Climate-Sensitive Growth and Yield Models and Their Application to Assisted Migration

Dawei Luo (dawei.luo@ubc.ca)
University of British Columbia
Gregory A. O'Neill
Kalamalka Forestry Centre, BC Ministry of Forests
Yuqing Yang
Alberta Environment and Parks
Esteban Galeano
Mississippi State University
Tongli Wang
University of British Columbia
Barb Thomas
University of Alberta

Research Article

Keywords: assisted migration, climate change, growth and yield, Universal Response Function, white spruce, lodgepole pine

Posted Date: November 21st, 2023

DOI: https://doi.org/10.21203/rs.3.rs-3627309/v1

Additional Declarations: No competing interests reported.

Abstract

Growth and yield (G&Y) of forest plantations can be significantly impacted by maladaptation resulting from climate change, and assisted migration has been proposed to mitigate these impacts by restoring populations to their historic climates. However, currently used genecology models for guiding assisted migration lack accounting for impacts of climate change on cumulative growth and requires assumption that responses of forest population to climate do not change with age. Using provenance trial data for interior lodgepole pine (*Pinus contorta* subsp. *latifolia* Douglas) and white spruce (*Picea glauca* (Moench) Voss) in western Canada, we integrated Universal Response Functions (URFs), representing the relationship of population performance with their provenance and site climates, into a G&Y model (Growth and Yield Projection System, GYPSY), to develop a climate-sensitive G&Y model for both species, and therefore to estimate climate change's impacts on G&Y of local and moving populations and guiding assisted migration. Our findings reveal that climate change is expected to have varying effects on forest productivity across the landscape, with partial areas projected to experience a slight increase in productivity by the 2050s, while rest areas projected to face a significant decline in productivity for both species. Adoption of assisted migration with optimal populations selected was projected to maintain and even improve its productivity at the provincial scale. The findings of this study highlight the importance of accounting for climate change in forest management practices and underscores the relevance and benefits of incorporating assisted migration approaches to mitigate the negative impacts of climate change.

1. Introduction

Forest populations normally display their highest fitness near their geographic or climatic origin. This phenomenon, known as local adaptation, has been extensively documented in widespread forest tree species (Leimu and Fischer 2008). Local adaptation is of great significance as it plays a fundamental role in our understanding of evolutionary, population, and conservation biology, and in formulating forest reforestation strategies intended to address climate change. Local adaptation also informs seed transfer practices in resource management and conservation of forest ecosystems to maintain population health, productivity, and resilience, especially in the face of rapidly changing environmental conditions (Ying and Yanchuk 2006).

The principle of "local is best" has long been upheld for seed transfer guidance in forest management. However, the escalating occurrence of maladaptation events in forest stands related to climate change has placed significant strain on geographically local populations (Hogg et al. 2017, Sperlich et al. 2020). Rapid climate change, relative to the long generation times and slow rate of migration and adaptation of temperate and boreal forests (Malcolm et al. 2002), significantly heightens the risk of maladaptation of naturally established forests and stands planted with local seed sources (Pedlar et al. 2012).

Growth and yield (G&Y) models are a widely used tool for estimating forest productivity and their predictions play a key role in supporting sustainable forest management decisions. Top height, which is defined as the average height of the dominant trees in the stand at a given age, and site index (SI), which normally refers to top height at age 50 (e.g total age 50), often play the role as stand productivity indicator (Skovsgaard and Vanclay 2008) and the main driver for many G&Y models (Mitchell 1975, Huang et al. 2009). Consequently, height-over-age curves are a fundamental component in these G&Y models. Although effects of climate change on growth and yield have been investigated by adjusting impacts to live crown (Yang et al. 2019), height increment, and diameter increment (Yang et al. 2019), the incorporation of climate effects into these G&Y models is primarily associated with naturally regenerated forests and plantations using local seed sources. In addition, it is also of great interest to explore the application of G&Y models in forest management strategies associated climate change risk, such as assisted migration, which is considered an efficient approach to addressing the risk of maladaptation of forest tree populations under climate change (Pedlar et al. 2012).

Local adaptation, which is typically assessed in provenance trials, is used to identify the need for assisted migration. Using data from provenance trials of interior lodgepole pine (*Pinus contorta* subsp. *latifolia* Douglas) across British Columbia and the southern Yukon, Canada, previous studies have investigated the feasibility of applying Universal Transfer Functions (UTFs) (O'Neill et al. 2008, Leites et al. 2012b) and a Universal Response Function (URF) (Wang et al. 2010) to predict growth responses of populations to a range of climate conditions, and therefore help provide guidance for assisted migration. In these UTF and URF models, test site climate is considered a reflection of the short-term environmental and genetic-by-environment interaction effect on the phenotype, while provenance climate is considered a reflection of the long-term genetic effect of natural selection on the phenotype (Leites et al. 2012b).

Although UTFs and URFs are mature tools and have been used widely, they still have several limitations in predicting the impact of climate change or seed transfer on forest productivity. First, UTF and URF functions use data from a single age, requiring the assumption that population responses to climate do not vary with tree age. Second, these functions are usually developed from relatively young (e.g., 5–20-year-old) provenance tests; therefore, the growth of the tested populations represents the impact of climate change on the population growth rate at their test climate and not the impact of climate change on the cumulative growth of local populations in operational plantations when the plantations reach the test climate or rotation age (O'Neill and Nigh 2011). These limitations could be addressed by G&Y models, in which cumulative growth over age is an essential component. For instance, Pooled Transfer Functions (PTFs), which relate standardized growth pooled across multiple sites and populations to climate transfer distance, were merged with a height over age curve for lodgepole pine (*Pinus contorta*) and used in productivity prediction and optimal seed source selection (O'Neill and Nigh 2011, Nigh 2014).

In Alberta, a fixed-zone, geography-based seed transfer system guides the collection, deployment and transfer of seeds collected from wild stands and seed orchards (AAF 2016). However, the province of Alberta is challenged by an ongoing reduction in its timber harvesting land base, combined with decreasing forest productivity driven primarily by climate change (Hogg et al. 2017). To further improve the practice of assisted migration, we propose exploring opportunities to combine G&Y models with genecology models (e.g. UTFs and URFs). In addition, we selected GYPSY, a widely used empirical G&Y model initiatively built for wild stand forest in Alberta, as the base model. In GYPSY, top height and SI are the main drivers and building top height curve is the first step for predicting stand volume yield. White spruce (*Picea glauca* (Moench) Voss) and lodgepole pine are two major commercial tree species in Alberta and have extensive field trials. Therefore, in this study, using Alberta as an example, we made use of height measurements from provenance trials for these two species to: (1) build a climate-sensitive G&Y model by integrating URFs into top height curves in GYPSY, which we then used to (2) investigate the effect of

climate change on productivity of geographically local populations of white spruce and lodgepole pine; and 3) provide guidance for assisted migration using a modified, climate sensitive G&Y model.

