

# Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution

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## Summary

1. Large differences exist in the predictions of plant responses to climate change among models that consider population variation and those that do not. Models that treat species as homogeneous entities typically predict net positive impacts of climate change on temperate forest productivity, while most studies that consider adaptive genetic variation within species conclude that the impacts of climate change on forest productivity will be negative.

2. We present a modelling approach that predicts plant responses to climate change using both ecological and genetic variables. The model uses growth data from multi-site provenance trials together with climate data for provenance source locations and test sites to predict distribution and productivity of tree populations under climate change. We used an extensive lodgepole pine *Pinus contorta* provenance data set to illustrate the model.

3. Spatially explicit predictions of the impacts of climate change on production were developed and suggested that different populations of lodgepole pine will respond very differently to climate change. Large production losses will be seen in many areas, although modest production increases may occur in some areas by 2085. The model further projects a significant redistribution of the species' potential habitat northwards and upwards in altitude over the next several decades.

4. *Synthesis and applications.* This study points to the need to consider population differences when modelling biotic responses to climate change, and suggests that climate change will render populations maladapted in many areas. The model also provides a key tool potentially to mitigate climate change impacts by identifying populations expected to be best adapted throughout the next generation of forests. Finally, the study highlights the value of wide-ranging long-term provenance tests in addressing key issues in ecology and climate change.

**Key-words:** adaptation, assisted migration, ecological modelling, forest productivity, growth response function, *Pinus contorta*, population differentiation, seed transfer, transfer function

## Introduction

By treating populations of a species as an undifferentiated collection of individuals with broad tolerances, many physiological and ecological, as well as growth and yield, studies conclude that global warming will have a net positive impact on forest productivity (herein considered only as area-based

tree stem volume) (Monserud *et al.* 1996; Coops & Waring 2001; van der Meer, Jorritsma & Kramer 2002; Nigh, Ying & Qian 2004; Briceño-Elizondo *et al.* 2006). While results vary considerably among experimental systems (Körner 2006), this view stands in stark contrast to a growing body of ecological genetics literature that suggests that the narrow climatic adaptation of individual populations of most conifer tree species (Langlet 1958; Morgenstern 1996; Beaulieu, Perron & Bousquet 2004) will render many populations maladapted or their potential distributions greatly altered towards the end of

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their rotation (Davis & Shaw 2001; Iverson & Prasad 2002; Rehfeldt *et al.* 2006; St Clair & Howe 2007). It is therefore worthwhile examining and validating the techniques used in the ecological genetics approaches to assess climate change impacts on forest productivity and species distributions with the aim of seeking refinements to these approaches.

Ecological genetics studies regarding the impacts of climate change on forest productivity are commonly based on provenance (i.e. transplant) tests. We use the term population to refer to a group of interbreeding individuals, and the term provenance to refer to the location from which a population originated. Provenance tests, established to identify locations of superior genotypes, have emerged serendipitously as ideal climate change laboratories (Mátyás 1994; Carter 1996). By testing populations from a range of source climates across a range of recipient climates, provenance tests reveal, *in situ*, effects of maladaptation associated with the growth of populations in disparate climates, overcoming the temporal and spatial restrictions inherent in controlled environment settings. Furthermore, by establishing provenance tests *in situ* and carrying them for many years, they sample the range of climatic extremes present at a test site, while integrating diverse effects of, and interactions with, biotic and abiotic environmental variables.

Two ecological genetic approaches using provenance test data have been developed to estimate the impacts of climate change on forest productivity. The transfer function approach, first described in the mid-1990s (Mátyás 1994; Mátyás & Yeatman 1992), followed by several refinements (Schmidting 1994; Persson & Beuker 1997; Rehfeldt *et al.* 2003; Wei *et al.* 2004), relates the growth of disparate populations to the geographical or climatic distance they were transferred to at the test site (e.g. test site climate minus provenance climate). Productivity impacts as a result of climate change are interpreted from the fitted curve as the productivity difference between a local population (zero transfer distance) and transferred populations. Some authors pool data from diverse and unrelated tests to develop a single curve (i.e. a pooled transfer function; Andalo, Beaulieu & Bousquet 2005; Carter 1996; Rehfeldt *et al.* 1999), assuming that the shape and position of transfer curves do not vary significantly in different locations (i.e. climates). However, several reports challenge this assumption by illustrating that sites do indeed differ in their sensitivity to seed transfer or in the climate of the optimum population at each site (Mirov, Duffield & Liddicoet 1952; Raymond & Lindgren 1990; Rehfeldt *et al.* 2003).

Conversely, a growth response function, also called a population response function or reaction norm, describes the growth of an individual population as a function of the climate at the test sites in which the population was grown (Roberds *et al.* 1990; Rehfeldt *et al.* 2002; Wang *et al.* 2006b). While these functions are ideal for directly inferring growth responses of a population to changing environmental conditions, all the preceding studies have identified large differences in growth response functions among populations, highlighting the need for a specific response function for each

population in order to obtain spatially explicit productivity estimates.

