Forest Tree Population Response to Climate Variability and Climate Change: Implications for Reforestation

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Forest Biology and Management

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Abstract

This dissertation aims to quantify the sensitivity and adaptive capacity of forest tree species to climate change in Canada and North America, with applications of guiding sustainable forest management through case studies focusing on Alberta. The general idea is that management interventions should focus on ecosystems, species or populations that are most likely to experience stress or mortality, or alternatively to focus on new forest management opportunities associated with warming climate conditions at high latitudes. The research addresses several specific problems at different spatial scales.

The research starts at the broadest scale, for North America, with a remote-sensing based vulnerability assessment of forest ecosystems to historical droughts. One of the most striking findings was a very high spatial diversity of vegetation response to historical climate variability. Broad continental patterns of vegetation response are readily apparent and conform to expectations, with southern interior ecosystems being limited by water availability and boreal populations limited by short growing seasons. However, within these broad geographic trends in growth response, finer scale (and often contradictory) response patterns emerge. For example, across the western boreal forest local patches show populations restricted in growth by warm summer temperatures and drought.

Next, a species-specific analysis investigates the adaptive capacity of an important boreal forest tree species, white spruce, using dendrochronological analysis. Results showed evidence for population differentiation in resistance and recovery parameters, but provenances conformed to approximately the same growth rates under drought conditions and had similar resilience metrics. The lack of populations with better growth rates under drought conditions is contrary to expectations for a wide-ranging species with distinct regional climate and we provide a counter example for drought tolerance traits, where assisted migration prescriptions may be ineffective to mitigate climate change impacts. An analysis of population response in the context of climatic conditions across Canada supports the view that northeastern Canada will provide a refugium for white spruce under climate change, while the species is sensitive to growth reductions under climate change in the western boreal.

In a case study for Alberta, a comprehensive series of genetic test plantations was analyzed to determine the optimal climate niche of selected planting stock. The results suggest 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. The case study provides a methodological template of how jurisdictions can determine feasibility as well as magnitude and direction of assisted migration prescriptions to adapt their reforestation programs to new planting environments.

When assisted migration is used to address climate change, tree seedlings may have to be moved to substantially colder environments in anticipation of climate warming over their life span. To assess the risk associated with moving planting stock north or to higher elevation, a climatic assessment of frost risk associated with assisted migration was performed. The results indicate that late spring and early fall frost risks do not change significantly for transfers toward the north. In contrast, moving planting stock toward higher elevation generally leads to a substantial increase in exposure to unseasonal frosts. In conclusion, transfers toward the north are preferable to transfers up in elevation in reforestation for the most important commercial tree species in western Canada that were evaluated in this study.

Lastly, the research explores how results may be translated to management prescriptions through an on-line seed selection tool for forest managers to identify the overall best planting stock for a reforestation site, synthesizing multiple criteria including vulnerability, adaptive capacity and growth of species and genotypes.

Preface

Thesis Chapter 2 has been submitted to a peer-reviewed journal under a title “Climatic vulnerabilities of ecosystems inferred from response function analysis of remote sensing data”, authored by Zihaohan Sang and Andreas Hamann. The study was conceived and designed by ZS. AH provided advice for analysis and interpretation. ZS performed the analysis. The first draft and revisions were carried out by ZS and AH.

Thesis Chapter 3 has been published in the peer-reviewed journal *Evolutionary Applications* under a title “Adaptive limitations of white spruce populations to drought imply vulnerability to climate change in its western range”, authored by Zihaohan Sang, Jaime Sebastian-Azcona Andreas Hamann, Annette Menzel and Uwe Hacke (*http://doi.org/10.1111/eva.12845*). The study was conceived by AH, AM and UH. JSA carried out the field sampling and JSA and AM contributed to method development. ZS performed the dendrochronology measurements and analysis and wrote the paper with revisions by all co-authors.

Thesis Chapter 4 has been submitted to the peer-reviewed journal under the title “Adapting reforestation programs to observed and projected climate change”, authored by Zihaohan Sang, Andreas Hamann, and Deogratias Rweyongeza. The study was conceived and designed by ZS and AH. DR contributed data and advice on analysis. ZS performed the analysis and wrote the first draft. DR and AH edited the manuscript.

Thesis Chapter 5 has been published to a peer-reviewed journal *Climate Risk Management* under the title “Assisted migration poleward rather than upward in elevation minimizes frost risks in plantations”, authored by Zihaohan Sang, Andreas Hamann, and Sally Aitken (*http://doi.org/10.1016/j.crm.2021.100380*). The study was conceived and designed by ZS, SA and AH. ZS performed the analysis and drafted the paper, with revisions from SA and AH.

Dedication

To the better and challenging future.

Acknowledgements

The process developing this thesis has been one of the most challenging yet rewarding processes that I have ever embarked on, and would not have been possible without the guidance of my supervisor Dr. Andreas Hamann. I appreciate the countless hours he spent on sharing ideas and editing this thesis. He believes in my ability even when this project went wrong and I started to question everything in my life. Without his help and support, I would not able to finish this thesis or the PhD degree.

I am also grateful for the scholarships that I received from University of Alberta, and I thank my committee members for reading my thesis, serving on my examining committee, and providing advice.

I would also want to thank my parents, who always did their best to provide me secure financial conditions for my study. I am very lucky to have their support and understanding for these years.

To my lab-mates at the Spatial Information System (SIS) lab, thank you for always being willing to help with any problems, and for the company that made the research environment supportive and encouraging.

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Chapter 1 - Thesis introduction, rationale and objectives

1.1. Background and rationale

Adapting natural resource management to new environmental realities is becoming ever more important, as efforts to limit greenhouse gas emissions appear to fall short. Moving seed sources poleward and to higher elevations, where planting environments are cooler, would help compensate for climate warming that has already occurred. This will ensure that climatic tolerances of species and locally adapted tree populations match current and future growing environments, thereby maintaining forest health and productivity.

Observed climate change in Alberta (two left panels below) amounts to approximately 1.4 °C relative to the beginning of the century, and recent decades of high annual CO_2 emissions make it likely that climate warming will continue as projected (Mahony et al. 2021)(Figure 1-1). Across the North American boreal forest, temperatures have on average increased by 1.5 to 2.5 °C, significantly exceeding the mean global temperature increase (Romero-Lankao et al. 2014). Warmer temperatures and reduced precipitation together have induced widespread impacts to the boreal forests and its ecosystems due to drought stress (Price et al. 2013). Across large regions, where water deficits limit growth, reduced forest productivity has been documented for western boreal tree species (Chhin and Wang 2008, Hogg et al. 2013, Chen et al. 2017). In some cases, drought periods have caused significant dieback and mortality (Allen et al. 2010, Michaelian et al. 2011, Worrall et al. 2013).

Several general options are available to address negative impacts of climate change and associated extreme events on natural and managed forest ecosystems (Millar et al. 2007).

Adaptive strategies for forest management include the protection of highly valued resources, resilience options to improve the capacity of ecosystems to recover after disturbance, and management response to facilitate the transition of ecosystems from current to new conditions. A cost-effective climate change adaptation strategy for the forestry sector is to move seed to more northern and higher elevation planting sites as part of ongoing reforestation programs.

Seed movement is, however, highly regulated by government authorities to match 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 climatic 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 could also expose 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., Rehfeldt 1995, Savolainen et al. 2007, Pluess et al. 2016, Collevatti et al. 2019).

Under climate change, the management approach of planting locally tested planting material needs to be called into question, because planting stock tested under past climatic 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 (Etterson et al. 2020, Bisbing et al. 2021). To address maladaptation of reforestation stock, assisted migration of locally adapted planting material has been proposed, primarily within species ranges (e.g., Peters and Darling 1985, Pedlar et al. 2011, Williams and Dumroese 2013, Aitken and Bemmels 2016, Park et al. 2018).

Moving seeds poleward and to higher elevations, where planting environments are cooler, would help to compensate for climate warming that has already occurred. This will increase the likelihood that climate conditions to which local populations are adapted match current and future growing environments, and thereby maintain forest health and productivity for the coming decades. Assisted migration prescriptions within and outside of current species ranges are already being implemented in Canada by moving some species and their populations (e.g., western larch, *Larix occidentalis*) to more northern locations or to higher elevation bands across seed zone boundaries to compensate for observed and projected climate change (Marris 2009, O'Neill et al. 2017, MFLNRO 2018, Natural Resources Canada 2020).

However, the benefits of assisted migration prescriptions have to be balanced against the inherent risk of major changes to management practices (Hotte et al. 2016). One potential problem that arises for long-lived tree species is that they may experience substantial climate change over the course of their lifetime. In order to match their optimum climatic niche with their most productive growing period, seeds and seedlings may have to be exposed to colder than optimal environments in anticipation of climate warming over the decades or centuries of their life span. Therefore, the risk of potential frost damage to planting stock that is to be moved to colder locations needs to be balanced against the benefit of more mature trees being better adapted to warmer growing environments decades later.

Any changes to management interventions come with some risk of unforeseen consequences, and it would therefore be wise to focus human interventions on regions, species, and local conditions that are most vulnerable to observed and projected climate change. As a tool for assessing the vulnerability of ecosystems to climate change, the strength of correlations between interannual climate variability and vegetation response can be a useful proxy for quantifying ecosystem vulnerability. Ecosystems or species close to critical climate thresholds will be more sensitive to anomalies (Dakos et al. 2012). This type of analysis can be carried out with any historical record of plant response to interannual climate variability or to climate extreme events. Dendroclimatology research can serve this purpose, but at larger scales, remote-sensing based vulnerability assessments could contribute to guiding conservation and management.