2. Materials and methods

2.1 Data Resources

2.1.1 Genetic trial data

The lodgepole pine trees used in this analysis were from 53 provenance field sites in Alberta, British Columbia, and Yukon containing 194 unique wild populations (Fig. 1, Table 1). The 'Illingworth Trial', established in 1974 with 140 range-wide lodgepole pine populations tested at 60 test sites (137 populations in 41 test sites were available for this analysis) (Ying et al. 1984). Within each site, 60 populations were tested in a randomized complete block design in which each population was tested in each of two blocks in a 3×3 tree square with 2.5 m spacing. The remaining 12 lodgepole pine sites in Alberta contained 13 to 39 populations with five-tree row plots in each of five to nine randomized complete blocks.

White spruce trees used in this analysis were from 17 sites installed in Alberta, with 176 unique wild populations tested (Fig. 1, Table 1). In 'Interior Spruce Climate Change/Genecology Trial', each test sites employed an incomplete block design with 119 populations grouped into one of 16 blocks, within which each population was tested in a four-tree row-plot. All remaining test sites contained 21 to 43 populations of spruce established in a randomized complete block design containing five to eight blocks, with each population represented in 5-9-tree-plots in each block.

Table 1
Summary of data sources, by species, trial series code, number (No.) of sites, region, number of populations (popns), establishment (Estab.) year and age of height measurements, used for analysis in this study.

Species	Trial series code	No. of sites	Region	No. of Popns	Estab. year	Age of height measurements
Lodgepole pine	G134	8	AB	39	1985–1990	10, 15, 20, 25
	Berland 5	1	AB	14	1980	4, 7, 10, 13, 16
	Marlboro 7	1	AB	16	1979	4, 7, 10, 13, 16
	Embarrass	1	AB	13	1980	4, 7, 10, 13, 16
	Illingworth	41	WNA	137	1974	32
White spruce	G103	9	AB	43	1981–1983	12, 15, 18, 21, 24, 27, 32
	G276	3	AB	21	1993&1994	10, 15, 18, 25
	G277	1	AB	39	1993	7, 10, 15, 18
	G366	1	AB	34	2005	3, 7, 11
	EP 670.71.12	2	AB	119	2005	3, 6, 10, 16
EP 670.71.12: Interior Spruce Climate Change/Genecology Trial;						
AB: Alberta;						
WNA: Western North America						

2.1.2 Climate data

ClimateBC V7.10 (https://climatebc.ca/), ClimateAB v3.21 (https://sites.ualberta.ca/~ahamann/data/climateab.html) and ClimateNA V7.10 (http://climatena.ca/) were used to generate values of 24 annual climate variables for the provenances and test sites located within British Columbia, Alberta, and other areas in western North America, respectively (Wang et al. 2012, Wang et al. 2016), as shown in Table A1 in Appendix. Climate variables without direct biological interpretation were removed (degree-days below or above 18℃). To reduce the number of independent climate variables to a more workable number, highly correlated climate variable pairs ($r > 0.9$) were identified for provenance and site respectively, and one variable from each pair was excluded, leaving 17 out of 24 site climate variables and 14 out of 24 provenance climate variables for lodgepole pine, and 11 out of 24 site and provenance climate variables for spruce.

2.1.3 Geographic data

Digital shape files for the natural range of white spruce and lodgepole pine (https://web.archive.org/web/20170127093428/ and https://gec.cr.usgs.gov/data/little/) were used to illustrate provenance locations. We used the Derived Ecological Phase (DEP, v2.0) digital map from Alberta government open data Derived Ecosite Phase v2.0 - Open Government (alberta.ca) (accessed in June 2023) and built a provincial site index layer using the estimated ecosite-based site index from Alberta ecosite guides (Beckingham and Archibald, 1996b, a). In this study, given the purpose of guiding assisted migration as a part of reforestation, we used site index estimates for post-harvest stands and imposed them onto the DEP maps (Fig. A1 in Appendix).

2.2 Data analysis

Competing vegetation was periodically removed at all sites so that growth of the subject trees was primarily a reflection of site climate, edaphic factors, and genetics. Consequently, we assume that each population was able to express its growth potential at each site. Therefore, we used population mean height at each site as the top height after excluding unhealthy trees marked as dead, crooked, browsed by animals, or showing signs of pest infection. All analyses were done in software *R* 4.2.3 (R Core Team 2018).

2.2.1 Universal Response Function (URF)

We first estimated population top height at each age and at each site using a linear mixed effect model, with the population as a fixed effect and the block as a random effect. Given the difficulty of addressing different measurement ages across trials, we then converted the height of each population tested at each site to the common ages of 16 for white spruce and 32 for lodgepole pine using the top height equations from GYPSY (Eqs. 1 and 2) (Huang et al. 2009). The height measurement from the age nearest the common age was identified and converted to height at the common age for those sites where height at the common age was not recorded. The original height was retained for sites with measurements taken at the common age.

$$HT_{i.Sw} = SI * (1 + \exp\left(b_1 + b_2\sqrt{\ln\left(1+50^2\right)} + b_3[\ln(SI)]^2 + b_4\sqrt{50}\right))/(1 + \exp\left(b_1 + b_2\sqrt{\ln\left(1+totage_i^2\right)} + b_3[\ln(SI)]^2 + b_4\sqrt{50}\right))$$ Eq. (1)

$$HT_{i.Pl} = SI * (1 + \exp\left(f_1 + f_2\sqrt{\ln(1+50)} + f_3(\ln(SI)) + f_4\sqrt{50}\right))/(1 + \exp\left(f_1 + f_2\sqrt{\ln(1+totage_i)} + f_3(\ln(SI)) + f_4\sqrt{50}\right))$$ Eq. (2)

Where HT_i is the top height (m) at a given total age i for white spruce ($HT_{i.Sw}$) and lodgepole pine ($HT_{i.Pl}$); SI is totage-based site index (top height at 50 years total age) assuming no climate change; totage = total age from the point of germination; $b_1, b_2, b_3, b_4, f_1, f_2, f_3, f_4$ = constants with no biological interpretation.

