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# Mitigating the effects of climate change on lodgepole pine site height in British Columbia, Canada, with a transfer function

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Provenance trials provide an opportunity to develop transfer functions that can be used to assess the effects of climate change on tree growth. A transfer function is available for lodgepole pine (*Pinus contorta* var. *latifolia*) in British Columbia, Canada, that predicts relative height (site height of a population divided by the site height of the local population) as a function of mean annual temperature transfer distance and mean annual temperature of the provenance. This model is modified to improve its fit and address some deficiencies. A dataset consisting of 2276 height observations from 136 populations planted at 40 test sites was fitted to a two-variable power/exponential function. Mean coldest month temperature and mean summer precipitation transfer distances were the predictor variables, and relative height at the age of 35 was the response variable. The transfer function was linked to a lodgepole pine height-age model to create a dynamic system that can be used to evaluate the effect of climate change on site height growth. The system can then be used to mitigate the effect of climate change on lodgepole pine site height growth by determining the expected height of seed from various provenances at the end of the rotation and selecting the optimal seed source. For an example stand, climate change is expected to reduce site height by ~0.77 m over an 80-year rotation. However, this reduction can be fully mitigated by planting the optimal seed source.

## Introduction

Climate change is expected to have significant effects on ecosystem functioning in British Columbia (BC), Canada, for example with hydrology, biodiversity and tree growth (B.C. Ministry of Water, Land and Air Protection, 2002; Spittlehouse, 2008). No more evident of this is the massive mountain pine beetle (*Dendroctonus ponderosae* Hopk.) outbreak in the interior of the province (Safranyik and Wilson, 2006). In BC during the twentieth century, the mean annual temperature has risen from 0 to 1.7°C, and precipitation has increased by 0–4 per cent per decade between 1930 and 2000 depending on the ecoprovince (B.C. Ministry of Water, Land and Air Protection, 2002). By the mid-twenty-first century, the temperature is predicted to increase 2.3°C above the climate normals from 1961 to 1990 whereas at the same time precipitation is predicted to increase by 8 per cent (Werner, 2011). The changes in climate are not expected to be uniform over the province (Werner, 2011), and the predicted changes are dependent on the assumed global circulation model and emissions scenario.

Changes in temperature and precipitation affect plant growth. Increased or decreased growth resulting from a changing climate has been reported (Boisvenue and Running, 2006) or is predicted (Wang *et al*., 2011). The optimum temperature for plant growth in cool temperate regions is between 8 and 25°C (Spurr, 1964; Oliver and Larson, 1996; Schulze *et al*., 2005; Hopkins and Hüner, 2009). The optimal environmental conditions under which photosynthesis occurs is controlled genetically, with the optimum temperature being lower for populations in colder climates (Ledig, 1976; Hopkins and Hüner, 2009). The growth response to temperature increases, reaches a plateau, and then decreases as temperature increases (Landsberg, 1986). This would suggest that, with a warming climate, there is opportunity for tree growth to be increased on cooler sites, but little growth increase could be expected when the temperature is in the optimal range. As temperatures increase beyond the optimal, growth will decrease until lethal temperatures are reached (Schulze *et al*., 2005). In the forested biogeoclimatic zones of BC (Meidinger and Pojar, 1991), the mean temperature of the warmest month ranges from ~11°C (in the Engelmann Spruce-Subalpine Fir zone) to ~18°C (in the Ponderosa Pine zone) (Spittlehouse, 2008). Trees in the warmer zones may often experience daily fluctuations in temperatures that are higher than optimal, but many areas of BC should remain in the optimal range under moderate climate change.

Excessively dry soils can inhibit tree growth (Kozlowski *et al*., 1991) although some species are better adapted to these conditions than others (Klinka *et al*., 2000). Summer droughts lead to reduced growth in trees; for example, large reductions in gross primary productivity have been linked to extreme drought

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conditions (Ciais *et al*., 2005). Precipitation frequency and amount are both related to the creation of drought conditions during the growing season (Wu *et al*., 2012).

Previously developed relationships between climate and site index, which is a measure of forest site productivity, show that climate variables are important predictors of site index for lodgepole pine (*Pinus contorta* var. *latifolia*) (Nigh *et al*., 2004; Monserud *et al*., 2006; Monserud *et al*., 2008). Inherent in these studies, though, is the assumption that the trees are adapted to the climate of the site. This assumption may not hold under a rapidly changing climate since there will be an adaptation lag (Mátyás and Yeatman, 1992). Consequently, the site index predicted by these methods will likely over-estimate height growth. Growth projections under a changing climate need to account for maladaptation.

Provenance studies are important for understanding genetic variation and for managing genetic resources for reforestation, restoration, and gene conservation. These types of studies were not originally designed as climate change experiments. However, fortuitously, they created climate change experiments by taking seed adapted to one climate and planting it in another climate. Mátyás (1994) recognized the potential of provenance studies for examining the effects of climate change on tree growth and proposed a modelling framework for doing so. The growth response to climate change is a function of the transfer distance of the population, or as Mátyás and Yeatman (1992) call it, ecodistance. Transfer distance is the difference between the climate at the planting site and the climate of the provenance (a provenance is defined as the geographic origin of a population). Climate is measured with variables such as mean annual temperature or mean annual precipitation. Using mean annual temperature as an example, a positive transfer distance means that a tree was planted at a site that is warmer than its provenance. Local populations (e.g. natural stands of trees) have a transfer distance of 0, indicating that the trees growing on a given site grew from seeds originating from a nearby source. Much work has been done recently in generating transfer functions (e.g. Andalo *et al*., 2005; Thomson and Parker, 2008; Thomson *et al*., 2009; Leites *et al*., 2012).

A transfer function for lodgepole pine height growth was developed for BC (O'Neill and Nigh, 2011). This function has mean annual temperature transfer distance as the independent variable and height as a proportion of the height of a local provenance as the dependent variable, with mean annual temperature of the provenance acting as a modifier of this relationship. There are, however, two deficiencies in this transfer function. Due to various sources of errors, an adjustment had to be made to the fitted model so that the response variable equalled the theoretically correct value of 1 for local provenances. This correction resulted in an approximate 7 per cent upwards adjustment in the fitted model, which is not large but nevertheless results in a model that is sub-optimal in terms of fit criteria. The other deficiency is a lack of precipitation transfer distance in the model. The purpose of this project is twofold:

(1) To improve the model of O'Neill and Nigh (2011) by incorporating a precipitation transfer distance into the transfer function, examining the potential for better predictor variables, and to minimize the adjustment needed to make the relative height equal to 1 for local provenances. O'Neill and Nigh (2011) found that precipitation transfer distance did not significantly improve their model. However, a different functional form for a multi-variable model is employed along with a more systematic approach to selecting predictor variables to achieve an improved transfer function.
(2) To examine how the revised transfer function, after linking it to the height-age model for lodgepole pine site height, can be used to mitigate the effects of climate change on height growth by identifying a provenance that is better adapted to the changing climate.

