



Adapting reforestation programs to observed and projected climate change

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Received: 22 September 2021 / Accepted: 17 February 2023
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Abstract

Reforestation programs generally rely on locally collected seed, which is assumed to be adapted to local climate conditions. To adapt to a changing climate, current methods of choosing reforestation seed should be revised to align seed movement with the magnitude and direction of climate change. In a case study for the province of Alberta, Canada, we analyzed options for seed transfer in white spruce (*Picea glauca* (Moench) Voss) based on the growth of more than 1000 white spruce genotypes spanning about 40 years of field testing. We used multivariate statistics with nine climate variables to match seed source and planting site climates to improve tree growth under the past and expected future climate conditions. We found that seed transfers can improve growth in some cases. However, the climate change vector does not always align with geographic gradients, which makes finding well-adapted seed sources difficult or impossible. This issue may partially be addressed by relying on additional silvicultural adaptation options to address climate change. Our case study provides a methodological template of how jurisdictions can determine the feasibility as well as magnitude and direction of assisted migration prescriptions to adapt their reforestation programs to new planting environments.

Keywords Forest management · Tree improvement · Tree breeding zones · Assisted migration · Climate change

1 Introduction

Many local government authorities that regulate reforestation programs provide guidelines for matching a seed source and planting site to avoid maladaptation. A mismatch between a seed source and planting environments could result in poor adaptation to general local climate conditions or climate extreme events (e.g., Grady et al. 2015; Isaac-Renton et al. 2018; Marquis et al. 2020). Long-distance movement of seed sources could also expose

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them to new pests and diseases (e.g., Sork et al. 1993; Wilhelmi et al. 2017). This in turn can cause increased mortality (e.g., Persson 1994) or reduced growth (e.g., Nagamitsu and Shuri 2021; Pedlar et al. 2021). In general, large geographic or climatic differences between the seed source and planting site should be avoided, because local populations are considered genetically best adapted to their native environments (e.g., Collevatti et al. 2019; Pluess et al. 2016; Rehfeldt 1995; Savolainen et al. 2007).

Seed transfer limits can be implemented in two ways. Allowable seed movement can be limited by geographic or climatic maximum distances from collection to planting location (e.g., Parker and van Niejenhuis 1996; Rehfeldt 1994), or by seed zone delineations where seed materials need to be collected and planted within the fixed areas (e.g., Campbell 1991; Parker and van Niejenhuis 1996). The magnitude of seed transfer limits or the size of seed zones can be determined by reciprocal transplant experiments, also referred to as provenance trials in forestry (e.g., Campbell 1986; Rehfeldt 1994; Ying and Yanchuk 2006). Latitude and elevation have been the primary variables for defining seed transfer limits in the past. However, with the need to adapt forestry to a changing climate, the current best practice is to adopt climate-based seed transfer guidelines (Ukrainetz et al. 2011).

Another more intensive management approach to produce reforestation stock is to test and select provenances or progeny from selected trees or controlled crosses for good growth and resistance to pests and diseases. Normally, this genotypic testing is over a wide range of environments to maximize the potential deployment area without maladaptation. Because improved planting stock has usually been tested over a wider range of climatic conditions, longer transfers can be allowed than for untested natural stand seedlots. Such tree improvement programs exist for 28 forestry species in Canada, while in the USA have improved seed for more than 70 species (FAO 2014). These testing and selection programs are usually organized by provincial jurisdictions and are meant to improve the growth and stability of planting stock over the tested environments.

Under climate change, this management approach of planting locally tested planting material needs to be called into question, because planting stock tested under past climate conditions may lag behind new, warmer planting environments (McKenney et al. 2009). Evidence of adaptation lag due to climate change has already been documented in major North America tree species (Bisbing et al. 2021; Etterson et al. 2020). To address the maladaptation of reforestation stock, assisted migration of locally adapted planting material has been proposed, primarily within species ranges (e.g., Aitken and Bemmels 2016; Park et al. 2018; Pedlar et al. 2011; Peters and Darling 1985; Williams and Dumroese 2013).

These management changes can often be implemented with minimal additional cost, because seeds are already being produced in seed orchards, or processed in centralized seed centers, grown in forestry nurseries, and transported over long distances to planting sites as part of regular reforestation operations. Matching planting stock with anticipated new environments is therefore mostly a technical challenge to determine the correct transfers and associated policies. The provinces of British Columbia, Alberta, Ontario, and Quebec have already partially implemented seed transfer rules to facilitate assisted migration through climate-based seed movement in their regular reforestation programs (O'Neill et al. 2017; O'Neill et al. 2008; Pedlar et al. 2011; Williamson et al. 2019). However, many of these assisted migration policies are implemented as "preliminary" and are based on incomplete information.