1.2. Thesis structure and objectives

The overall objective of this PhD research is to quantify the sensitivity of forest tree populations to climate variability and climate change at different scales: (1) At the broadest scale, for North America, I conduct a remote-sensing based vulnerability assessment of forest ecosystems to historical droughts; (2) Next, I conduct species-specific analyses of adaptive capacity for important boreal tree species in Canada using dendrochronological analysis; (3) In a case study for Alberta, I analyze a comprehensive series of genetic test plantations to determine the optimal climate niche of selected planting stock; (4) To assess the risk associated with moving planting stock north or to higher elevation, I carry out a climatic assessment of frost risk associated with assisted migration; Lastly, the research explores how results may be translated to management prescriptions through an on-line seed selection tool for forest managers to identify the overall best planting stock for a reforestation site, synthesizing multiple criteria including vulnerability, adaptive capacity and growth of species and genotypes.

In my **first research chapter**, I assess the vulnerability of forest types and forest ecosystems of North America to climate change. Vulnerability of trees, species, and ecosystems can be inferred through a historical biology approach that relies on records of past response to climate variability and climate extreme events to infer future response. This correlative analytical approach has some conceptual limitations, but is still widely used at various scales (dendrochronology, permanent inventory plot analysis, isotopic analysis, carbon flux tower networks, etc.). In this study, I carry out a classical dendroclimatological response function analysis, but using a remotely sensed cumulative annual Enhanced Vegetation Index (EVI) on forested ecosystems in lieu of tree ring width to determine limiting climatic factors for tree growth. High quality EVI time series data are only available since 2000, and two decades are considered short to make inferences from a correlative historical biology approach. Nevertheless, this study represents a first attempt of mapping patterns of limiting climatic factors at large scales and high resolution for forested ecosystems.

In **my second research chapter,** I evaluate the drought vulnerability of white spruce populations in a range-wide provenance trial. I use dendrochronology to identify climate responses to tree growth, especially under drought events. To highlight genetic differences among populations, tree cores were collected and sampled from white spruce provenance trail, containing individuals from range-wide provenances across boreal forest. During the study period, two drought events were identified in 1999 and 2002. Using tree ring width as a proxy for tree health, drought resistant and resilient differences were quantified for white spruce populations. The correlations were computed between drought responses and their normal local climate conditions. Secondly, the correlations were computed between drought responses and their normal local climate conditions. This study is designed to exam the drought adaptation of white spruce populations across boreal forest.

In my **third research chapter,** I investigate and predict the performance of genotypes under different climatic environments, represented by 9 controlled parentage program (CPP) regions in Alberta, for future seed selection. More specifically, I examine the validity of the “local is best” expectation, and examine the stability of populations, provenances and families under expected climate change through single- or multiple- variable response function for white spruce populations. Further, I make seed transfer recommendations that improve the multivariate climate match, accounting for observed climate change, and improving growth under both, past and anticipated future climate.

In my **fourth research chapter,** I compare the potential frost risk changes when tree seedlings have to be moved to higher latitude or higher elevation. When assisted migration is used to address climate change, tree seedlings may have to be moved to substantially colder environments in anticipation of climate warming over their life span. Such management practices increase the likelihood of maintaining forest health and productivity for the coming decades, but young seedlings would be exposed to higher frost risk after being planted to regions colder than the historical climate condition they adapted. In this chapter, I used current seed zones in Alberta and British Columbia to quantify the frost risk changes using interpolated daily climate data since 1980. Further, the estimated frost risks were compared between provenances and targeted northern and elevated seed zones for both spring and fall, and I make seed transfer recommendations to limit frost damages for forest assisted migration.

All research chapters, even though they cover different methodologies and different disciplines have a common aim: to aid reforestation activities and contribute scientific knowledge for economic, social, and ecological benefits. The results of the four research chapters are synthesized in a conclusion chapter at the end of the thesis.

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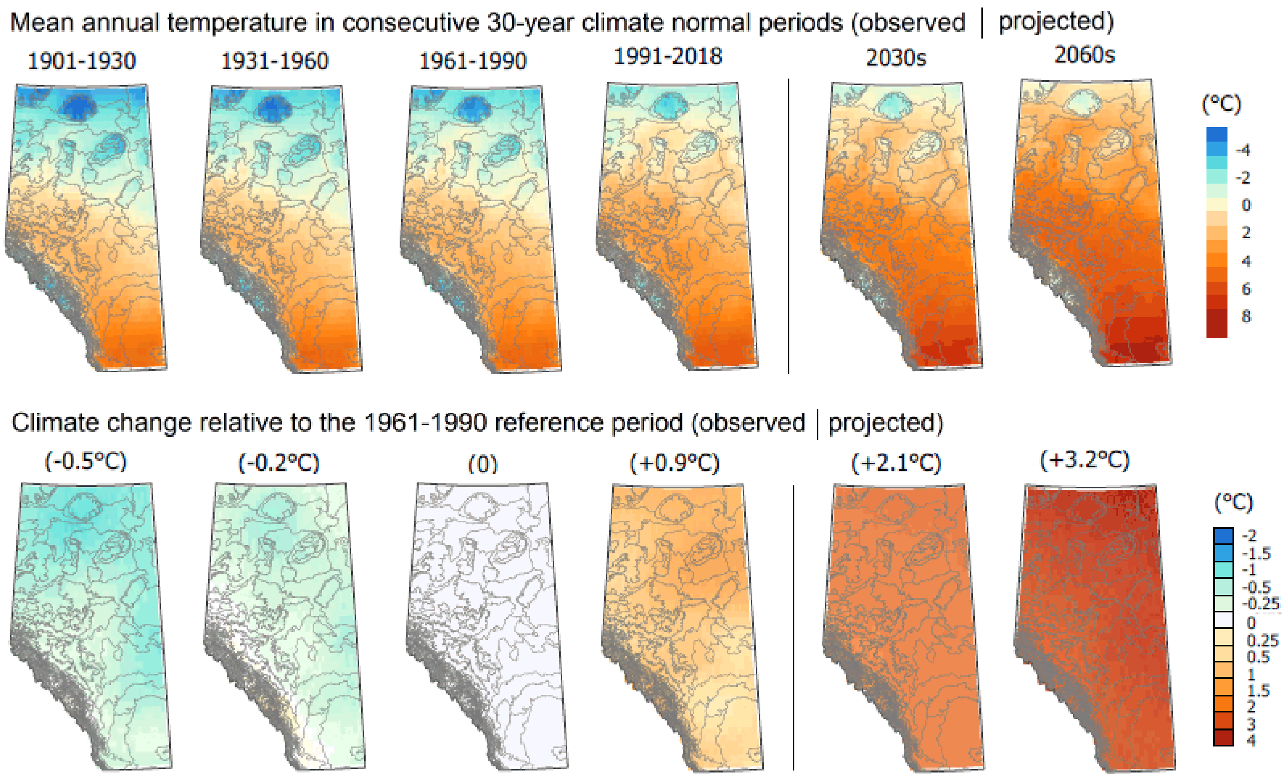

Figure 1-1. Observed and projected climate change for Alberta in 30-year climate normal intervals. Projections are based on CMIIP6 multi-model projections (Mahony et al., 2021).

Chapter 2 - Climatic vulnerabilities of North American ecosystems: a remote-sensing based response function analysis

2.1. Summary

Remote-sensing based vulnerability assessments to climate change are a research priority of critical importance for landscape-scale efforts to prioritize conservation and management of ecosystems. Limiting climatic factors can serve as a proxy for quantifying ecosystem vulnerability, since theory predicts that ecosystems close to critical climate thresholds will be more sensitive to interannual variation in limiting climate factors. Here, we propose a response function analysis applied to time series of enhanced vegetation index (EVI) data for continental-scale vulnerability assessments. The approach is derived from dendrochronological analysis, accounting for lagged response to climate variability and memory effects from the previous growing season. Mapping multivariate response function coefficients for North America reveal predominantly positive response to warm temperature anomalies across the Pacific Northwest, arctic and eastern boreal ecosystems. Vegetation types with negative responses, predominantly due to drought vulnerability, can be found across the continent, including a distinct geographic band across the western boreal forest. Mixed responses at local scales are also a common observation, and can be used to test hypotheses of interactions among climatic and non-climatic factors. We discuss applications of our assessment method for natural resource management in the context of climate change.

2.2. Introduction

As a tool for assessing the vulnerability of ecosystems to climate change, the strength of correlations between interannual climate variability and vegetation response can be a useful proxy for quantifying ecosystem vulnerability. Ecosystems or species close to critical climate thresholds will be more sensitive to anomalies (Dakos et al. 2012), which is an essential element of edge detection theory (Bathiany et al. 2020). Critical climate thresholds can apply relatively uniformly to members of natural species assemblages, allowing for ecosystem-level detection of vulnerabilities to climate change (Trisos et al. 2020). While natural resource managers and conservationists are primarily concerned with abrupt ecological disruption due to threshold transgressions at the edge of species and ecosystem tolerance limits (Millar and Stephenson 2015), the importance of gradual transitions has recently been pointed out in a meta-analysis of 4600 empirical climate change impact reports (Hillebrand et al. 2020). While threshold transgressions threaten profound changes to ecosystems, they are less frequent than gradual ecosystem and species responses to climate change. Comprehensive vulnerability assessments should detect both response types, threshold transgressions and gradual changes, to infer vulnerability of species or ecosystems.