Then for each species, we built URFs (Eq. 3) to predict population top heights at the common age using estimated population top height (from Eqs. 1 and 2) and various combinations of retained site and provenance climate (section 2.1.2) as independent variables. Among the retained site and provenance climate variables, we systematically examined combinations ranging from one provenance and one site climate variable to three provenance and three site climate variables. This analysis resulted in the identification of 390,677 candidate URFs for lodgepole pine and 53,361 candidate URFs for white spruce distributed across nine categories of climate variable combinations (Table 2). We selected the URF that had the largest R^2 within each category of climate variable combination. A 10-fold cross-validation was applied to the retained candidate URFs for each category of climate variable combination using prediction efficiency (EF, Eq. 4) and residual means square error of prediction (RMSEP, Eq. 5) as the validation metrics. In the end, the candidate URF with the lowest RMSEP was selected as the final model for each species.

$$HT_{jt} = exp\left(a_1 * x_j + a_2 * x_t + a_3 * x_j^2 + a_4 * x_t^2 + a_5 * x_j * x_t\right) + \epsilon_{jt}$$ Eq. (3)

$$EF = 1 - [\sum(Y_k - \widehat{Y_k})^2 / \sum(Y_k - \bar{Y})^2]$$ Eq. (4)

$$RMSEP = \sqrt{\sum_{k=1}^{n}(Y_k - \widehat{Y_k})^2 / n}$$ Eq. (5)

where HT_{jt} is the estimated mean height for the jth population estimated at test site t; x_j is the provenance climate variable for the jth population (averaged during 1961–1990 normal period); x_t is the climate variable for tth test site (averaged from planting year until measurement age); $a_1 - a_5$ are coefficients to be determined; n is the number of observed values; Y_k is the kth observed value; $\widehat{Y_k}$ is the kth predicted value; $\bar{Y}$ is the average of the observed values.

2.2.2 Merging URF into top height curves

We merged the URFs into top height curves in GYPSY using the revised procedure of merging PTF into height curves from O'Neill and Nigh (2011) and Nigh (2014). In the first step, we estimated top height at age 32 for lodgepole pine and at age 16 for white spruce using URFs (Eq. 3). The plantation climate in the first step was averaged from planting year to each age in final climate-sensitive top height curves (e.g., age i, i ranges from 1 to 80, corresponding annual plantation climate was year 1 to 80). Climate values during the 1961–1990 normal period were used to represent the provenance climate, given that this normal period is commonly used as a reference for estimating climate change (Wang et al. 2012, Wang et al. 2016). In the second step, top height was substituted into top height equations (Eqs. 1–2) to solve for the corresponding SI, as GYPSY requires SI to be determined before generating top height curves. In the third step, the solved SI was used to generate a set of top height curves for the given provenance-plantation climate combination (e.g., a curve for each year's plantation climate from establishment to rotation). The top height curves generated in the third step represent 80 different static climates. Therefore, in the last (fourth) step, we built a climate-sensitive top height curve using top height values extracted from the set of climate non-sensitive top height curves generated in the third step. Top height value at age one was retained, while for each climate non-sensitive curve built on plantation climate at age i (i > 1), annual height increment at age i was extracted and added to top height values calculated at age i-1. These extracted single-age height values were assembled as the final climate-sensitive top height curve. The future climate change scenario is described below in section 2.2.3. The flow chart is shown in Fig. A2 in Appendix, where four climate non-sensitive top height curves instead of 80 are used for a simplified visualization.

A 10-fold validation was applied to the final climate-sensitive G&Y model (top height-age curves) using EF (Eq. 4) and RMSEP (Eq. 5) as validation metrics, and top height values from other measurement ages, with corresponding life span averaged climate at each age, were taken as the validation sets. In addition, using the SI layer generated from DEP as the validation set, we also calculated a pixel-wise correlation coefficient for the spatial validation using averaged climate in the normal period 1961–1990 as both provenance and site climate.

2.2.3 Application of the climate-sensitive G&Y model

In the subsequent analysis, future climate values including annual and normal period means were obtained from an ensemble climate projection, which is an averaged prediction from 13 General Circulation Models (GCMs). Shared Socioeconomic Pathway (SSP) 245 was selected as the climate change scenario. SSP245 indicates a climate change scenario described in CMIP 6 (Coupled Model Intercomparison Project Phase 6), in which climate protection measures are being taken, with an additional radiative forcing of 4.5 W/m² by the year 2100 (Eyring et al. 2016).

Predicting climate change impacts on local populations

The provincial map was generated using a grid set covering Alberta with a resolution of 0.5º. To simplify the visualization, we selected 2055 - representing the climate normal for 2041–2070 - as the year when total height reached age-50, and the corresponding 30-year climate average was used as site climate under which trees will be growing. The climate average in normal period 1961–1990 was used as the provenance climate.

The SI maps demonstrate the effects of climate change at the time point of age-50. To demonstrate the cumulative effects of climate change on yield curves, we selected one test site and built top height curves for each species. Large inter-annual variation in climate values resulted in fluctuations in top height curves; therefore, to capture the long-term trend of climate change and to produce smooth top height curves, a log regression was fitted to the life span averaged climate for each age. The estimated climate values were then used in the climate-sensitive G&Y models to produce top-height curves.

Identifying effects of selecting optimal populations

Using the climate-sensitive G&Y model, we identified the provenance climate in normal period 1961–1990 of the population expected to generate the tallest trees at age-50 (year 2055) at provincial scale for the purpose of assisted migration. To achieve this goal, for each plantation location from the provincial map, we scanned the natural range within the province using a grid with an adjustable resolution (e.g. 0.5º or 1,000 random points, while only 100 random points were selected for calculation efficiency) and applied the climate-sensitive G&Y models to the 100 grid points to identify the climate of the population expected to yield the greatest growth, with corresponding 30-year climate average was used as provenance and site climate.

A visual inspection revealed that the mountainous regions of southwestern Alberta were expected to undergo significant changes in precipitation due to climate change (Fig. A3 in Appendix), surpassing the climatic conditions in provenance trials. These regions closely matched locations where the SI exceeded 25m when considering optimal populations under the climate change scenario (Figs. 4–5). To minimize the risk associated with extrapolation, we decided to exclude sites with an SI greater than 25m.

The procedure of optimal population selection was also applied to the above selected two test sites, with corresponding annual climate average used.

3. Results

3.1 Universal response function (URF)

The final URF model for lodgepole pine (R^2 = 0.527) contained three provenance climate variables (MCMT.p, TD.p and CMD.p) and three site climate variables (MCMT.s, DD5.s, and PAS.s), while the final URF for white spruce (R^2 = 0.680) contained three provenance climate variables (AHM.p; NFFD.p, and Eref.p) and three site climate variables (MAP.s, SHM.s, and FFP.s) (Table 2, Table A2 in Appendix). In the 10-fold validation, the selected URF for lodgepole pine had a RMSEP equal to 1.88m and EF equal to 0.637, while the selected URF for white spruce had a RMSEP equal to 0.75m and EF equal to 0.673 (Fig. 2).

Table 2

Results of R^2, AIC, number (No.) of test sites and population (popn) residual mean square error of predictions (RMSEP), and prediction efficiency (EF) for fitting Universal Response Functions (URFs) with various combinations of site and provenance climate variables to population top height of lodgepole pine at age 32 and white spruce at age 16; results of spatial validation (pixel-wise spatial correlation) for climate sensitive growth and yield (G&Y) models for lodgepole pine and white spruce.