We present a novel universal transfer function (UTF) growth model based on ecological (i.e. site climate) and genetic (i.e. population adaptation) factors that is developed using transplant experiment growth data. The model allows forest productivity in current and future climates to be predicted for any population in any location as a function of the regional climate of the planting site and the climate of the provenance, effectively combining transfer function and growth response function models into a variable transfer function model. We also present a novel approach to estimate future species' distributions by truncating the lower end of estimated growth responses to climate. Finally, we demonstrate the use of the UTF by estimating the current and future growth and distribution of lodgepole pine *Pinus contorta* Dougl. ex Loud. in British Columbia (BC), Canada, using one of the most comprehensive provenance tests in the world.

## Methods

### MATERIALS, EXPERIMENTAL DESIGN AND MEASUREMENTS

Trees used in this study belong to the BC Ministry of Forests and Range's lodgepole pine provenance test (EP 657.06, the Illingworth test), which consists of 140 populations tested at 62 sites (Ying, Illingworth & Carlson 1984). Populations planted in the test were selected in a stratified random manner across six Canadian and two USA physiographic regions (Illingworth 1969) from southern California (34°N latitude) to central Yukon (64°N latitude), encompassing most of the species' range and the three main varieties (*latifolia*, *contorta* and *murrayana*). Seed of each population, collected between 1966 and 1968, was bulked from collections of 50–100 cones from each of 15 trees. Test sites in the Illingworth trial were also selected in a stratified random sampling scheme: five sites in each of 12 geoclimatic regions in interior BC and two sites in the Yukon, encompassing 12 degrees of latitude (49°–61°), 21 degrees of longitude (114°–135°) and 1220 m of altitude (610–1830 m).

An incomplete testing design tested 60 of the 140 populations at each site, so that each population was tested at 30–40 sites. Within each site, a randomized complete block design was used, with one nine-tree square plot of each population planted in each of two blocks. The two Yukon sites contained six blocks, each comprising 40 populations. In total, 69 120 seeds were sown in 1971 and resultant seedlings were transplanted to the sites in spring 1974 at 3 × 3-m spacing. Total height (HT) and diameter at breast height (d.b.h.) were measured at 43 of the 62 sites in autumn 2005, after 32 field growing seasons (35 growing seasons from seed).

### POPULATION MEAN PRODUCTION AT EACH TEST SITE

Survival at the 43 sites ranged from 32% to 96% ( $\bar{X}$  = 81%). To calculate individual tree stem volume (m<sup>3</sup> tree<sup>-1</sup>; VOL), HT and d.b.h. were used to calculate the volume of a cylinder, which was then multiplied by a taper factor, TF:

$$TF = \frac{576/\pi}{343896 + (0.211534 \times HT)} \quad \text{eqn 1}$$

which ranged from 0.47 to 0.53 (Honer 1967). Arithmetic mean VOL was then calculated for each population at each site based on the surviving trees. Finally, the area-based production (volume per hectare,  $\text{m}^3 \text{ha}^{-1}$ ; VPH) of each population at each site was calculated as:

$$\text{VPH} = \text{VOL} \times \text{SURV} \times 1600 \quad \text{eqn 2}$$

where SURV is the population mean survival proportion and 1600 is the number of seedlings planted per hectare in the tests and in many reforestation sites.

#### CLIMATE DATA

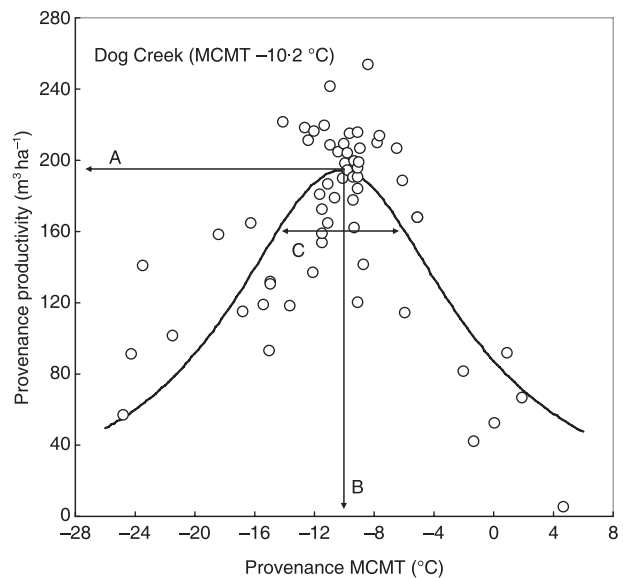
Mean values of nine annual climate variables for the 30-year period centred on 1975 were obtained for each provenance and test site from ClimateBC© (Hamann & Wang 2005; Wang *et al.* 2006a), a computer program that extracts and downscales PRISM© (Daly *et al.* 2002) monthly climate means ( $2.5 \times 2.5$  arcmin) and derives biologically important seasonal and annual temperature- and precipitation-related climate variables for specified locations based on latitude, longitude and altitude. Climate data for 39 USA provenances not covered by ClimateBC (i.e. provenances south of  $47^\circ\text{N}$  latitude or east of  $113^\circ$  longitude) were calculated using ANUSPLIN© (Hutchinson 2000) with methods described by Rehfeldt (2004). Details regarding the estimation of the nine derived climate variables can be found in Wang *et al.* (2006a).