Remote-sensing based vulnerability assessments to climate change is a research priority of critical importance, as few other methodological approaches could guide conservation and management priorities at continental or global scales. Previous work on developing remote-sensing based metrics to assess vulnerability includes a number of valuable methods. Seddon et al. (2016) developed a vegetation sensitivity index based on seasonally detrended multivariate climate time series, where coefficients of variables are weighted by their significance in a principal component regression. Another widely applied method estimates resistance (response to climate anomaly) and resilience (speed of recovery) metrics from Normalized Difference

Vegetation Index (NDVI) time series (De Keersmaecker et al. 2015). Li et al. (2018) added interpretative values by evaluating resistance and resilience of vegetation in the context of climatic exposure. Li et al. (2020) added a stability component to resistance and resilience metrics to arrive at a more comprehensive vulnerability score. Another comparable approach, relies on a linear mixed-effects model to quantify the strength of the association between precipitation/aridity and an EVI-based estimation of primary productivity (Maurer et al. 2020). All these methods yield a single metric of vulnerability for decision support. While these indices deliver valuable information, they generally do not allow inferring the nature of the vulnerability because the indices are not time- and variable- specific.

A conceptually different approach to vulnerability assessments is to evaluate long-term historical trends in ecosystem health and productivity. In the context of remote sensing, these trends are referred to as greening and browning. For example, Sulla-Menashe et al. (2018) observed greening in the eastern North American boreal forests, which is more humid, and browning in the western boreal, where forests are more prone to moisture stress. Pan et al. (2018) documents the risk of reversal from long-term greening to browning in the warmer future due to evapotranspiration demand. Both of these remote sensing based observations have also been confirmed through historical tree ring records suggest observed global warming shifted climatic drivers of tree growth from temperature-limited to moisture-constrained (Babst et al. 2019). Generally, western North America has seen declines in growth, while the northeast has been described as a climate change refugium (e.g., D'Orangeville et al. 2018). The studies point to the importance of a multivariate climate gradient from cold/wet to warm/dry conditions for assessing ecosystem vulnerability.

In summary, previous remote sensing indices have focused on evaluating ecosystem stability based on short term responses to interannual climate variation, or by tracking trends over time.

Both approaches have identified evapotranspiration demand as one major climatic drivers of tree growth in a warming world. Furthermore, while the potential of threshold transgression of species and ecosystems is well grounded in ecological theory, gradual responses (positive and negative) as well as their causes should also be quantified. This justifies the need for different approach to assessing ecosystem sensitivity and vulnerability. Our objectives are therefore to: (1) develop a remote sensing based multivariate sensitivity index that conveys the nature of potential ecosystem vulnerabilities, e.g. conveying where and during which month of the year forests are likely becoming vulnerable to climate-induced physiological stress associated with drought and high temperatures; (2) apply this multivariate index to the North American continent, mapping the behavior of growth and the underlying climatic driving factors; and (3) to associate these patterns of vegetation response with regional long-term climatic conditions, as well as non-climatic factors, such as forest stand age, elevation, and topo-edaphic factors, with the purpose of testing hypotheses of interactions among climatic and non-climatic factors. We discuss applications for natural resource management in the context of climate change.

2.3. Materials and methods

2.3.1. Remote sensing data

Satellite remote sensing offers an effective way of consistently measuring and monitoring large forest areas. For example, the Enhanced Vegetation Index (EVI) as a measure of vegetation greenness have been used to derive metrics related to primary productivity. As a proxy for annual productivity of forests, we used 17 years (January 2003 to December 2019) of 16-day 500 m EVI records accessed from Moderate Resolution Imaging Spectroradiometer (MODIS)

Vegetation Indices (MOD13A1, Collection 6). This MODIS dataset was pre-processed to reduce the noise of surface reflectance associated with solar and view angles (Huete et al. 2002) and achieved stage 3 validation (out of 4 levels), with the database validated against ground-based sample locations with comprehensive spatial and temporal coverage (Didan et al. 2015). The dataset was obtained through NASA Land Processes Distributed Active Archive Centre, U.S. Geological Survey/Earth Resources Observation and Science Centre (https://lpdaac.usgs.gov), comprising 391 layers (layer for 2016 Aug1 was missing from the database, but imputed for this study as explained below).

The quality of EVI records varied among seasons and regions, usually showing a high percentage of missing values across high latitudes areas and during winter months. Records flagged as poor quality (classified as 'Lowest quality', 'Quality so low that it is not useful', 'L1B data faulty', 'Not useful for any other reason/not processed') were excluded from further analysis. Also excluded from this analysis were human-managed ecosystems and grasslands, according to the vegetation classification according to the MCD12Q1 international Geosphere-Biosphere Programme (IGBP) classification (Sulla-Menashe and Friedl 2018). Thus, the analysis includes needle-leaf and broadleaf forests, shrub lands, arctic tundra and dry savannas with at least 10% tree coverage (legend classes 1 through 9).

After filtering out low-quality observations, agriculture areas and rangeland land cover, we rescaled the spatial resolution from original 500 m to 2 km by averaging the available measurements per temporal interval. This step resulted in more complete time series for a given 2 km pixel. Incomplete time series with less than 300 (out of 391) observations were removed. The remaining missing values of grid cells were estimated with the seasonally decomposed missing value imputation, implemented with the *na_seadec()* function of the *imputeTS* package for the R programming environment (R Core Team 2020). This data cleaning approach resulted in gap filling of 1.5% of all data over the entire study area and 17 year time period. To quantify the annual productivity for a response function analysis, we summed the EVI value above 0 per 2 km pixel per year, for each year from 2003 to 2019.

2.3.2. Climate data

We generated spatially interpolated monthly climate grids from 2002 (a year prior to the start of EVI data coverage) to the end of 2019 using the software ClimateNA v7.01 (Wang et al. 2016), which is available at http://climatena.ca. The ClimateNA software extracts monthly historical time series of interpolated climate data for particular locations and variables of interest. The interpolated climate grids are based on the Parameter Regression of Independent Slopes Model (PRISM) interpolation method (Daly et al. 2008). In this study, we used 72 monthly variables, including three monthly sets of temperature variables: maximum, minimum and average monthly temperature, and three sets of precipitation-related variables: monthly precipitation, monthly relative humidity and a monthly climate moisture index developed by Hogg (1997). In total, the response function analysis relies on 1224 monthly climate grids for the North American continent to support the response function analysis.

2.3.3. Climatic response function analysis

Plant response to climate can have lagged effects that vary with vegetation type, soil conditions, variable type and general macroclimatic region. One widely used approach to flexibly allow for different lags for different variables is a response function analysis, where Pearson’s correlation coefficients or multiple regression coefficients between annual response variable and monthly predictor variables are evaluated. Pearson correlation coefficients describe the strength of the correlation, whereas regression coefficients describe the magnitude of effects. The temporal window of this analysis is usually specified from the end of last growing season (e.g., last year's September) to the end of current year's growing season (e.g., current August). We implemented this approach in a per pixel analysis of EVI values across 17-year study period. Note that additional response-function techniques exist for dendrochronology analysis allowing statistical inference from individual tree response to populations (Fritts et al. 1971, Zang and Biondi 2015). However, in this case we work directly with the statistical population of EVI values and applications of inferential statistics would not be appropriate. Here, we simply use Pearson correlation coefficients between monthly climate variables and annual sums of EVI values to identify limiting climate factors throughout the year.

For the purpose of concise reporting, we clustered EVI grid cells with similar response coefficients using recursive partitioning for 14 groups (details shown in Appendix B). The cluster analysis was carried out through multivariate recursive partitioning implemented with the *mvpart()* function of the *mvpart* package for the R programming environment (R Core Team 2020). The number of groups was pre-set with the *rpart.control()* option to obtain 14 clusters that explained over 40% of the total variance in response coefficients. To confirm the robustness of this approach, another divisive clustering technique (k-means) was also used with the same number of clusters, yielding similar results. However, we used recursive partitioning for its speed and ability to handle very large datasets. For a regionally structured discussion of the results, we further created manual delineations of regions of the continent that had similar composition of response function clusters.

2.4. Results

2.4.1. Climatic response on a continental scale

To visualize continental patterns of limiting climate factors, we mapped remotely sensed vegetation response summarized into 14 clusters of grid cells that show similar vegetation response to interannual climate anomalies (Fig. 2-1). To allow a regional discussion of results, we further impose an arbitrary delineation into regions with similar composition of response functions (Fig. 2-1a). This delineation is simply meant to communicate a geographic location on the map and is not used in analysis. For a first visualization of broad continental patterns, cluster means from recursive partitioning were colored based on a scale generated by subtracting temperature from precipitation coefficients. Grid cells limited by high temperature and low precipitation are located on the red end of the color ramp and grid cells limited by cold temperatures and high precipitation values are indicated in blue (Fig. 2-1b and 2-1c).

Although other combinations are possible, most clusters (or geographic regions) can be ordered along a gradient from being limited by warm temperature and low precipitation (Fig. 2-1c, upper left) to being primarily limited by cold temperature, with precipitation having smaller additional negative effect (Fig. 2-1c, lower right). Two regions deviate to some extent from this diagonal positioning: The Taiga West region showed positive correlation of both temperature and precipitation with EVI, and Boreal East has stronger negative association with moisture condition. An important consideration in reading this map correctly is that response coefficients (colors) only indicate how vegetation responds to a local annual climate anomaly, relative to average climate conditions at this grid cell. The coefficients (colors) do not allow an inference on absolute values of vegetation response, nor do they represent the effect of absolute climate values at different locations. To give a simplified, univariate example, a positive (blue) temperature coefficient indicates a relative increase of EVI-inferred productivity at this location in response to a year with higher temperature than average for this location.

Broad geographic trends in limiting climate factors are readily apparent (Fig. 2-1b), with expected patters of northern and high elevation ecosystems cold-limited and southern interior regions of the continent most drought limited. However, there is also a remarkable regional diversity of response functions, which is summarized in Table 2-1. Generally, there are few landscapes with high uniformity of vegetation response, such as arctic ecoregions that are dominated by only a few clusters with similar thermal limitations, resulting in the lowest response function variances across the North America study area (e.g. Table 2-1, regions: TW, HP, PN). In contrast, southern and mountainous regions cover almost all clusters from 1 to 14, resulting higher variances (Table 2-1, regions SU, TS, T). Given similar latitude, eastern boreal forest ecosystems have a more homogenous response than the western and interior ones, with about half the variance in response coefficients (Table 2-1, regions BW, BSW, BC versus BE, TN, TE). This is also visible in the map, with discrete moisture-constrained patches in the central and western portions of the boreal forest apparent (Fig. 2-1b, red patches).