## Data

The data used for this project were from a large lodgepole pine provenance trial. Five test sites were selected in each of 12 geoclimatic regions giving 60 extant sites throughout BC and southern Yukon (Wu and Ying, 2004). The geoclimatic regions were delineated primarily on latitude and precipitation regimes (Ying *et al*., 1985), and eight of the geoclimatic regions had lodgepole pine as a major component of the natural forest. A randomized complete block design was established at each test site with two blocks of each population in a $3 \times 3$ tree square plot. One-hundred and forty-two samples from populations from southern California to central Yukon were planted at these sites in the spring of 1974 with 3-year-old seedlings. A subset of the populations were planted at each test site because it was not practical to plant all populations at all sites. Each subset contained populations that were indigenous to the region, most populations from neighbouring regions and some populations from extremes of the range of lodgepole pine. The experiment was re-measured on an ~3-year schedule with the latest height measurement being taken after the trees had 32 growing seasons in the field (making the trees 35 years old). The dataset available for analysis contained 136 provenances from 40 interior sites giving a total of 2276 observations.

The response variable of interest is site height (referred to as height from here on), which is the average height of the two tallest trees in the plot. This definition was chosen because it approximates the definition of site height adopted in BC. Site index in BC is defined as site height at breast height age of 50. It can be estimated from height if age is also known, which is critical to the implementation of the transfer function. Height was standardized by dividing the height of a population by the average height of the local population. This allows the data from sites with different inherent productivities to be pooled without explicitly taking into account the factors affecting the productivity of the sites (Rehfeldt *et al*., 1999). A definition for a local population was developed since local populations were not planted at the test sites (Schmidtling, 1994). Local populations are defined as those with the following three characteristics:

(1) The difference between the mean annual temperature of the provenance and the test site is $<1$.
(2) The difference between the natural logarithm of the mean annual precipitation of the provenance and the test site is $<0.3$.
(3) The difference between the latitude of the provenance and the test site is $<2.5$ degrees.

Climate data for each test site and provenance were obtained from the ClimateWNA (version 4.62) software (Wang *et al*., 2012).

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ClimateWNA predicts 20 annual climate variables for the reference period of 1961–1990 for western North America (Table 1). The climate predictions are made from latitude, longitude, and, if available, elevation. The downloadable software and more information about ClimateWNA are available at http://www.genetics.forestry.ubc.ca/cfcg/ClimateWNA/ClimateWNA.html.

The potential predictor variables are climate transfer distances of the provenances. Distance is expressed as the difference in climate between the seed's provenance and that of the test site. That is, transfer distance (txXXX) = XXX_S − XXX_P, where XXX is a climate variable from Table 1, '_S' indicates that the climate variable is for the planting site and '_P' indicates that the climate variable is for the provenance. For example, txMAT = MAT_S − MAT_P, i.e. the mean annual temperature of the test site minus the mean annual temperature of the provenance.

The natural logarithm of the precipitation variables MAP, MSP and PAS were taken before the transfer distance was calculated. This was done for two reasons. First, it results in the transfer distances for these variables to be closer to the scale of most of the other transfer variables. More importantly, the logarithmic transformation results in smaller transfer distances as precipitation increases for a given change in precipitation. For example, suppose Provenances A and B had MAPs of 1800 and 500 mm, respectively, and seed from both provenances were moved to sites 100 mm drier. Provenance A should have a much smaller transfer distance than Provenance B since wetter sites are less sensitive to changes in precipitation than drier sites (Wang *et al.*, 2011). Taking the difference of logs has the effect of making a larger transfer (on the untransformed scale) necessary on wetter sites to obtain the same response as on drier sites.

**Table 1** Annual climate variables predicted by ClimateWNA version 4.62

| Variable | Acronym | Units |
|---|---|---|
| Mean annual temperature | MAT | °C |
| Mean coldest month temperature | MCMT | °C |
| Mean warmest month temperature | MWMT | °C |
| Continentality (MWMT − MCMT) | TD | °C |
| Mean annual precipitation | MAP | mm |
| Mean summer (May–September) precipitation | MSP | mm |
| Annual heat to moisture index | AHM | °C $mm^{-1}$ |
| Summer heat to moisture index | SHM | °C $mm^{-1}$ |
| Degree-days below 0°C | DDLT0 | °C days |
| Degree-days above 5°C | DDGT5 | °C days |
| Degree-days below 18°C | DDLT18 | °C days |
| Degree-days above 18°C | DDGT18 | °C days |
| Number of frost-free days | NFFD | # days |
| Frost-free period | FFP | # days |
| Beginning of frost-free period | bFFP | Julian date |
| End of frost-free period | eFFP | Julian date |
| Estimated extreme minimum temperature of a 30 year normal period | EMT | °C |
| Precipitation as snow | PAS | mm |
| Annual reference evaporation | $E_{ref}$ | mm |
| Annual climatic moisture deficit | CMD | mm |

# Methods

## *Developing the transfer function (Objective 1)*

A parsimonious version of the model fit by O'Neill and Nigh (2011) was used as the basis for the transfer function:

$$Ht_p = \frac{x^{b_0}}{\exp(x^{b_1})} + \varepsilon, \quad (1)$$

where $Ht_p$ is the site height of a population in a plot divided by the site height of the local provenance, $x$ is a simple linear function of a transfer distance for a climate variable (i.e. $x = a_0 + a_1\, txXXX$), $txXXX$ is as defined earlier, $a_0, a_1, b_0$ and $b_1$ are model parameters, exp is the exponentiation function and $\boldsymbol{\epsilon}$ is a random error that has the usual assumption of being i.i.d. N(0, $\sigma^2$). The transfer function should be positive, unimodal and be able to take on symmetric and asymmetric shapes. Other functions like the Cauchy or polynomials are also potential transfer functions (Mátyás and Yeatman, 1992; Thomson and Parker, 2008). However, the asymmetrical nature of the data (Figure 1a) makes the Cauchy function a poor choice for this transfer function. Polynomials have poor extrapolation properties and choosing the degree of the polynomial without overfitting the model can be difficult, particularly with a large dataset. The chosen transfer function (equation (1)) can take on a range of shapes from skewed to symmetrical. The parameters of this model interact in a complicated way, but generally parameters $a_0$ and $a_1$ are related to the location and steepness of the curve, respectively, and parameters $b_0$ and $b_1$ are related to the shape, asymmetry, and maximum value of the model.

One objective of this work was to incorporate both temperature and precipitation variables into the transfer function. To meet this objective, the following strategy was adopted to select a set of predictor variables from the 20 potential variables that were available; however, it is not necessarily optimal in terms of obtaining the best fitting model. The potential variables were divided into precipitation-related variables (txMAP, txMSP and txPAS), variables with both temperature and precipitation information (txAHM, txSHM and txCMD) and temperature-related variables (all remaining variables). Variable $E_{ref}$ is predicted from temperature (Wang *et al.*, 2012); hence, it is a temperature-related variable. Variable CMD is calculated from $E_{ref}$ and precipitation (Wang *et al.*, 2012), making it a variable with both temperature and precipitation information. The classification of the other 18 variables should be more obvious. The 20 single-variable models were fitted using maximum likelihood (procedure NLMIXED, SAS Institute Inc., 2004). Parameters with large $P$-values were removed from the model provided that their removal reduced Akaike's Information Criterion (AIC) (Burnham and Anderson, 1998). The fitted models were ranked using the AIC. This analysis showed that there was one temperature-related variable (txMCMT) and two precipitation-related variables (txMAP and txMSP) that were potential candidate variables for the transfer function.