A 400-m digital elevation model of BC was systematically subsampled (i.e. every 16th point was retained) to generate a fine-scale ( $1.6 \times 1.6$  km) grid of 370 205 point locations. ClimateBC was used to estimate values of the nine climate variables at each grid point. Values were obtained for four 30-year climate normal periods: 1961–90, 2011–40, 2041–70 and 2071–2100, hereafter referred to by their midpoints, 1975, 2025, 2055 and 2085. ClimateBC generates future climate estimates by overlaying high-resolution climate baseline data (1961–90 normals) with changes estimated by global circulation models (GCM) (Hamann & Wang 2005; Wang *et al.* 2006a). We chose the A2 'enterprise' scenario (scenario CGCM2), implemented through the Canadian Global Circulation Model of the Canadian Centre for Climate Modelling and Analysis, because its estimates of changes for disparate BC locations for mean annual temperature and precipitation (MAT and MAP) by the 2080s (average of  $4.0^\circ\text{C}$  and 7% increase, respectively) closely match the average of 32 international SRES scenarios ( $4.0^\circ\text{C}$  and 9% increase). CGCM2 predictions were downscaled in ClimateBC from a  $3.75^\circ$  grid to a  $1^\circ$  grid using ANUSPLIN (Hutchinson 2000), and further downscaled to a 400-m grid using bilinear interpolation (Wang *et al.* 2006a). According to the CGCM2 A2 scenario, expected increases in mean monthly cold month temperature (MCMT) from the (1975) baseline are  $1.4^\circ\text{C}$ ,  $2.9^\circ\text{C}$  and  $4.3^\circ\text{C}$  for years 2025, 2055 and 2085, respectively, in warmer regions of the study area ( $-8$  to  $-10^\circ\text{C}$  1975 MCMT) and  $1.7^\circ\text{C}$ ,  $4.3^\circ\text{C}$  and  $7.4^\circ\text{C}$  for the same years, respectively, in colder regions of the study area ( $-16$  to  $-18^\circ\text{C}$  1975 MCMT).

#### UNIVERSAL TRANSFER FUNCTION

##### Step 1: develop a transfer function for each test site

At each test site, an individual transfer function relating individual provenance climate variables (e.g. MCMT<sub>p</sub>) to population production (VPH<sub>p</sub>) was fitted to the Cauchy function using non-linear regression, PROC NLIN (SAS 1994):



**Fig. 1.** Scatterplot and fitted transfer curve of lodgepole pine provenance production as a function of provenance MCMT ( $^\circ\text{C}$ ) at the Dog Creek test site. Also shown are the Cauchy curve parameters: A, the estimated production of the expected optimum provenance; B, the climate value of the expected optimum provenance; C, the range of climate values at 80% of A (i.e. the climate range of provenances adapted to the Dog Creek climate).

$$\text{VPH}_p = \frac{A_s}{1 + \left( \frac{\text{MCMT}_p - B_s}{C_s} \right)^2} \quad \text{eqn 3}$$

where  $A_s$ ,  $B_s$  and  $C_s$  are the fitted function parameters for each site (Fig. 1). The Cauchy function was selected because it is biologically appropriate and its parameters are easily interpreted from key features of the fitted relationship (i.e. width, height and position of the vertex) (Raymond & Lindgren 1990; Lindgren & Ying 2000). Preliminary analysis indicated that the strongest relationships (transfer functions) involved MCMT (mean  $R^2 = 0.48$ ). Step 1 therefore identified a set of three parameters, A, B and C, for each of the 43 MCMT transfer equations (i.e. one set of parameters at each test site).

To account for the apparent asymmetry in the individual transfer functions at some sites, 25 asymmetric peak functions, including the Weibull and gamma function, were also examined using Table Curve (version 4; Jandel Scientific Software, Corte Madera, California). However, because of the marginal improvement in fit ( $R^2$  increased from 0.48 to 0.51 on average) and the additional calculations that were required to relate features of asymmetric curves to their coefficients, asymmetric functions were abandoned.

##### Step 2: develop equations to predict transfer function parameter values from site climate

A UTF should be constructed only if one or more of the parameters differ significantly among test sites, otherwise transfer functions would not differ significantly among test sites and a single pooled transfer function would suffice. Preliminary analysis examined differences among sites for each of the three parameters by adding 'site' as a random factor to the model fitted in step 1 using non-linear mixed model regression PROC NL MIXED (SAS 2004). The random

coefficients regression was moderately strong (pseudo  $R^2 = 0.59$ ) (Schabenberger & Pierce 2002) and  $t$ -tests of site parameters ( $A_s$ ,  $B_s$  and  $C_s$ ) showed that the variance of each parameter differed from zero ( $P < 0.0001$  for all parameters), indicating that the parameters differed significantly among sites.

Having demonstrated significant variation among sites for all transfer function parameters, a UTF was developed to recognize site-to-site variation in transfer curve shape or position on the  $x$ -axis by relating transfer function parameters to site climate in multiple regression. Once fitted, the equations predicting each transfer function parameter were substituted into the general transfer function equation (equation 3), resulting in a variable or 'universal' transfer function that predicts production of any population growing at any site (i.e. plantation) in the study area (interior BC) based on the climate of the site and climate of the provenance. Importantly, the UTF allows spatially explicit estimation and mapping of expected production of any population growing in any location or climate.

