936. Growth of Douglas fir Trees of Known Seed Source, US Department of Agriculture, Washington, DC, Technical, Bulletin No. 537, p. 40.

Read, R.A., 1980. Genetic variation in seedling progeny of ponderosa pine provenances. Forest Sci. Monogr. 23, 1–59.

Rehfeldt, G.E., 1979. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) populations. I. North Idaho and North-East Washington. Heredity 43, 383–397.

Rehfeldt, G.E., 1982. Ecological adaptations in Douglas-fir populations. II. Western Montana. In: USDA Forest Serv. Intermountain Res. Stn. Res. Paper INT-295, p. 8.

Rehfeldt, G.E., 1983. Ecological adaptations in Douglas-fir populations. III. Central Idaho. Can. J. Forest Res. 13, 626–632.

Rehfeldt, G.E., 1986a. Adaptive variation in *Pinus ponderosa* from Intermountain Regions. I. Snake and Salmon River Basins. Forest Sci. 32, 79–92.

Rehfeldt, G.E., 1986b. Adaptive variation in *Pinus ponderosa* from intermountain regions. II. Middle Columbia river system. In: USDA Forest Serv. Res. Pap. INT-373, p. 9.

Rehfeldt, G.E., 1988. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). IV. Montana and Idaho near the Continental Divide. West. J. Appl. Forest 3, 101–105.

Rehfeldt, G.E., 1989. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*): a synthesis. Forest Ecol. Manage. 28, 203–215.

Rehfeldt, G.E., 1990. Genetic differentiation among populations of *Pinus ponderosa* from the upper Colorado River basin. Bot. Gaz. 151, 125–137.

Rehfeldt, G.E., 1991. A model of genetic variation for *Pinus ponderosa* in the Inland Northwest (USA): applications in gene resource management. Can. J. Forest Res. 21, 1491–1500.

Rehfeldt, G.E., 1993. Genetic variation in the *Ponderosae* of the southwest. Am. J. Bot. 80, 330–343.

Rehfeldt, G.E., 1994a. Adaptation of *Picea engelmannii* populations to the heterogeneous environments of the Intewrmountain West. Can. J. Botany 72, 1197–1208.

Rehfeldt, G.E., 1994b. Evolutionary genetics, the biological species, and the ecology of the interior cedar-hemlock forests. In: Proceedings of the Conference: Interior Cedar-Hemlock-white Pine Forests: Ecology and Management, Spokane, WA, March 2–4, Department of Natural Resource Sciences, Washington State University, Pullman, WA.

Rehfeldt, G.E., 2004 Interspecific and intraspecific variation in *Picea engelmannii* and its congeneric cohorts: biosystematics, genecology, and climate-change. In: General Technical Report 134, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, Colorado.

Rehfeldt, G.E., Crookston, N.L., Warwell, M.V., Evans, J.S., 2006. Empirical analyses of plant–climate relationships for the western United States. Int. J. Plant Sci. 167, 1123–1150.

Rehfeldt, G.E., Jaquish, B.C., 2010. Ecological impacts and management strategies for western larch in the face of climate-change. Mitig. Adapt. Strat. Glob. Change 15, 283–306.

Rehfeldt, G.E., Jaquish, B.C., López-Upton, J., Sáenz-Romero, C., St Clair, J.B., Leites, L.P., 2014a. Comparative genetic responses to climate for the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: realized climate niche. Forest Ecol. Manage. 324, 126–137.

Rehfeldt, G.E., Jaquish, B.C., Sáenz-Romero, C., St Clair, J.B., López-Upton, J., Leites, L.P., 2014b. Comparative genetic responses to climate for the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Reforestation. Forest Ecol. Manage. 324, 147–157.

Rehfeldt, G.E., Tchebakova, N.M., Parfenova, E., 2004. Genetic responses to climate and climate change in conifers of the temperate and boreal forests. Rec. Res. Develop. Gene Breed 1, 113–130.

Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, R.A., Kuzmina, N.A., Milyutin, L.I., 2002. Intraspecific responses to climate in *Pinus sylvestris*. Glob. Change Biol. 8, 912–929.

Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L., Hamilton, D.A., 1999. Genetic responses to climate in Pinus contorta: niche breadth, climate change, and reforeastation. Ecol. Mongr. 69, 375–407.

SAS Institute, 2008. SAS User's Guide: Statistics, Release 9.2, SAS Institute Inc., Cary, NC.

Sorensen, F.C., 1994. Genetic variation and seed transfer guidelines for ponderosa pine in central Oregon. In: USDA Forest Service Research Paper PNW-RP-472.

Sorensen, F.C., Weber, J.C., 1994. Genetic variation and seed transfer guidelines for ponderosa pine in the Ochoco and Malheur National Forests of central Oregon. In: USDA Forest Service Research Paper PNW-RP-468.

Sorensen, F.C., Mandel, N.L., Aagaard, J.E., 2001. Role of selection versus historical isolation in racial differentiation of ponderosa pine in southern Oregon: an investigation of alternative hypotheses. Can. J. Forest Res. 31, 1127–1139.

Stephan, B.R., 1980. Testing Douglas fir provenances for resistance to *Rhabdocline pseudotsugae* by infection trials. Eur. J. Forest Pathol. 20, 152–161.

Squillace, A.E., Silen, R.R., 1962. Racial variation in ponderosa pine. Forest Sci. Monogr. 2, 1–27.

St Clair, J.B., Mandel, N.L., Vance-Borland, K.W., 2005. Genecology of Douglas Fir in western Oregon and Washington. Ann. Bot. 96, 1199–1214.

St Clair, J.B., Howe, J.T., 2007. Genetic maladaptation of coastal Douglas-fir seedlings to future climates. Glob. Change Biol. 13, 1441–1454.

Tchebakova, N.M, Rehfeldt, G.E., Parfenova, E.I., 2003. Redistribution of vegetation zones and populations of *Larix sibirica* Ledeb. and *Pinus sylvestris* L. in Central Siberia in a warming climate. Siberian Ecol. J. 10, 677–686 (in Russian).

Turesson, G., 1925. The plant species in relation to habitat and climate. Hereditas 6, 147–236.

Wang, T., Hamann, A., Yanchuk, A., O'Neill, G.A., Aitken, S.A., 2006. Use of response functions in selecting lodgepole pine populations for future climates. Glob. Change Biol. 12, 2404–2416.

Wells, O.O., 1964. Geographic variation in ponderosa pine. I. The ecotypes and their distribution. Silvae Genet. 13, 89–103.

Worrall, J.J., Rehfeldt, G.E., Hamann, A., Hogg, E.H., Marchetti, S.B., Michaelian, M., Gray, L.K., 2013. Recent declines of *Populus tremuloides* in North America linked to climate. Forest Ecol. Manage. 299, 35–51.