In the next step of the analysis, the two combinations of the potential predictor variables (i.e. txMCMT/txMAP and txMCMT/txMSP) were fitted to the following two-variable version of model (1):

$$Ht_p = \frac{x^{b_0} \cdot y^{d_0}}{\exp(x^{b_1}) \cdot \exp(y^{d_1})} + \varepsilon, \quad (2)$$

where $x$ and $y$ are simple linear functions of transfer distances for the temperature- and precipitation-related variables, respectively (i.e. $x = a_0 + a_1\, txXXX$ and $y = c_0 + c_1\, txYYY$), $txXXX$ is the transfer distance for a temperature-related variable, $txYYY$ is the transfer distance for the moisture-related variable, $c_0$, $c_1$, $d_0$ and $d_1$ are model parameters and all other variables are as previously defined. A multiplicative, as opposed to an additive, model was chosen so that the two-variable transfer function maintains a biologically reasonable behaviour. For example, the model retains the property that $Ht_p$ approaches zero as one variable increases or decreases conditional on the other variable being fixed at some value.

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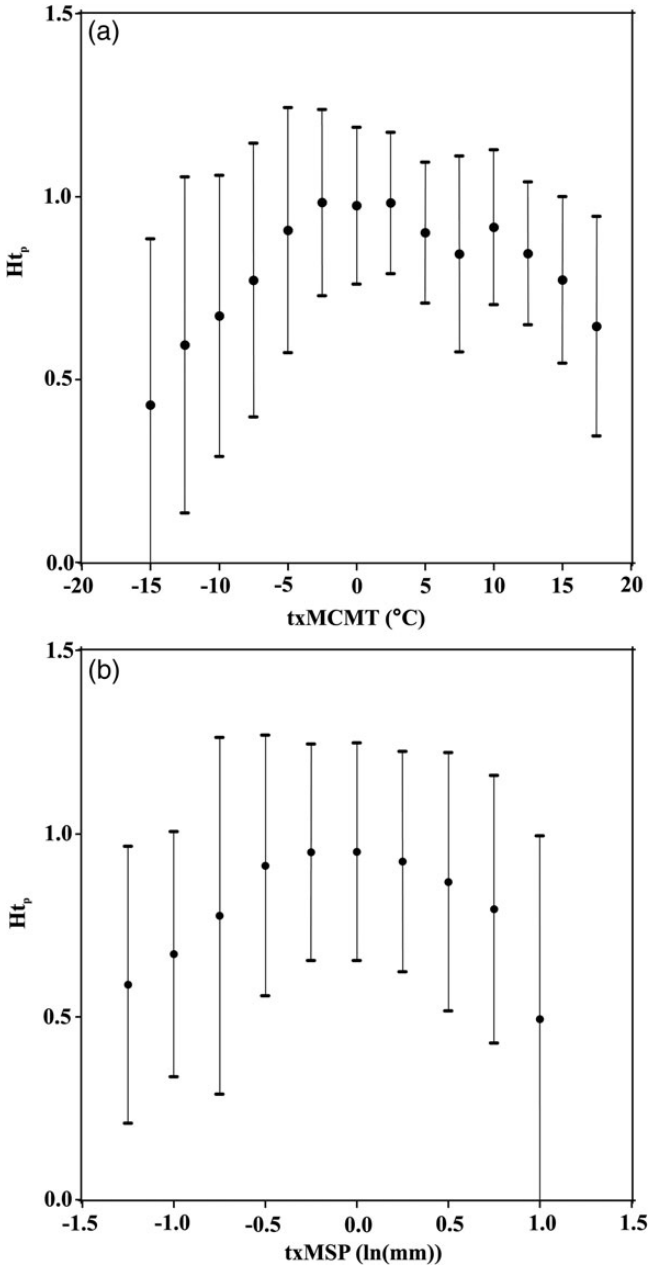


**Figure 1** Relationship between $Ht_p$ and txMCMT (a) and txMSP (b) using binned data. The mean and 2 SD for each bin is graphed at the midpoint of the bin.

Procedure MODEL in SAS (SAS Institute Inc., 2004) was used in the re-fitting because it was important at this point in the analysis to restrict the model to return a value of $Ht_p = 1$ when $txXXX = 0$ and $txYYY = 0$. This restriction is based on the theoretical consideration that $Ht_p$ is, by definition, 1 for local populations and is part of Objective 1. By setting $Ht_p = 1$, $txXXX = 0$ and $txYYY = 0$ in equation (2) and rearranging terms (excluding the error term), the following equation was programmed in the RESTRICT statement in procedure MODEL to achieve the desired outcome.

$$a_0{}^{b_0} \cdot c_0{}^{d_0} = \exp(a_0{}^{b_1}) \cdot \exp(c_0{}^{d_1}) \cdot$$

As with the single-variable models, non-significant parameters were removed from the model provided that their removal reduced the AIC and the AIC was used to guide model selection.

The residuals of the final fitted model were evaluated for normality (with a Q − Q plot and a histogram) and homoscedasticity (with plots of the residuals against the independent variables and the predicted values of $Ht_p$). A $t$ test was used to check whether the mean of the residuals was significantly different from 0 at a 95 per cent significance level. Model fit was evaluated by binning the data into appropriate classes (which depend on the independent variables in the final fitted model) and using a $t$ test to determine whether the mean of the residuals in each bin was different from 0 at a 95 per cent significance level.

## *Mitigating the effects of climate change on height growth (Objective 2)*

The intended primary application for the transfer function is to link it to a height-age model for lodgepole pine to account for climate change. This system can then be used to select a seed source that will mitigate the effects of climate change on site height.

The Batho and García (2013) lodgepole pine height-age model was linked to the transfer function to demonstrate the mitigation procedure. This model is as follows:

$$h = a_q\{1 - [1 - (h_0/a_q)^{0.8297}]exp[-q(t - t_0)]\}^{1/0.8297}, \quad (3)$$

where $a_q = 12313q^{1.645}$, and $q$ must be iteratively solved from two known age-height pairs, one of which can be (0.5, 1.3) (see Batho and García (2013) for more details). This model is base-age invariant and estimates height ($h$) at a specific breast height age ($t$) from a known height ($h_0$) and breast height age ($t_0$), i.e. $h = f(t, h_0, t_0)$. The base-age invariance property allows site index (i.e. height at the age of 50) to be obtained from a known ($t_0$, $h_0$) without inverting the model. By linking the transfer function to a height-age model, a dynamic system is created where multiple height-age trajectories are required to model height in a changing climate. The response variable in the transfer function is height relative to height of the local provenances. Using relative height allows data for sites with different productivities to be pooled in the analysis. However, the effect of site productivity on height growth needs to be incorporated back into the system when it is applied. This is done by using site index of the local provenance to select the height-age trajectory that will be adjusted for climate change.