2.4.2. Monthly response function analysis

Monthly response functions for specific climate variables reveal in greater detail at what time of the year specific variables have a positive or negative impact on vegetation productivity (Fig. 2-2). While continent-wise responses function clusters are provided as Supplement Appendix A, we focus here on a number of regional examples to illustrate the analytical approach. For instance, the savannas in Southern Texas and Northeast Mexico (region DM: Dry forest, Mexico) are predominantly drought limited. In this region, only drought-limited clusters 1, 2 and 5 occur with significant frequency (Table 2-1, last row). A specific example is shown in Fig. 2-

2a for cluster #1, which has strong negative correlations with temperature and high positive correlations for moisture variables, especially for the climate moisture index (CMI), which indicates water deficits between March and August.

At the opposite end of the spectrum, the regions Pacific Central (PC), Pacific North (PN), and taiga ecosystems of the Hudson Bay (TH) are dominated by cluster #14 (Table 2-1, upper right), with year-round limitations by cold temperatures, and with precipitation having slightly negative effects in June and July (Fig. 2-2b and Appendix A for cluster #14 across all regions). In the more southern regions influenced by Pacific climate, cluster #14 still occurs at lower frequencies, but at lower elevation, there are strong drought limitations with the most frequent cluster being #5 (Region SU, Fig. 2-2c). In these oak or pine dominated forests, drought is a prevalent limiting factor throughout the year, especially in July.

For eastern temperate forest ecosystems from south to north (TS, TC, and TN), a gradient of limiting factors emerges from the response function analysis (Fig. 2-2 d-f). Southern pine forests of the United States have diverse response functions with the dominant clusters being #1 and #3 (other clusters found in this region are discussed below). These clusters are moisture limited from April to August (Fig. 2-2d). This moisture limitation is reduced for Temperate Central region, where cluster #3 is dominant (Fig. 2-2e), followed by temperate mixed forests of the Great Lakes, with further reduced moisture limitations (Fig. 2-2f). For northeastern regions we see increasing cold limitations and negative effects of moisture variables during the growing season (Fig. 2-2g).

Another notable continental pattern is the latitudinal sequence of Boreal Southwest (BSW), to Boreal West (BW) to Taiga West (TW), with both the northern and southern adjoining regions less limited by evapotranspirative demand (Fig. 2-1b). The red patches in the central Boreal West

(BW) region represent cluster #3, indicating growth limitations driven by warm summer temperatures (Fig. 2-2h).

2.5. Discussion

2.5.1. Inferring vulnerability to climate change

Both our response function analysis and other research approaches suggest that drought may play an important role in limiting growth of forested ecosystems in the future for a variety of regions of North America. Climate change impacts for high latitudes of North America, where the warming signal is strongest have already been relatively well documented. While high-latitude boreal ecosystems are generally expected to benefit from warming trends, widespread greening trends that was initially observed in remote sensing in response to climate change have in many cases reversed to browning trends in the most recent decade (Phoenix and Bjerke 2016). For the North American boreal, browning, or trend reversals from greening to browning are prevalent in western Canada and Alaska (de Jong et al. 2011, Ju and Masek 2016, Pan et al. 2018). This corresponds to diagonal band (dominated by response cluster #3) across the western boreal forest that we also see in this study, where warm summer temperatures and water deficits in spring and fall are limiting factors (Figs. 2-1b, 2-2h). Our interpretation is that initial greening observed in the 1980s to 1990s reversed to browning because of drought limitations by increasing evapotranspiration demands, as inferred by response cluster #3.

Tree ring studies have also pointed to drought-limitations in the western boreal of Alaska (Barber et al. 2000, Trugman et al. 2018) and western Canada (Girardin et al. 2016, Hogg et al. 2017). In contrast to western boreal forest ecosystems, eastern boreal forest suggests the forest productivity could benefit from up to 2 °C warming, and the Northeast might serve as a climate refugia for boreal forest species (D'Orangeville et al. 2016, D'Orangeville et al. 2018). This is generally also supported by our response function analysis that suggests a favorable growth response to higher temperatures in the east (Fig. 2-1b, 2-2g).

2.5.2. Inferring causes of local response

Seddon et al. (2016) pointed out that a remote sensing index can serve as a the first step towards addressing why some regions and locations appear to be more sensitive than others, and with the detailed information from response function analysis, we can interpret the results in the context of candidate variables and test hypotheses regarding the causes of local sensitivity of forest ecosystems and forest stands. A good example is the central boreal forest, where we find a patchwork of forest stands that are cold limited versus summer-drought limited in close proximity. A comparison with stand age (Fig. 2-3a) reveals a striking "lock and key" pattern, where drought limitations are most pronounced in medium-aged stands (20-50 years) that are growing fast and have high transpiration rates during the growing season. Both young forest stands (0-20 years) and older forests (>50 years) appear less vulnerable to drought, which could be due to young stands having not yet developed a significant transpiration capacity and older stands having a lower density of larger trees, or possibly better access to groundwater. The response is region-specific, and age class structure has for example no effect on response functions in most regions of the eastern boreal forest (Fig. 2-3b), also apparent at larger scales (Fig. 2-1b). Age class structure has also been documented as an important driver of how forest stands respond to climate change in western Canada in research that relies on forest inventory plots (McMillan and Goulden 2008, Peng et al. 2011, Luo and Chen 2013). Responses can vary significantly due to region, topoedaphic factors, and species composition.

Another example for high local variability in vegetation response functions can also be found throughout the western montane regions from Alaska to Mexico, which generally contain the same response function clusters but at different frequencies (Fig. 2-4). Here, the type of vegetation responses are driven by steep gradients of climatic and topo-edaphic factors associated with elevation gradients. High elevation positions generally fall into thermal-limited clusters (in blue toned colors), but low elevations show stronger drought sensitivity (in orange colors). Such response gradients have, for example been documented for dry forest and Sierra ecoregions (Herrmann et al. 2016), using a remote sensing-based approach. Also, Davis et al. (2019) document threshold transgressions for tree regeneration at low elevation due to drought limitations.

2.5.3. Implications and management applications

Our analysis revealed high spatial heterogeneity of climatic response coefficients across most ecosystems. As a consequence, response to anthropogenic climate change will almost always be locally variable, and mitigation strategies need to be carefully tailored toward local circumstances. For example, to mitigate drought sensitivity of fast growing or dense forest stands (e.g., Young et al. 2017), silviculture interventions may including thinning to reduce overall evapotranspiration rates of fast growing forest stands and thereby make the trees overall more resistant to drought episodes (Sohn et al. 2016, Wang et al. 2019). Such a prescription would, however, only be effective where response coefficients have identified this type of vulnerability during the growing season.

The high local and regional diversity in growth climate responses also offers an explanation for contradictory findings in studies from the same general region using similar methods. One example is research across the interior boreal forest of Alaska, where some studies report declines of spruce growth (Barber et al. 2000) , while others documented overall increases in productivity (e.g., Sullivan et al. 2017). We find this particular region very diverse in local response coefficients, so that a diversity of vegetation response from individual research studies would not be unexpected. Climate change impacts and corresponding management interventions to mitigate those impacts would similarly need to be tailored to local circumstances in this region.

This study indicates that time series records of remotely sensed vegetation response are now of sufficient length and quality to infer limiting climatic factors, and map them at high resolution. We further provided examples how vegetation response function types can be linked non-climatic factors, such as forest stand age, drainage, nutrient regimes and other topo-edaphic factors, which may contribute to resilience or exacerbate vulnerabilities. We believe this analytical approach could prove useful for mapping climate vulnerabilities at spatial scales that can support local management interventions to mitigate climate change impacts, especially when validated by ground observations such as long-term forest inventory plots that is usually available to local forest managers (e.g., Das et al. 2021).

2.6. Literature cited

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Table 2-1. Response function cluster composition (in percent) for North American regions as shown in Fig. 2-1(a). High percentage values are highlighted with a darker background color. The variance in response function values across all growing season variables is provided as metric of the heterogeneity of vegetation response functions within each region.