Here, we investigate how reforestation practices can be adapted to ensure future forest health and productivity, considering a multivariate climate environment, multivariate climate change, and the predicted growth response of provenances and families to the climate change vector. We develop our analysis as a case study for a commercially important boreal tree species, white spruce (*Picea glauca* (Moench) Voss) in Alberta. Approximately

43 million improved white spruce seedlings are planted per year to regenerate forests after harvesting, where white spruce accounts for 40% of the harvested conifer volume (Government of Alberta 2020). The objective of this paper is to provide a methodological template of how jurisdictions can develop proactive adaptation strategies for their reforestation programs in anticipation of future climate change. We also determine the magnitude and direction of assisted migration prescriptions that are required to address climate change that has already occurred. Management changes that compensate for the adaptational lag that already exists would have the highest priority for implementation to mitigate the negative impacts of climate change.

2 Methods

2.1 Provenance and progeny data

The Alberta tree improvement program for white spruce is organized into regions locally known as Controlled Parentage Program (CPP) regions. In this paper, we refer to them as “breeding regions.” The tree improvement program for white spruce includes nine breeding regions, each covering approximately 2° of latitude with an elevation range of about 400 m. To allow forest companies to operate effectively, breeding regions are defined by the operators (private companies or cooperatives), who carry out the testing of planting stock for suitability within their chosen region of operation. Therefore, breeding region boundaries may substantially overlap, allowing different commercial forest breeding programs to operate on the same land base in Alberta (Fig. 1a).

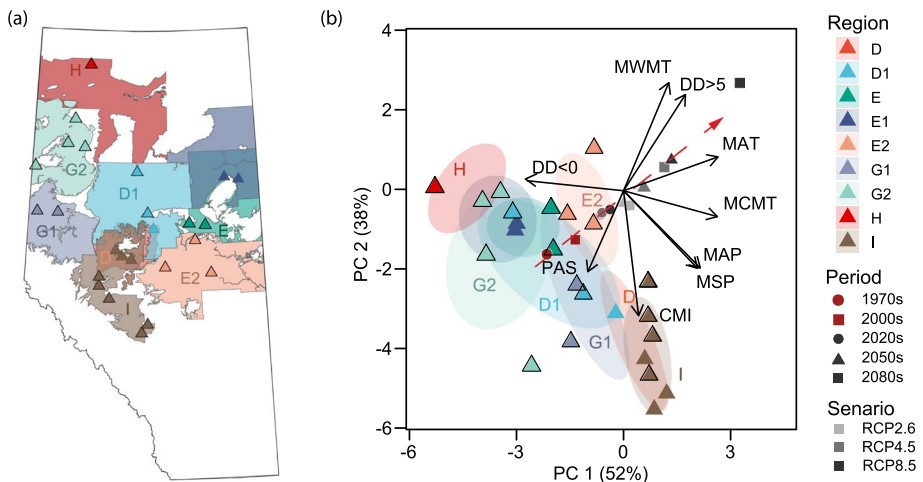


Fig. 1 Geographic locations of nine Alberta white spruce breeding regions (a), and their climatic conditions described with nine climate variables in a principal component plot (b). For climate variable abbreviations, see Table 2. Test sites are indicated by triangles, and the range of climate normal conditions (1970s) within breeding regions are indicated by colored 80% ellipses. Note that the ordination includes future climate projections, which leads to the origin of the vectors (point 0, 0) being located outside the 1970s climate mean

Each white spruce tree breeding program has its own series of progeny trials, testing selected half-sib families within its own region, but also testing sources from other breeding regions or from outside of Alberta. In total, there are 11 series of progeny trials with a total of 30 test sites (2 to 5 sites per series), each testing between 50 and 300 half-sib families (~ 100 families on average). In addition, Alberta has five provenance trials series, where bulk seed collections from forest stands are tested across breeding regions throughout Alberta. The largest series has 11 test sites with 86 provenances, other trial series consists of 1, 2, or 4 sites, testing on average 40 provenances. The entire testing program includes approximately 125,000 trees from around 1000 half-sib families (where female parents are known) and 180 provenances (that represent a general collection location) in Alberta. Table 1 shows the combined number of families and provenances in field tests among and within white spruce breeding regions in Alberta.

Test plantations comprise a number of experimental designs that vary in plot size, block size, and number of replications. Earlier trials have randomized complete block designs with few replications and row-tree plots. Later trials have incomplete block α -designs with single-tree plots. Due to differences in planting dates, tree heights used in this study were measured under various ages ranging from 7 and 32 years. To account for individual age and test site conditions, height measurements were converted to percent height relative to the local population. For this purpose, “local” includes all populations and families that were sampled from and tested within the same breeding region. A value of 100% height growth for any provenance or family, therefore, represents the average growth, expected from local seed sources. Provenance and family mean performance (relative to local sources) was then analyzed as a function of the source breeding region and test site breeding region with a linear mixed model. We used best linear unbiased estimates (BLUEs) to estimate family and provenance means, previously carried out by Gray et al. (2016).