Species	Climate variable	R^2	AIC	No. site	No. popn	RMSEP (m, 10 fold)	EF (10 fold)	Pixel-wise spatial correlation
Lodgepole pine	TD.p; MAT.s	0.395	13474.6	53	194	2.29	0.463	0.616
	TD.p; MCMT.s; DD5.s	0.453	13208.5	53	194	2.15	0.527	0.688
	TD.p; TD.s; eFFP.s; EXT.s	0.478	13083.1	53	194	2.06	0.564	0.496
	MAT.p; TD.p; MAT.s	0.419	13369.9	53	194	2.21	0.498	0.658
	TD.p; CMD.p; MCMT.p; DD5.s	0.485	13050.3	53	194	2.06	0.567	0.654
	TD.p; Eref.p; MCMT.s; eFFP.s; EXT.s	0.524	12855.3	53	194	1.98	0.598	0.560
	MAT.p; TD.p; CMD.p; MAT.s	0.457	13194.2	53	194	2.17	0.516	0.662
	MAT.p; TD.p; CMD.p; MCMT.s; DD5.s	0.503	12962.3	53	194	1.99	0.596	0.668
	MAT.p; TD.p; CMD.p; MCMT.s; DD5.s; PAS.s	**0.527**	**12833.0**	**53**	**194**	**1.88**	**0.637**	**0.680**
White spruce	MCMT.p; MAP.s	0.603	1565.8	17	176	0.96	0.447	0.188
	MCMT.p; MAP.s; FFP.s	0.634	1520.8	17	176	0.91	0.502	0.220
	MAT.p; MAP.s; SHM.s; FFP.s	0.593	1593.1	17	176	0.87	0.554	0.208
	MCMT.p; AHM.p; MAP.s	0.622	1539.6	17	176	0.95	0.467	0.241
	MCMT.p; AHM.p; MAP.s; FFP.s	0.654	1490.5	17	176	0.90	0.519	0.235
	AHM.p; Eref.p; MAP.s; SHM.s; FFP.s	0.687	1438.1	17	176	0.75	0.663	0.126
	MCMT.p; Eref.p; RH.p;MAP.s	0.649	1500.0	17	176	0.91	0.511	0.276
	MCMT.p; MSP.p; SHM.p; MAP.s; FFP.s	0.672	1462.5	17	176	0.88	0.542	0.227
	AHM.p; NFFD.p; Eref.p; MAP.s; SHM.s; FFP.s	**0.700**	**1416.1**	**17**	**176**	**0.75**	**0.673**	**0.100**

Note: p and s refer to provenance and site; full names of each climate variables are listed in Table 2; bold font indicates the selected URFs.

3.2 Climate-sensitive G&Y models

Validation of climate-sensitive G&Y model

During the 10-fold cross-validation process, in which height measurements from other ages were used as validation sets, the climate-sensitive G&Y models yielded high EF values. Specifically, lodgepole pine achieved an EF value of 0.831, while white spruce achieved an EF value of 0.735 (Fig. 2). In terms of spatial validation for climate-sensitive G&Y models, where the SI values derived from the DEP were used as validation sets, the pixel-wise spatial correlation was 0.680 for lodgepole pine, while only 0.100 for white spruce (Table 2).

Predicting climate change impacts on local populations

Application of the climate-sensitive G&Y model at the provincial scale revealed strong impacts of climate change on forest productivity. The anticipated climate change (Fig.S3 in Supporting Information) was projected to have negative impacts on SI of lodgepole pine in central Alberta, while a positive impact on SI was projected in mountainous areas located in the southwest and part of northern Alberta (Fig. 3). In the case of white spruce, a slight increase in SI was projected for the mountain area in southwestern Alberta and part of northern Alberta, while a decrease was projected in most central areas. The case study conducted on two selected test sites revealed that the anticipated climate change may have mixed effects on forest productivity. Specifically, in site G346a, the changing climate was projected to improve height growth. However, in site G354a, the changing climate was anticipated to negatively impact top height yield (Fig. 5).

Identifying effects of selecting optimal populations

Regardless of species, the selection of optimal populations was projected to maintain and even enhance the SI in most areas (Fig. 4). In the test sites G346a, selecting the optimal population from within the natural range in Alberta had the potential to further enhance the SI at this site. In site G354a, the selected optimal population could mitigate the projected negative impacts (Fig. 5).

4. Discussion

4.1 Model performance

Using provenance URFs developed from comprehensive sets of provenance data, we were able to modify G&Y model to simulate the impacts of climate change on forest productivity. With the objective of being able to predict climate change impacts, performance of the final climate sensitive G&Y models in this study were assessed through a 10-fold cross validation and a spatial validation. The 10-fold cross-validation results indicated that the climate sensitive G&Y models had good predictive accuracy and predictive power, with an EF equal to 0.831 for lodgepole pine and 0.735 for white spruce. In the spatial validation, we obtained a pixel-wise spatial correlation of 0.680 for lodgepole pine, while a considerably lower value of 0.100 was obtained for white spruce. It is important to note that the low spatial validation values for white spruce may, in part, be attributed to SI layer derived from ecosite, which relied solely on mean SI values. The absence of precise SI productivity information at the provincial scale for spatial validation could potentially compromise the validity of the spatial validation. Therefore, the final model selection was primarily relied on the 10-fold cross validation.

Both temperature and precipitation-related variables played important roles in the final climate sensitive G&Y models. Temperature-related variables are normally the most important climate factors influencing geographic patterns of provenance performance for tree species (Leites et al. 2012a, Leites et al. 2012b). Conifer species exhibit different growth rates, phenology events, and metabolic activity that are mainly associated with temperature (Guo et al. 2020). The low temperature in winter and early spring are generally considered as an important factor limiting survival and growth for conifers due to its potential frost damage (Pearce 2001). Freezing temperatures can also lead to dehydration due to extracellular freezing of water (Jeffree et al. 1987). In contrast, although increasing temperature may result in a longer growing season and higher carbon sequestration (Keenan et al. 2014), the potential damage caused by overly high temperature, accompanied by relatively limited water availability, may reduce photosynthesis, and therefore inhibit growth and even lead to increased mortality (McDowell et al. 2016, Hogg et al. 2017). Under global warming, the challenge of rising temperature appears to outweigh its benefit, given that most areas in Alberta are predicted to have limited change in precipitation, as suggested by our results. Although we demonstrated our analysis using SSP245, the final model could be easily applied to different climate change scenarios to estimate changes in the productivity and identify the optimal populations for assisted migration and reforestation.

