

Use of response functions in selecting lodgepole pine populations for future climates

T. WANG*, A. HAMANN*, A. YANCHUK†, G. A. O'NEILL† and S. N. AITKEN*

*Department of Forest Sciences, University of British Columbia, Vancouver, BC, Canada V6T 1Z4, †Research Branch, B.C. Ministry of Forests, Victoria, British Columbia, Vancouver, BC, Canada V8W 9C2

Abstract

Although growth response functions have previously been developed for lodgepole pine (*Pinus contorta* Dougl. ex Loud.) populations in British Columbia, new analyses were conducted: (1) to demonstrate the merit of a new local climate model in genecological analysis; (2) to highlight new methods for deriving response functions; and (3) to evaluate the impacts of management options for existing geographically defined seed planning units (SPUs) for reforestation. Results of this study suggest that new methods for anchoring population response functions, and a multivariate approach for incorporating climate variables into a single model, considerably improve the reliability of these functions. These functions identified a small number of populations in central areas of the species distribution with greater growth potential over a wide range of mean annual temperature (MAT). Average productivity of lodgepole pine is predicted to increase (up to 7%) if moderate warming ($\sim 2^\circ\text{C}$ MAT) occurs in the next few decades as predicted, although productivity would substantially decline in some SPUs in southern BC. Severe global warming ($> 3^\circ\text{C}$ MAT) would result in either a drastic decline in productivity or local populations being extirpated in southern SPUs. New deployment strategies using the best seed sources for future reforestation may not only be able to mitigate the negative impact of global warming, but may even be able to increase productivity in some areas.

Keywords: climate change impacts, facilitated migration, forest productivity, growth response function, local adaptation, *Pinus contorta*, seed deployment

Received 7 February 2006; revised version received 20 May 2006 and accepted 3 April 2006

Introduction

The importance of using seed sources adapted to their plantation environments for reforestation has long been recognized, based on observed differences among populations within species for survival, growth and resistance to biotic and abiotic stresses. Geographic patterns of genetic variation for traits related to adaptation to climate (e.g. timing of initiation and cessation of growth, cold and drought hardiness and growth rates) are associated with climatic gradients in temperature and moisture (Aitken & Hannerz, 2001). These observations have typically lead to forest policies that require the use of local seed sources for reforestation, in order to minimize the risk of maladaptation. This has been a widespread, appropriate, risk-averse practice for the

past several decades. However, this assumption of 'local is best' assumes that offspring planted locally for reforestation are going to experience a climate similar to that experienced by their parents, grandparents and more distant ancestors. We now know that this is increasingly unlikely due to climate change.

Substantial evidence that we are in an unprecedented period of rapid global climate change is accumulating. Both weather data (IPCC, 2001; Petit, 2001) and observed biological responses to increased temperature over the past 30 years (Bradshaw & Holzapfel, 2001; IPCC, 2001; Chmielewski & Rotzer, 2002; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Chuine *et al.*, 2004) support this notion. Plant phenology, particularly the timing of onset of growth in the spring, has advanced for some species during this period of warming (Menzel & Fabrian, 1999; Post & Stenseth, 1999). Altitudinal range limits of some plant species are rising, and are predicted to climb an average of 400–600 m over the

Correspondence: T. Wang, 3041-2424 Main Mall, Vancouver, BC, Canada V6T 1Z4, e-mail: tlwang@interchg.ubc.ca

next century (Kullman, 2002), a distance that exceeds current allowable transfers for seed from place of collection to planting sites for most forest tree species in British Columbia. Thus, climate change adaptation strategies should be viewed as part of the risk management component of a sustainable forest management plan (Spittlehouse, 2005). In reforestation, seed deployment policy will need to adapt to climate change by taking population responses to climate into consideration.

Response functions of populations to various climatic conditions can be modeled if data are available from comprehensive provenance trials (i.e. seed collected from many locations and planted in common garden experiments on many sites spanning a wide range of climatic conditions, Matyas, 1994; Rehfeldt *et al.*, 1999). In this manner, spatial climatic variation is substituted for temporal trends. Response functions can then be used to predict the performance of each population under both current and predicted future climates. By comparing response functions among populations, the most suitable populations can be selected for each planting site under particular climate change scenarios. The development of response functions also requires a climate model that accurately predicts climatic variables for each test site. Although population and provenance are slightly different by definition (the former is defined by interbreeding while the latter emphasizes the geographical origin of a sample of genotypes), they will be used interchangeably in this study.

The lodgepole pine 'Illingworth provenance trial' established in British Columbia in 1974 (Illingworth, 1978), with 140 provenances tested at 60 test sites, may be the most comprehensive provenance test in the world. In a landmark analysis of this trial, Rehfeldt *et al.* (1999) predicted climatic variables for test sites using polynomial functions driven by latitude, longitude and elevation, developed from multiple regressions using weather station data. Response functions were then developed for most of the populations. Using these response functions, impacts of climate change on growth performance and survival were predicted for a number of climate change scenarios (Rehfeldt *et al.*, 2001).

With the recent commercial availability of the climate model PRISM (parameter-elevation regressions on independent slopes model; Daly *et al.*, 2002), we were able to make comparisons between this model and the polynomial functions developed by Rehfeldt *et al.* (1999). We found in a previous study (Hamann & Wang, 2005) that predictions of climatic variables using elevation-adjusted PRISM data were considerably improved over those of the polynomial models, especially for precipitation-related variables. Therefore, we felt it worthwhile to reanalyze the provenance trial data in

light of the new climatic model. Notably, a new version of this high-resolution climate model has further improved the predictions of climatic variables (Wang *et al.*, 2006). We have also attempted to improve methods of data analysis to deal with unbalanced field experimental design and effects of multiple climatic variables on growth.

Seed Planning Units (SPUs) are the geographic units of seed management for reforestation in British Columbia. Characterizing growth responses of genotypes from a SPU over different environments is important for planning seed deployment across SPUs for future climates. Therefore, the development of response functions for SPUs is necessary in addition to the response functions for individual populations.

The objectives of this study are to: (1) improve the accuracy of response functions by using the improved climate model and analytical methods; (2) develop growth response functions for both populations from specific seed source locations and populations when seed sources are aggregated over each SPU; (3) examine variation in patterns of growth response to climates among populations; and (4) predict impacts of climate changes on productivity of lodgepole pine in British Columbia with different seed deployment strategies.

Materials and methods

Plant materials

The extensive provenance trials for lodgepole pine established by the BC Ministry of Forests in 1974 (Illingworth, 1978) incorporated a range-wide collection of 140 populations (provenances) from New Mexico to the Yukon, planted at 60 test sites in interior British Columbia and two sites in the southern Yukon (Fig. 1). Of the 140 populations, 107 were *ssp. latifolia* [Engelmann] Critchfield. An unbalanced design tested 60 populations at each site. Most of the populations tested at each site were from the local region, but considerable overlap occurred across the test sites between regions. In particular, 10 populations, seven of them *ssp. latifolia*, were tested over all sites as reference populations. Populations from *ssp. contorta* [Doug. Ex Loud.] Critchfield and *ssp. murrayana* [Greville and Balfour] Critchfield were tested only at a few test sites and generally experienced high mortality, and are therefore not included in the current analysis.

