

Linking population genetics and tree height growth models to predict impacts of climate change on forest production

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Abstract

Changes to forest growth models used widely in global change research and sustainable forest management are needed to account for expected climate change impacts. We provide a new approach that dynamically merges height–age functions prevalent in forest growth models with transfer functions prevalent in population adaptation research to better represent changes to forest productivity as climates gradually change. Our simulations with data from an extensive provenance test of lodgepole pine (*Pinus contorta*) in British Columbia, Canada, suggest that **climate change will reduce production in lodgepole pine forests established today by at least 7–13% at the end of this century** – considerably less than most predictions based solely on transfer or response functions, which do not integrate impacts as climate gradually changes. This work illustrates the need for forest productivity models to consider the changing climate in which a population is growing relative to the static climate of its origin. It also demonstrates the value of long-term provenance trials in assessing the dynamic impact of climate change on forest productivity, and serves as an example of how provenance trials may be exploited in other forest productivity models or other research fields to assess plant responses to climate.

Keywords: forest productivity, growth and yield, height–age model, maladaptation, population adaptation, provenance test, site index, transfer function

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Introduction

Forests provide many ecosystem services and commodity products, supply a repository of two-thirds of terrestrial biodiversity (Millennium Ecosystem Assessment, 2005), and their response to global climate change will affect mitigation efforts required to reach stabilization targets for atmospheric CO₂ concentrations (Kurz, 2010). Accurate estimates of future forest productivity, therefore, provide critical inputs into global biodiversity, economic and carbon balance models (Waide *et al.*, 1999; Mittelbach *et al.*, 2001; McMahon *et al.*, 2010), and are central to sustainable forest management (Davis *et al.*, 2001; Porté & Bartelink, 2002). However, as many forest productivity models were designed for use in a static climate, methods are needed to incorporate climate models into forest growth prediction systems (Purves & Pacala, 2008).

Provenance tests, in which forest tree populations from a range of source climates are grown in one or

more test climates, were established in many countries in the last century to identify locations of superior commercial genotypes, and later, to assess maximum distances that seedlings used in reforestation could be transferred before displaying unacceptable levels of maladaptation (Morgenstern, 1996). Transfer functions developed from provenance test data relate population growth to the climate distance trees in provenance tests are transferred (i.e. test site climate minus provenance climate), quantifying, degree of local adaptation (Wu & Ying, 2004) and impacts of seed transfer on growth (Raymond & Lindgren, 1990). Serendipitously, provenance tests have emerged as ideal climate change laboratories because they reveal, *in situ*, the growth of populations in future climates (Mátyás, 1994). Accurate estimates of climate change impacts to tree growth may be expected from transfer functions because they reflect the effects of multiple, interacting biotic and abiotic environmental factors, including a range of climate extremes, using large, long-term studies in natural environments.

Provenance tests indicate that populations of trees incapable of migrating or evolving apace with climate

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change (Aitken *et al.*, 2008) will become increasingly maladapted and slower growing in climates expected towards the middle and end of the current century, despite the emergence of more favourable growing conditions in many areas. Provenance tests suggest that for most species, climate change will result in a decline in growth, or a slight increase for a few decades, followed by a decline (Rehfeldt *et al.*, 1999a; Beaulieu *et al.*, 2004; St. Clair & Howe, 2007; Reich & Oleksyn, 2008). In recognition of the need to incorporate population adaptation into forest growth models, a biophysical model was used to predict site index at harvest (ca. 65 years after planting) on the basis of climate expected at harvest (Beaulieu & Rainville, 2005). (Site index, a commonly used measure of forest productivity, is the height of the tallest or largest diameter trees on a site at a reference age – often 50 or 100 years; e.g. SI₅₀.) An estimate of the impact of climate change on growth rate at harvest obtained from a transfer function was then used to adjust site index at the time of harvest. Finally, yield tables interpreted forest tree volume from adjusted site index at harvest. Refinements to this model are needed to account for the gradually changing impacts of climate on population adaptation, site productivity and their interaction.

Subsequently, component functions of a widely used forest productivity model – Forest Vegetation Simulator – were adjusted to take into account the effects of a gradually changing climate (Crookston *et al.*, 2010). Effects of climate change on adaptation (interpreted from transfer functions), viability and site index were estimated periodically during the growth of the forest, and a logic model used to select the single factor expected to govern growth most strongly, which was then used as a growth modifier for that period. We propose an alternative approach that merges height growth and population adaptation models, recognizing site productivity to be a function of – not independent of – the adaptation of the trees on a site.