	Clusters														Area (km^2)	Variance
Region Name	1	2	3	4	5	6	7	8	9	10	11	12	13	14		
PN (Pacific North)	0	0.1	0.1	0.9	0.5	1.7	4.4	3.3	2	1	3	0	3.9	79	404,920	0.015
PC (Pacific Central)	0.7	2	0.2	0.9	2.1	3.1	3.2	5.6	9.6	2.1	4.5	2.2	7	56.8	582,716	0.032
HP (Hudson Plain)	0	0	0.2	0.4	0.6	0.5	5.3	0.9	1.4	2.4	3.7	6.4	5.2	72.9	631,692	0.015
TW (Taiga West)	0	0	0.4	0.1	0.3	1.8	1.3	1.1	0.1	0.5	0.1	81	9.6	3.7	754,284	0.010
TE (Taiga East)	0	0.1	0.1	1.6	0.9	0.5	5.7	0.4	0.6	33.9	28.9	3.7	6.8	16.8	747,188	0.016
BW (Boreal West)	0	0.2	10	6.3	3	25.2	5	5.5	4.5	1.9	3.3	9.7	17.9	7.7	651,916	0.030
BC (Boreal Central)	0	0.1	3	1.4	1	3	13.8	11.2	3.2	8	7.5	2.9	10.8	34.1	619,536	0.027
BSW (Boreal Southwest)	0	0.2	1.1	4.8	1.6	13.8	2.7	3.5	14	6.4	7.9	3.3	22.1	18.6	314,676	0.026
BE (Boreal East)	0	0.2	0	1.3	1	0.5	6.6	2.2	2.7	8.1	57.4	2.7	4.1	13.1	488,376	0.016
MN (Montane North)	0.1	0.2	2.4	5.2	9.2	11	23.9	9.2	8.4	1	3.2	5.4	6.3	14.5	906,088	0.029
MC (Montane Central)	1	1.9	0.8	5.8	5.7	7.8	3.4	8.7	18.1	3.8	20.2	0.9	9.1	12.8	599,036	0.030
TN (Temperate North)	0	0.3	1.7	2.8	0.7	4.7	26.6	28.5	5.2	8.2	10.5	1	6	3.8	1,017,252	0.018
TC (Temperate Central)	2.9	1.1	35.1	8	2.4	10.2	7.3	19.3	4.6	2.7	3.5	0	1.7	1.1	823,532	0.028
TS (Temperate South)	14.3	4.4	14.3	3.1	4.1	7.8	7.6	8.8	13.2	5.6	3	0.4	4.7	8.6	902,712	0.051
T (Tropical)	4.4	6.5	5.3	1.6	23.6	9.4	12	3.9	5.6	3.1	0.8	0.6	11.7	11.4	824,308	0.043
SU (Sierra, US)	18.4	11.9	0.4	3.9	20.7	5.9	5.7	12	3.3	1.2	4.2	0.1	1.4	10.9	381,200	0.060
SM (Sierra, Mexico)	8.1	6.6	2.5	2.8	16.9	6.9	2.5	1	44	3.8	1.3	0.2	0.9	2.6	672,552	0.026
DU (Dry forest, US)	5.9	13.6	6.4	4.9	13.8	10.8	2.8	8	21.6	3	5.7	0.2	0.2	2.9	528,936	0.033
DM (Dry forest, Mexico)	47.7	17.9	2.8	1.3	14.2	4.4	3.7	0.5	4.4	0.2	0.1	0.8	1.6	0.3	719,180	0.034

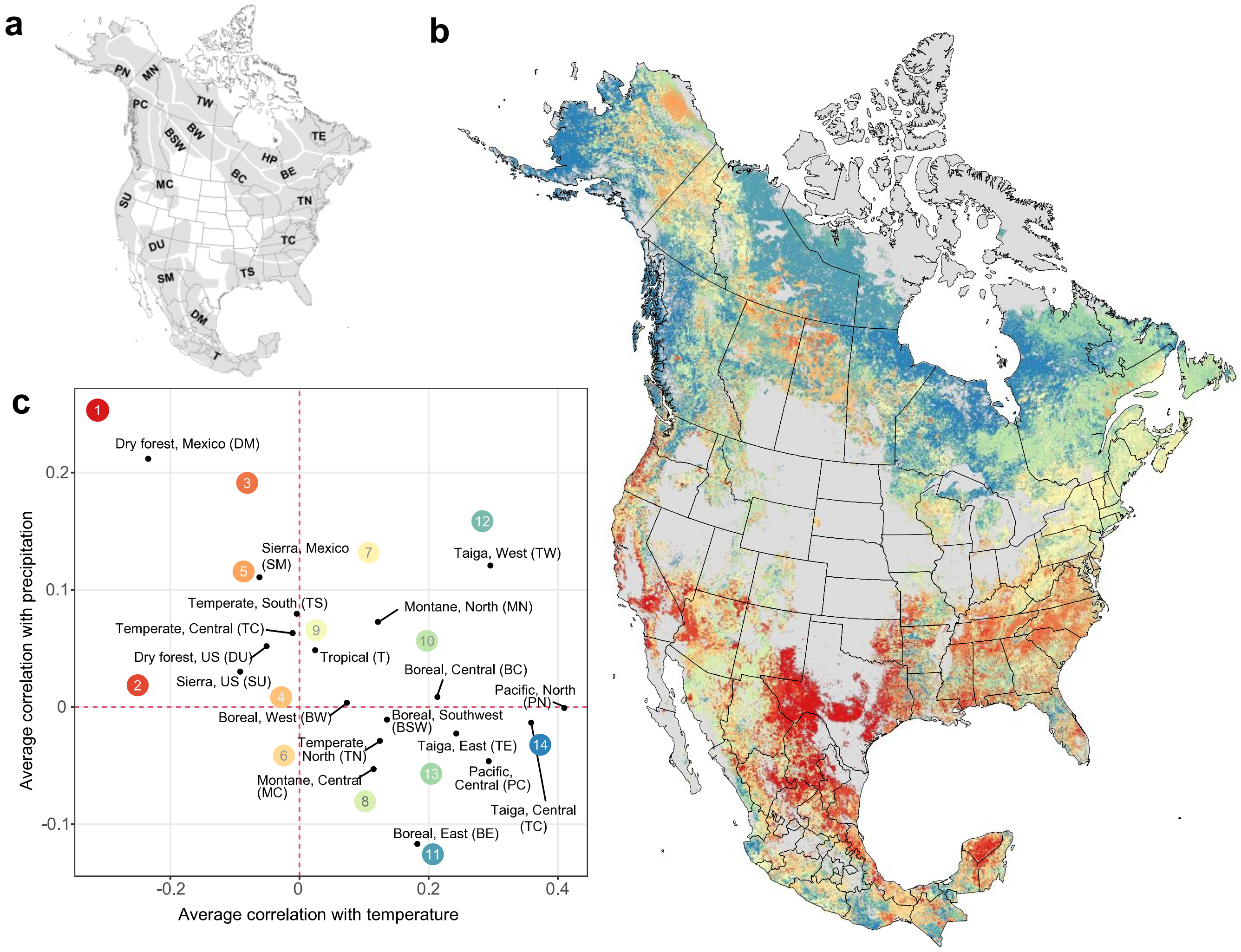

Figure 2-1. Climatic response function clusters across North America. Clusters are based on similarity of grid cells in correlations between annual cumulative EVI and monthly climatic variables (including maximum, minimum and average monthly temperature, monthly precipitation, relative humidity and a climate moisture index). Clusters were colored from most to least limited by high temperature and low precipitation by subtracting temperature from precipitation coefficients and applying linear color ramp (c). Clusters of similar vegetation response were then mapped across North America (b), and summarized for regions with similar cluster composition (a). Light gray in (b) represents excluded ecosystems or no data.

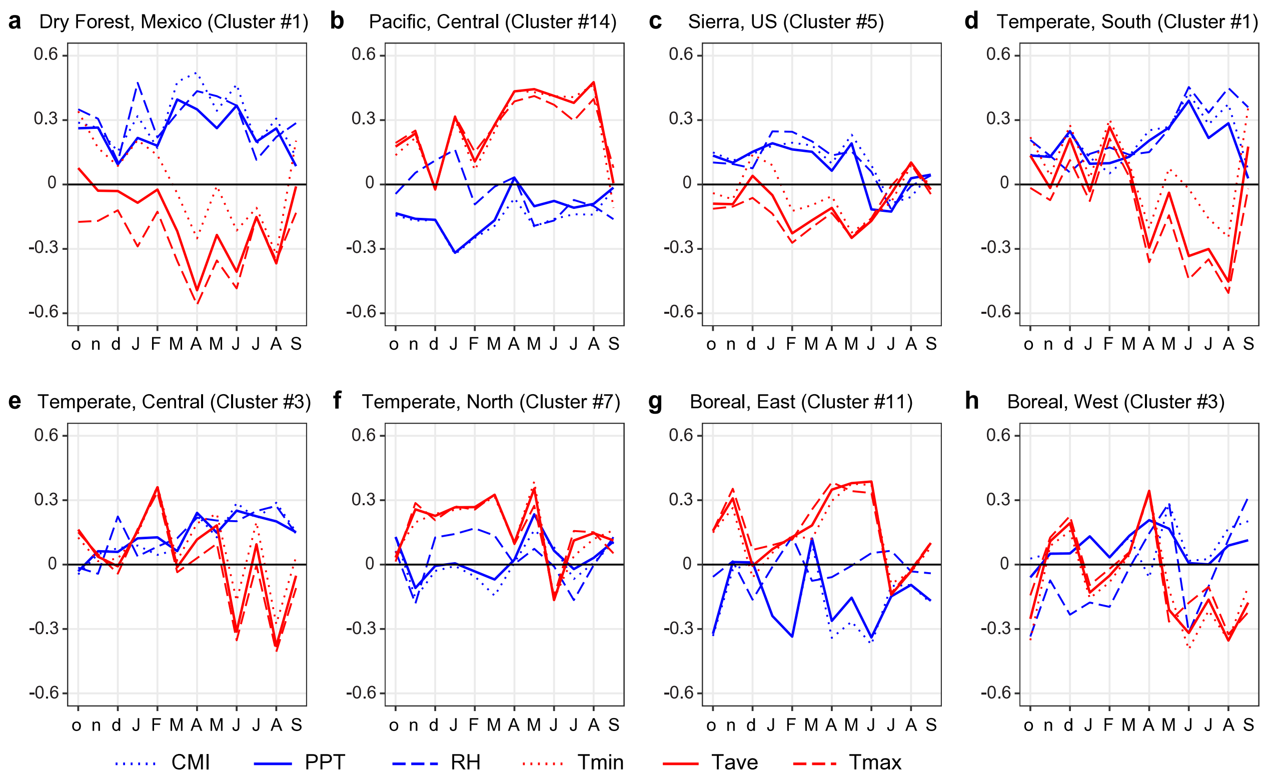

Figure 2-2. Region-specific monthly response functions for selected clusters. Graphs show the correlation of monthly climate variables with cumulative annual EVI values (Tmin – mean monthly minimum temperature, Tmax – mean monthly maximum temperature; Tave – mean monthly temperature; CMI – climate moisture index, PPT – mean monthly precipitation, RH – mean monthly relative humidity). Response function of clusters may vary slightly among different regions. Continental cluster averages for all 14 clusters are provided as Appendix A.