SPUs and sample distribution

In British Columbia, seed transfer is constrained within Seed Planning Zones (SPZs) that are largely delineated by combining variants of the Biogeographic Ecological

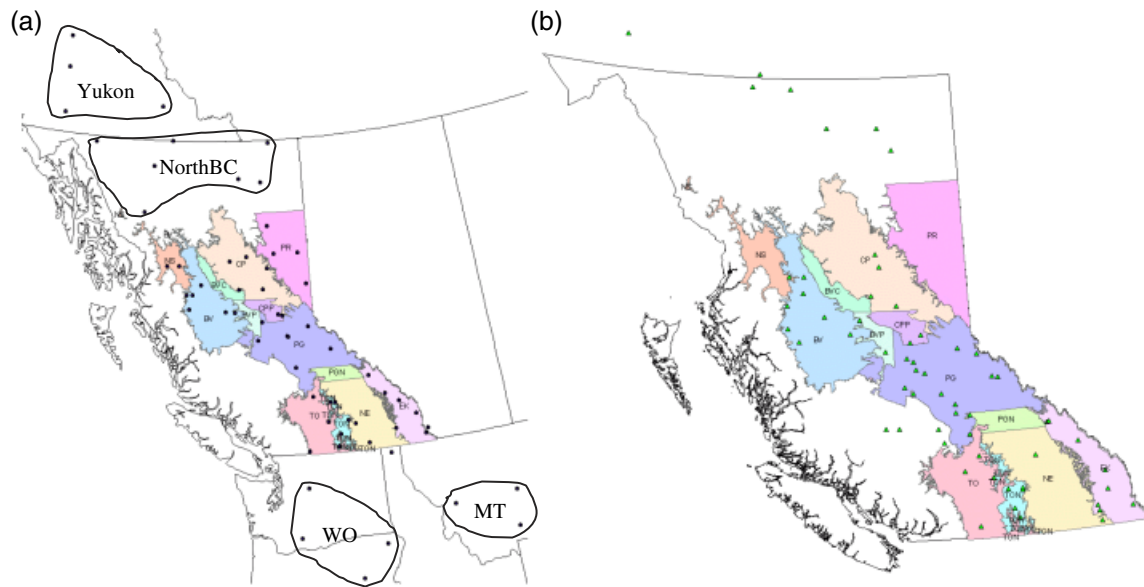


Fig. 1 (a) Locations of provenances (black dots), seed planning units (grayscaled polygons) and regions (white polygons); and (b) location of the 62 test sites (green triangles).

Table 1 Predicted changes in productivity of each SPU with increased MAT for local and optimal seed deployment (%), relative to current MAT with local seed source

SPU	Local seed source					Optimized seed source						
	MAT	+1 °C	+2 °C	+3 °C	+4 °C	+5 °C	+0 °C	+1 °C	+2 °C	+3 °C	+4 °C	+5 °C
CPhigh	-0.0	26.8	41.4	44.3	35.6	15.6	9.1	42.9	64.0	73.0	82.5	85.2
CPlow	1.6	6.7	7.5	2.6	-7.8	-23.6	8.8	14.4	18.9	20.0	16.1	7.2
NShigh	0.2	43.3	75.5	97.2	109.1	111.4	38.7	71.1	100.0	120.9	139.4	147.1
NSlow	2.9	0.6	-3.8	-13.1	-27.4	-46.6	16.5	22.5	24.3	21.2	13.2	0.4
BVhigh	0.8	2.7	-0.1	-8.2	-21.6	-40.1	15.6	19.4	22.1	19.2	10.8	-2.9
BVlow	2.0	8.8	12.3	10.6	3.8	-8.0	16.1	24.3	28.8	31.3	28.3	19.9
PGhigh	1.0	19.7	32.7	39.4	40.1	34.9	16.2	36.3	45.9	56.0	59.6	56.9
PGlow	3.0	1.0	-2.3	-10.0	-21.8	-37.9	1.9	5.3	4.1	-1.5	-11.6	-25.9
PRhigh	1.2	6.4	7.5	3.4	-5.8	-20.0	38.8	52.3	58.1	63.5	62.2	54.3
PRlow	1.0	6.4	6.9	1.7	-9.0	-25.0	4.1	12.3	16.5	18.2	14.0	4.0
NEhigh	1.3	6.9	6.0	-2.6	-18.9	-42.9	2.7	17.7	31.1	42.0	46.3	44.3
NElow	4.3	0.3	-3.3	-10.9	-22.3	-37.5	0.0	0.3	-3.3	-10.9	-22.3	-37.5
EKhigh	0.9	10.1	10.2	0.4	-19.0	-48.0	16.3	40.1	52.4	64.0	69.4	67.8
EKlow	3.5	-10.5	-28.4	-53.6	-86.0	-100	7.1	7.5	3.2	-5.8	-19.5	-37.8
TOhigh	2.3	-5.5	-20.4	-44.5	-77.9	-100	16.4	20.5	22.4	19.0	10.4	-3.5
TOlow	4.6	-26.3	-63.2	-100	-100	-100	43.6	26.4	0.6	-34.0	-74.8	-100
Average*		6.9	6.9	0.9	-9.1	-24.1	10.8	21.0	25.3	25.6	21.1	12.3

Predictions in shaded cells are beyond the MAT range of test sites.

*Weighted average by the area of lodgepole pine plantation in each SPU.

SPU, seed planning unit; MAT, mean annual temperature.

Classification (BEC) system (Meidinger & Pojar, 1991) into continuous landscape units. Within SPZs, the deployment of orchard seed (Class A) is further restricted to elevational bands called SPUs. There are eight SPZs (NS, CP, PR, BV, PG, TO, NE and EK) and

five overlapping SPZs (BVC, BVP, CPP, PGN and TON), which can be classified into either of the two neighbor SPZs; Fig. 1) and 16 SPUs (not including the ones from overlapping SPZs; Table 1) for this species in BC. Of the 16 SPUs, 14 SPUs have populations included in the

provenance trials. Populations in geographic areas outside of BC's SPZs were grouped into four geographic regions: Yukon, northern BC, Montana (MT) and Washington/Oregon (WO), shown in Fig. 1. The population in Idaho near the BC border was lumped into a BC SPU (NElow). To facilitate comparison among so many populations and to make the results of this study directly applicable to practical seed management in this province, most of the analyses were conducted at the SPU level (i.e. populations from each SPU or each geographic region were pooled together, and referred to as a 'SPU population' or a region).

Climate variables

Values of eight climate variables used in previous studies (Rehfeldt *et al.*, 1999, 2001) were predicted for each provenance and test site for a reference period (1961–1990) using our recently developed high-resolution climate model ClimateBC v2.2 (Wang *et al.*, 2006). For provenances beyond the coverage of ClimateBC, the climate variables were predicted using elevation-adjusted PRISM data based on the methodology described in Hamann & Wang (2005). The eight climate variables include mean annual temperature (MAT), mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), continentality (TD, which is the difference between MWMT and MCMT), mean annual precipitation (MAP) and mean summer precipitation (MSP), as well as two moisture indices: annual heat-moisture index [AHM: (MAT + 10)/(MAP/1000)] and summer heat-moisture index [SHM: MWMT/(MSP/1000)]. The eight climate variables were also predicted for three future 30-year periods centered on 2025, 2055 and 2085 using ClimateBC and based on ensemble averages generated by the global circulation model CGCM2-A2x of the Canadian Centre for Climate Modeling and Analysis (Flato *et al.*, 2000). This model is one of the two most updated Canadian models, and predicts more rapid warming than the other one (CGCM2-B2x). The years predicted for MAT to increase by 1, 2, 3, 4 and 5 °C were approximated by linear interpolation of the above predictions between reference period and 2085. The five scenarios were predicted to occur in years 2018, 2041, 2064, 2087 and 2110, respectively, based on predicted changes averaged across all SPUs. MAP is predicted to increase slightly, approximately 1.8%, with each 1 °C increase in MAT.

Statistical analysis

All statistical analyses were conducted using SAS (SAS-Institute-Inc., 1989). As the relationships between survival and climate variables are generally weak, only

20-year height and volume per hectare were used in the analysis. Height growth is the most heritable of growth-related traits for this species (Wang *et al.*, 1999) and also has the strongest relationship with climate variables found in this study. Thus, it was used to develop methodology for the development of response functions. Volume per hectare integrates growth and survival, and was used for predictions of impacts of climate change on productivity.