#### SPATIAL APPLICATION OF UNIVERSAL TRANSFER FUNCTION

Production (VPH) of native forests in 1975 was estimated for each of the 370 205 grid points by inserting values of 1975 site and provenance climate variables for each grid point into the UTF. To assess the impact of climate change on the production of naturally established or planted forests of native (i.e. local) populations, production was again estimated at each grid point by inserting site climate values obtained from climate coverages for 2025, 2055 and 2085 (see Climate data above) into the UTF. As future production estimates are desired for native forests (i.e. for seed adapted to the local climate of 1975 or earlier), provenance climate values for 1975 were used in the UTF to estimate future production. The resulting production estimates therefore describe the expected production (VPH) of a 32-year-old-stand in each of the target years. Production in each of the four target years was mapped using ArcView.

The mapped VPH = 40 m<sup>3</sup> ha<sup>-1</sup> contour for 1975 coincided well with the current natural distribution range of lodgepole pine var. *latifolia* (Hamann & Wang 2006). West of the Coast Mountains, lodgepole pine var. *latifolia* is competitively excluded by other species. Therefore, to illustrate how climate change may impact the natural distribution of lodgepole pine var. *latifolia* only those areas of interior BC where VPH is > 40 m<sup>3</sup> ha<sup>-1</sup> were mapped.

## Results

#### UNIVERSAL TRANSFER FUNCTION

Individual transfer equations relating VPH to MCMT<sub>P</sub> (equation 3 and Fig. 1) in step 1 were moderately strong (mean  $R^2 = 0.48$ ) and significant ( $P < 0.0001$ ) for all 43 sites, and standard errors of site parameters ( $A_s$ ,  $B_s$  and  $C_s$ ) were small, averaging 11, 0.8 and 1.3, respectively.

In step 2 the following equations were selected to predict transfer function parameters  $A_s$ ,  $B_s$  and  $C_s$  from test site climate:

$$A_s = 61.19 + 61.70MAT_s - 6.69MAT_s^2 + 8.29ADI_s - 0.189ADI_s^2 - (1.54 \times MAT_s \times ADI_s) \quad \text{eqn 4}$$

$$B_s = -3.85 + 0.72MCMT_s \quad \text{eqn 5}$$

$$C_s = 10.10 + 0.16MCMT_s - 0.082ADI_s \quad \text{eqn 6}$$

where ADI is annual drought index (Wang *et al.* 2006a). Regression equations 4–6 were all significant ( $P = 0.0002$ ,  $< 0.0001$  and  $0.0038$ , respectively) and accounted for 48%, 76% and 25% of the variation in  $A_s$ ,  $B_s$  and  $C_s$ , respectively.

#### IMPACTS TO PRODUCTION AND DISTRIBUTION IN THE LODGEPOLE CASE STUDY

Expected changes in production and potential habitat of lodgepole pine in interior BC predicted by the UTF are large and highly variable in time and space (Table 1 and Figs 2 and 3). By 2085, production will have declined 31–59% (i.e. on average from 155 m<sup>3</sup> ha<sup>-1</sup> to 86 m<sup>3</sup> ha<sup>-1</sup>) in the 'pine basket' central interior region where the species is currently most productive and abundant (i.e. where the 1975 MCMT is between  $-8$  °C and  $-11$  °C). In warmer (lower altitude and southern) areas impacts will be moderately negative ( $-12\%$  to  $-21\%$ ) in the near future but strongly negative ( $-64\%$  to  $-70\%$ ) by 2085. Only in colder areas (northern and high altitude),

**Table 1.** Expected mean production (VPH) of lodgepole pine at age 32 for 11 MCMT bands in BC in years 1975, 2025, 2055 and 2085. Also shown is the mean percentage change in production of each band relative to production in 1975. Bands where productivity estimates are based on extrapolations are shown in grey

1975 mean cold month temperature band (°C)	1975			2025		2055		2085	
	m <sup>3</sup> ha <sup>-1</sup>	m <sup>3</sup> ha <sup>-1</sup>	% change from 1975	m <sup>3</sup> ha <sup>-1</sup>	% change from 1975	m <sup>3</sup> ha <sup>-1</sup>	% change from 1975	m <sup>3</sup> ha <sup>-1</sup>	% change from 1975
< -16	80	107	34	102	28	70	-12		
-16 to -15	79	106	35	111	40	86	9		
-15 to -14	68	100	47	114	68	98	44		
-14 to -13	62	101	63	122	99	111	80		
-13 to -12	69	114	64	137	97	126	82		
-12 to -11	118	151	28	154	31	122	4		
-11 to -10	149	165	11	151	1	103	-31		
-10 to -9	162	165	2	142	-121	90	-44		
-9 to -8	154	143	-7	112	-27	64	-59		
-8 to -7	144	127	-12	94	-35	51	-64		
> -7	102	81	-21	56	-45	30	-70		