Integrating URFs into top height curves offers a comprehensive strategy that harnesses the strengths of both genecology models and G&Y models. This integration presents a promising opportunity to enhance existing climate-sensitive methodologies for the selection of optimal populations for plantation sites. Prior research merging climate variables into G&Y (e.g., height increment curves, diameter increment curves) used data from permanent sample plots (PSPs) (Yang et al. 2019), which often overlooked population effects and their interaction with the environment. In contrast, merging PTF into G&Y curves (O'Neill and Nigh 2011, Nigh 2014) using data from provenance trials integrates population's variation to climate, thereby furnishing valuable insights for the selection of suitable seed sources. It is worth noting that by standardizing height at each site, differences in productivity among sites were removed in PTFs. Without a site climate variable as input, variation in site productivity cannot be determined. To address this, supplementary information such as the estimated SI across different locations becomes imperative before implementing a merged G&Y model with PTFs. Consequently, our study modified top height curves in GYPSY using URFs, which included genetic effects of populations, climate effects, and their interaction. While both URFs and UTFs perform similarly (Zhao and Wang 2023), incorporation of provenance, site climate, and their interactions in URFs, provides a more intuitive approach for identifying the optimal population or plantation site compared to UTFs (O'Neill et al. 2008). This updated climate-sensitive methodology to identify the climate of the most productive seed source could obviate the assumption of a quarter of rotation age to match historic climate of populations and future climate of plantations (O'Neill et al. 2008, Ukrainetz et al. 2011, O'Neill et al. 2017).

4.2 The effects of climate change on forest productivity

In previous studies that examined the growth responses of different populations to different climate conditions, the variation of forest productivity has shown a strong geographic pattern, which was closely associated with latitude. For instance, in British Columbia, significant reductions in stand yield for lodgepole pine were predicted in most areas based on provenance trial data, except for an increase in stand yield observed in northern regions (O'Neill et al. 2008). In Alberta, by using stem analysis on trees from natural stands, a decreasing trend of aboveground biomass for white spruce was reported throughout most areas of the province, except in northern areas where an increase in aboveground biomass was observed (Hogg et al. 2017). Our study indicated similar geographic patterns in which elevation played a more important role. Decreased productivity was predicted in central Alberta, while increased productivity was projected in the southwestern mountain areas and partial northern areas. In Alberta, the southern mountains areas are colder than the central regions and are therefore more likely to be the leading edge for species migration under climate change.

4.3 Implications for forest management

Alberta's seed transfer system constrains seed transfer to within the fixed seed zone (wild stand seed sources) or breeding region (orchard seed) from which a seed source originates (AAF 2016). The findings of this study, however, underscore the critical importance of integrating climate change considerations into forest management practices. Populations that are currently well adapted to prevailing climates may face challenges in the future due to changing climatic conditions. Therefore, alternative seed transfer systems which are flexible enough in responding to climate change are urgently needed. Combining URFs with GYPSY enables the interaction between genotype and environment to be further delineated and explored in the long-term. These long-term simulation results may provide a valuable insight into forest management strategies and policy. Considering these results, program managers responsible for reforestation initiatives may consider reassessing and realigning their objectives to account for potential maladaptation and explore opportunities for assisted migration. Although we used Alberta as an example to demonstrate the application of the climate sensitive G&Y, it's important to note that this approach is not restricted to a particular geographic area. The adaptability of climate-sensitive G&Y models extends to various tree species by incorporating corresponding G&Y models relevant to distinct regions and corresponding provenance trials.

The optimal population with the maximum productivity was often projected not to be near their geographic origin under climate change, as indicated by the difference between optimal and local populations. Previous studies have reported that ecological optimum (competitively exclusive) of a population is often not equal to its physiological optimum (competitively excluded) (Leites et al. 2012a, Rehfeldt et al. 2018). This finding of non-local optimality also supports the idea of 'gene swamping' (Aitken et al. 2008), in which there exists a net flow of pollen from the center of a species' distribution where populations are dense (large numbers of trees/ha) toward peripheral populations where densities are lower. This net flow of pollen can result in an evolutionary lag among peripheral populations, such that their adaptation is more like those from the central populations than one would expect from their climate (Aitken et al. 2008). This difference between 'ecological optimum' and 'physiological optimum' combined with expected exacerbation of the evolutionary lag under climate change, further indicates the necessity of matching populations with the climate to which they are best adapted to maintain forest productivity.

In our study, we specifically focused on predicting productivity within the fundamental niche rather than the realized niche. The fundamental niche represents the full range of environmental conditions that populations of a species are expected to be adapted to, excluding factors such as inter-species competition, physical barriers, historical events, and human impact (Aitken et al. 2008, Zhao and Wang 2023). By considering the fundamental niche, we aimed to capture the potential productivity of populations under optimal conditions, unconstrained by the limitations imposed by competition and other external factors. One of the key applications related to the predictions within the fundamental niche is assisted migration. Assisted migration involves moving populations to new locations outside their historical range to address rapid environmental changes (Pedlar et al. 2012). By relocating populations to ensure that anticipated climate conditions are matched with the optimal populations, assisted migration seeks to maximize site productivity in forest ecosystems. Therefore, the prediction of productivity within the fundamental niche aligns well with the objectives and principles of assisted migration.

5. Conclusion

This study explored a new method for estimating the effect of climate change on G&Y and an alternative approach for guiding assisted migration. Taking advantage of existing provenance trials, and the model GYPSY, we built URFs and climate sensitive G&Y models. Throughout the validation process, we found that the final models had good predictive efficiency. Our findings indicate that climate change is likely to have diverse effects on growth and yield of both species studied. The feasibility and effectiveness of implementing assisted migration as a climate change adaptation strategy are also highlighted. By accounting more accurately for climate change impacts and employing proactive measures such as assisted migration, forest managers can help mitigate at least some of the impacts of climate change on forest productivity.

Declarations

Acknowledgements

This analysis includes data sharing from the provincial ministry of Forestry and Parks, the forest industry in Alberta, the Government of Alberta, and the Government of British Columbia (BC). Funding for this manuscript has been provided through the Industrial Research Chair in Tree Improvement held by B.R. Thomas (NSERC: IRC461040-13) supported by the Natural Sciences and Engineering Research Council (NSERC), Alberta-Pacific Forest Industries Inc., ANC Timber Ltd., West Fraser Mills Ltd. (including Hinton Wood Products, Blue Ridge Lumber, Sundre Forest Products, Alberta Plywood), Canfor Ltd. (Grande Prairie and Whitecourt divisions), Weyerhaeuser Company Ltd., (Grande Prairie and Pembina Timberlands), the Huallen Seed Orchard Company and the Government of Alberta.

Declaration

Funding

Funding for this manuscript has been provided through the Industrial Research Chair in Tree Improvement held by B.R. Thomas (NSERC: IRC461040-13) supported by the Natural Sciences and Engineering Research Council (NSERC), Alberta-Pacific Forest Industries Inc., ANC Timber Ltd., West Fraser Mills Ltd. (including Hinton Wood Products, Blue Ridge Lumber, Sundre Forest Products, Alberta Plywood), Canfor Ltd. (Grande Prairie and Whitecourt divisions), Weyerhaeuser Company Ltd., (Grande Prairie and Pembina Timberlands), the Huallen Seed Orchard Company and the Government of Alberta.

Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Availability of data and material

Data supporting this research was made available from forest industry companies and the government of Alberta, the government of British Columbia, data available upon request.

Code availability

Code available upon request to corresponding author.

Author Contribution

Dawei Luo, Gregory A. O'Neill and Barb R. Thomas conceived the ideas and designed methodology; Dawei Luo drafted the article and conducted most data analysis; Yuqing Yang aided the data analysis; Barb R. Thomas supervised the project and provided funding; O'Neill and Barb R. Thomas acquired the data; all authors contributed critically to the drafts and gave final approval for publication.

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Figures

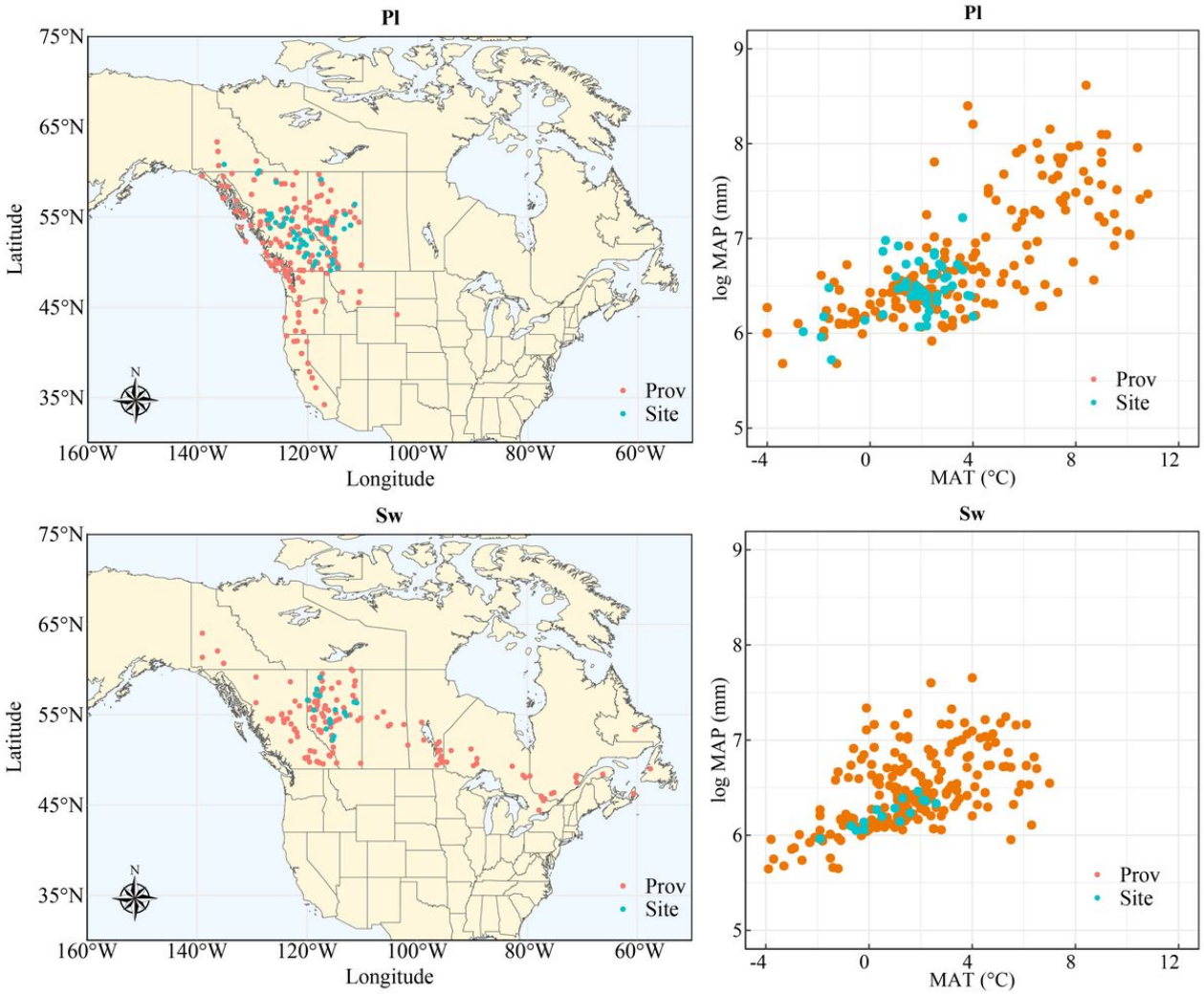

Figure 1

Locations of the test site (Site) and provenance (Prov) of the populations of white spruce (Sw) and lodgepole pine (Pl) trials used in this study. Mean annual temperature (MAT) and log mean annual precipitation (MAP) of provenances and test sites.