Growth response functions describe the performances of populations across planting environments (Matyas, 1994; Rehfeldt *et al.*, 1999). Univariate and multivariate quadratic response functions were developed for each population based on the following regression models respectively:

$$Y_i = b_0 + b_1X_1 + b_2X_1^2 + e_i, \quad (1)$$

$$Y_i = b_0 + b_1X_1 + b_2X_1^2 + b_3X_2 + b_4X_2^2 + \dots + e_i, \quad (2)$$

where Y_i is the mean height or productivity of a population (or a SPU population) at the test site (or in the SPU) i ; b_0 is the intercept; b_1 , b_2 , b_3 and b_4 are regression coefficients; X_1 and X_2 are two climate variables for the test site (or in the SPU) i ; and e_i is the residual.

A function describing the relationship between the growth performance of populations and their source climate for a given individual test site was necessary to improve and validate growth response functions. As this function reflects the performance of transferred populations relative to local ones at a given test site, we defined it as 'individual transfer function' in contrast to the general transfer function (Campbell, 1974) that is based on pooled data across all test sites. It bears no relationship to the meaning of transfer function in control theory. A univariate quadratic function was used to develop individual transfer functions for some of the test sites:

$$Y_i = b_0 + b_1X_1 + b_2X_1^2 + e_i, \quad (3)$$

where Y_i is the mean height or productivity of the population i at a given test site, b_0 is the intercept, b_1 and b_2 are regression coefficients, X_1 is a climate variable for source location of the population i ; and e_i is the residual.

Impacts of climate change on productivity of each SPU were predicted based on multivariate response functions of the SPU population, while the impacts on overall productivity across SPUs were averages weighted by the area of lodgepole pine plantation in each SPU. For the two SPUs (BVhigh and NShigh) that did not have populations tested, the parameters for their growth response functions were approximated through linear interpolation based on SPUs' MAT and

log-transformed AHM (LnAHM). Predicted productivities for overlapping SPUs were averages of the two neighboring SPUs. The impacts were predicted for five climate change scenarios: MAT increased by 1, 2, 3, 4 and 5 °C. Intervals for 90% confidence were also estimated for each prediction based on the corresponding confidence intervals of multivariate response functions for SPU populations.

Results and discussion

Improvements of growth response functions using anchor points

Although the Illingworth test is one of the most comprehensive provenance trials in forestry, the majority of test sites are located within a relatively narrow range of MAT (1–5 °C; Fig. 2a), the single most effective variable for predicting height growth in lodgepole pine (Rehfeldt *et al.*, 1999). Owing to the unbalanced experimental design, many provenances were not tested in the coldest environments (at the left of the distribution

in Fig. 2a). For these provenances, it is difficult to establish reasonable relationships between their performance and climate variables for the test sites. As shown in Fig. 2b, radically different response curves (with poor determination coefficients) may be equally plausible for populations that are not tested at climatic extremes. Therefore, it is critical to have observations at the extremes of the climatic gradients of interest.

Rehfeldt *et al.* (2001) addressed this problem using a predefined maximum breadth of the fundamental niche of this species, and properties of quadratic functions ($r_1 + r_2 = -\beta_1/\beta_2$ and $r_1 \times r_2 = \beta_0/\beta_2$, where r_1 and r_2 are the roots, β_0 is the intercept, and β_1 and β_2 are regression coefficients). The maximum breadth of the fundamental niche was determined from response curves of the eight standard provenances (seven *ssp. latifolia* provenances and one *ssp. contorta* provenance) tested over all test sites. Response curves having a fundamental niche wider than the maximum fundamental niche were adjusted using the maximum fundamental niche.

We took a different approach in this study. For provenances that were not tested at some or all of the

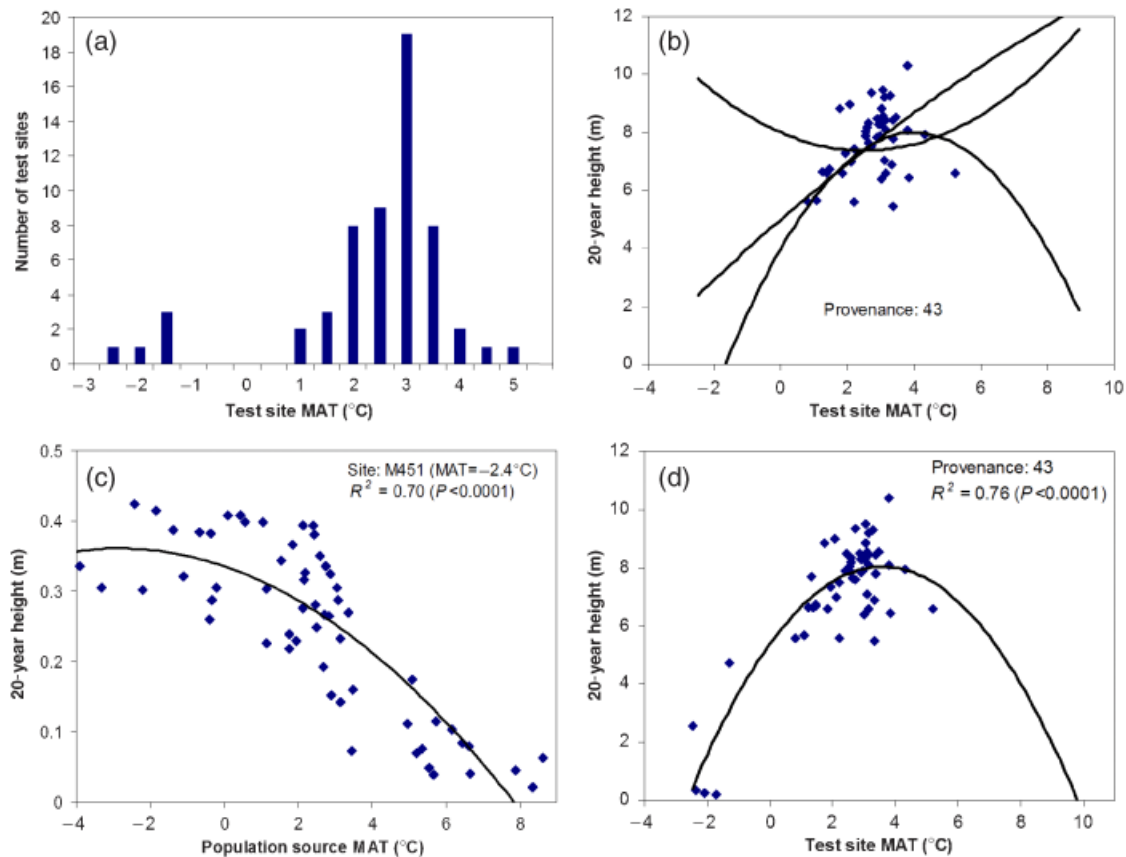


Fig. 2 (a) The distribution of test sites against mean annual temperature (MAT); (b) possible forms of growth population response functions for provenance 43 which was not tested at cold sites; (c) transfer function for site M451 which was used to estimate one of the five anchor points used in (d); and (d) population response function for provenance 43 established with anchor points included.