The procedure for linking the transfer function to the height-age model is as follows (also described in the online appendix to O'Neill and Nigh (2011)):

(1) Determine the site index for the local population of lodgepole pine (SI) at the planting site assuming pre-1990 conditions.
(2) Estimate the height of the local population at a total age of 35 ($h = H_{35}$) using the height-age model with $h_0 = SI$, $t_0 = 50$ and $t = 35 - YTBH$ (YTBH is number of years to breast height and converts total age into breast height age; YTBH is estimated from site index using the YTBH model in Nigh (1999)).
(3) Determine MCMT_P and MSP_P, which are the values of MCMT and MSP of the provenance, respectively, in 1990, from ClimateWNA.

For each year in the simulation, perform the following steps:

(1) Calculate transfer distances txMCMT (= MCMT_S − MCMT_P) and txMSP (= MSP_S − MSP_P), where MCMT_S and MSP_S are MCMT and MSP for the site at the current year of the simulation (see equations below).
(2) Estimate $Ht_p$ with the fitted transfer function and txMCMT and txMSP as predictor variables.
(3) Estimate the climate-adjusted site index ($h = SI_{adj}$) from the height-age model with $t = 50$, $h_0 = H_{35} \cdot Ht_p$ and $t_0 = 35 - YTBH$.

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(4) Project the height 1 year using the height-age model with $h_0 = SI_{adj}$, $t_0 = 50$ and $t$ as determined below.

At the end of the simulation, the adjusted height-age trajectory consists of conjoined segments of height-age trajectories. Joining each segment involves shifting the height-age trajectory defined by $SI_{adj}$ left (or less likely right) until this new trajectory joins up with the last endpoint (call it $H_{last}$) of the climate-adjusted height-age trajectory being constructed. The age at which the height trajectory based on $S_{adj}$ joins up with $H_{last}$ can be calculated by algebraically inverting the height-age model so that $t = f^{-1}(h, h_0, t_0)$. Now the new segment of the height-age trajectory can be projected 1 year from the height-age model starting at the point $h = H_{last}$ and $t = f^{-1}(h, h_{01}, t_{01})$ where $h_{01} = SI_{adj}$, and $t_{01} = 50$. Without this adjustment, the resulting height-age trajectory would have a saw-tooth profile.

After linking the height-age model to the transfer function, the system is used to select a seed source that can potentially mitigate the effects of climate change on height growth. An example will illustrate how this is done. An arbitrary cutblock east of Williams Lake, British Columbia, was selected for this illustration. This cutblock is in the Sub-Boreal Pine-Spruce moist cool subzone (denoted SBPSmk) (Steen and Coupé, 1997). A site index of 20 m was assumed for this site, which is the site index for zonal sites in the SBPSmk (Ministry of Forests, Lands and Natural Resource Operations, 2011). The latitude and longitude of the approximate centre of this cutblock are 52° 12′ 50.3″ and 121° 38′ 26.6″, respectively, and the elevation is ~1050 m. The site was assumed to be regenerated with a local provenance of lodgepole pine at the beginning of the growing season in 2000, and a rotation age of 80 years was assumed for the stand.

Several climate change scenarios are built into ClimateWNA (Wang *et al.*, 2012) and are available for the simulation. The CGCM3 A2 Run 4 projection was chosen based on the recommendation of Murdock and Spittlehouse (2011) because this scenario 'has been most widely used in BC and will thus be the most comparable to other work' (Murdock and Spittlehouse, 2011). Latitude, longitude, and elevation of the cutblock were used in ClimateWNA to estimate MCMT and MSP 1961–1990 normals. ClimateWNA was also used to predict MCMT and MSP for the selected scenario at years 2020, 2050, and 2080 from latitude, longitude, and elevation. The values of MCMT and MSP are (−9.2, 248), (−6.3, 297), (−4.6, 288) and (−3.2, 283) in 1990, 2020, 2050 and 2080, respectively. To obtain values for MCMT and MSP at intervening years, a cubic polynomial model was fit to these data with year (= year − 1990) as the independent variable.

A strategy to mitigate the effect of climate change on height growth by wisely selecting the source of the seed to be planted at this site can now be developed. The height-age model/transfer function system is used in a simulation approach to examine this proposition. Recalling that the example site has an MCMT and MSP of −9.2°C and 248 mm, respectively, simulations were done by varying MCMT_P and MSP_P from −10 to −1°C in steps of 0.1 and from 200 to 450 mm in steps of 5, respectively. These values were used as input to the height-age model/transfer function system, and a simulation was run for each starting value. The combination of MCMT_P and MSP_P that resulted in the greatest predicted height after 80 years was identified as the optimal climate for the seed provenance.

A 95 per cent confidence interval for the optimal simulation was obtained through bootstrap methods (Davison and Hinkley, 1997). Algorithm 6.1 (model-based resampling in linear regression) in Davison and Hinkley (1997) was used to obtain 1000 sets of parameter estimates for the transfer function (equation 2). Then, a grid of points spanning the range of the predictor variables was established (txMCMT: −20 to 20 in steps of 1; txMSP: −2 to 2 in steps of 0.1), and $Ht_p$ was predicted at each grid point using each of the 1000 set of parameter estimates. A 95 per cent confidence interval at each grid point was obtained by identifying the 2.5th and 97.5th percentile of the estimated $Ht_p$. To ease the use of the confidence interval, the transfer function was fit to these sets of 2.5th and 97.5th percentile points across the grid.

## Results

### *Developing the transfer function (Objective 1)*

Table 2 contains the results of the analysis of the AIC's from the fitting procedures. This table presents the logarithm of the likelihood (Log(L)), AIC, Δ AIC and Akaike weight (Anderson *et al.*, 2000). Δ AIC is the difference between the AIC of the model and the AIC of the model with the smallest AIC. The Akaike weights are the likelihood of a given model and can be interpreted as the approximate probability that the model is the best model from the set of models that were considered.

The results in Table 2 for the one-variable models indicate that one temperature-related variable (txMCMT) and two precipitation-related variables (txMAP and txMSP) were potential candidates for the transfer function. Variables txAHM, txSHM and txCMD, which incorporate both temperature and precipitation information, had substantially poorer fits than the best single-variable temperature and precipitation models. Therefore, these three variables were no longer considered to be potential variables for the transfer function.