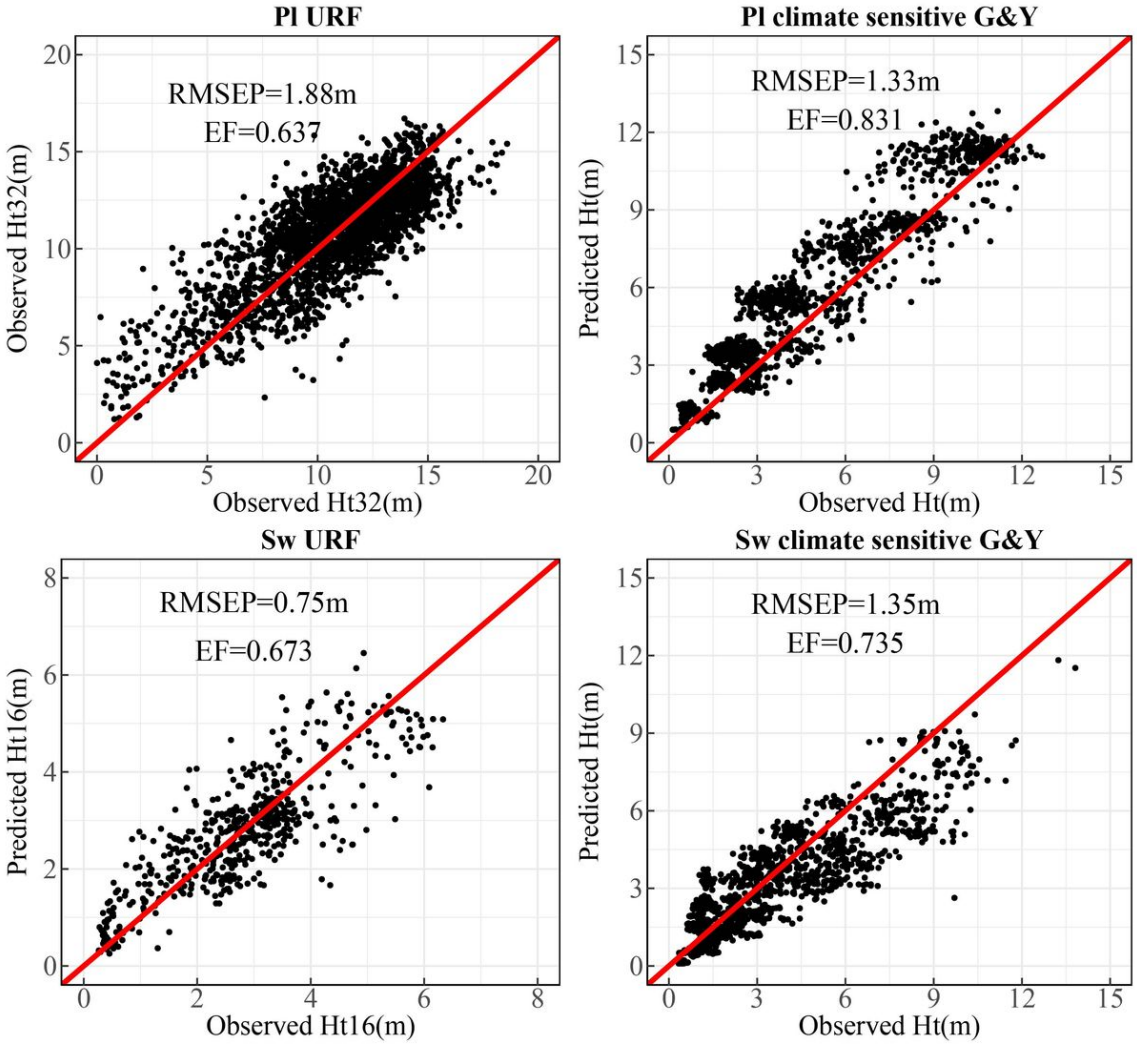

Figure 2

Results from the 10-fold cross validation for the selected Universal Response Function (URF) for height estimated at age-32 (Ht32) for lodgepole pine (Pl, top left), and height estimated at age-16 (Ht16) for white spruce (Sw, bottom left); results from the 10-fold cross validation for the selected climate sensitive growth and yield (G&Y) model for Pl (top right) and Pl (bottom right); RMSEP is residual means square error of prediction; EF is prediction efficiency.

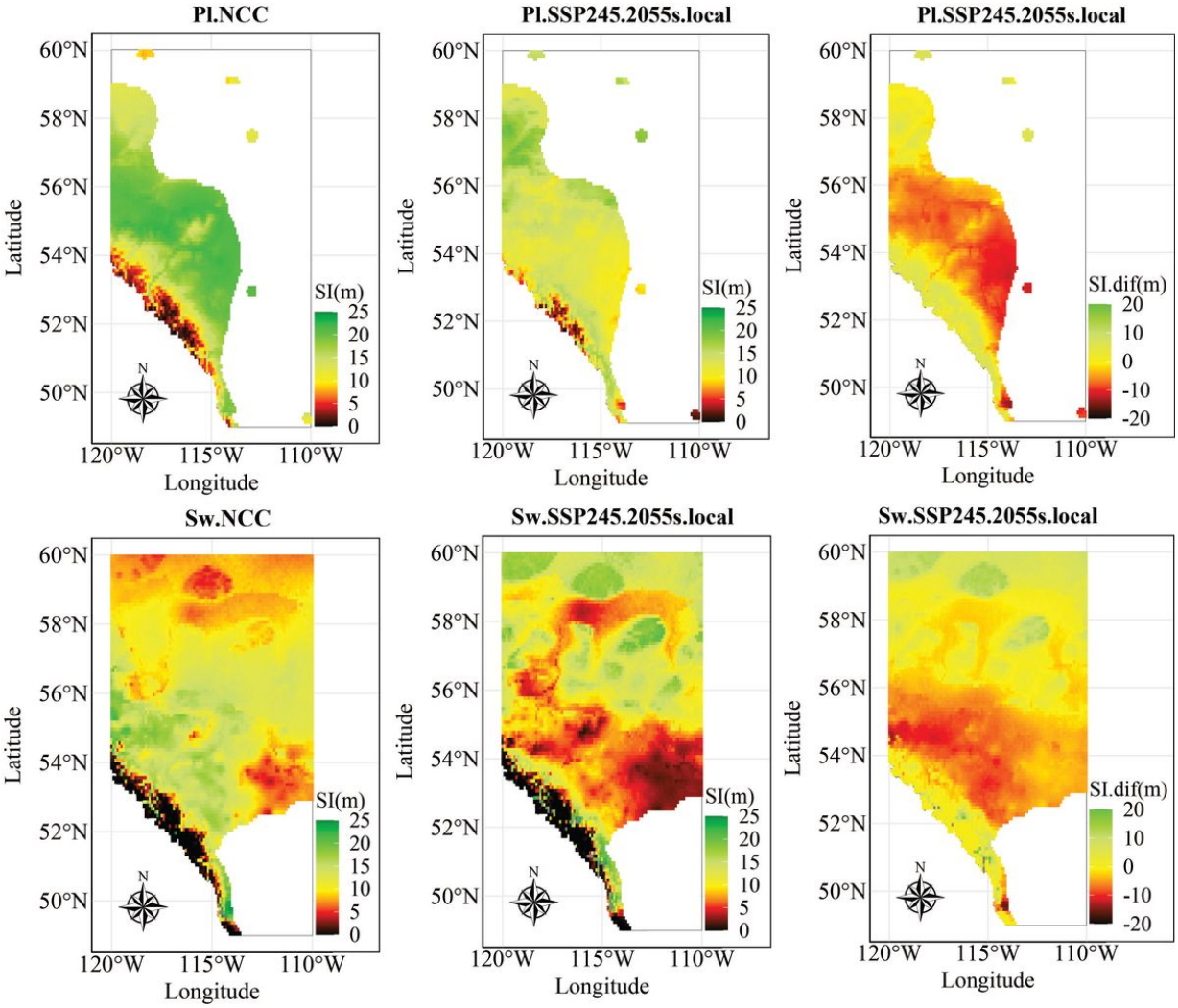

Figure 3

Site index (SI) and site index change (SI.dif) for the local populations of lodgepole pine (Pl) and white spruce (Sw) under no climate change (NCC) and Shared Socioeconomic Pathways (SSP) 245 in 2055s (averaged from 2041-2070) within each species' current natural distribution in Alberta.