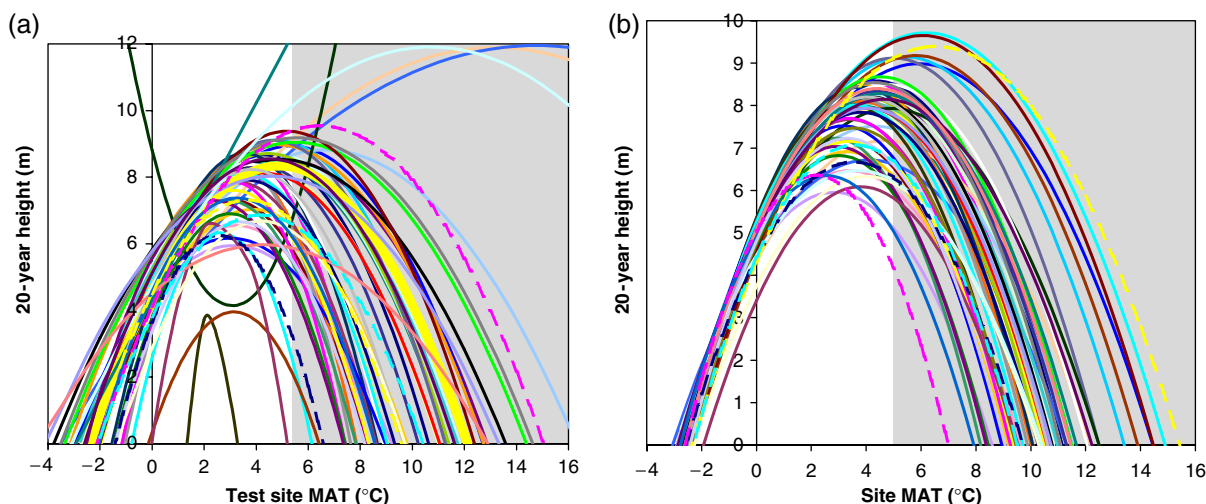


Fig. 3 Population response curves for 20-year height developed without (a) and with (b) predicted anchor points. Shaded areas are beyond the mean annual temperature (MAT) range of test sites.

five coldest test sites where MAT was $<0^{\circ}\text{C}$, their growth performances at these sites were estimated from individual transfer functions developed using model [3]. For example, the provenance #43 was not present at any of the five coldest sites (Fig. 2b). Its 20-year height at test site M451 was estimated from the individual transfer function for this site (Fig. 2c, the regression curve) based on its source MAT. Using the same method, its 20-year heights at the other four coldest sites could also be estimated. The estimated values (Fig. 2d, the five points on the left end) were then used together with observed values from other test sites to develop an improved growth response function. As the estimated values for the cold test sites were critical to anchor the ‘low MAT’ tail of response functions, we call them ‘anchor points.’

Response curves for all provenances differed considerably depending on whether predicted anchor points are used (Fig. 3). When anchor points are not used (Fig. 3a), quite a few biologically impossible curves are estimated. Over 20% of the curves in Fig. 3a had very low R^2 values (<0.20). Those curves with poor fit or without a sensible fundamental niche would have to be dropped from further analysis or arbitrarily modified to meet the maximum breadth of fundamental niche (Rehfeldt *et al.*, 1999, 2001). Population response functions became more realistic and the fit of curves improved after the inclusion of anchor points. For example, the R^2 of the population response function for the provenance shown in Fig. 2b and d increased from 0.28 to 0.76, and the average R^2 over all populations increased from 0.48 to 0.64 when up to five cold-site anchor points were added.

All provenances were very short at the five coldest sites (e.g. tallest provenance <0.70 m at three of the

five sites) relative to the heights of provenances at the remaining sites (e.g. tallest provenance >7 m at each site) and were estimated fairly accurately with statistically significant transfer functions ($R^2 = 0.40\text{--}0.70$; $P < 0.0001$). Consequently, the error inherent in the height of any provenance estimated from the five transfer functions is small compared with the error associated with response functions fitted without values from cold sites (i.e. sites having an MAT $<0^{\circ}\text{C}$). Anchor points therefore provide substantial improvement in response function estimation, particularly in the low MAT region of the response.

The range of the roots is much narrower at both the low and high ends of MAT in Fig. 3b (anchor points used) than in Fig. 3a (anchor points not used). Obviously, different conclusions could be drawn from these two figures in term of the pattern of adaptation to different environments for this species. Shift in peaks and fundamental niches among populations along MAT gradients for growth would be a significant feature based on the result shown in Fig. 3a, although not to the same extent as reported in previous studies (Rehfeldt *et al.*, 1999, 2001). However, Fig. 3b suggests that among-population variation in growth is small at colder temperatures and greater at warmer sites. This pattern of adaptive variation among populations is consistent with the pattern obtained from the seven populations that were tested at all test sites (no predicted anchor points needed) shown in Fig. 4. A similar pattern was also found among populations of larch and interior Douglas-fir in this province (B. Jaquish, BC Ministry of Forests, unpublished data).

Figure 3b shows that the best populations outperformed others over a large range of MAT and the

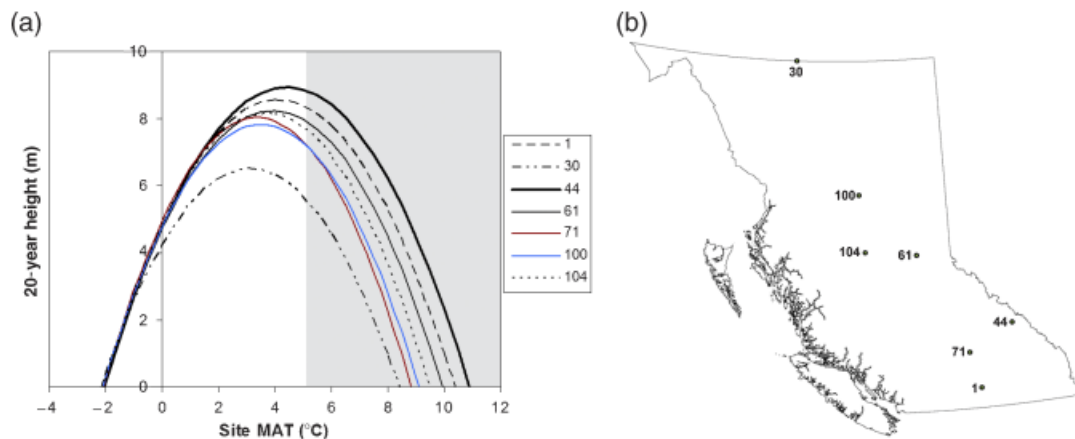


Fig. 4 Height growth response curves for the seven reference populations that were tested at all test sites (a) and the source locations of the populations (b). Shaded areas are beyond the mean annual temperature (MAT) range of test sites.

fundamental niche of the best populations is wider than Rehfeldt's predefined fundamental niche (Rehfeldt *et al.*, 2001). Despite dramatic improvement in the R^2 of the response functions achieved by applying anchor points, the growth response functions established in this study still possess considerable uncertainty due to the uneven distribution of the test sites along the temperature gradient (Fig. 2a) and the assumption of symmetrical temperature response functions. There is a large gap between MAT -1.3 and 1 °C, thus the left side of a response curve is entirely dependent on the five (cold sites) points. In particular, the absence of test sites at locations warmer than MAT 5 °C considerably compromises the confidence of predictions for climate conditions beyond this point (shaded areas in Figs 3 and 4). Therefore, predictions using these response functions need to be interpreted with caution particularly for projections past, say, 2055 when many test sites will have MATs higher than 5 °C.

Improvement of response functions using multivariate analysis

Of all climate variables analyzed, the quadratic function of MAT explained the largest amount of environmental variation in height (64% on average) for populations planted in various environments. This is well in agreement with previous studies (Rehfeldt *et al.*, 1999, 2001). Inclusion of an additional variable, LnAHM, explained an additional 6% of the total variation, on average. All other climate variables made either no significant contribution or had an inconsistent effect on the model across populations. The interaction between MAT and LnAHM was not significant, accounting for only 0.3% of the total variation, and was ignored in further analyses.

AHM better reflects soil moisture than does precipitation alone, as it considers both moisture source (precipitation) and evapotranspiration (related to temperature). Furthermore, predicted changes in precipitation are small relative to predicted changes in temperature according to predictions of the global circulation model CGCM2-A2x (Flato *et al.*, 2000). Therefore, changes in AHM should reflect growth impacts due to climate change better than changes in MAP alone, and in combination with MAT should provide reasonably robust predictions of population performances in multivariate response surfaces.