To capture the effects of dynamic population adaptation on forest growth, we propose incorporating population responses to climate change inferred from transfer functions into conventional height growth models (also called site index or height–age models) which drive many forest growth models used in forest research (Davis *et al.*, 2001; Crookston & Dixon, 2005; Skovsgaard & Vanclay, 2008) and forest management (Schumacher, 1939; Edwards & Christie, 1981; Milner, 1988). Further, transfer functions are developed from provenance tests where each population experiences a ‘new’ climate beginning at establishment. Consequently, growth of a transferred population relative to a nontransferred (local) population effectively describes the impact to growth rate at a given amount of climate

change. However, many fields of forest research and management require the accrued impact of climate change on forest production at some future date, which will likely be considerably smaller than growth rate impacts at that date because forests established today will experience climate change only gradually as it arises. By adjusting annual height growth functions based on annual changes to growth, cumulative impacts of a changing climate on forest tree volume can be quantified for established populations from any climate.

Using growth data from 32-year-old trees from one of the widest ranging provenance tests in the world – the Illingworth lodgepole pine (*Pinus contorta*) field trial – we developed a transfer function that predicts height as a function of mean annual temperature (MAT) transfer distance and the MAT of the provenance. Expected annual change in MAT was used in the transfer function as the effective transfer distance of local seed each year to predict annual change to height growth, which was used to adjust the height growth trajectory each year.

To explore the range of potential impacts of climate change on forest productivity, we ran our algorithm using three temperature trajectories representing a range of possible future climates and populations from three disparate provenance climates. The adjusted height growth functions produced by the algorithm were then used in a stand growth model to examine potential volume growth impacts associated with climate change.

Materials and methods

Analysis overview

To model the effect of climate change on site productivity, we first developed a pooled transfer function (Schmidtling, 1994) using data from an extensive lodgepole pine provenance test to estimate change in site height associated with climate transfer distance (climate of the test site minus climate of the provenance). ‘Site height’ – defined here as the height of the tallest trees in a stand – at a reference age reflects site productivity, and was estimated for each population at each site by calculating the average height of the two tallest live trees of each population at each site.

Relationships describing temporal trajectories of climate change (i.e. climate variable vs. year) in the study area (the range of lodgepole pine in interior BC) were used with the transfer function to adjust BC’s height growth equation (i.e. height–age function) for lodgepole pine (Thrower *et al.*, 1994). Details of these procedures are described next in an iterative algorithm, and Steps are keyed to Appendix S1 and animated slides in Movie S1. To demonstrate the adjusted height growth function, we compared estimated height growth for a

'no climate change scenario' (control) with each of the three scenarios for each of three climatically disparate provenances. Finally, we input site height values estimated from the adjusted height growth model into a stand growth model to estimate the changes to site productivity associated with climate change.

Provenance data

Growth data used for this project were obtained from the British Columbia (BC) Forest Service's long-term lodgepole pine 'Illingworth' provenance trial (Rehfeldt *et al.*, 1999a) which consists of populations from 140 provenances from southern California to central Yukon planted at 62 sites throughout the BC interior and southern Yukon. (We refer to a 'population' as a set of intermingling individuals and 'provenance' as their geographic origin). The populations were planted as 3-year-old seedlings at a 2.5 m spacing in the spring of 1974 in an incomplete design such that each population was tested at 30–40 test sites. Within each site, a randomized complete block design was used, with one 3 × 3 tree square plot of each population planted in each of two blocks. Height, diameter and survival were recorded after 32 years in plantation at 42 of the 62 sites. These data were supplemented with data from two additional lodgepole pine provenance tests located on Vancouver Island that were of similar age, design and population base as the Illingworth trial, producing a final dataset containing 173 populations and 44 test sites.

Climate data

Mean values of four annual temperature variables and four annual precipitation variables for 1961–1990 were obtained for each provenance and test site using ClimateBC[®] (Hamann & Wang, 2005; Wang *et al.*, 2006a), a computer application that extracts and downscales PRISM[®] (Daly *et al.*, 2002) monthly climate means from a 2.5 × 2.5 arcmin grid, and derives biologically important seasonal and annual climate variables for specified geographic locations. (For a list of the eight climate variables, see Wang *et al.*, 2006b.) Values of the eight climate variables at all of the interior BC provenance and test site locations were also obtained for three 30-year periods centred on 2025, 2055 and 2085 for each of three general circulation models (GCMs) and emission scenarios (CGCM2 A2, CSIRO2 B1 and HADLEY3 B2, hereafter called simply 'climate scenarios') (IPCC, 2007) using ClimateBC. These three climate scenarios were selected from among a wide range of climate scenarios illustrated in the Regional Analysis Tool of the Pacific Climate Impacts Consortium (<http://pacificclimate.org/tools/regionalanalysis/>) to represent a range of possible future climate and emission scenarios.

We wished to determine the trajectories of each variable in each of the three scenarios over time in the study area. As the populations and test sites sampled the study area geographically uniformly (Ying *et al.*, 1984), values of each variable were averaged across the populations and test sites for each period and climate scenario. Trajectories of each variable over time were then developed by fitting equations to predict each vari-

able using year as the independent variable in linear or quadratic regression models. Fitted equations were used to generate climate values each year from 1975 to 2100 for each climate scenario (Fig. 1).