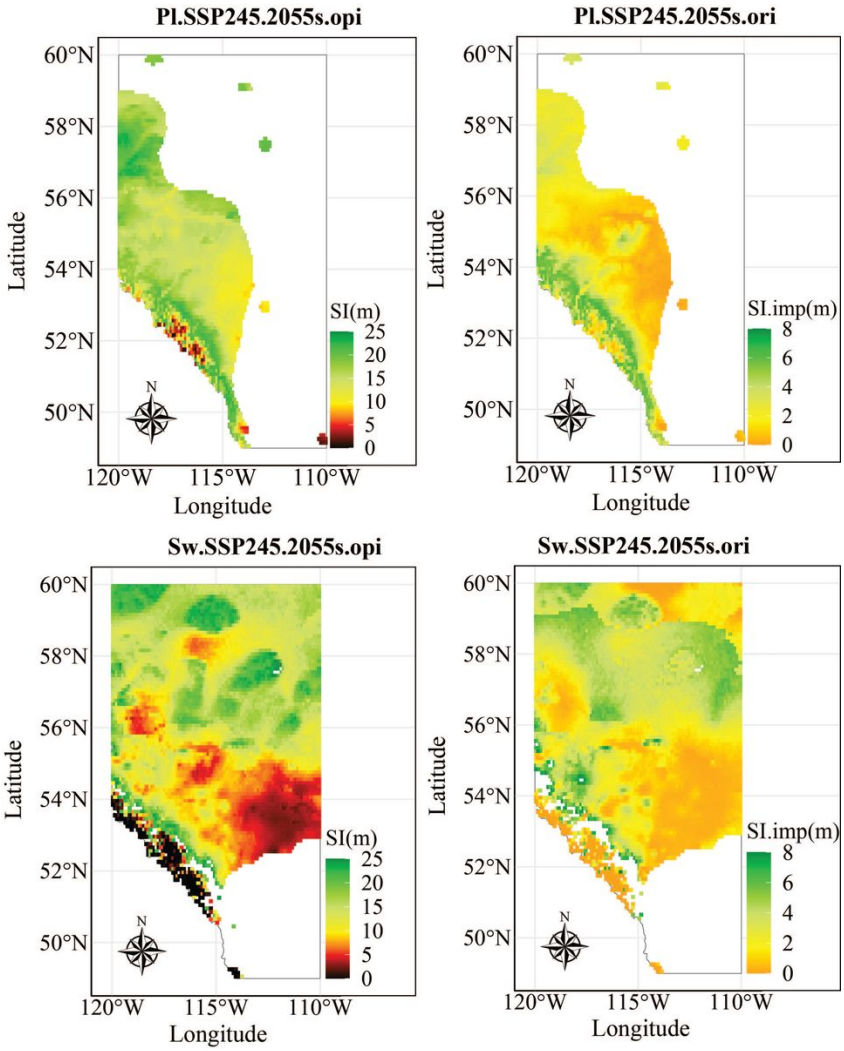

Figure 4

Site index (SI) and site index improvement compared to local populations (SI.imp) for the optimal populations (.opi) of lodgepole pine (Pl) and white spruce (Sw) under SSP245 in 2055s (averaged from 2041-2070) within species natural range in Alberta.

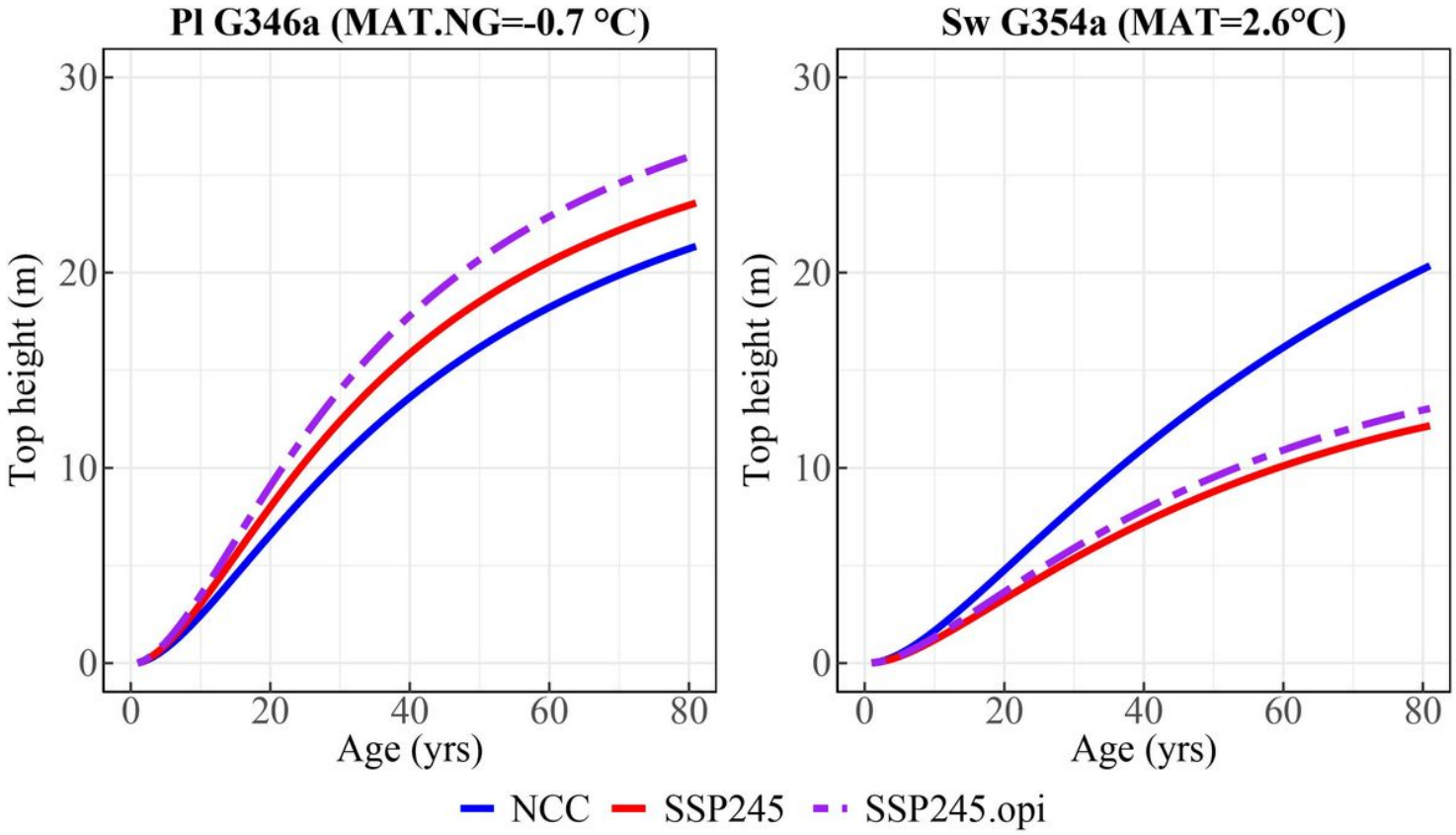

Figure 5

Case study of climate sensitive grow and yield (GYPSY) models for lodgepole pine (Pl) growing at site G346a and white spruce (Sw) at site G354a under no climate change (NCC) and under Shared Socioeconomica Pathway (SSP) 245; optimal population (.opi) is selected based on grid scanning (100 random points) that cover the natural range within Alberta.

Supplementary Files

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- Appendix.docx