The two-variable model fit with variables txMCMT and txMSP is the best transfer function from of the set of candidate models based on the AIC. Moreover, this model does not require a significant adjustment in the parameter estimates to ensure that $Ht_p$ is 1 for local populations. Therefore, this model was chosen as the transfer function. The results of the fitting of txMCMT and txMSP

**Table 2** Results of the predictor variable selection process

| Variable | log(L) | AIC | Δ AIC | Weight |
|---|---|---|---|---|
| Single-variable model – temperature variables | | | | |
| txMAT | 870 | −1730 | 773 | 0.000 |
| txMCMT | 1257 | −2503 | 0 | 1.000 |
| txMWMT | 656 | −1301 | 1202 | 0.000 |
| txTD | 1207 | −2404 | 99 | 0.000 |
| txDDLT0 | 824 | −1637 | 866 | 0.000 |
| txDDGT5 | 788 | −1566 | 937 | 0.000 |
| txDDLT18 | 787 | −1566 | 937 | 0.000 |
| txDDGT18 | 645 | −1280 | 1223 | 0.000 |
| txNFFD | 915 | −1820 | 683 | 0.000 |
| txFFP | 891 | −1722 | 781 | 0.000 |
| txbFFP | 729 | −1449 | 1054 | 0.000 |
| txeFFP | 1010 | −2010 | 493 | 0.000 |
| txEMT | 1056 | −2101 | 402 | 0.000 |
| tx$E_{ref}$ | 775 | −1540 | 963 | 0.000 |
| Single-variable models – precipitation variables | | | | |
| txMAP | 775 | −1539 | 0 | 0.622 |
| txMSP | 774 | −1538 | 1 | 0.378 |
| txPAS | 628 | −1246 | 293 | 0.000 |
| Single-variable models – temperature and precipitation variables | | | | |
| txAHM | 665 | −1322 | 100 | 0.000 |
| txSHM | 716 | −1422 | 0 | 0.500 |
| txCMD | 716 | −1422 | 0 | 0.500 |
| Two-variable models | | | | |
| txMCMT/txMAP | 1260 | −2525 | 171 | 0.000 |
| txMCMT/txMSP | 1356 | −2696 | 0 | 1.000 |

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to equation (2) are in Table 3, and the estimated correlations between the parameter estimates are in Table 4. The final fitted model is as follows:

$$HT_p = \frac{x^{2.893661} \cdot y}{\exp(x^{0.884667}) \cdot \exp(y^{3.947990})}, \quad (4)$$

with $x = 3.742500 + 0.142890$ *txMCMT* and $y = 0.736660 + 0.217510$ *txMSP*.

Parameter $d_0$ was set to 1 (i.e. taken out of the model) because it was not significantly different from 1 at $\alpha = 0.05$. Some of the parameter estimates are highly correlated. Figure 1 shows the relationship between $Ht_p$ and txMCMT (a) and txMSP (b). The data were binned when producing these graphs to better show these relationships since they were somewhat obscured by the variability in the data. The mean value and $\pm 2$ SD are plotted at the midpoints of the bins to show the trend and the variability. The mean of the residuals from the fitted model is $-0.0011841$, which is not significantly different from 0 at $\alpha = 0.05$. The Q − Q plot of the residuals (not shown) indicated a slight departure from normality, and a histogram (not shown) showed a slight skewness in the distribution of the residuals. However, the distribution of the residuals was unimodal, and the departure from normality was slight and was not considered to be serious enough to warrant further action. Plots of the residuals *vs* txMCMT, txMSP and the predicted values of $Ht_p$ did not show any evidence for rejecting the hypothesis that the residuals were homoscedastic (Figure 2). The fitted transfer function is shown in Figure 3.

For the fit analysis, the following bins were defined for variable txMCMT:

- txMCMT $\leq -10$
- $-10 <$ txMCMT $\leq -5$
- $-5 <$ txMCMT $\leq 0$
- $0 <$ txMCMT $\leq 5$
- $5 <$ txMCMT $\leq 10$
- txMCMT $> 10$

and the following bins were defined for variable txMSP:

- txMSP $\leq -1$
- $-1 <$ txMSP $\leq -0.5$
- $-0.5 <$ txMSP $\leq 0$
- $0 <$ txMSP $\leq 0.5$
- $0.5 <$ txMSP $\leq 1$
- txMSP $> 1$.

In all, 28 *t* tests were made (7 of the 36 bins were empty and 1 bin had only one observation and hence could not be tested). Table 5 shows the results of the multiple comparisons. The Holm multiple comparison procedure (Bretz *et al.*, 2011) was applied to get an experiment-wise significant level of $\alpha = 0.05$. The only bin for which the hypothesis that the average residual is 0 can be rejected is ($5 <$ txMCMT $\leq 10$, $0 <$ txMSP $\leq 0.5$) ($P = 0.00043$). I conclude that the model fits well across the observed range of both txMCMT and txMSP.

**Table 3** Results of the final fitting of the transfer function (equation 2)

| Parameter | | | | |
|---|---|---|---|---|
| Name | Estimate | SE | MSE | $R^2$ |
| $a_0$ | 3.742500 | 0.504119 | 0.0178 | 0.4947 |
| $a_1$ | 0.142890 | 0.030163 | – | – |
| $b_0$ | 2.893661 | 0.273922 | – | – |
| $b_1$ | 0.884667 | 0.083051 | – | – |
| $c_0$ | 0.736660 | 0.009128 | – | – |
| $c_1$ | 0.217510 | 0.022630 | – | – |
| $d_1$ | 3.947990 | 0.915769 | – | – |

Parameter $d_0$ is set to 1.
MSE, mean squared error for the model.

### *Mitigating the effects of climate change on height growth (Objective 2)*

The fitted models that predict MCMT and MSP are as follows:

$$\text{MCMT} = -9.2 + 0.12667 \cdot y - 0.00117 \cdot y^2 + 0.00000556 \cdot y^3,$$

$$\text{MSP} = 248 + 3.28889 \cdot y - 0.06667 \cdot y^2 + 0.00038272 \cdot y^3,$$

where *y* is the year in the simulation minus 1990. These models are specific to the chosen latitude, longitude and elevation and should not be used elsewhere, nor should they be extrapolated.

Figure 4 shows three height trajectories. Seed adapted to the local climate would have a height growth pattern under a no-climate change scenario as shown by the solid line. Seed

**Table 4** Estimated correlations between the parameter estimates from the fitting of the transfer function (equation 2)

| | | Parameter | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | $a_0$ | $a_1$ | $b_0$ | $b_1$ | $c_0$ | $c_1$ | $d_1$ |
| Parameter | $a_0$ | 1.000 | – | – | – | – | – | – |
| | $a_1$ | 0.993 | 1.000 | – | – | – | – | – |
| | $b_0$ | −0.920 | −0.954 | 1.000 | – | – | – | – |
| | $b_1$ | −0.984 | −0.994 | 0.975 | 1.000 | – | – | – |
| | $c_0$ | −0.197 | −0.105 | −0.139 | 0.050 | 1.000 | – | – |
| | $c_1$ | 0.286 | 0.180 | 0.087 | −0.124 | −0.825 | 1.000 | – |
| | $d_1$ | −0.250 | −0.148 | −0.145 | 0.079 | 0.849 | −0.941 | 1.000 |