Transfer function

Data from individual transfer functions at multiple sites can be combined to develop a 'pooled' transfer function that is more robust than individual transfer functions (Schmidtling, 1994; Carter, 1996; Rehfeldt *et al.*, 1999b). However, pooling data can obscure the effects of seed transfer at different locations, and because pooling requires population responses to be standardized to account for productivity differences among test sites (Rehfeldt *et al.*, 1999a), absolute growth differences among populations cannot be compared. As our objective was to illustrate integration of transfer functions with height growth models and to assess relative impacts of climate change on growth of different populations, absolute heights were not needed, allowing us to pool the data to develop a robust transfer function for the entire study area and simplifying the analysis.

Therefore, we standardize each population's site height by expressing it as a proportion (HTp) of the average site height of 'local' populations growing at each test site. We defined 'local' populations as those that originated within 2.2 °C MAT, 0.3 log units of mean annual precipitation and 2.5° of latitude from the test site. These limits were selected on the basis of individual transfer functions constructed from the current dataset, and sought to be sufficiently restrictive to ensure that populations identified as 'local' were no more than

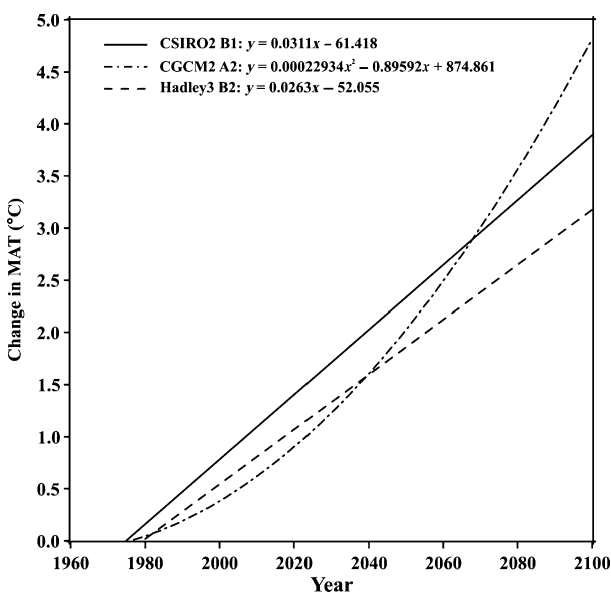


Fig. 1 Mean annual temperature trajectories. Results of the fitted relationships describing the expected trajectory of changes in mean annual temperature in the study area according to three general circulation models and emission scenarios.

3% shorter than the predicted height of a population at zero transfer distance, while being sufficiently inclusive to ensure that all sites contained at least three local populations.

In preliminary analyses, we developed transfer functions using the standardized site height data pooled from all sites to identify climate transfer distance variables most strongly influencing growth of transferred populations. Quadratic models using each of the eight climate variables individually and in all possible combinations of temperature and precipitation variables were developed to predict HTp. These analyses indicated that HTp was not significantly related to any of the four precipitation variables, nor did the precipitation variables significantly contribute to any of the two-predictor variable models. Of the four temperature variables, MAT was most strongly related to HTp. However, including a second temperature variable with MAT did not significantly strengthen the model. Therefore, further transfer function refinements involved models that used MAT as the only independent climate transfer distance variable.

Pooled transfer functions were developed using standardized site height (HTp) to predict population HTp as a function of population MAT transfer distance (txMAT = MAT of the test site – MAT of the provenance). Responses may differ greatly for transfers from 5 to 8 °C MAT vs. transfers from –2 to 1 °C MAT (O'Neill *et al.*, 2008), even though both situations involve +3 °C MAT transfer distance. Therefore, provenance MAT (MAT_P) was also included in the model as an independent localizing variable, allowing the transfer function to vary across provenances having different climates. The selected model was based on the Weibull probability density function (Yang *et al.*, 1978) which had the strongest fit, smallest (most negative) Akaike Information Criteria value, and the smallest estimated mean-squared error among several candidate models. The selected model took the form:

$$\text{HTp}_{ij} = \mu_i + \left[x_{ij}^{b_0} \times \exp(-x_{ij}^{b_1}) \right] + \varepsilon_{ij}, \quad (1)$$

$$x_{ij} = a_0 + (a_1 \times \text{txMAT}_{ij}) + (a_2 \times \text{txMAT}_{ij} \times \text{MAT}_P),$$

where i = the 1, 2, 3, ..., 173rd provenance tested at the j = 1, 2, 3, ..., 44th test site; a_0 , a_1 , a_2 , b_0 , and b_1 are model parameters; exp is the exponentiation function for natural logarithms; ε_{ij} are the random error terms which are assumed to be independently and normally distributed with mean = 0 and variance = σ^2 ; μ_i is a random-effects parameter having provenance as the subject, and all other variables are as previously defined. The random-effects parameter is assumed normally distributed with a mean of 0 and an unknown variance, allowing each provenance to take on a unique value in the transfer function. Fit of the Weibull transfer function was evaluated using the likelihood ratio test R^2 (Magee, 1990).