Growth response surfaces developed based on two environmental gradients (MAT and LnAHM) for both height and productivity [volume per hectare ($\text{m}^3 \text{ha}^{-1}$)] are demonstrated for the SPU population NElow in Fig. 5. The response surfaces displayed a bell shape for both traits, suggesting that lodgepole pine populations have both an optimum temperature and optimum soil moisture. The 'optimum' population MAT varied between 3.1 and 5.9 °C with an average of 4.0 °C, whereas the optimum AHM varied between 12.5 and 18.2 with an average (across all populations) of 15.1 , based on 20-year height. The R^2 value of the height response surface (0.77) is considerably greater than that of the productivity response surface (0.48). This is primarily due to variation in survival rather than tree size in calculating a volume per hectare estimate. Volume per hectare consolidates variation in height, diameter and survival and should therefore offer a truer estimate of area-based productivity impacts than its constituent traits. However, productivity estimates also incorporate any error associated with estimation of these component traits. Survival can be particularly affected by nonclimate factors (e.g. establishment success after planting and some forms of animal damage). Thus, a substantial

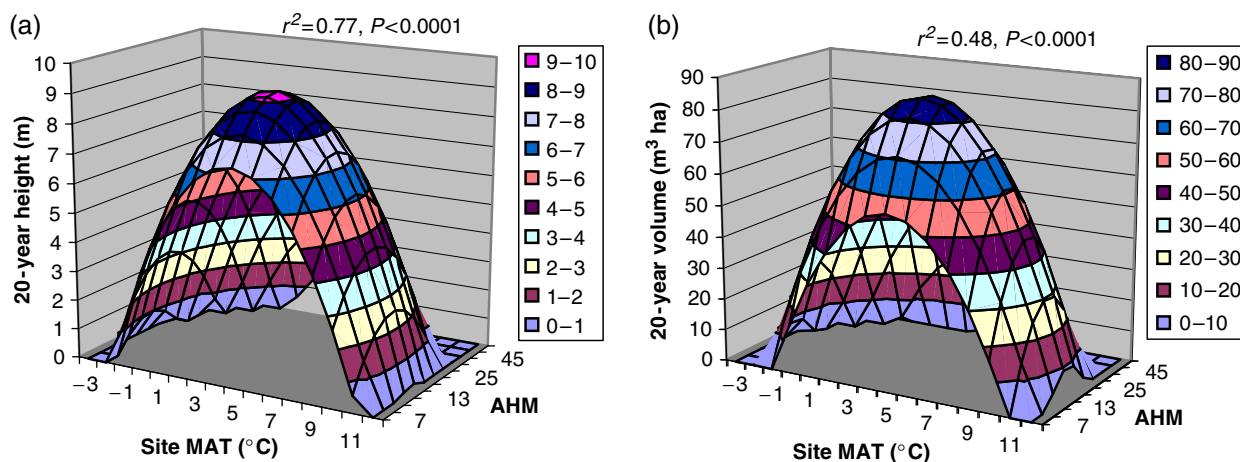


Fig. 5 Growth response surfaces on site mean annual temperature (MAT) and mean annual heat-moisture index (AHM) for 20-year height (a) and volume per hectare (b) of the seed planning unit population NElow.

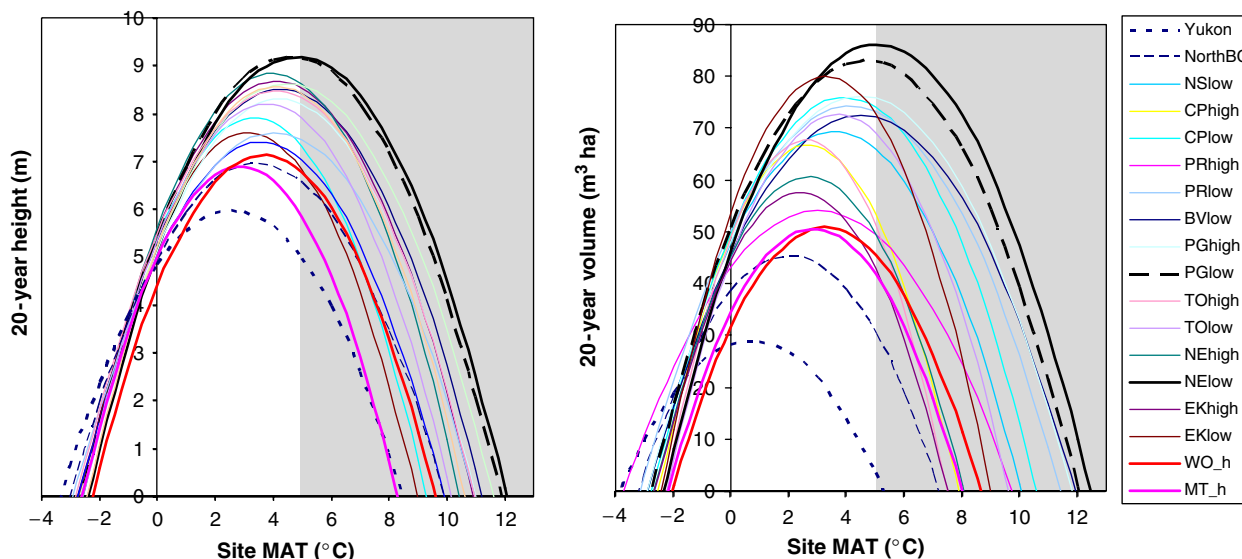


Fig. 6 Growth response curves of seed planning unit populations and regions for 20-year height and volume per hectare against mean annual temperature (MAT) at each population’s optimum annual heat:moisture index (AHM). Shaded areas are extrapolations beyond the MAT range of test sites.

proportion of survival differences among populations cannot be directly attributed to adaptation to climate. The small plot size (i.e. nine tree square plots) restricts our ability to make meaningful volume per unit area projections; however, the pattern of variation with temperature and AHM is very similar in both Fig. 5a and b.

Variation in growth responses to climate among SPU populations

To facilitate comparisons among the 14 SPU populations and the four regions, growth response functions

were developed and plotted at the optimum AHM value of each response function (Fig. 6). NElow and PGLow populations outperformed others across a wide range of MATs. The superiority of these two SPU populations was particularly obvious at MATs warmer than 3.0 °C, indicating they are potentially suitable seed sources for warmer planting sites and for future climates. Populations from both the north (northern BC and Yukon) and the south (MT and WO) not only underperformed populations from the central area studied, but also had relatively narrow fundamental niches in term of MAT in comparison with central