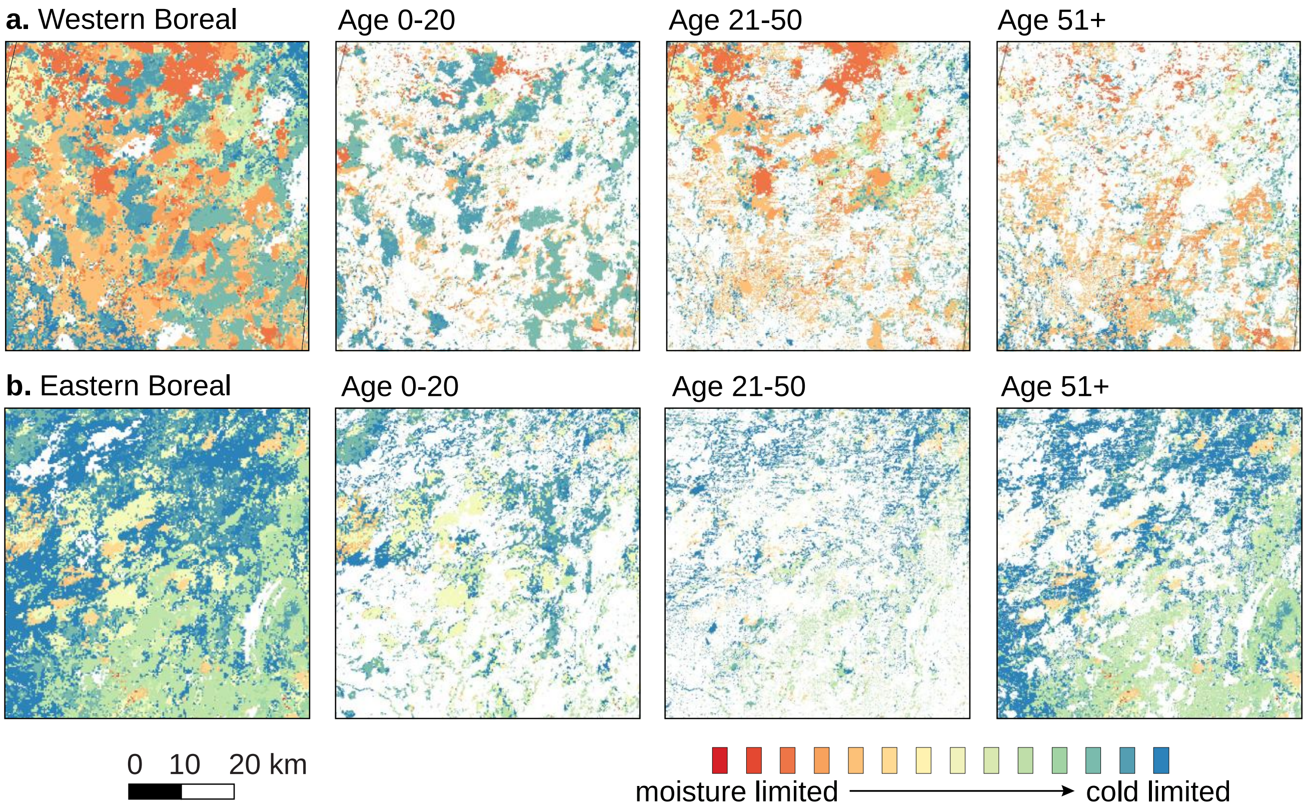

Figure 2-3. Forest age structure and the distribution of clusters in (a) western boreal and (b) eastern boreal region. Given the correlation values, 14 clusters were plotted from moist limited (red colors) to thermal limited (blues). Forest age estimation from Pan *et al.* (2011) has been cut into three categories: 0-20, 21-50, and over 51. The 0-20 aged forest areas fit the records from Canadian National Fire Database. For each group, pixels in corresponding age class will be covered by black color.

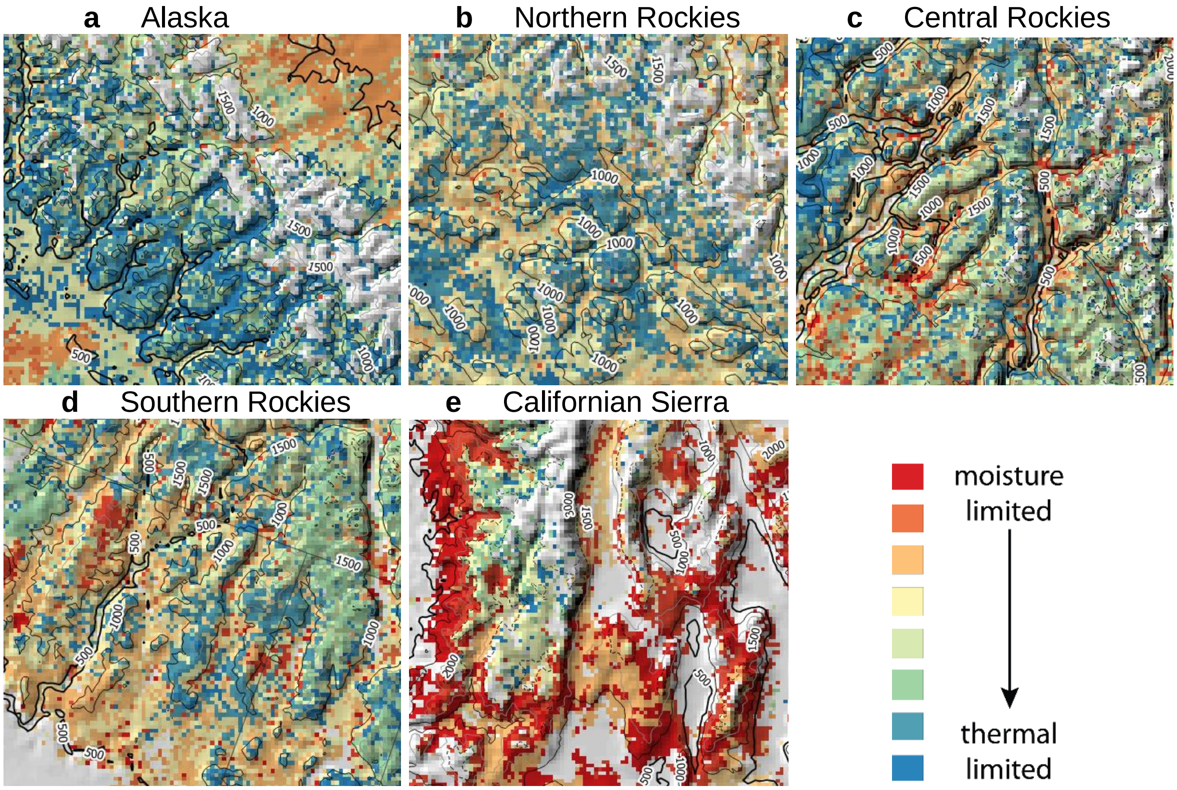

Figure 2-4. Distribution of climatic response clusters in six western mountane regions from north (a) to most southern (e). The same response function clusters occur in all regions at different frequencies, with low-elevation drought-limited clusters most frequent in the south, and high-elevation cold-limited clusters most frequent in the north.

Chapter 3 - Lack of genetic population differentiation in white spruce implies vulnerability to drought in its western range: implications for assisted migration

3.1. Summary

A cost-effective climate change adaptation strategy for the forestry sector is to move seeds to more northern and higher elevation planting sites as part of ongoing reforestation programs. This is meant to match locally adapted populations with anticipated environments, but adaptive traits do not always show population differences suitable to mitigate climate change impacts. For white spruce, drought tolerance is a critical adaptive trait to prevent mortality and productivity losses. Here, we use a 40 year old provenance experiment that has been exposed to severe drought periods in 1999 and 2002 to retrospectively investigate drought response and the adaptive capacity of white spruce populations across their boreal range. Relying on dendrochronological analysis under experimentally controlled environments, we evaluate population differences in resistance, resilience and recovery to these extreme events. Results showed evidence for population differentiation in resistance and recovery parameters, but provenances conformed to approximately the same growth rates under drought conditions and had similar resilience metrics. The lack of populations with better growth rates under drought conditions is contrary to expectations for a wide-ranging species with distinct regional climates. Populations from the wettest environments in the northeastern boreal were surprisingly drought tolerant, suggesting that these populations would readily resist water deficits projected for the

2080s, and supporting the view that northeastern Canada will provide a refugium for boreal species under climate change. The findings also suggest that white spruce is sensitive to growth reductions under climate change in the western boreal. The study highlights that population differentiation in adaptive capacity is species and trait specific, and we provide a counter example for drought tolerance traits, where assisted migration prescriptions may be ineffective to mitigate climate change impacts. For resource managers and policy makers, we provide maps where planning for widespread declines of boreal white spruce forests may be unavoidable.

3.2. Introduction

Since the beginning of the 20th century, mean annual temperature across the North American boreal forest has increased by 1.5 to 2.5 °C, significantly exceeding the mean global temperature increase (Romero-Lankao et al. 2014). In the western boreal, climate conditions have also become drier by around 10% in mean annual precipitation (Mbogga et al. 2009, Romero-Lankao et al. 2014). Warmer temperatures and reduced precipitation together have induced widespread impacts to the boreal forests and its ecosystems due to drought stress (Price et al. 2013). Across large regions, where water deficits limit growth, reduced forest productivity has been documented for western boreal tree species (Chhin and Wang 2008, Hogg et al. 2013, Chen et al. 2017), or in some cases have caused significant dieback and mortality (Allen et al. 2010, Michaelian et al. 2011, Worrall et al. 2013).