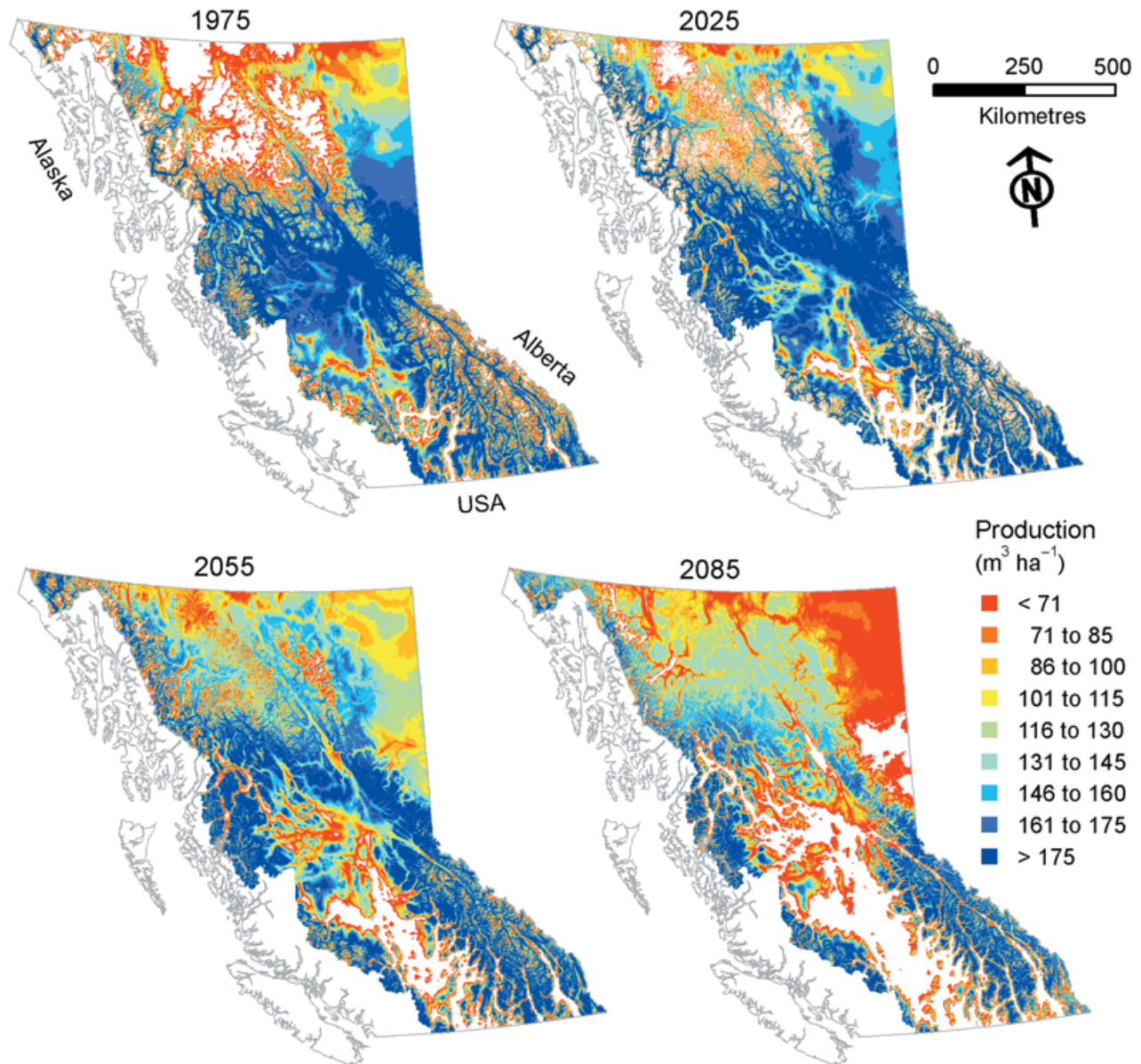


Fig. 2. Absolute production and potential range of lodgepole pine at age 32 in interior BC in 1975, 2025, 2055 and 2085 estimated using the UTF. Areas where estimated production is  $< 40 \text{ m}^3 \text{ha}^{-1}$  (the approximate distribution limits of lodgepole pine) are shown in white.