The pooled transfer function was fitted using the maximum likelihood method in the NLMIXED procedure of SAS (SAS OnlineDoc®9.1.3; SAS Institute Inc., Cary, NC, USA, 2004). Standardization of site heights resulted in the model predicting HTp = 0.93 at txMAT = 0. The function was therefore raised so that HTp = 1.00 at txMAT = 0 by multiplying predicted HTp values by $1/\text{HTp}_0$, where HTp_0 is the predicted value of HTp at txMAT = 0.

To assess bias in the final transfer function, the mean error in predicted values (predicted HTp minus observed HTp) was examined across the range of txMAT. Errors were averaged by 1-degree txMAT classes. Ninety-five per cent confidence intervals were calculated for each mean, and mean errors and their 95% confidence intervals were plotted against txMAT class. Significant bias was assumed when the confidence interval did not include zero. Slight bias (over-estimation) may exist in the prediction of HTp at txMAT = 5 (Fig. S1). However, as the error analysis involves multiple dependent comparisons, it is a nonconservative test of bias, that is, the true 95% confidence envelope would be wider than the intervals calculated here.

Height–age model adjustment

Growth of trees in BC's Tree and Stand Simulator, TASS (Mitchell, 1975) is driven by height–age models that differ among species. Site productivity for each species is defined by the user, using site index which identifies a growth trajectory (height–age model).

Site productivity is assumed to be temporally invariant in stand growth models. However, as transfer functions indicate, impacts of climate change on growth will differ each year. Consequently, site productivity, as represented by site index, will also vary annually. The following five-step algorithm was developed to adjust the trajectories of the height–age model for a lodgepole pine stand to reflect a changing climate (see Supporting Information for details).

Current site index (SI_{50} in metres), current stand age (A , in years), simulation start and stop date (Start_y and Stop_y, in years), and choice of GCM are input (Step 1). Height at ages A (HT) and 32 (HT32) are predicted using the height–age model and the current site index (Steps 2 and 3).

To account for dynamic height growth associated with a dynamic climate, the site index is recalculated annually ($\text{SI}_{50\text{adj}}$) by an amount corresponding to the expected impact of climate change on height growth, as interpreted from the transfer function (Steps 4a–4d). After site index is re-estimated, annual height is projected using $\text{SI}_{50\text{adj}}$ in the height–age model, creating annual trajectory increments (Steps 4e and 4f). A saw-tooth profile for the height–age trajectory is avoided by connecting the trajectory increments associated with the previous site index and the adjusted site index, and is achieved by adjusting age (A_{adj}) to the age expected of a tree of height = HT at $\text{SI}_{50\text{adj}}$. Values of A and HT at $\text{SI}_{50\text{adj}}$ are output at the end of each round of simulation from the adjusted height–age function. Central to the operation of the algorithm is the connection of height, site index and age in our height–age equation, allowing any one variable to be calculated using the other two.

Evaluating the effects of climate change on height and volume growth

Impacts of climate change on lodgepole pine height growth were examined by adjusting the lodgepole pine height–age model using the fitted transfer function and the height–age

model adjustment algorithm described before. The simulation was run using three levels of provenance MAT (MAT_P = -1.0, 2.0 and 5.0 °C) and the three climate scenarios for each provenance climate. MAT_P values of -1.0, 2.0 and 5.0 °C were chosen as starting conditions when calculating txMAT as these values span the range of MATs found in the distribution of managed lodgepole pine in the study area. All simulations used site index = 20 m, and simulation start and stop dates of 2010 and 2100. A control (no climate change) height-age curve was developed using txMAT = 0.

To examine how climate change impacts to height growth translate into volume impacts, each of the adjusted height-age curves was input into TASS. TASS is an individual tree distance-dependent growth and yield simulation model in which individual tree growth processes and mortality are driven mainly by height and intertree competition, and individual tree volumes are aggregated to obtain stand volume. Stand growth was simulated for 90 years, beginning in 2010, with an initial density of 1200 stems per hectare. Total volume was reported for each year in the simulation.

Results

The fitted transfer function (Fig. 2 and Table 1) ($R^2 \approx 0.60$; MSE = 0.01285) provides strong evidence that populations of lodgepole pine are differentiated on the basis of MAT of the provenance (lack of differentiation would result in flat functions), and suggests that population height growth will decline as climates warm. All parameters were significantly different from 0 at $\alpha = 0.05$, and the intercept differed significantly among provenances ($\sigma^2_\mu = 0.016254$; $P < 0.001$).