White spruce (*Picea glauca* (Moench) Voss) is one of the most common and widely distributed boreal forest species in North America. The species is also commercially important and comprises roughly a quarter of the Canadian forest inventory (Natural Resources Canada 2013). Dendrochronological and inventory plot based research has identified the species as sensitive to growth reductions under warming and increased moisture deficits expected under climate change projections. Water deficits limit the range of white spruce at the southern fringe (Chhin et al. 2004, Chhin and Wang 2008, Lu et al. 2019). Further, droughts caused significant mortality of white spruce (Peng et al. 2011). Barber et al. (2000) and Hogg et al. (2017) showed that moisture stress reduced growth due to recent climate trends, and D'Orangeville et al. (2018) predict that white spruce is more sensitive to growth reductions under increased temperature than other boreal species.

To address negative impacts of climate change and associated extreme events on natural and managed forest ecosystems, several general options are available (Millar et al. 2007). Adaptive strategies for forest management include the protection of highly valued resources, resilience options to improve the capacity of ecosystems to recover after disturbance, and management response to facilitate the transition of ecosystems from current to new conditions. A cost-effective climate change adaptation strategy for the forestry sector is to move seeds to more northern and higher elevation planting sites as part of ongoing reforestation programs (Lenoir et al. 2008, Pedlar et al. 2012, Aitken and Bemmels 2016). This is meant to match locally adapted populations with anticipated environments, but adaptive traits do not always show population differences suitable to mitigate climate change impacts.

A commonly used approach to study local adaptation of populations, the adaptive capacity of a species, and genetic variability in adaptive traits are provenance and progeny field trials. In these experiments seeds from different origins, sometimes with a known pedigree, are grown in a common garden to reveal intra-species genetic variance. Provenance and progeny trials for white spruce have been evaluated for disease resistance (Alfaro et al. 1996), wood quality (Beaulieu et al. 2002), and survival and growth (Li et al. 1997, Lu et al. 2014, Gray et al. 2016). Resistance to drought and other climate extreme events are not normally reported from provenance experiments, but they have been assessed in natural stands through tree ring analysis (e.g., Fritts 1974, Fritts et al. 1991, Jacoby and Darrigo 1995). Using tree ring analysis in common garden experiments is a useful, new research approach that combines the strength of historical biology analysis with population genetic and genomic inferences (Montwé et al. 2015, Montwé et al. 2016, George et al. 2017, Housset et al. 2018).

Here, we contribute a dendrochronological analysis of white spruce provenances from throughout the range sources of the species, grown for almost four decades in a common garden experiment at a centrally located test site that already experienced above-average water deficits compared to the species range under normal conditions. The test site has been exposed to severe drought periods in 1999 and 2002 that caused significant growth reductions and mortality of tree species in the region, offering a unique opportunity to study drought response of genotypes in a common garden environment where environmental variation is uniform and experimentally controlled. Specifically, we (1) quantify drought resistance, recovery, and resilience of boreal spruce populations from throughout the range; we (2) evaluate drought tolerance traits in the context of long-term growth performance and survival, and (3) we interpret correlations between drought tolerance and growth metrics in the context of the origin climate of provenances to infer local adaptation. The results are discussed in the context of sensitivity to growth reductions under climate change, and possible climate change adaptations strategies to maintain health and productivity of one of the ecologically and commercially most important boreal forest tree species.

3.3. Materials and methods

3.3.1. Plant material and sampling design

White spruce seedlings from 43 provenances across Canada were planted at a common garden trial near Calling Lake, Alberta, (55°17’N, 113°09’W, 625 m ASL). Planting stock consisted of containerized seedlings, germinated in 1978 and planted in 1982. This field trial is a randomized complete block design with 5 blocks, 5-tree row plots with 2.5 m × 2.5 m spacing. Two border rows were planted to minimize edge effects. Tree height and survival was evaluated at age 32, and the diameter at breast height (DBH), approx. 1.3 m above the ground, was measured at age 27.

For dendrochronological analysis, we used a subsampling design with 33 of 43 provenances. Where the original sampling design had local clusters of samples, sometimes from near identical locations, we selected one provenance to arrive at a well distributed geographical and climatic representation of growing conditions throughout the range of the species (Figure 3-1). Within each block of the experimental design, one tree was randomly selected per provenance (5 blocks × 33 provenances = 165 trees in total). The relatively small sample size was chosen to minimize potential injuries on these valuable genetic trials, and was based on a power analysis of the number of samples needed detect population differences in growth and drought tolerance traits. Two cores were sampled in 2017 from each individual at north and south sides of the stem with an increment borer at approximately 0.5 m stem height to capture growth data since the late 1980s while coring well above areas of growth influenced by the root collar. Ring-width values from the two cores per tree were averaged prior to statistical analysis.

3.3.2. Dendrochronology analysis

Core samples were preserved in plastic straws with slices for air circulation. After air drying for two weeks, a total 324 increment cores were glued in wooden cores mounts (six cores were too broken to reconstruct). Then, cores were prepared using a belt sander with progressively finer grains (400, 240, 100 grains per inch) and scanned at 6400 DPI (Epson Perfection V800 Pro). Scans were analyzed with WinDENDRO software, version 2016a (Regent Instruments Canada Inc., Québec). Tree ring series were cross-dated in WinDENDRO and errors such as missing rings were corrected prior to generating final cross dating statistics with the program COFECHA (Holmes 1983, Grissino-Mayer 2001).

To evaluate the cross-dating reliability of the complete chronology (from 1988 to 2017), we calculated the Expressed Population Signal (EPS) according to Wigley et al. (1984) for all 165 individuals. An exceptionally high value (EPS=0.99) suggested near perfect cross dating, but this is an expected result for trees grown in a randomized common garden where environmental variation is experimentally controlled. In natural stands, an EPS of 0.85 is considered sufficiently consistent (Speer 2010).

Cross-dated chronologies were then subjected to detrending, because ring width is not only controlled by growing conditions but also by the age of the tree, with the ring widths near the pith being largest. In standard dendrochronological research, this age-related trend is removed by subtracting a spline function fitted to each chronology. The residual after detrending is then converted to a standardized chronology with a mean of one and interannual growth variation expressed in units of standard deviations for further analysis (Cook et al. 1990). However, fitting individual splines to trees grown in a common garden experiment for detrending might partially remove population differences. We therefore used a common spline function that has the same shape for all trees. Further, in our common garden trial, where all trees have the same age and were grown under controlled environments, the absolute growth value carries important information. We therefore did not work with standardized ring widths, but reversed the standardization after detrending using the original average and standard deviation of each tree ring chronology. The detrending was implemented with a smoothing parameter of 0.7, a relatively stiff spline, fitted to the combined normalized chronology data with the *smooth.spline()* function of the stats package (R Core Team 2020).

To quantify white spruce resilience to the two drought events, we calculated indices for resistance, recovery, and resilience (Lloret et al. 2011). Resistance was calculated as the ratio of the radial growth during the drought over growth before the drought (higher resistance value indicates a small growth reduction during the event). Recovery was measured as the mean post-disturbance growth divided by the growth during the drought year (high recovery values indicate a strong rebound of growth after disturbance). The resilience index is the ratio of growth performance after and before the disturbance to quantify permanent damage (a resilience value below one suggests the tree failed to recover to the pre-disturbance performance after the drought).

In our common garden experiment, the two-year period between the first and second drought event was not long enough for trees to fully recover from the very first drought event. We therefore used five years before the first drought (1993-1997) and five years after the second drought (2003-2007) as pre-disturbance and post-disturbance reference periods for calculation of indices for both drought events.

3.3.3. Climatic characterization

Climate data of seed source origins were obtained using the software ClimateNA v5.21 (Wang et al. 2016). We used the climate period 1961-1990 as a representation of normal climate conditions. The period is a compromise between weather station coverage and representing climate conditions to which populations are putatively adapted. Prior 1961, weather station coverage becomes sparse leading to inaccurate climate estimates, and subsequent to 1990 there is a significant anthropogenic warming signal. Provenances were grouped into six regions considering geographic location of the provenances (Fig. 3-1a) as well as climate conditions summarized by a principal component analysis (Fig. 3-1b). The groups approximately corresponded to the Canadian Ecoregion classifications (Boreal Cordillera, Boreal Plains, Boreal Shield, Maritime Mixedwood, Montane Cordillera, and Temperate Mixedwood), and we use these names throughout the text when referring to populations of white spruce within these regions. Principal component analysis was implemented with the *princomp* () function of the stats package using the correlation matrix. We also generate maps of current and projected water deficits for the range of white spruce with the same ClimateNA v5.21 software package, using gridded data publicly available at *http://tinyurl.com/ClimateNA.*

To more precisely characterize growing conditions at the planting site, we obtained daily weather records from a meteorological station in Calling Lake (Station ID 3061117), at approximately 4 km distance to the planting site, operated by the Government of Canada (*http://climate.weather.gc.ca*). The weather data included daily average, maximum, minimum temperature (°C) and the daily amount of snow and precipitation (mm). We calculated water deficits on a daily scale, based on a reference evapotranspiration (ET_0) estimated with Hargreaves and Samani (1985) method, also used by the ClimateNA v5.21 software package.