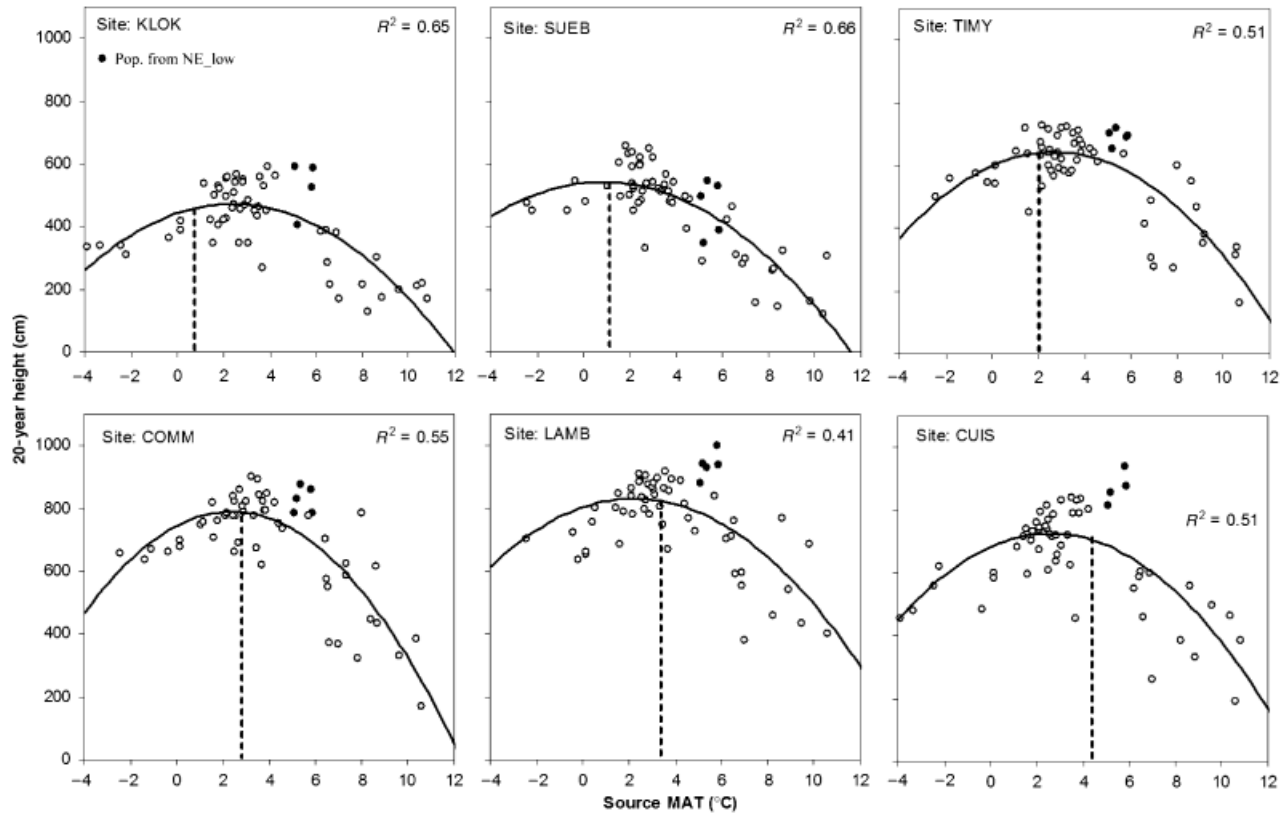


Fig. 7 Individual transfer functions (the trend curves) for six test sites from a range of mean annual temperatures (MATs) showing the superiority in 20-year height of populations from the seed planning units NElow (●) over other populations (○). The vertical dashed line indicates the site MAT.

populations. Interestingly, populations from south of the most productive area, MT and WO, did not perform better on warmer sites in BC than local ones, suggesting that these populations cannot take advantage of warmer conditions.

In order to validate these results based on growth response functions, the superiority of 20-year height of populations from the best SPU, NElow, was examined relative to other populations at six test sites (Fig. 7). A transfer function is also plotted to show the expected performance at a given MAT. These sites were chosen because they covered a range of MAT from 0.7 to 4.3 °C and included at least four provenances from the NElow SPU. Figure 7 shows that populations from NElow are among the top performers at the four cooler sites (MAT < 3.0 °C) and significantly outperformed others at the two warmer sites (> 3.0 °C).

The best performing populations were from the center of the distribution of this subspecies at lower elevations in the south of the province. This area is also the most productive in the province for this species, suggesting that environments in the center of the species' ecological niche produce the best genotypes

for growth and adaptation. This result is consistent with a previous study for seedling height growth of the same genetic materials (Chiune & Aitken, 2006). They found the best performers at a very warm test site on Vancouver Island (MAT = 9.7 °C) were also from the NElow area and called this area the 'epicenter of height growth potential' (I. Chiune, CNRS Montpellier, personal communication). A recent growth chamber study found that NElow populations are again the best performers at warmer temperatures, with even a wider range of MAT tested (1–13 °C) for 1-year-old seedlings (P. Smets, University of BC, unpublished data).

Our results suggest that if climate changes as predicted, seed sources from the central area studied, NElow and PGLow, will be the best choices for most of the SPUs in the province. These seed sources performed better than local SPU populations even under current climates. Therefore, it will be beneficial to deploy these seed sources in most SPUs in the near future if these seed sources do not perform more poorly than local sources in other important traits, such as stem and wood quality and disease resistance. A previous study (Wu & Ying, 1998) showed that populations from

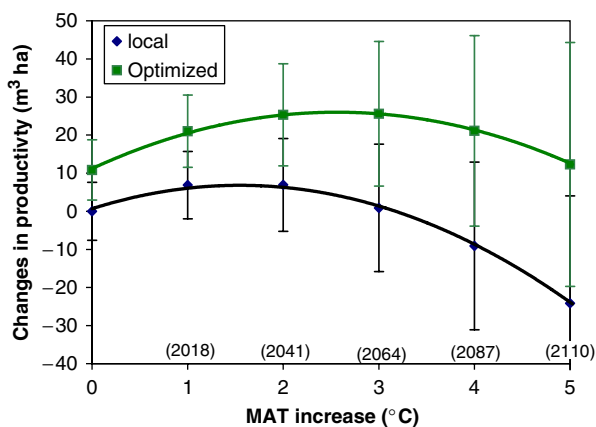


Fig. 8 Predicted changes in productivity of lodgepole pine across all seed planning units in BC for local seed vs. most productive seed source for future climates. Each increase of 1 °C in mean annual temperature (MAT) is accompanied by an increase of 1.8% increases in mean annual precipitation. Error bars indicate the 90% confidential interval for predicted means.

NElow are more resistant than most populations to the two major diseases of this species, western gall rust (*Endocronartium harknessii*) and needle cast (*Lophodermella concolor*), and the resistance of these populations is stable across planting sites.

Impacts of global warming on productivity

Productivities of lodgepole pine in each SPU were predicted for future climates using multivariate growth response functions based on MAT and LnAHM. Predicted impacts of climate change in productivity of lodgepole pine varied substantially among SPUs, primarily depending on the current MAT of each SPU (Table 1). For SPUs with higher MATs in southern BC (TOlow, EKlow, TOhigh and NElow), a moderate increase in MAT (+1 or +2 °C) would result in considerable reduction in productivity if current seed deployment policy is applied (Table 1 and Fig. 9a). Further warming (> +3 °C) would either drastically reduce productivity or extirpate local populations (> +3 °C for TOlow and > +5 °C for EKlow and TOhigh) in these SPUs (Table 1 and Fig. 9b). Negative impacts would also occur in SPUs in central BC if MAT increases by 3 °C or more. On the other hand, productivity would increase in SPUs for degrees of warming simulated in northern BC and could increase as much as 100% (NShigh). These predictions generally agree with what has been suggested in previous studies that negative impacts of global warming on productivity of this species are greater in the south than in the north (Rehfeldt *et al.*, 1999, 2001).

The variation in predicted changes in productivity also depends on genetic variation among SPU populations represented by the differences in growth response functions shown in Fig. 6. For example, NElow is predicted to be the best seed source in term of productivity and the range of adaptation, thus the negative impact of temperature increase in this SPU is predicted to be much smaller than in TOhigh, although NElow has a higher MAT than TOhigh.

Overall productivity across all SPUs is predicted to increase by about 7% as MAT increases to approximately 1.5 °C over current temperature, in approximately 2030 (Fig. 8). However, the productive range of the species will shift northward and upward in elevation with this warming (Table 1 and Fig. 9). Warming beyond 2 °C in MAT is predicted to result in an overall productivity decline from maximum levels to below current levels when MAT increases by about 3.2 °C (predicted by 2069). If MAT increases by 4 °C, along with a 7.2% increase in MAP, as is predicted to occur by 2087, overall productivity across all SPUs will decline by 9% on average, relative to current levels (Fig. 9b).