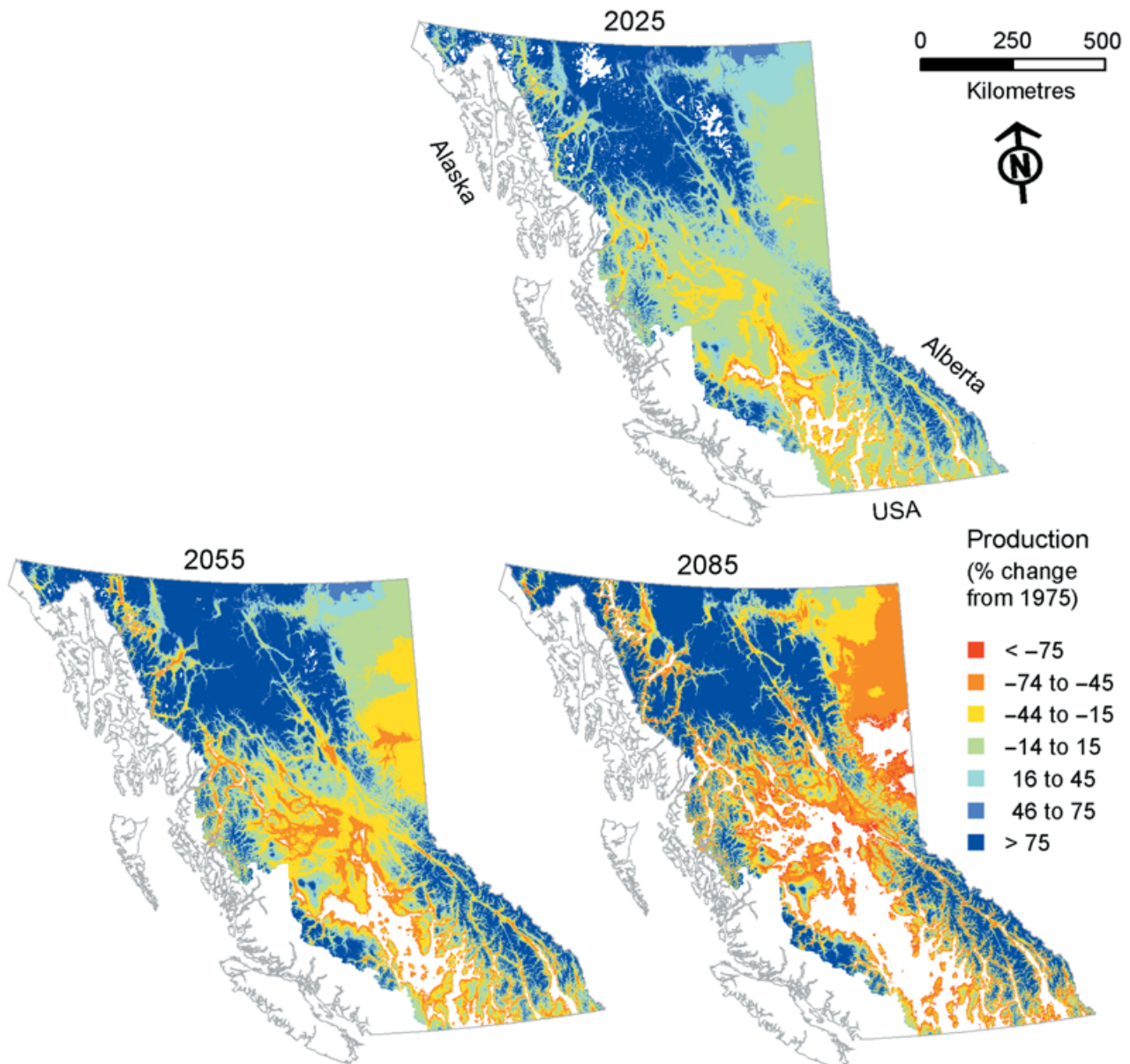
where the (1975) MCMT is  $-12^\circ\text{C}$  to  $-15^\circ\text{C}$  and current estimated production marginal ( $62\text{--}69 \text{ m}^3 \text{ha}^{-1}$ ), will production increase. Substantial changes to potential lodgepole habitat are also predicted. By 2085, a large area in the central and southern interior will no longer be able to support lodgepole pine forest, while new potential lodgepole pine habitat will be acquired in the north.

## Discussion

### ECOLOGICAL APPLICATIONS OF THE UNIVERSAL TRANSFER FUNCTION

The UTF provides three significant refinements to our understanding of biotic responses to climate change. First, it

demonstrates that populations differ greatly in growth responses to climate change because of differences in local adaptation, and that these differences can be accounted for by modelling variable transfer functions for each climate (step 2). Differences among populations in their climatic tolerances and responses to climate change are known to be large and patterned closely on climatic variation, as we (Table 1) and others have shown (Eriksson *et al.* 1980; Beaulieu, Perron & Bousquet 2004). Different responses to climate among populations have been attributed to the fact that native populations on the extremes of a species' climatic range display their fastest growth in climates that are more moderate than in climates where they are native (Rehfeldt, Wykoff & Ying 2001; Rehfeldt *et al.* 1999) and may be associated with 'swamping' of peripheral populations by pollen from more



**Fig. 3.** Production in 2025, 2055 and 2085 relative to 1975 for lodgepole pine at age 32 in interior BC estimated using the UTF. Areas where estimated absolute production is  $< 40 \text{ m}^3 \text{ ha}^{-1}$  (the approximate distribution limits of lodgepole pine) are shown in white.

central populations (Mimura & Aitken 2007). As a result, populations from opposing ends of an 'environmental stress' axis will exhibit opposite responses to a shift in climate. Accounting for these differences has a profound impact on estimates of current and future production and species' distribution.

Secondly, the ability of the UTF to make spatially explicit predictions of biotic responses to climate change represents a significant refinement over existing models that utilize provenance test data (i.e. pooled transfer functions and growth response functions). The pooled transfer function approach assumes that transfer functions are constant in all environments, an assumption we have shown to be inappropriate. The growth response function approach develops specific response functions for each tested population (Rehfeldt,

Wykoff & Ying 2001; Wang *et al.* 2006b) but they cannot be applied to other populations.