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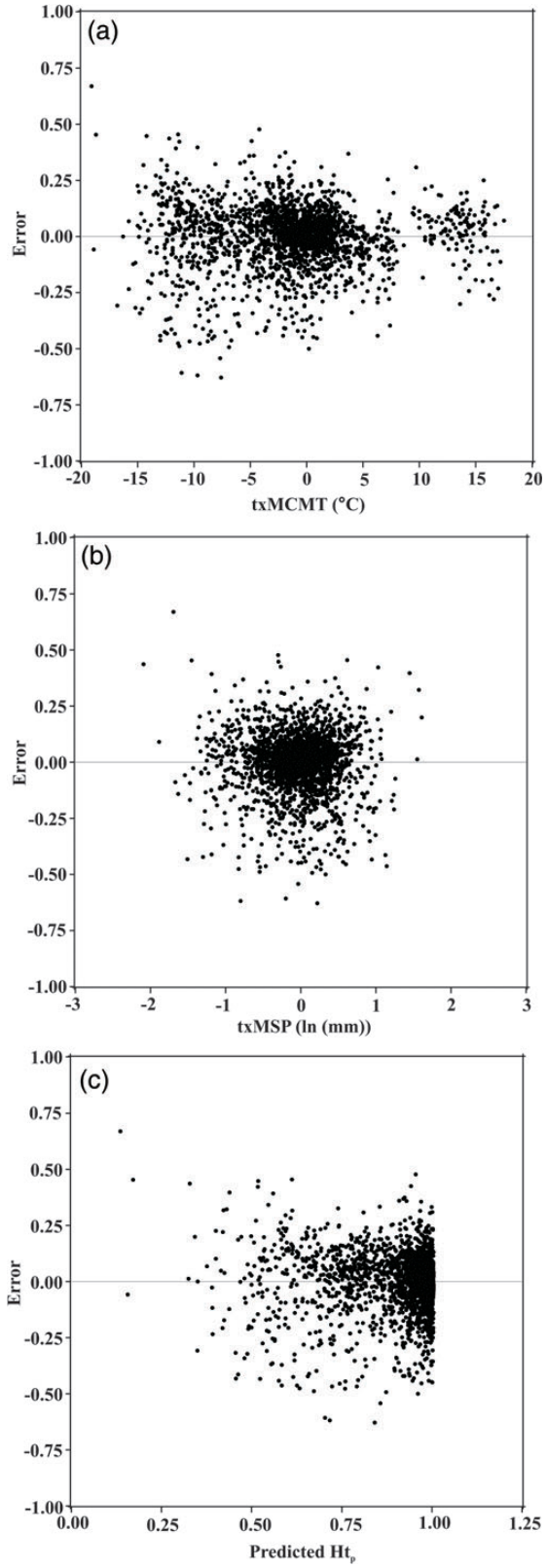


**Figure 2** Plot of the residuals (errors in predicted $Ht_p$ from the fitted model, equation (4)) *vs* txMCMT (a), txMSP (b) and predicted $Ht_p$ (c).

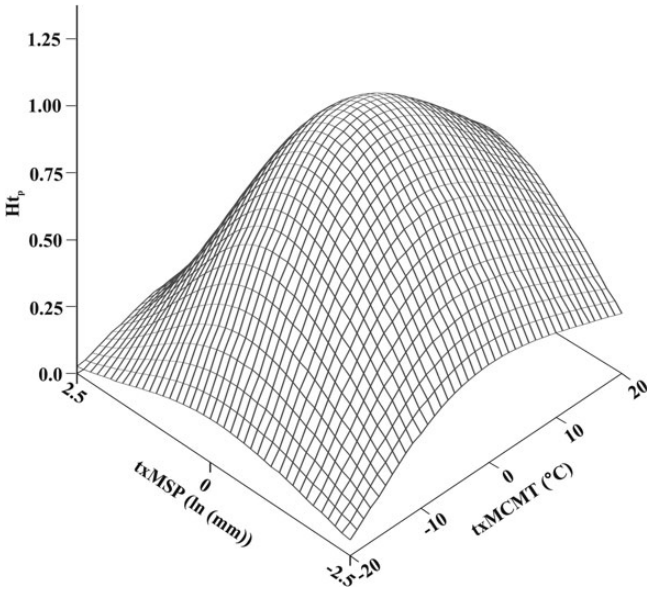


**Figure 3** The fitted transfer function (equation (4)).

adapted to the local climate under the CGCM3 A2 Run 4 scenario is indicated by the dash/dot line. The optimal seed source under the CGCM3 A2 Run 4 scenario is shown as the dashed line. Under the CGCM3 A2 Run 4 climate change scenario, the height of the trees from a local seed source at the end of an 80-year rotation would be 23.23 m and the height of the trees from the optimal seed source would be 24.00 m, a difference of 0.77 m. The height trajectories for the local population/no climate change scenario and the optimal population/CGCM3 A2 Run 4 scenario are nearly identical.

The functions for the upper and lower bounds of the confidence interval for the transfer function are as follows:

$$\text{Upper: } HT_p = \frac{x^{3.172812} \cdot y}{\exp(x^{0.962669}) \cdot \exp(y^{3.647405})},$$

where $x = 3.346843 + 0.115268$ *txMCMT* and $y = 0.736373 + 0.200150$ *txMSP*;

$$\text{Lower: } HT_p = \frac{x^{2.675551} \cdot y}{\exp(x^{0.820740}) \cdot \exp(y^{4.083578})},$$

where $x = 4.194259 + 0.174693$ *txMCMT* and $y = 0.734951 + 0.240851$ *txMSP*.

The $R^2$ statistics for the fitted upper and lower bounds of the 95 per cent confidence interval are 0.9984 and 0.9981, respectively. Therefore, these functions can be used in place of the bootstrapped values without loss of much accuracy. Recalling that the predicted height at the age of 80 for the optimal seed source is 24.00 m, its 95 per cent confidence interval is (23.96, 24.03). A different way to examine the confidence intervals is to consider which seed source would be optimal had the upper and lower confidence intervals for the transfer function been used in the simulations instead of the fitted transfer function. The optimal seed source for the lower confidence level would be MCMT = −4.9°C and MSP =