Response functions developed in this study also allow identification of the SPU with the most productive seed for each SPU at different MATs. By using seedlots from the SPU best adapted to future climates in each SPU (i.e. by optimizing seed source selection or facilitated migration), productivity is predicted to increase with mild global warming in almost all SPUs (Table 1). In the event of more severe warming ($\geq +3$ °C MAT), productivity will increase slightly, or losses will be mitigated in most SPUs. However, a substantial decline in productivity appears inevitable in some warm SPUs even with use of optimal seed sources. The optimization would be most effective in SPUs that have relatively poor performing local populations.

Our analysis suggests that if optimal seed sources were used instead of local sources, productivity would increase by 14–36% among the 16 SPUs. For example, if MAT increases by 2 °C along with a 3.6% increase in MAP, overall productivity across SPUs is predicted to increase by about 7% if local seed is deployed. If the optimal seed source is used for each SPU, a 18% additional gain in overall productivity could be achieved (25% gain in total). If MAT increases 4 °C along with a 7.2% increase in MAP, overall productivity will decrease by 9% for current local populations, but a 23% increase could be achieved if optimal seed sources are deployed. The difference in overall productivity between using optimal seed sources and just using the local sources are surprisingly large. Not surprisingly, the effect of seed source optimization increases with the degree of increase in MAT (Fig. 8). Our predictions

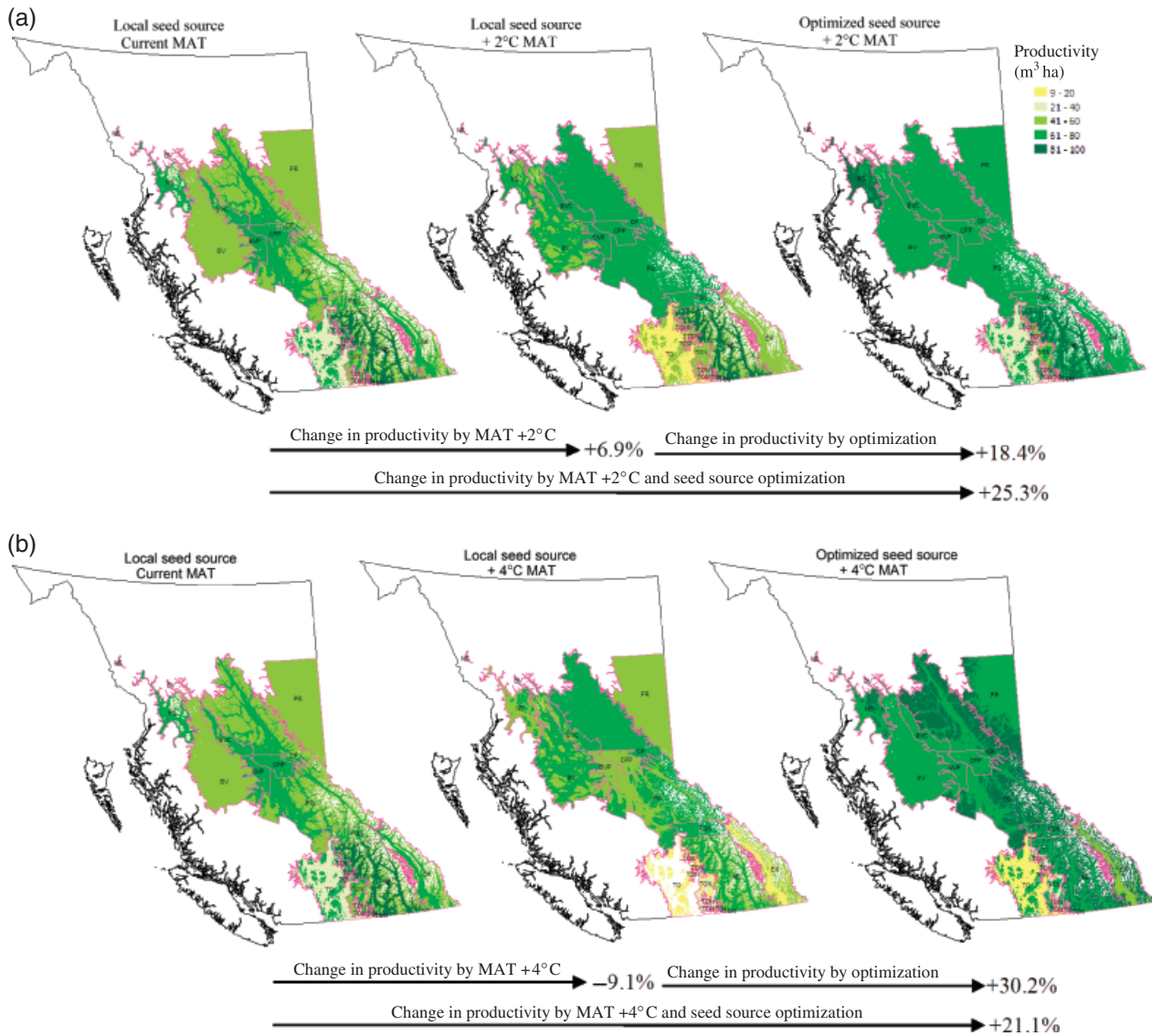


Fig. 9 Maps of predicted productivity of seed planning units for mean annual temperature to increase by 2 (a) and 4 °C (b) and mean annual precipitation to increase by 3.6 (a) and 7.2% (b) in years 2041 and 2087, respectively.

somewhat agree with what has been suggested in previous studies that redistribution of genotypes in changed climate is an effective measure to prevent the productivity of this species from drastic decline (Rehfeldt *et al.*, 1999, 2001).

Optimization of seed deployment will not only increase predicted growth if climate changes, but could also improve the overall growth potential by 10% under current climatic conditions. This is not surprising as we have known for a few decades both theoretically and experimentally that local seed sources are safe in the absence of additional information, but are not necessarily optimal (Namkoong, 1969). The potential to increase productivity through seed source optimization

under current climatic conditions can also be seen in Fig. 7 (e.g. the peak of the transfer function occurred at a MAT 1.5 °C warmer than local MAT at the KLOK test site). In general, the potential to increase productivity is greater in colder (<1 °C) and warmer (>4 °C) environments than intermediate ones. However, this potential was not revealed through a general transfer function using pooled data from all test sites (Rehfeldt *et al.*, 1999) as variation in individual transfer functions among test sites may have canceled out each other.

As the 90% confidence intervals of productivity predictions (Fig. 8) are wide, particularly for large increases in MAT, predicted values should be interpreted with caution. These wide confidence intervals primarily

result from two factors. First, response functions for volume per hectare based on MAT and AHM represent only 40–50% of the total variation. As indicated earlier, a large proportion of variation in this trait cannot be modeled with climatic variables. Other nonclimatic factors are also important, but they could not be included in the response functions (e.g. variation in soil among test sites); however, these should not change the relative performance of the various populations studied. Second, values of MAT at all test sites are below 5 °C, while future climates for many sites in BC are predicted to be well above this level in 60–80 years. This is reflected by the large increase in confidence intervals beyond this point. In addition, although there are many GCMs available and they are being improved all of the time with greater understanding of natural processes, experts do not agree on which climate model is most likely to be correct. Thus, deep uncertainty exists in predictions of future climates. Furthermore, growth response functions do not incorporate expected impacts of climate change on forest productivity associated with other factors not modeled in these estimates, such as increased fire frequency (Flannigan *et al.*, 2000; Filmon, 2004; Fried *et al.*, 2004) or pest damage (Volney & Fleming, 2000; Woods *et al.*, 2005). For example, the current mountain pine beetle (*Dendroctonus ponderosae*) epidemic resulting from a decade of winters devoid of lethal cold temperatures is causing monumental destruction of lodgepole pine forests in BC (Eng *et al.*, 2005). Therefore, the uncertainty can be well beyond the confidence intervals.