Height-age curves for lodgepole pine adjusted to account for future climate change suggest that because of climate change height growth of local (native) populations will decline slightly throughout the 90 years of the simulation (Fig. 3a and b). Differences among the nine height-age curves were small, but were somewhat greater when height growth was translated to total volume growth using a stand growth model (Fig. 3c and d). Volume losses at age 90 averaged 10% across all nine simulations, ranging from 7% (MAT_P = 5 °C; Hadley B2) to 13% (MAT_P = -1 °C; CSIRO B1). Impacts to volume increased as MAT_P decreased, and were marginally larger for the CGCM2 and CSIRO2 models than for the Hadley3 model. Simulations performed in this study were also conducted using sites more and less productive (i.e. site indices 25 and 15 m) than the site simulated in the present analysis, but the relative impacts of climate change on production at these sites differed negligibly from those reported here (i.e. at site index = 20 m).

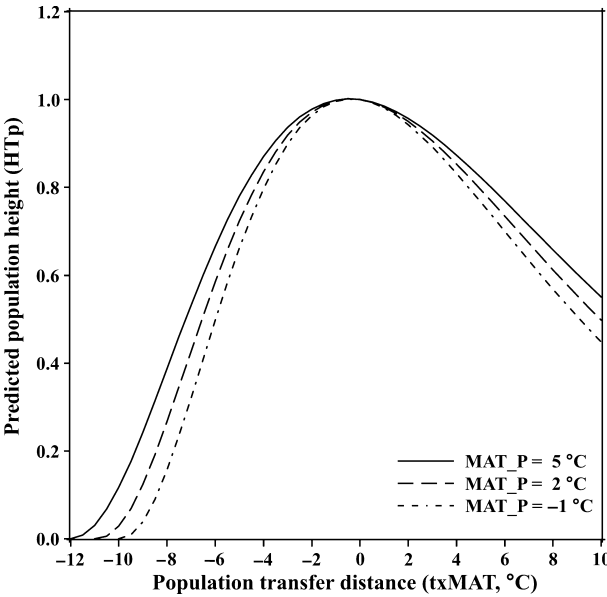


Fig. 2 Transfer functions for three lodgepole pine populations. Predicted height (HTp – height at age 32 as a proportion of the height of local populations) is a function of population transfer distance in units of mean annual temperature (txMAT). The equation is fitted for lodgepole pine in British Columbia for populations at sites having mean annual temperatures (MAT_P) of -1, 2 and 5 °C.

Discussion

Methods described in this report offer a new conceptual basis and practical approach to predict climate change impacts on forest productivity. Transfer functions developed from provenance tests are merged

Table 1 Results of fitted transfer function for lodgepole pine height using the Weibull model

Parameters	Estimate	SE	MSE*	R ²
a ₀	2.892	0.3026	0.01284	0.599
a ₁	0.2793	0.05760		
a ₂	-0.008219	0.003035		
b ₀	2.512	0.2472		
b ₁	0.9492	0.09208		

Transfer function predicts standardized site height (HTp – height as a proportion of the average site height of ‘local’ populations at each test site) as a function of mean annual temperature (MAT) transfer distance (txMAT = MAT of the test site – MAT of the provenance) and provenance MAT (MAT_P). See Eqn. 1 for transfer function model.

*MSE – mean-squared error is the estimate of the variance of the random error term. Significance of all parameters <0.0001, except a₂ (P = 0.0068).

incrementally with site height functions to reveal the gradual and cumulative impacts of a gradually changing climate on forest growth. The approach recognizes the importance of population responses to climate in forest productivity modelling and the ability of transfer functions to reveal those responses accurately. By modifying height growth functions, the approach capitalizes on a widely used and universally recognized driver of forest productivity (i.e. tree height growth), allowing height growth

responses to climate change to be incorporated into stand-level growth models where tree-to-tree competition is considered. Use of height growth functions also allows cumulative impacts of climate change on growth rate to be integrated over time to quantify impacts on forest volume (i.e. area-based tree volume). Further, incremental (i.e. annual) adjustment of growth rate recognizes that differing trajectories of GCMs and transfer functions can result in differing cumulative impacts to forest volume.