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**Table 5** Results of the model fit analysis. Multiple comparisons were done to test the hypothesis that the mean of the residuals in a bin was significantly different from 0. In each cell, the first line is the mean of the residuals, the second line is the number of observations, and the third line is the p-value

| | txMCMT | | | | | |
|---|---|---|---|---|---|---|
| | $\leq -10$ | $-10 \rightarrow -5$ | $-5 \rightarrow 0$ | $0 \rightarrow 5$ | $5 \rightarrow 10$ | $> 10$ |
| txMSP | | | | | | |
| $\leq -1$ | 0.06562 | −0.05933 | −0.08262 | N/A | N/A | N/A |
| | 37 | 31 | 3 | 0 | 0 | 0 |
| | 0.07603 | 0.03717 | 0.14662 | N/A | N/A | N/A |
| $-1 \rightarrow -0.5$ | 0.03005 | −0.02182 | −0.00346 | 0.01166 | −0.03379 | N/A |
| | 59 | 55 | 45 | 52 | 7 | 0 |
| | 0.23008 | 0.34976 | 0.86904 | 0.45964 | 0.08189 | N/A |
| $-0.5 \rightarrow 0$ | −0.00694 | −0.00456 | 0.00378 | −0.00964 | −0.03152 | 0.03238 |
| | 54 | 76 | 376 | 309 | 34 | 41 |
| | 0.79938 | 0.76687 | 0.54874 | 0.06242 | 0.05801 | 0.04098 |
| $0 \rightarrow 0.5$ | 0.01553 | −0.02083 | 0.00630 | −0.00249 | −0.07388 | 0.01994 |
| | 27 | 70 | 407 | 291 | 47 | 76 |
| | 0.64787 | 0.33076 | 0.27760 | 0.68754 | 0.00043 | 0.13141 |
| $0.5 \rightarrow 1$ | −0.02549 | −0.06440 | 0.03511 | 0.01885 | 0.01809 | 0.03174 |
| | 29 | 39 | 39 | 40 | 6 | 6 |
| | 0.52540 | 0.07147 | 0.12658 | 0.40349 | 0.81507 | 0.37681 |
| $> 1$ | −0.03683 | 0.08719 | N/A | 0.14277 | N/A | N/A |
| | 13 | 6 | 0 | 1 | 0 | 0 |
| | 0.54146 | 0.54334 | N/A | N/A | N/A | N/A |

320 mm resulting in a predicted height of 23.97 m at the age of 80. At the upper confidence level, the optimal seed source would be MCMT = −5.7°C and MSP = 340 mm and results in a predicted height of 24.04 m. Note that these confidence intervals do not consider error from the height-age model or from the climate change scenario, which could be substantial.

## Discussion

This research derives a transfer function that predicts relative height ($Ht_p$) at total age of 35 from the transfer distance of the mean coldest month temperature (°C, MCMT) and the mean summer precipitation (mm, MSP, where the summer months are May to September). Relative height is site height of a population divided by the site height of the local trees at the same age. The transfer distance is the difference between the MCMT or MSP of the planting site and the seed's provenance. The climate data are predicted with the ClimateWNA ver. 4.62 model (Wang *et al.*, 2012). The transfer function is therefore calibrated to these climate predictions. Using climate data from other sources, including measured data, may result in biased estimates of $Ht_p$ from the transfer function.

The transfer function is plotted in Figure 3. Maladaptation due to a changing climate reduces lodgepole pine height as the climate warms/cools and/or becomes wetter/drier. Although it is not obvious from Figure 3, the transfer function peaks near, but not at, txMCMT = 0 and txMSP = 0 (the local population). This suggests that local populations may not be optimally adapted to their site, i.e. moving seed to a slightly drier and/or warmer climate will result in marginally better height growth. This could be the result of past climate change and the presence of an adaptation lag, especially with a rapidly changing climate (Mátyás and Yeatman, 1992; Wu and Ying, 2004). However, this effect is very slight, as are the transfer distances resulting in the maximum relative height. The effect could also be an artefact of the definition of local population that was adopted for this study since true local populations were not planted at the test sites.

Winter temperature rather than growing season temperature was the best temperature predictor of height in the transfer function. Others have also found winter temperatures to be good predictors of height in transfer functions (Thomson and Parker, 2008; Thomson *et al.*, 2009). Some adapted traits such as time of bud set and bud break are associated with cold temperatures in the winter (Howe *et al.*, 2003), which may play a large role in determining height growth.

It was necessary to develop the strategy outlined earlier to find predictor variables that resulted in a good fitting model while avoiding severe multicollinearity. Plots of $Ht_p$ *vs* transfer distance showed at least a weak relationship for all climate variables, making all climate variables potential predictor variables. Therefore, a variable selection strategy was developed since all variables could not be included in the transfer function. The climate variables are derived directly or indirectly (i.e. from model predictions) from basic temperature and precipitation measurements (Wang *et al.*, 2012). Therefore, the predictor variables were expected to be correlated (Sen and Srivastava, 1990; Bonate, 1999), which can be a serious issue (Nigh *et al.*, 2004). For some climate variables, multicollinearity is obvious, for example, between NFFD, eFFP and bFFP (NFFD = eFFp − bFFP). This makes a two-variable transfer function,



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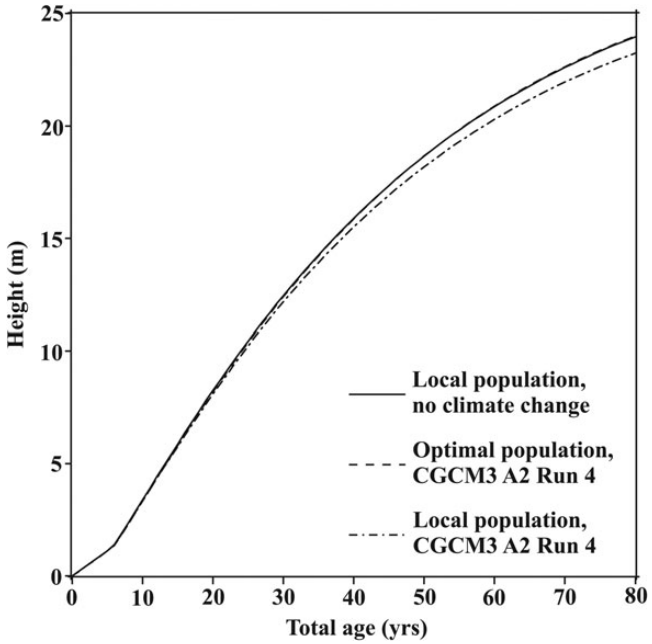


**Figure 4** Height trajectories of the local population under both a no climate change scenario and a CGCM3 A2 Run 4 climate change scenario, and the height trajectory of the optimal population under a CGCM3 A2 Run 4 climate change scenario.

one variable being temperature-driven and the other being precipitation-driven, attractive both biologically and statistically. The Pearson correlation coefficient for the two variables in the transfer function is 0.21, which is small enough to avoid multicollinearity issues.

The modifications made to the O'Neill and Nigh (2011) transfer function may seem minor but they do have fairly significant effects. To better understand these effects, the mean and variance of the errors (actual $Ht_p$ − predicted $Ht_p$) were calculated with the data used in this project. The predicted values were calculated from three models (designated a, b, and c for ease of reference): (a) model (3) above, (b) the adjusted transfer function developed by O'Neill and Nigh (2011) and (c) the O'Neill and Nigh (2011) model re-fitted using procedure MODEL with the RESTRICT statement to condition the model to return a value of $Ht_p = 1$ when txMAT = 0 (results of this analysis are not shown). This re-fitting eliminated the need for the *post hoc* adjustment to achieve the conditioning. The mean (standard deviation in parentheses) of the residuals for models a, b and c are −0.001184 (0.1334), −0.01169 (0.1445) and −0.02346 (0.1462), respectively. The mean of the errors for models b and c are significantly different from 0 at $\alpha = 0.05$, but not for model a. While the effect of each change in the O'Neill and Nigh (2011) model cannot be easily disentangled, it is clear that together these changes significantly improved the performance of the model. In particular, it appears that using txMCMT instead of txMAT and including txMSP in the transfer function eliminated a source of bias. This is also evident from the data analysis. Equation (4) fitted without the RESTRICT statement resulted in a model that predicted a value of $Ht_p$ very close to 1 when txMCMT = 0 and txMSP = 0.