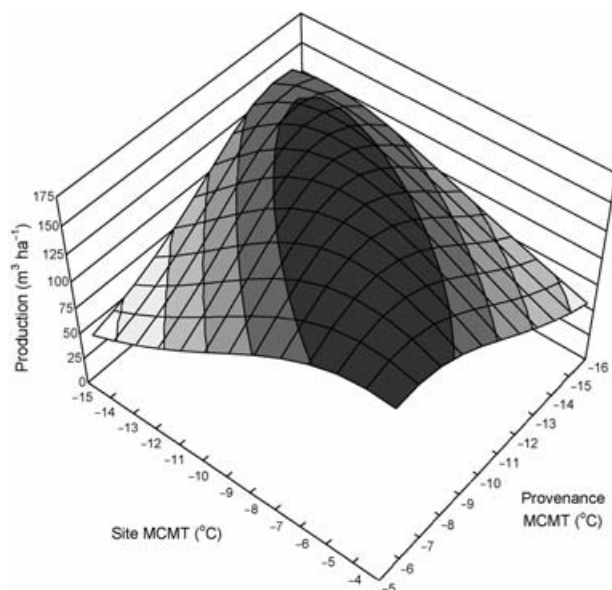
Thirdly, by truncating mapped future production estimates from the UTF using an estimated production contour that coincides with the current distribution limit, potential future species' distributions (i.e. the fundamental niche) can be mapped in a way that accounts for population differentiation, addressing a significant shortcoming of species distribution models (Aitken *et al.* 2008). The biological basis for this observation is not evident from our study and is likely to differ among regions where factors limiting species abundance differ. None the less, the finding presents a new opportunity to refine future species distribution models that capitalize on the many advantages of transplant (i.e. provenance test)

experiments for assessing climate change impacts (see the Introduction).

#### INTERPRETING THE UTF

This two-stage approach of fitting transfer curves at each site, and then fitting the estimated transfer curve parameters of all sites to their climate variables, allows direct interpretation of how transfer curves vary in different climates. For example, equation 6 indicates that the  $C$  parameter of the transfer function increases with site MCMT and declines with site ADI, implying that the MCMT<sub>S</sub> range from which suitable provenances may be selected is more restricted in cold and droughty environments. As an alternative to the UTF, a universal 'response' function, having the same input variables and application as a UTF, could have been developed by first fitting a growth response function to each tested population and then relating growth response function parameter values to the climate of the origin of the populations (i.e. the provenances).

A simplified UTF was developed to illustrate the combined influence of a single site climate variable (MCMT<sub>S</sub>) and a single provenance climate variable (MCMT<sub>P</sub>) on production (Fig. 4). To develop this UTF,  $B_S$  and  $C_S$  were predicted in linear regression using MCMT<sub>S</sub> alone, and  $A_S$  was predicted from MCMT<sub>S</sub> and its square, so that production could be predicted solely from MCMT<sub>P</sub> and MCMT<sub>S</sub>. Model accuracy is forfeited; indeed production responses to changes in site and provenance climate are considerably dampened relative to responses predicted by the full model (Table 1 and Fig. 2). However, Fig. 4 effectively illustrates the narrow MCMT range in which each population grows well, and how the MCMT of the most productive provenance at each site varies



**Fig. 4.** A simplified UTF in which expected production of lodgepole pine is predicted as a function of a single provenance and site climate variable (i.e. MCMT). The function can be used to estimate production for a provenance from any climate when grown in any climate.

with site MCMT. In fact,  $MCMT_P \approx MCMT_S$  along the surface ridge in moderate climates, supporting the notion that, in a static climate, local populations are generally the most productive. However, at extreme MCMT<sub>S</sub> the line formed by matching provenance and site MCMT departs slightly from the ridge, possibly because of an evolutionary lag associated with recent climate change (e.g. in the century before the seed was collected) and our use of contemporary (1961–90) climate values of provenances instead of climate values prevalent during the preceding century when the recent ancestors of the tested trees were naturally selected.

#### IMPACTS OF CLIMATE CHANGE TO PRODUCTION

Trends observed in this study add to the growing body of ecological genetics literature that suggests that the long-range impact of climate change on stem volume growth in boreal and sub-boreal forests will be negative, notwithstanding modest absolute increases in some cold areas, but even these are contingent on the availability of adequate seed sources and seed dispersal and the presence of sufficiently developed soils. Somewhat similar conclusions were drawn from growth response functions developed using age-20 growth from the same lodgepole pine provenance tests used here (Rehfeldt, Wykoff & Ying 2001; Wang *et al.* 2006b); however, lack of a spatially explicit approach in these studies precluded more detailed comparison with our results. Recognizing the important role that water availability and interactions among climate variables can play in modelling impacts of climate change on forest production and distribution (Andalo, Beaulieu & Bousquet 2005; Elith *et al.* 2006), we also attempted to incorporate precipitation and additional temperature variables into transfer functions along with MCMT in step 1; however, improvement in the strength of the transfer functions was marginal.