2.2 Climate data

The climate of white spruce breeding regions and testing sites were extracted from spatially interpolated climate data using the software package ClimateNA v6.40a (Wang et al. 2016), which integrates a high-resolution climate grid with historical anomaly data and

Table 1 Number of genotypes transferred for testing among breeding regions and tested within the same breeding region (diagonal highlighted in italic)

Tested in region	No. of test sites	Number of genotypes transferred from breeding region									
		D	D1	E	E1	E2	G1	G2	H	I	
D	4	<i>113</i>	112	0	1	1	23	1	2	214	
D1	3	52	<i>132</i>	7	11	4	12	34	73	39	
E	4	52	119	<i>33</i>	11	14	3	2	3	38	
E1	2	4	12	32	<i>11</i>	10	1	2	3	2	
E2	3	77	22	0	1	<i>1</i>	21	2	3	187	
G1	2	3	3	0	1	1	<i>74</i>	3	2	2	
G2	4	4	41	6	11	1	76	<i>99</i>	74	2	
H	1	3	37	7	12	1	28	35	<i>76</i>	2	
I	8	114	111	0	2	2	27	4	3	<i>219</i>	

future climate projections. The high-resolution interpolated climate grid is based on the Parameter Regression of Independent Slopes Model (PRISM) interpolation method for a 1961–1990 baseline climate period (Daly et al. 2008). For historical anomaly data, we use CRU-TS 4.04 (Harris et al. 2020), and future climate projections were obtained from the Coupled Model Inter-comparison Project Phase 6 (CMIP6) (Eyring et al. 2016), using a 2021 release of model projections (Mahony et al. 2021). The software version used for this analysis is available for download at <http://tinyurl.com/ClimateNA>. The latest version of the software is maintained at <http://ClimateNA.ca>.

We used this software to estimate historical and projected climate values for given latitude, longitude, and elevation positions of the seed sources and planting sites. The general climate of breeding regions was characterized by estimating for 1-km resolution gridded climate data across each seed zone. Nine biologically relevant variables were selected that are often associated with the climatic adaptation of tree populations. They include mean annual temperature (MAT), mean coldest month temperature (MCMT), mean warmest month temperature (MWMT), mean annual precipitation (MAP), growing season precipitation (MSP), a climate moisture index (CMI), precipitation as snow (PAS), growing degree days above 5 °C (DD>5), and chilling degree days (DD<0). For details on these variables and their estimation, see Wang et al. (2016).

Observed and projected climate change was quantified for 30-year climate normal periods. Observed climate change is represented by the difference between the 1961–1990 and 1991–2020 climate averages (referred as 1970s and 2000s, respectively). Future projections are based on 15 AOGCMs and 10 GCMs from CMIP6 multi-model dataset x 3 Emission Scenarios (RCP2.6, RCP4.5, and RCP8.5) under 3 future climate normal periods (2011–2040, 2041–2070, 2071–2100), hereafter referred to as 2020s, 2050s, and 2080s, respectively. We evaluated future climate projections of individual models, as well as an ensemble average. A multivariate one-dimensional climate change vector was calculated as an overall mean from the individual model × RCP scenario combinations.

2.3 Analysis

Climate gradients were summarized by principal component analysis (PCA), implemented with the *princomp()* function of the R programming environment (R Core Team 2021). Principal component scores were generated for 1-km resolution gridded climate data and mapped to visualize major independent climate gradients, covering the distribution of white spruce in Alberta. The climatic conditions of each breeding region were plotted with the *stat_ellipse()* function of the *ggplot2* package for the R programming environment. For context, we also climatically characterized and plotted ellipses for the natural habitat of white spruce (outside breeding regions) as well as climate conditions outside the species natural distribution range, using the Alberta Natural Subregion ecosystem delineations (Alberta Parks 2015). The frequency of white spruce under different climate conditions was derived from inventory plots (Alberta Biodiversity Monitoring Institute 2020), publicly available at <http://abmi.ca> and <http://tinyurl.com/1t5o0cfe>.

Subsequent analysis revealed that observed and projected climate change can be described by an approximately linear vector (i.e., observed climate change, and short-term, medium-term, and long-term projections all point in the same multivariate direction). We, therefore, carried out an additional rotation of the first two principal component planes, which accounted for 90% of the variation in the original climate variables. First, a

projected climate change vector was determined by calculating an average ensemble for the 2050s from all individual climate models, relative to the 1961–1990 normal climate. This average multivariate vector in the direction of the climate change was expressed in principal component scores, which were generated by applying the *predict()* function to the *princomp()* object, using R base package functions. Subsequently, the PC1 and PC2 scores were matrix-multiplied with a rotation matrix $[[\cos(\alpha), -\sin(\alpha)], [\sin(\alpha), \cos(\alpha)]]$, where α is the angle of the climate change vector relative to the x -axis. Matrix algebra operations were implemented with R base package functions (R Core Team 2021).

To highlight the population responses under future climate, we classified the current breeding regions into two groups that form a temperature series parallel to the climate change vector. The two series along the climate change vector differ in moisture-related climate variables (MAP, MSP, CMI, PAS) and are orthogonal to the climate change vector towards warmer temperatures (MAT, MCMT, MWMT, DD>5, DD<0). For visualization, we divided each series into three equal sections, representing cold, medium, and warm temperature conditions within the current white spruce habitat. This division (of two moisture classes by three temperature series) created six climatic regions, covering the current and future white spruce habitat in Alberta. We use this visualization to provide suggestions for the geographic magnitude and direction of assisted migration along the observed multivariate climate trend as well as anticipated future climate change.