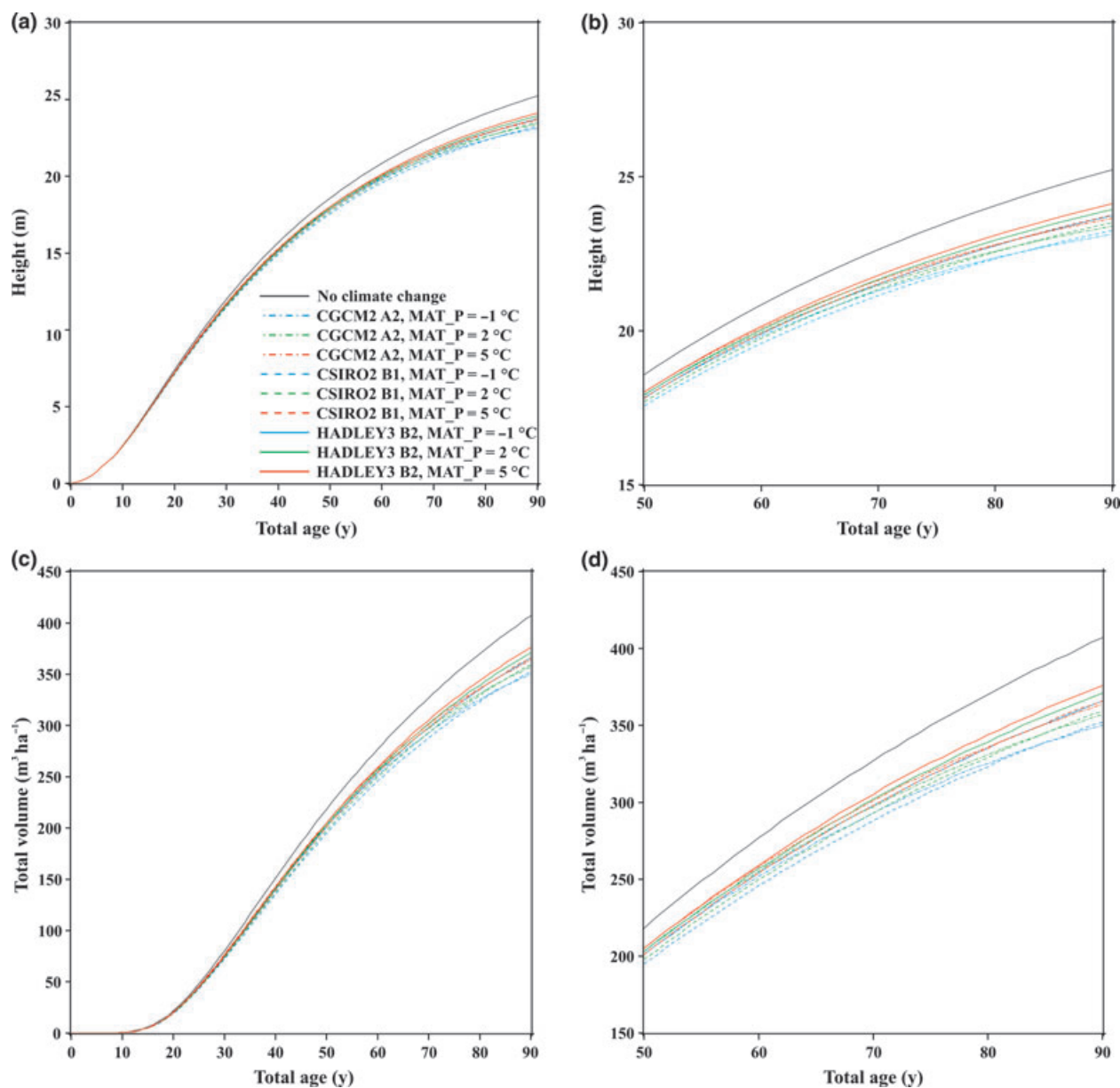


Fig. 3 Growth curves. Predicted height–age (a and b) and volume–age (c and d) curves for populations of lodgepole pine from three climatically disparate locations in British Columbia (mean annual temperatures -1 , 2 and 5 °C) adjusted to account for climate change during the period 2010–2100 according to three general circulation models and emission scenarios. Also shown are the height–age and volume–age curves in the absence of climate change.

Several of these features are of consequence to the wider climate change community seeking to exploit new methods to study climate change impacts and adaptation strategies. We illustrate an approach to integrate different components of growth (adaptation and site productivity) that have different, sometimes opposite, responses to climate change, using techniques from different disciplines (transfer functions from population genetics, and height growth functions from forest productivity modelling).

The study also demonstrates the value of provenance tests in climate change research, and serves as an example of how they may be exploited in other fields, such as physiology, ecology, entomology and pathology, to examine plant responses to climate change. Just as we use transfer functions for height to adjust a statistical model, so too could transfer functions for physiological traits or other morphological traits be used to adjust process models to help account for expected changes to climate and soil properties over time. Indeed, some process-based models may provide superior estimates of rotation-age stand productivity in future climates because they can accommodate seasonal and interannual variation in climate and soil properties, as well as rising atmospheric CO₂ concentrations (Mäkelä *et al.*, 2000). Their computational complexity and the large number of parameters and data they require present challenges for use in forest management (Mohren & Burkhart, 1994; Porté & Bartelink, 2002), but significant advances are reported and interest in mixed models is increasing (Landsberg, 2003).