### *Linking the transfer function to a height-age model*

Lodgepole pine site height at the end of an 80-year rotation is predicted to be 24.00 m provided seed from a site with MCMT = −5.3°C and MSP = 330 mm was planted at the example site. The height trajectory for this population is shown in Figure 4. The 95 per cent confidence interval for this trajectory is very narrow and hence for clarity is not plotted. The confidence interval is narrow because, over most of the simulation, txMCMT and txMSP are relatively close to 0, at which point the fitted response function and its confidence interval converge to 1. A scan of the test site and provenance data and available climate station data did not reveal any sites with values for MCMT and MSP close to the optimal values and that would also support lodgepole pine (one site with an MCMT and MSP close to the optimal value was a coastal site). It may be the case that no seed source exists with the optimal MCMT and MSP. However, if seeds from a provenance with the optimal MCMT and MSP are available, then it is possible to mitigate the effects of climate change and perhaps even see a slight gain in height over pre-climate change rotations. These results are contingent on the assumptions in the models and the simulations. In particular, if the climate does not change according to the predictions from the selected climate change scenario, then there is a risk of not achieving the expected height response from the selected seed source. In practice, the simulations should be run with a range of climate scenarios to at least partly address the risk associated with basing a seed selection decision on uncertain climate scenarios. Furthermore, the results for site height do not extrapolate to volume, both at the tree and stand level, because climate change also affects tree taper (Nigh and Smith, 2012) and will likely affect mortality, both of which will have an effect on tree and/or stand volume.

The height response surface for the simulations is shown in Figure 5. The local and optimal populations are indicated by dots on the response surface. This response surface is relatively flat, indicating that seed from many different provenances will give a close-to-optimal response. The reason for this is because the climate is constantly changing which results in no one population being optimal over the whole rotation. To show this, the line joining the local and optimal populations both on the response surface and on the base of the graph shows the path of the optimal population in 10-year increments as the climate changes. That is, the line joins the optimal population if that population had been chosen after 10, 20, 30, …, 70 years of growth. The optimal population changes the most in the first few years of the simulation, most likely because the climate model predicts a large change in MSP from 1990 to 2010, after which the MSP is relatively constant or slightly declining.

The dynamic nature of this system makes it critical that the height-age models, the site index and the transfer function are all based on compatible assumptions about the climate. Care must be taken in choosing a site index. The necessity for consistency can be seen by looking at a hypothetical situation. Suppose two site indexes are available for the simulations: one based on pre-1990 growth and the other based on pre-2010 growth. The second site index will be lower due to the effects of climate change on height growth and hence will give different results in the dynamic height growth system.

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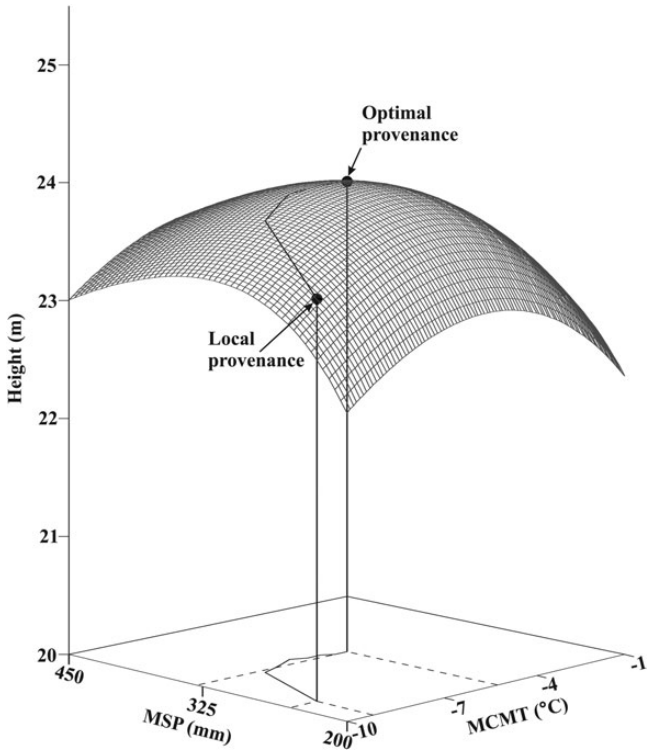


**Figure 5** Height response surface for a suite of provenances under assumed starting conditions and the CGCM3 A2 Run 4 climate change scenario. The two dots on the surface show the local provenance and optimal provenance at an 80-year rotation. The line joining the local and optimal provenances shows the optimal provenances as chosen after 10, 20, . . ., 70 years in the simulation.

The Batho and García (2013) lodgepole pine height-age model forms the benchmark for the system. Most of the data in the model development dataset are based on height growth prior to 1990. Although the climate in Canada changed prior to 1990, the change has been small enough (Zhang *et al.*, 2000) to have minimal effect on height growth as evaluated by the transfer function. Since future climate change is expected to be more rapid than past change, the benchmark period (pre-1990) is assumed to be relatively constant in terms of climate change. In the procedure linking the transfer function to the height-age model, the site index and the climate of the provenance used to calculate the transfer distance should also be based on the benchmark period (e.g. 1990). Using a later year may not capture the full effect of climate change on the transfer distance and may bias the site index relative to the benchmark period.

The transfer function was developed with data from trees growing during and after the benchmark period. However, any climate change that occurred during the time the sample trees were growing would cancel out when calculating transfer distance because both the local and the test populations experienced the same the climate change. Similarly, the relative height would also be unaffected by climate change because the sample trees and local trees would have experienced the same climate change. Furthermore, the amount of climate change outside of the benchmark period is small compared with the distance that the seed was moved.

A common way to estimate site index is from trees growing on a site. If a pre-1990 site index is not available, it may still be possible to estimate the site index from height and age data from site trees. This would be done by varying the pre-1990 site index in small increments and running the simulation system until the estimated height and age is the same as the observed height and age at the year these data were collected. Note that txMCMT and txMSP would be set to 0 for years prior to 1990 in the simulation.

## Conclusion

A transfer function was developed for lodgepole pine in BC that predicts relative height from the transfer distance for MCMT and MSP. The effect of climate change on lodgepole pine height growth can be assessed when the transfer function is linked to the height-age model for lodgepole pine. This dynamic system shows that height will decrease as climate change progresses. However, the negative effect on height growth may be partially or fully mitigated by using the system to assess the growth of non-local populations and planting the optimal population.

This research demonstrates the value of provenance trial data in applications other than those for which the data were intended. In particular, provenance data are especially well suited for developing transfer functions that can be integrated into height-growth systems to evaluate and mitigate the effects of climate change.

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## Conflict of interest statement

None declared.

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