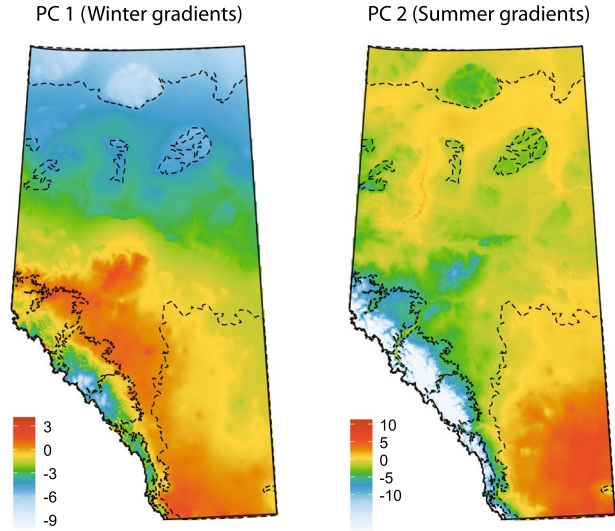
3 Results

3.1 Climatology of breeding regions

Using principal component analysis (PCA), we can describe the climatic pattern of Alberta in two independent dimensions. These are defined by two PCA axes, which together accounting for 90% of the total variance in the original nine climatic variables (Fig. 1). The first PCA axis (PC1) explains for 52% of the variance and primarily represents MAT and winter season temperature (MCMT and DD<0). The second PCA axis (PC2) accounts for 38% of the total variance and primarily represents temperature variables (MAT, MWMT, and DD>5) and climate moisture index (CMI). Precipitation variables (MAP, MSP, and PAS) were equally represented in both PC1 and PC2. As an alternative geographic visualization of principal components PC1 and PC2, we also map the principal component scores of each grid cell (Fig. 2). Red areas in the PC1 map indicate especially mild winters (c.f., Fig. 1, high MCMT and low DD<0 values), whereas red areas in the PC2 map are associated with hot summers (high MWMT values) and dryness (low CMI values).

In this PCA ordination, breeding regions align along a diagonal (Fig. 1b), from a cooler and drier climate (upper left) to warmer and moister conditions (lower right). At the cold and dry end of this gradient, breeding regions H and G2 in northwestern Alberta (Fig. 1, red and light green, respectively) are distinguished by long, cold winters (low MCMT and high DD<0) and low precipitation (vector values of MAP and MSP pointing in the opposite direction). In contrast, breeding regions in the Rocky Mountains' foothills (I, D, and G1; Fig. 1 southwest corner) have moist and mild winters (high CMI, MAP, MSP, and MCMT values). Breeding regions G2 and E2 diverge slightly from this diagonal. Region

Fig. 2 Climate gradients expressed as principal component scores for nine climate variables, explaining 90% of the total variation in original climate variables. Principal component scores of 1km grid cells for Alberta indicate where they are located in the principal component ordination, i.e., the color legends correspond to the PC1 and PC2 values in Fig. 1b



E2 is characterized by low precipitation as snow (PAS) and higher annual temperatures (MAT, DD>5), whereas G2 tends toward the opposite.

Because of having considerable geographic overlap, breeding regions also overlap in their climatic ranges (Table 2). In addition, the size and topographic complexity of the breeding regions determine climatic variability within the breeding region. For example, breeding regions D1, G1, and I have diagonally stretched ellipses in the direction of precipitation vectors, indicating variable moisture conditions within these breeding regions. A further observation is that region G2 covers northern high-elevation areas with one test site (Fig. 1 lower left). Due to its unusual high elevation, this test site does not represent typical climate conditions of the breeding region (i.e., a test site well outside the corresponding breeding region ellipse).

Table 2 Geographic and climatic summary statistics for breeding regions of Alberta. The ranges are given from the 5th to the 95th percentile

Region	Geographic characteristics			Climatic variables		
	Latitudinal range	Longitude range	Elevation (m)	MAT (°C)	MAP (mm)	CMI (mm)
D	54.26~55.16	-116.87~-114.62	695~1026	1.7~2.3	544~647	8.9~26.9
D1	54.84~56.69	-117.12~-113.32	535~750	-0.8~1.7	432~563	-4~15.7
E	54.99~56.94	-112.92~-110.2	394~637	-0.8~0.7	445~476	0.7~6.8
E1	55.89~57.94	-112.97~-110.15	281~576	-1.6~0.1	408~466	-0.7~7.4
E2	53.45~54.8	-114.66~-110.35	567~727	0.9~2.2	423~531	-4.8~7.1
G1	54.48~55.9	-119.87~-117.42	625~960	1.1~2.3	458~640	1.3~22.9
G2	56.14~58.11	-119.86~-117.53	534~879	-1.7~0.9	415~480	-3.3~11.3
H	57.19~59.09	-119.59~-114.35	275~528	-2.2~-0.2	386~438	-5.2~3.8
I	52.72~55.08	-117.48~-115.15	759~1167	1.7~2.5	562~649	11~26.8

3.2 Observed and projected climate change

Observed climate change for the breeding regions is indicated in Fig. 1 by red symbols. The 1961–1990 climate normal (referred to as 1970s) across all breeding regions is indicated by a red circle, and their overall climate shift based on the subsequent 1991–2020 climate normal (referred to as 2000s climate) is indicated by a red square. Projected climate change from 168 individual model-emission scenario combinations for the 2020s, 2050s, and 2080s are shown as thin gray lines (Fig. 3). The model and scenario averages across these lines are shown by gray symbols. The analysis reveals that climate change projections show only moderate uncertainty up to the 2050s and that projected climate change vectors are in the same direction as observed climate change trends between the 1970s and the 2000s.