This report highlights the need to distinguish results of transfer or response¹ functions, which describe the impact to growth of populations when grown in a new climate, from results of analyses such as the present, which model growth impacts to a population established in its local climate and growing in a gradually changing climate. In the former, points on transfer and response function curves effectively describe the relative impact to growth rate at a given amount of climate change; in the latter, impacts at each point in time are integrated to estimate total growth of local populations across a gradually changing climate.

Consequently, growth impacts predicted at the end of the current century using transfer and response functions are often large and highly variable (ca. +40% to –80%), depending on growth variable, model type, geographic region and species (Rehfeldt *et al.*, 1999a, 2002; Andalo *et al.*, 2005; Wang *et al.*, 2006b; Savolainen *et al.*, 2007; Savva *et al.*, 2007; O'Neill *et al.*, 2008; Crookston

et al., 2010). In contrast, predictions that integrate growth across transfer functions are able to consider growth throughout the life of a stand, including the first few decades when climate change and maladaptation are minor, and are therefore more moderate (e.g. 7–13% in this report) than the aforementioned impacts described in transfer and response functions. This distinction is of consequence in models of global CO₂ sequestration, biodiversity modelling, and other fields of global change biology, where future forest tree *height* or *volume* is of vital concern, such as studies of species distribution modelling, succession and competitive exclusion (Loehle, 2003; Purves & Pacala, 2008) and in the field of forest management, where sustainable harvest rate is based on harvest-age volume.

Conceptual views of climate change impacts to forest growth

Our approach to the study of forest growth calls for genotype to be considered as an integral part of site productivity. Changes to site productivity as a result of climate change can be assessed by examining changes to site and provenance climate. (See schematic representation in Fig. 4.) Provenance climate – the climate in which a population has evolved – will change only gradually over several tree generations via natural selection and migration. Therefore, vector A illustrates how forest productivity of locally adapted populations currently differs across the landscape. If populations evolve over several tree generations to be adapted to their new climates, vector A could also be used to interpret future site productivity at that time (Nigh *et al.*, 2004; Beaulieu & Rainville, 2005; Monserud *et al.*, 2008; Crookston *et al.*, 2010). Changes to forest productivity over the course of a single tree generation will follow vector B.

Changes to growth shown in transfer functions represent the combined direct effects of changes to climate, and indirect effects of changes to climate on soil factors and the level of adaptation of the population to the new climate and soil factors. Consequently, changes to forest productivity shown in vector B (Fig. 4) track changes shown in transfer functions (Fig. 2). (Subtracting MAT_P from site MAT of vector B in Fig. 4 results in a transfer distance axis shown in a transfer function.) Transfer functions, therefore, should be used to adjust incrementally a height growth function (site index) suited for a site at the time of plantation establishment. Further, adjusting a height growth function using a transfer function may be a more biologically reasonable conception of how climate change will affect forest growth than interpreting growth using a logic model to identify a single operative function for each iteration of the model (Crookston *et al.*, 2010).

¹A response function relates growth of a population to the climates of the sites where it is tested.

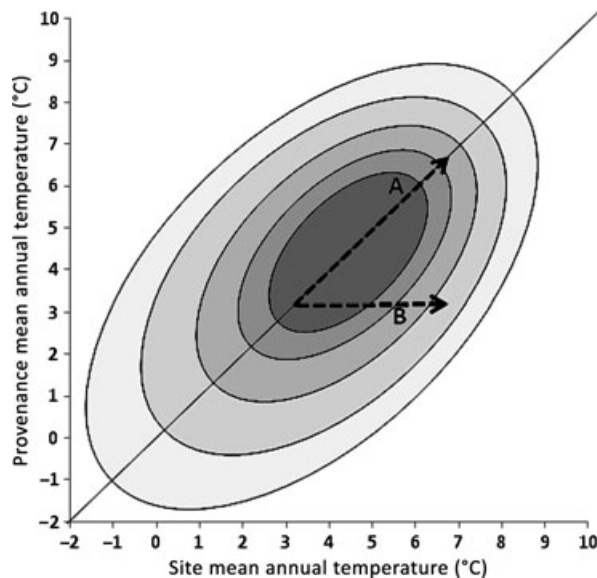


Fig. 4 Universal transfer function. The relationship of forest productivity with site and provenance climate is shown in this schematic based on a three-dimensional representation of a universal transfer function (O'Neill *et al.*, 2008, fig. 4). The climate variable mean annual temperature (MAT) is used for illustration. Darker shades represent greater productivity. Only site MAT changes over the life of a stand; provenance MAT is fixed at the time of stand establishment. Therefore, vector B, which is similar to the transfer function in Fig. 2, illustrates the expected change in forest productivity as climate changes over the next century. Vector A illustrates how forest productivity of locally adapted populations currently differs across the landscape.