Conclusions

As climate changes, the general ‘local is the best’ rule for seed transfer will no longer be valid. Reliable growth response functions are critical in formulating new seed deployment strategies to mitigate the impacts of global warming. Comprehensive provenance trials for lodgepole pine and a high-resolution climate model, ClimateBC, enabled the development of growth response functions to evaluate seed deployment options in British Columbia.

Predicted anchor points based on transfer functions produced response curves with a reasonable temperature range and improved the response functions (average R^2 increased from 0.48 to 0.64 for 20-year height). Otherwise, a large number of response functions (over 20%) with very low R^2 values (<0.20) or with unrealistic fundamental niches would either need to be discarded or arbitrarily modified. The use of anchor points in development of response functions also altered the general pattern of adaptation detected across populations. Application of a multivariate approach to climate

further improved response functions (average R^2 increased from 0.64 to 0.70).

Comparisons of response functions for different SPU and peripheral populations revealed an ‘epicenter’ pattern of growth potential and adaptation. Populations originating from this epicenter showed the best performance and broad adaptation.

Predicted impacts of climate change on productivity in SPUs suggest that productivity averaged across all SPUs will increase in the near future if climate warms as predicted. The productivity will peak (+7%) with an increase of 1.5 °C in MAT and 2.7% in mean annual precipitation (predicted by 2030). However, productivity averaged across all SPUs will decline if warming continues beyond this point and is predicted to drop below current levels if MAT increases by 3.2 °C or more (predicted by 2069). Facilitated migration will considerably improve productivity if climate changes. The increase in productivity could be as high as 36% relative to using local seed as currently prescribed by forest management policy. Facilitated migration of seed would also increase productivity (or at a minimum, not negatively affect productivity) even under current climatic conditions. In addition, the most desirable seed sources found in this study, NElow, are reported to be the most resistant to some important fungal diseases. Further work is necessary to evaluate the deployment of these superior populations, either from wild sources or from current breeding programs and seed orchards, with respect to other important traits (e.g. stem form and wood properties), in order to be ready to deploy these populations as soon as possible.

Acknowledgements

We greatly appreciated three anonymous reviewers for their helpful comments. Funding for this study was provided by the Forest Investment Account through both the BC Forest Science Program and the Forest Genetics Council of BC and a joint Strategic Grant to Aitken and Yanchuk from NSERC and the BIOCAP Canada Foundation.

References

- Aitken SN, Hannerz M (2001) Genecology and gene resource management strategies for conifer cold hardiness. In: *Conifer Cold Hardiness* (eds Bigras F S, Columbo S), pp. 23–53. Kluwer Academic Press, New York.
- Bradshaw WE, Holzapfel CM (2001) Genetic shift in photoperiodic response correlated with global warming. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, **98**, 14509–14511.
- Campbell RK (1974) A provenance-transfer model for boreal regions. *Norsk Institutt for Skogforskning*, **31**, 544–546.

- Chmielewski FM, Rotzer T (2002) Annual and spatial variability of the beginning of growing season in Europe in relation to air temperature changes. *Climate Research*, **19**, 257–264.
- Chuine I, Aitken SN (2006) Height growth determinants and adaptation to temperature in pines: a case study of *Pinus contorta* and *Pinus monticola*. *Canadian Journal of Forest Research*, **36**, 1059–1066.
- Chuine I, Yiou P, Viovy N *et al.* (2004) Historical phenology: grape ripening as a past climate indicator. *Nature*, **432**, 289–290.
- Daly C, Gibson WP, Taylor GH *et al.* (2002) A knowledge-based approach to the statistical mapping of climate. *Climate Research*, **22**, 99–113.
- Eng M, Fall A, Hughes J *et al.* (2005) Provincial-level projection of the current mountain pine beetle outbreak: an overview of the model (BCMPB v2) and results of year 2 of the project. In: *Natural Resources Canada*. Canadian Forest Service, Pacific Forestry Centre, Victoria, BC.
- Filmon G (2004) *Firestorm 2003* Provincial review of the 2003 fire season [online]. Available from <http://www.2003firestorm.gov.bc.ca/>
- Flannigan MD, Stocks BJ, Wotton BM (2000) Climate change and forest fires. *Science Of The Total Environment*, **262**, 221–229.
- Flato GM, Boer GJ, Lee WG *et al.* (2000) The Canadian Centre for Climate Modelling and Analysis global coupled model and its climate. *Climate Dynamics*, **16**, 451–467.
- Fried JS, Torn MS, Mills E (2004) The impact of climate change on wildfire severity: a regional forecast for northern California. *Climatic Change*, **64**, 169–191.
- Hamann A, Wang TL (2005) Models of climatic normals for genecology and climate change studies in British Columbia. *Agricultural and Forest Meteorology*, **128**, 211–221.
- Illingworth K (1978) Study of lodgepole pine genotype-environment interaction in B. C. In: *Proceedings International Union of Forestry Research Organizations (IUFRO) Joint Meeting of Working parties: Douglas-fir provenances, Lodgepole Pine Provenances, Sitka Spruce Provenances and Abies Provenances*. pp. 151–158. Vancouver, British Columbia, Canada.
- IPCC (2001) *Third Assessment Report of the Intergovernmental Panel on Climate Change IPCC (WG I & II)*. Cambridge University Press, Cambridge.
- Kullman L (2002) Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology*, **90**, 68–77.
- Matyas C (1994) Modeling climate-change effects with provenance test data. *Tree Physiol*, **14**, 797–804.
- Meidinger D, Pojar J (1991) *Ecosystems of british columbia*. BC. Min. For. Special Report Series No. 6. 330 pp.
- Menzel A, Fabrian P (1999) Growing season extended in Europe. *Nature*, **397**, 659.
- Namkoong G (1969) Nonoptimality of local races. In: *Proceedings of the 10th Southern Conference on Forest Tree Improvement*, June 17–19. pp. 149–153. Texas A&M University/Texas and Texas Forest Service, College Station/Houston, Texas.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Petit M (2001) Mankind facing the additional anthropogenic greenhouse warming. *Comptes Rendus de l'Academie des Sciences Series IIA Earth and Planetary Science*, **333**, 775–786.
- Post E, Stenseth NC (1999) Climate variability, plant phenology and northern ungulates. *Ecology*, **80**, 1322–1339.
- Rehfeldt GE, Wykoff WR, Ying CC (2001) Physiologic plasticity, evolution, and impacts of a changing climate on *Pinus contorta*. *Climatic Change*, **50**, 355–376.
- Rehfeldt GE, Ying CC, Spittlehouse DL *et al.* (1999) Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. *Ecological Monographs*, **69**, 375–407.
- SAS-Institute-Inc. (1989) *SAS/STAT(R) User's Guide, Version 6, Fourth Edition*. SAS-Institute-Inc, Cary, NC.
- Spittlehouse DL (2005) Integrating climate change adaptation into forest management. *Forestry Chronicle*, **81**, 691–695.
- Volney WJA, Fleming RA (2000) Climate change and impacts of boreal forest insects. *Agriculture, Ecosystems and Environment*, **82**, 283–294.
- Walther GR, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Wang T, Aitken SN, Rozenberg P *et al.* (1999) Selection for height growth and Pilodyn pin penetration in lodgepole pine: effects on growth traits, wood properties, and their relationships. *Canadian Journal of Forest Research*, **29**, 434–445.
- Wang T, Hamann A, Spittlehouse DL *et al.* (2006) Development of scale-free climate data for western Canada for use in resource management. *International Journal of Climatology*, **26**, 383–397.
- Woods A, Coates KD, Hamann A (2005) Is an unprecedented dothistroma needle blight epidemic related to climate change? *Bioscience*, **55**, 761–769.
- Wu HX, Ying CC (1998) Stability of resistance to western gall rust and needle cast in lodgepole pine provenances. *Canadian Journal of Forest Research*, **28**, 439–449.