Notably, some variables are nearly orthogonal to the climate change vector (MAP and MSP), i.e., they are independent and not expected to change in the future (Fig. 1b). Although precipitation is generally expected to increase under future climate change scenarios, these changes are relatively small compare to the geography of the precipitation gradients. Because of warming temperatures, moisture deficits are expected to slightly increase across breeding regions (CMI). The vectors parallel to the climate change trajectory are for MAT, DD>5, and MWMT. Hence, we can expect notably warmer and longer growing seasons that potentially benefit spruce growth in previously thermal-limited regions. Precipitation as snow (PAS) is the climate variable expected to decrease the most due to warmer winters. For additional reference, projected changes for climate variables across all nine breeding regions are provided in Table 3.

A visualization of the same PCA that includes the climate space of montane, subarctic, parkland, and grassland natural subregions of Alberta suggests that some breeding regions may become marginal environment for spruce in the future (Fig. 3). Current white spruce frequencies are the highest in the climate space where breeding regions are situated

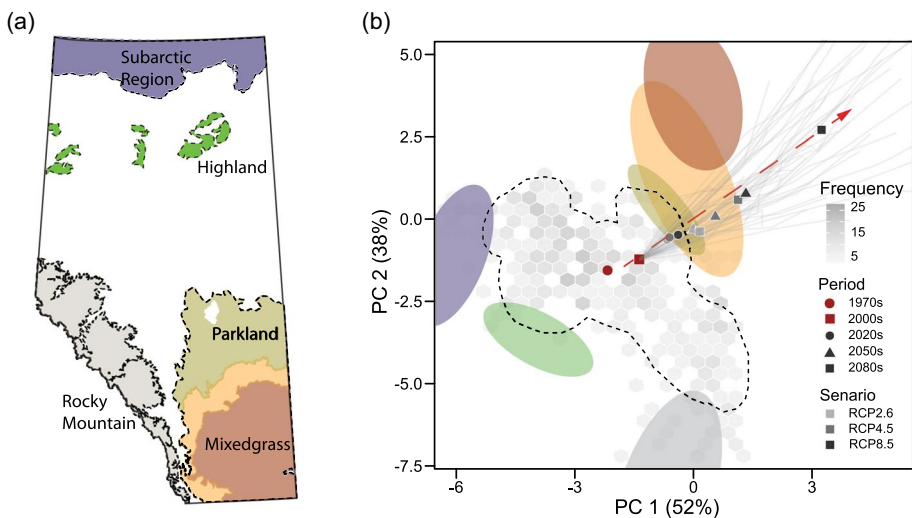


Fig. 3 The climate space of white spruce breeding regions (dashed line), adjacent ecosystems (colored 80% ellipses), and spruce frequencies for different climatic conditions (hexagons). The ordination is otherwise identical to Fig. 1

(Fig. 3b, hexagons), and the dashed line represents the climate space where productive forestry operations with white spruce are possible under historical climate conditions. Regions too cold for commercial forestry operations include the northern subarctic (Fig. 3 map purple area), montane and submontane ecosystems within the Rocky Mountain area (gray), and subarctic highlands (green). The southern boreal parklands (light green) have historically been too dry to support white spruce forestry operations, and grassland ecosystems (brown) are outside of the natural distribution of the species. The transition between parkland and grasslands (shown in light orange) contains the white spruce natural distribution boundary.

Projected climate conditions for the 2020s suggest that the historical climate across all breeding regions will shift close to the boundary of where white spruce forestry is currently practiced under any RCP scenario (Fig. 3, gray circles). For the 2050s and the RCP8.5 emission scenario, the climate of current breeding regions would fall within the parkland-mixed grass transition zone (Fig. 3, gray triangles), corresponding to the historical range limits of the species. By the 2080s, breeding region climates are projected to reach non-analog conditions to current Alberta climates under the RCP8.5 emission scenario (Fig. 3, black square). The more optimistic scenarios (RCP 2.6 and 4.5) would indicate breeding region climates equivalent to the grassland-parkland transition climates by the 2080s, which is the historical range limit of the species in Alberta.