Inferences and limitations of this study

Impacts to forest growth reported in this study corroborate previous genecology reports (Schmidtling, 1994; Carter, 1996; Rehfeldt *et al.*, 1999b, 2002; Andalo *et al.*, 2005; Savolainen *et al.*, 2007) in showing that populations will become maladapted with moderate to severe climate change. However, results of this report suggest that even minor changes in MAT will result in growth loss throughout the study area. In contrast, several other reports that use individual or regional transfer functions suggest that warming may increase growth or survival slightly, particularly for northern populations in the short- to moderate-term (Rehfeldt *et al.*, 2001, 2002; Wang *et al.*, 2006b; Savolainen *et al.*, 2007; O'Neill *et al.*, 2008; Reich & Oleksyn, 2008). The discrepancy between our results and those of others, including those that used the Illingworth data, may be explained primarily by our pooling of data to create a single transfer function. The only other pooled MAT transfer function that used the Illingworth data obtained results identical to ours (i.e. vertex at zero transfer distance – Rehfeldt *et al.*, 1999a). Had we used

individual or regional transfer functions (Savolainen *et al.*, 2007) or random coefficients models (i.e. a universal transfer or response function – see O'Neill *et al.*, 2008; Wang *et al.*, 2010), our model may have had greater spatial nuance that may have enabled detection of different responses to climate change in different parts of the species' range. We chose to pool the data into a single function to simplify an already complex analysis. However, in practice, where provenance trials contain sufficient test sites, use of regional transfer functions or random coefficients models should be considered. Our inclusion of data from two coastal test sites not used in previous reports, use of an asymmetric transfer function, as opposed to a symmetric function, and use of 'site height' in lieu of average height may also have contributed to differences between our pooled function and the individual or regional transfer functions of others.

Climate change impacts to forest productivity reported here represent a conservative estimate of potential negative impacts, as the intensity and frequency of pest epidemics and fires is expected to increase as the climate changes (Harvell *et al.*, 2002; Fried, 2004; Kirilenko & Sedjo, 2007). Indeed, mountain pine beetle has devastated many of the plantations used in this study. Although the severity of this outbreak is exceptional among North American tree species, it highlights the need to consider factors other than adaptation and site productivity that may affect forest productivity. Also, our analysis used only height growth impacts represented in transfer functions to examine accrued growth impacts due to climate change during the simulation. Impacts of climate change on survival are unrepresented in our study, and may further reduce realized site productivity in some regions (Rehfeldt *et al.*, 1999a; Savolainen *et al.*, 2007; Reich & Oleksyn, 2008). Also, our model applies primarily to forests after the establishment phase; impacts of climate change on flowering, seed production, germination and establishment are not represented, so caution should be used in applying the model to situations where the regeneration phase is assumed (Bugmann, 2001). Large reductions in forest production were predicted for most species and climate scenarios when the effects of climate change on adaptation (interpreted from transfer functions), viability and site index were used to model impacts of climate change (Crookston *et al.*, 2010). Impacts on survival inferred from climate – species occurrence relationships were identified as the dominant factor-driving reductions in volume production, although impacts to survival estimated in this manner appear to be somewhat greater than when estimated directly using survival transfer functions (see Rehfeldt *et al.*, 1999a, fig. 9). Therefore, we are currently seeking

methods to integrate survival transfer functions into existing mortality functions used in forest growth models so as to account for the complex interactions of growth and survival.

In addition, by using a single transfer function developed from 32-year-old trees, we assume that transfer function shape does not change with time. A fuller representation of climate change impacts at each age would be achieved using transfer functions specific to each age. Climate change may also alter the relationship between site height and the distribution of heights of trees in a stand (Ledig & Kitzmiller, 1992). As height growth curves apply to the tallest trees in a stand, adjusted height growth curves could over-estimate stand growth if growth of a stand as a whole (average tree growth) is more impacted by climate change (or seed transfer) than are the tallest trees. Finally, different species may respond to climate change differently, leading to changes in interspecies competition that may affect forest productivity (Aitken *et al.*, 2008). The need to accommodate interspecies competition, and in particular, shifts in interspecies competition is recognized (Di Lucca *et al.*, 2009) and will introduce new challenges to many forest growth models. Despite these sources of uncertainty, integrating changes to height growth dynamically into a height growth model should improve estimates of forest productivity in a changing climate.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Algorithm to merge transfer function and height–age curves. The algorithm below is used to adjust height–age curves for the effects of climate change on height growth. Steps shown here are linked to steps in the Animated Slides in Movie S1.

Fig. S1. Transfer function bias assessment. Results of lodgepole pine transfer function model bias assessment showing mean error of height predictions (HTp) and its standard error as a function of seed transfer distance in units of mean annual temperature (txMAT).

Movie S1. Iterative algorithm. An iterative procedure is illustrated for adjusting height growth (site index) curves using transfer function information. Annual impacts to height growth are inferred from a transfer function and this information is then used to adjust annual segments of the height growth curve. Steps are keyed to Appendix S1.

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