#### POPULATION ADAPTATION IN FOREST PRODUCTIVITY MODELS

Many studies predict increases in forest productivity as a result of climate change (Cumming & Burton 1996; Bergh *et al.* 2003; Johnston & Williamson 2005; Briceño-Elizondo *et al.* 2006). Invariably, these analyses do not account for maladaptation arising from a changed climate, basing their predictions on productivity–climate relationships or process-based models developed from adapted populations, or requiring populations to migrate or adapt at a pace sufficient to allow them to thrive in the face of rapid climate change, a scenario that appears untenable (Rehfeldt *et al.* 1999; Davis & Shaw 2001; Jump & Peñuelas 2005). Predictions made in these studies may be realized only if harvest sites are replanted with populations adapted to future climates (i.e. assisted migration); they do not reflect the expected growth response of native populations.

The current study and, with rare exceptions, all others we encountered that have considered population adaptation, are generally pessimistic regarding the potential impacts of

climate change on productivity of native forests (Carter 1996; Rehfeldt 2004; Andalo, Beaulieu & Bousquet 2005). In all of these reports, the sensitivity of native populations to climate change was attributed to population adaptation to climate. Many conifer species are widely distributed; however, populations within those species are finely adapted to their native climatic environments. While the palaeobiology record demonstrates that most conifer species have tolerated large and repeated changes in climate through widespread migration (Jackson & Overpeck 2000), the magnitude of species' redistributions and the ensuing evolutionary lag that accompanied those events may well have resulted in prolonged periods of ecological disturbance that today would have significant negative social, environmental and economic ramifications.

#### LIMITATIONS OF THE UTF

The accuracy of predictions from UTF is related to the extent and sampling intensity of provenance tests, as well as climate model and GCM accuracy. An important weakness of our study, indeed of most provenance tests established for conventional purposes (i.e. superior provenance identification), arises from a paucity of test sites representative of future climates: the warmest site in our test is at MCMT (1975)  $-7.4$  °C, yet 77% of interior BC will experience MCMT warmer than  $-7.4$  °C by 2085. Consequently, more than one-third of the impact predictions in Table 1 are extrapolations. It is therefore imperative to consider carefully the biological appropriateness of UTF coefficients and variables, and to remain cognisant of the uncertainty associated with long-range predictions.

The UTF, as we have presented it, is driven by site and provenance climate variables. Future refinements could incorporate other important non-climatic determinants of plant productivity and species' distributions (e.g. site factors such as slope position, soil texture and soil nutrients); however, as most of these factors will not be greatly affected by climate change, they will not significantly improve estimates of climate change impacts.

Climate change is expected to reduce forest productivity because of increased fire frequency and extent (Flannigan 2000; Fried 2004) and increased pest damage (Volney & Fleming 2000; Harvell *et al.* 2002). While the current mountain pine beetle *Dendroctonus ponderosae* epidemic in BC is causing monumental destruction of lodgepole pine (Eng *et al.* 2005) and has been linked to recent climate warming (Carroll *et al.* 2004), the degree and extent of the impacts of this climate change-related epidemic are thus far anomalous among temperate conifers. Future impacts of this and other pests and fire are highly uncertain. In addition to pest-related impacts, there is also evidence that commercially important stem form and wood quality traits may be negatively impacted by climate change (G. A. O'Neill, unpublished data), suggesting that estimates of impacts to forest production based on volume alone, as calculated in most ecological genetics studies, may further underestimate economic impacts associated with climate change.

Competitive interactions among species in multispecies stands may be altered by climate change, providing another potential source of error in UTF estimates. Interactions among species may mitigate some of the negative impacts on forest production predicted in this single-species model. Stand growth and species distribution models capable of considering mixed species stands and dynamic height–age functions are required to assess forest growth better in future climates.

#### ADDITIONAL APPLICATIONS OF THE UTF

In addition to estimating climate change impacts on forest growth and species' distributions, the UTF has at least two immediate applications. Seed transfer regulations exist in most forestry jurisdictions to ensure that seedlings are planted in environments where they are adapted and productive. However, there currently exists no quantitative method of assessing the effectiveness of the myriad of alternative seed transfer regulation systems or methods used to calculate acceptable transfer distances. Using samples of provenances and planting locations representative of those available or anticipated, production across a jurisdiction could be estimated for alternative seed transfer systems and distances using the UTF.

Planting seedlings adapted to a future climate (i.e. assisted migration) is recognized as a key forest management strategy to mitigate negative impacts associated with climate change (Ledig & Kitzmiller 1992; Rehfeldt *et al.* 2003; Sonesson 2004; Hulme 2005) and in some cases may enhance a site's productivity in a future climate (Rehfeldt, Wykoff & Ying 2001; Wang *et al.* 2006b). However, the climate of the optimum population for each planting site (i.e. the optimum climate migration distance) can be difficult to determine, especially in heterogeneous environments (Millar, Stephenson & Stephens 2007), and is likely to depend on local adaptation and the expected rate of climate change in each location (St Clair & Howe 2007). Knowing the current and future climate of each location, the UTF could be used to identify the climate of the population expected to be best adapted over the life span of the forest in each location.

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