3.3 Breeding region alignment under climate change

For subsequent analysis of how spruce populations may respond to climate change, and which seed sources would be the best adaptive fit under projected climate change, we carry

Table 3 Average historic climate for the 1961 to 1990 period (1970s), given in absolute values, and observed or projected climate change relative the 1970s baseline averaged across nine white spruce breeding regions of Alberta. Projected climate change values do not differ substantially among the individual breeding regions (e.g., for the 2050s, RCP4.5, Δ MAT ranges from 2.8 to 3.1 °C)

Code	Climate variable (unit)	Observed		Projected 2020s		Projected 2050s		Projected 2080s	
		1970s	2000s	RCP4.5	RCP8.5	RCP4.5	RCP8.5	RCP4.5	RCP8.5
MAT	Mean annual temperature (°C)	0.5	+0.7	+1.7	+1.9	+3.0	+3.8	+3.6	+6.0
MCMT	Mean coldest month temp (°C)	-18	+2.3	+2.1	+2.5	+3.8	+4.8	+4.5	+7.4
MWMT	Mean warmest month temp (°C)	15.6	+0.4	+1.7	+1.8	+2.7	+3.7	+3.4	+6.1
DD>5	Degree days above 5 °C	1206	+43	+257	+283	+434	+595	+554	+1014
DD<0	Degree days below 0 °C	1936	-208	-301	-349	-525	-647	-619	-965
MAP	Mean annual Precipitation (mm)	483	+1	+19	+22	+34	+40	+40	+51
MSP	Mean summer precipitation (mm)	320	+1.4	+7.9	+10	+16.1	+17.2	+16.4	+13.3
CMI	Climate moisture index (mm)	8.7	-0.9	-3.4	-3.5	-5.3	-7.6	-7.3	-15.5

out an additional rotation of the plane represented by PC1 and PC2. The rotation aligns the x-axis of Fig. 4 with the average climate change vector (Fig 3, red dashed). The rotation of the coordinate system results in the y-axis representing the moisture gradient, which is largely independent of the climate change vector (c.f., individual variable vectors in Figs. 4 and 1). Breeding regions are differentiated along this moisture gradient that is not expected to be affected by climate change. We, therefore, divided the climate space into dry and moist series, each containing a gradient from cool to warm along the climate change vector (Fig. 4). The lower series in the graph contains moister breeding regions (Fig. 4, green to blue) and the upper series represents the drier breeding regions (Fig. 4, orange to red). The moist series comprises the Rocky Mountain Foothills and includes breeding region I, D, and G2. The remaining breeding regions fall into the dry series.

3.4 Transfer function analysis of populations

The growth response of trees, when moved along these climate gradients can be described by transfer functions, which can then be used to predict a climate change response. In this case study, the population-level response along the projected climate change vector appears minimal relative to the within-region variability, but some trends are apparent (Fig. 5). Transfers among breeding regions in the dry series (Fig. 5a) from the warm climate bin (Region E2) to the medium climate bin (E1, E, D1) all suggest small growth improvements under observed and projected climate change. This is inferred from the positive slope of test site panels E1, D1, and E, where the E2 population outperforms the local sources by about 5%. The transfer from planting stock originating in the medium climate bin (E1, E, and D1) to colder environments is not well tested except for some data from regions G2 and H. Given the available data, the medium temperature sources again outperform the local sources from cooler environments (i.e., corresponding to a transfer from the center

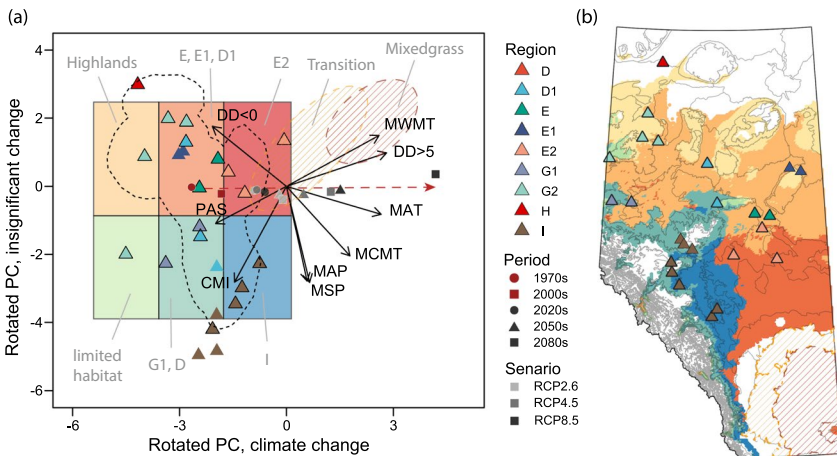


Fig. 4 The climatic space of the principal component analysis of Fig. 1 rotated toward the climate change vector so that the y-axis represents climate variables that do not change (a). Colored boxes represent a dry (upper) and a moist (lower) temperature series, spatially plotted across Alberta (b). For climate variable abbreviations, see Table 2

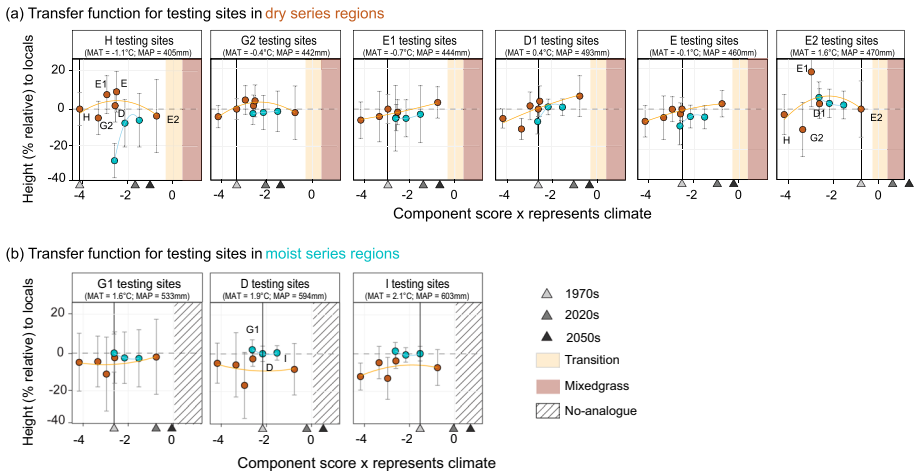


Fig. 5 Transfer functions of white spruce growth when transferred among breeding regions. We separate transfer functions for the dry and moist series as defined by the climatic bins in Fig. 4. Each panel represents the results of testing genotypes in one breeding region, with the header including mean annual temperature (MAT) and mean annual precipitation (MAP) of test sites, and the vertical line indicating the multivariate climate score. The *x*-axis in this graph corresponds to the *x*-axis in Fig. 4 and represents the projected climate shift of the vertical line by the 2020s and 2050s is indicated by triangles on the *x*-axis

towards the left). The transfer among breeding regions in the moist series (Fig. 5b) does not result in notable changes in growth. The regions are climatically too similar in the direction of the climate change vector to discern a substantial difference in the growth among G1, D, and I sources compared to the variance within regions.

4 Discussion

4.1 Matching planting stock to changing environments

Results from this study illustrate the challenges of managing seed transfer to address climate change in an environment with a complex climatology. In the physical world, natural climate gradients to which populations are adapted are created primarily by topography and latitude. It would simplify prescriptions if we could migrate species along those latitudinal and elevation gradients (north and up in elevation) to compensate for climate warming. However, this analysis shows that multivariate climate change does not cooperate to make such prescriptions possible in many cases. Predominant climatic gradients in the landscape (Fig. 1, ellipses arranged diagonally) do not align with observed and projected climate change (Fig. 1, red arrow), and matching appropriately adapted source populations to anticipated future climate conditions is not always possible. Since the drivers of climate gradients in Alberta are common elsewhere (elevation gradients in mountainous areas, and maritime to continental gradients), this difficulty likely applies to many regions of the world.

Nevertheless, some straight forward transfer recommendations to address climate change are possible for our case study: within the dry-series of breeding regions, transfers

from warmer to cooler environments result in better growth based on both historical data and projected growth response under future climate change. This example aligns with the general expectation that seed sources from warmer, southern regions may benefit from assisted migration to cooler northern environments (Lu et al. 2014; Prud'homme et al. 2018). In other cases, options are limited. Southern dry breeding regions are expected to become unsuitable because of moisture deficits that would only support grassland ecosystems, and for the southern montane regions, we have no test sites that would allow for inferences on how white spruce may respond to no-analogue climate conditions under projected climate change. However, Schneider (B37 2013) suggests that these warm and moist foothill regions would still support forest ecosystems by the 2080s. In contrast, it would be hard to imagine that commercial forestry could still be supported under grassland-type climate conditions by the 2050s or 2080s. Others have also pointed out that white spruce populations will face potentially dramatic declines across the southern boreal forest due to drought-induced mortality or growth reductions under projected climate change (Aubin et al. 2018; Boulanger et al. 2017; Peng et al. 2011).

The magnitude of observed and projected climate change relative to the climatic breadth of breeding regions suggest that assisted migration prescriptions should be implemented where possible. In Alberta, white spruce is a commercial species with a rotation age of 60–100 years depending on climate, site conditions, and the intensity of silviculture management. With such a long rotation, climate change adaptation could target mid-rotation as a point of reference for the choice of reforestation seed (an approximately 1.5 bin shift in Fig. 4). Observed climate change by the 2000s already represents a 0.5 bin shift. As a consequence, a very conservative assisted migration prescription could safely target a 1 bin shift along the multivariate vector to compensate for observed climate change. Such a general prescription would invariably enhance or maintain growth while improving the match between climate conditions to which planting stock is adapted. A moderate movement of an approximately 1 bin climatic distance (Fig. 4) should also not increase the risks of exposing vulnerable seedlings to substantially colder planting conditions, where they may be damaged by unseasonal frosts.

4.2 Consideration of genetic factors in seed transfer

In order for an assisted migration prescription to yield any benefits, genetic differentiation among populations is a necessary. However, it should be noted that the absence of differentiation among populations in growth observed in field trials is not evidence that important genetic differentiations do not exist. Differentiation in adaptive traits may only be revealed, when genotypes are subjected to rare extreme events (that may not have occurred at a specific test plantation), or if they experience general climate conditions substantially outside their climatic niche. A good example for this phenomenon is panel H versus all other panels of Fig. 5a. While the populations of the moist series do not reveal any significant differences at most planting sites, the population of Region G1 does show substantial differentiation when transferred to the coldest site (Region H). A general precautionary principle that should govern assisted migration should therefore be to match the historic origin climate of seed sources with anticipated future environments, even if growth data from provenance experiments shows no evidence of population differentiation. In provenance testing, the absence of genetic differentiation is not considered evidence of genetic homogeneity or low risks.

A consistent genetic differentiation that is revealed through the reciprocal transplant experiments among breeding regions in Alberta are different growth responses of dry series versus wet series breeding region sources. Seed sources from dry series show better growth under dry regions (Fig. 5a), and seed sources from wet series (G1, D, and I) tend to have better performance under wet series sites than sources from dry series (Fig. 5b). Cross-over interaction among genotypes would suggest that transfers among wet and dry series climates should be generally avoided. Recommended transfers would be from red to orange, orange to yellow, and blue to green regions (Fig. 4). Our results align with climatic transfer limits for both moisture and precipitation gradients observed in wind-pollinated boreal species in other studies based on provenance testing (Pedlar et al. 2021). Generally, a cross-over genotype \times environment interaction for precipitation is strong evidence for local adaptation and was also previously documented for white spruce based on the analysis of a provenance trial series by Rweyongeza (2011).

An important genetic consideration that is not covered in this study is an analysis of within-region genetic variability and differences in the climatic niche breadth and tolerance limits of individual families tested in the Alberta tree improvement programs. Follow-up research may systematically search for genotypes that have a stable and superior growth response over a wide range of environmental conditions, especially warmer test site conditions than their origin climate. Such an analysis would benefit from being carried out on data from individual test sites, rather than breeding region means as in this study. Furthermore, site conditions within regions can be highly variable, accounting for the large standard errors in Fig. 5. Some of these local site factors may compensate for climate change, e.g., moist sites or slopes with a northern aspect, could allow current genotypes to be successfully deployed under climate change for longer than average conditions of climate regions would suggest. Therefore, the option of site-specific guidelines without long-distance transfer of seed sources could be researched through dedicated trials.

4.3 Silvicultural climate change adaptation options

In addition to matching planting stock to anticipated future environments through assisted migration, other options for climate change adaptations are available (Millar et al. 2007). While projections of grassland-type climates are concerning, mature white spruce may exhibit considerable tolerance to maintain growth under dry conditions as opposed to younger, regenerating trees (Peng et al. 2011). While the range of white spruce may be limited by the capacity of seedlings to establish, planted forests using robust nursery-grown planting stock may not necessarily be as vulnerable as species range limits imply. Once established, saplings may grow well, even when outside their optimal climate niche, and persist in the long term (Bisbing et al. 2021). Limiting stocking density in plantations can limit transpiration rates and thereby increase their resilience to drought events or drier conditions becoming a limiting factor for growth (Elkin et al. 2015; Fernandez-de-Una et al. 2015), especially for seedlings with superior growth potentials which tend to have reduced drought adaptability (Cappa et al. 2022).

In this study, we lack test site data that quantify the climatic tolerances of spruce (i.e., where growth rapidly declines near the transition to grasslands in Fig. 5). Similarly, it is uncertain how far silvicultural interventions, such as the use of nursery stock, appropriate spacing to minimize stand evapotranspiration, and control of competing vegetation could expand the climatic niche space that supports commercial white spruce forestry operations.

Silvicultural trials and genetic tests could be established under drought and heat-limited environmental conditions to inform the viability of maintaining spruce forestry in Alberta and to discover genotypes that are best suited for what may become marginal habitat conditions in the future. Meanwhile, other empirical research approaches, such as species distribution modeling, remote sensing, or dendrochronology can be used to quantify the climatic tolerances of reforestation species, which can complement results from genetic test plantations for dependable assisted migration prescriptions (e.g., Gray et al. 2011; Sang et al. 2019).

Another consideration to guide the choice of genotypes and species in reforestation under climate change is the vulnerability to pests and diseases. For the study region, milder winters favor the survival of insect pests, and warmer temperatures can lead to accelerated reproductive cycles of pests and diseases (e.g., Gauthier et al. 2015). Abiotic stresses, such as drought periods and heat waves may further weaken forest trees' defenses and tolerance to insects and pathogens (e.g., Jactel et al. 2019; Weed et al. 2013). Populations that are optimally matched to their climate niche are usually also the most resilient genotypes to pest and disease problems. Therefore, migrating planting stock in response to climate change can have beneficial effects not only on growth but also on forest health.

Acknowledgements This analysis uses data published as Electronic Supplementary Material to Gray et al. (2016). We thank the Government of Alberta and 12 forestry companies that originally contributed their progeny and provenance data to make this analysis possible.

Funding Funding for this study was provided by the NSERC Discovery Grant RGPIN-330527-20 to AH and Desmond I Crossley Memorial Scholarship in Forestry to ZS.

Data availability Provenance testing data for white spruce underlying this analysis are publicly available as Appendix Table S1 to Gray et al. (2016): <https://doi.org/10.1007/s11295-016-0983-1>, and climate data used in this analysis is available at <http://tinyurl.com/ClimateNA>. The authors will share additional derived datasets generated as part of this analysis upon request as well.

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