3.3.4. Statistical analysis

Taking advantage of the randomized complete block design, regional means of drought response metrics and field measurements were estimated with a mixed model approach and Best Linear Unbiased Estimates (BLUEs) for the average and standard error of each region. For measurements of height and DBH, we evaluated 25 trees per provenance planted in 5-tree row plots with a linear mixed model with blocks and plots within blocks specified as random effects. Regions were specified as a fixed factor and provenances nested within regions were also treated as a random effect. The analysis was implemented with the *asreml*() and *predict*() functions of the asreml package (Gilmour et al. 2015) based on the following linear model:

$$Y_{ijklm} = \mu + R_{i} + Prov(R)_{ij} + B_{k} + Plot(B)_{lk} + e_{ijlkm}$$

where Y is the measurement of individual m of Provenance j from Region i planted in Plot l within Block k. The overall mean is denoted as μ and the experimental error as e. The model effects *R*, *Prov(R), B* and *Plot(B)* denote Region, Provenance within Region, Block, and Plot within Block, respectively.

The survival rate of white spruce from each region was estimated by fitting generalized linear mixed model (GLMM) for binomial data with the *glmer*() function of the lme4 package (Bates et al. 2015). Since only one tree per provenance of each block was sampled for drought resilience analysis, our linear mixed models for drought indices specify regions as fixed effects and blocks as random effects. For multiple pairwise statistical comparisons among regions, we corrected the α-value with a Tukey adjustment, implemented with the *cld*() function of emmeans package (Lenth 2018). The residuals of each mixed model were visually checked for meeting assumptions of the respective distributions of errors.

Associations among climate of origin and provenance means of traits measured in the common garden experiment were assessed with the non-parametric Spearman correlation coefficient, implemented with the *cor.test()* function of the R base package (R Core Team 2020). Significance of correlations was adjusted for multiple inference using Holm’s method (Rice 1989), implemented with the *adjust()* function of the R base package.

3.4. Results

3.4.1. Chronologies and test site climate

All chronologies shared a strong growth reduction in 1999, corresponding to a low precipitation period from 1997 winter to 1999 (Fig. 3-2D, first gray bar Drought 1, area colored red below normal expectation). The precipitation shortage was especially noticeable during the summers when most precipitation falls at the test site in a normal year. This drier-than-normal period was also remarkably warm (Fig. 3-2B), causing a severe moisture deficit that resulted in reduced growth for all provenances (Fig. 3-2A and 3-2C). The second pronounced growth reduction (Fig. 3-2, Drought 2) occurred in 2002, coinciding with an unusually cold spring and a moderately dry summer during the year. Growth of provenances did not fully recover before this second drought period, and the response to the second drought might therefore be influenced by the first drought period as well. This second drought in 2002 was shorter than the first in 1999 at the study site, but it is still recorded as one of the most serious prairie droughts in the last several decades (Bonsal and Regier 2007, Wheaton et al. 2008). The average growth response of regional populations was reasonably precise and constant over time as indicated by standard errors of around 0.3 mm ring width.

3.4.2. Provenances and origin climate

Most geographic groups of provenances had distinct regional origin climates, except the Montane Cordillea region, which comprises a variety of climates due to complex topography (Fig. 3-1b). The vectors represent the strength and directions of correlations of climate variables with the first two principal components. Provenances with high scores in the first principal component (PC1) (right side of Fig. 3-1b) experienced a long growing season (MAT, MCMT, opposite DD < 0) and high moisture availability (MAP, MSP, PAS, opposite SHM). Provenances that score high for the second principal component (PC2, y-axis of Fig. 3-1b) experienced low growing season temperature variables (MWMT, DD > 5, FFP). Together, PC1 and PC2 explained 82.5% of total variance in climate variables.

The coldest and driest climate of the sample design was found in the Boreal Cordillera and Boreal Plains ecoregion of western Canada (Fig. 3-1, Table 3-1). The eastern neighboring area, the Boreal Shield ecoregion comprising Ontario and Quebec sources, showed similar temperature conditions but twice the precipitation, which results in a lower annual moisture deficit. Maritime Mixedwood provenances from the east coast received the highest precipitation, the smallest moisture deficit, and the warmest winters. The southeastern Temperate Mixedwood ecoregion of southern Ontario had high annual moisture deficits due to high temperature. Montane Cordillera of the west coast was characterized by maritime climate with cool summers, relatively mild winters and a low continentality score.

3.4.3. Regional population differentiation

Best linear unbiased predictions (BLUEs) of regional population means were estimated with a generalized linear mixed-effects models (GLMMs) for survival rate, and a linear mixed-effects models (LMMs) for all other traits (Table 3-2). Conforming to the expectations that local sources would be best adapted to the climate of the planting site, provenances from the local region (Boreal Plains) had the lowest mortality and showed good growth performance, with one of the highest height and diameter values measured after 32 and 27 growing seasons, respectively. Populations from Temperate Mixedwood (southern Ontario) and Boreal Shield (Ontario and Quebec) showed overall growth performance as competitive as local sources with the latter one originating from regions approximately 5 °C warmer and double the annual precipitation compared to the test site (Table 3-1). The excellent growth performance of the non-local sources from the Boreal Shield did not significantly compromise survival (Table 3-2). In contrast, the sources close to the west coast and east coast had inferior growth performance and low survival rates at the central test site.

3.4.4. Population response to drought

Regional population differentiation was also readily apparent in annual growth increments with the local provenances, Boreal Shield and Temperate Mixedwood sources being the best performers during the pre- and post-disturbance periods (Fig. 3-2A). During the drought periods, provenances from all regions behaved similarly with reduced ring width increments, but the decreased measurements in percent of the pre-disturbance productivity (resistance) were inversely proportional to the normal growth rates before disturbance: 31% loss of growth (i.e. 69% resistance in 1999) for the most resistant Boreal Cordillera sources versus over 56% reduction for the sources from the Temperate Mixedwood and Boreal Shield regions (Table 3-2). For the 2002 drought, the percent reduction in growth was less differentiated (Fig. 3-2), with no significant regional differences in resistance (Table 3-2). Provenances from all regions recovered approximately to their pre-disturbance levels, indicating no permanent damage after two consecutive drought events. Unlike the 1999 event, the 2002 growth reduction showed no statistically significant regional differences of resistance or recovery.

3.4.5. Genetic adaptation to local climate conditions

Seed sources originating from warm and wet origin climate showed superior growth potential at our test site (Fig. 3-3). Height and diameter positively correlated to long and moist growing seasons of the provenance origin climate. In contrast, a high survival rate was closely associated with dry environments and cold, prolonged winters. Climate variables that showed strong correlations with height and diameter were not associated with survival rates. Resistance for the 1999 drought was negatively related with growing season length and summer precipitation of the provenance origin climate, which mirrored associations with height and diameter. Therefore, trees from warm and moist climate conditions grow well, but also experience the proportionally largest growth reductions under drought conditions. For the climate conditions during the 2002 drought period, characterized by a cool spring and dry summer, correlations among provenance origin climate and drought metrics were weak ($r < 0.5$) (Fig. 3-3). Provenances from continental climates (dry, hot summers with cold winters) maintained better growth under the 2002 climate conditions. Since the recovery index is an inverse calculation of the resistance values under full recovery, matching, but opposite correlations for recovery and resistance indices were observed for each disturbance. No genetic differentiation and no strong associations were identified between resilience and the origin climate of provenances, indicating that provenances have comparable drought resilience, with all regional populations avoiding permanent damage from the drought episodes.

3.5. Discussion

The general expectation for widespread forest trees that occur over a wide range of environmental conditions is to find genetic population differentiation in growth and adaptive traits. Local sources are expected to have the highest fitness, and often also the highest growth rates (Morgenstern 1996). Our data for white spruce partially conforms to these expectations. Local sources from the Boreal Plains ecoregion were among the top performers. Boreal Shield and Temperate Mixedwood sources from eastern Canada slightly outperformed the local sources, but for the Temperate Mixedwood provenances, fitness appears to be compromised based on the lower survival rates. Growth measurements generally conform to comparable trials in eastern Canada that also showed populations from the southern fringe of the boreal forest have the highest growth potential, even when transferred to northern test sites (e.g., Lu et al. 2014).

A possible explanation for this observation is that southern populations already lag behind their optimal niche due to climate warming that has occurred over the last several decades. Alternatively, adaptation to biotic factors may explain the superior growth potential of Temperate Mixedwood sources from southern Ontario. In warmer mixed forest ecosystems, competition for light from other species causes higher selection pressure for fast growth, causing individuals to allocate less resource to survival adaptions (Loehle 1998). When such sources are moved northward beyond their optimal climatic niche, their fitness could be compromised as indicated by lower survival rates (Table 3-2). Similar to Andalo et al. (2005), we find that population differentiation in growth and survival is related to the temperature of the provenance origin. Here, the winter temperature of the origin was correlated with survival and the growing season length was associated with growth (Fig. 3-3).

The most notable result from this range-wide provenance experiment is that no obvious adaptation in growth and survival were observed in response to various precipitation regimes (Fig. 3-3), conforming to the finding of equal drought resilience even when provenances from throughout the natural range were exposed to extreme drought conditions that severely impacted the annual growth of all provenances (up to over 50% growth reduction compared to a normal year). While resistance and recovery metrics significantly varied among populations (Table 3-2), no crossover interactions were observed where a provenance with lower growth under favorable moisture conditions exceeds productive provenances under drought conditions (Fig. 3-2). No population was able to maintain a substantially higher level of productivity under drought constraints. This implies that the species as a whole may lack genetic variation and adaptive capacity to maintain growth under drought, also supported by findings for the species in eastern Canada (Lu et al. 2016). That said, our sampling design did not cover a sufficient amount of samples from isolated or marginal populations at the southern boreal fringe, where such adaptation may still be found.

Nevertheless, our results are different to what has been observed for other boreal and temperate conifers. For example, lodgepole pine, which overlaps with white spruce in the west, lacks adaptive capacity for drought conditions in northern populations of the Boreal Cordillera but shows distinct adaptations to drought in southern populations (Montwé et al. 2016). Douglas-fir showed a trade-off between growth performance and drought tolerance, with the provenances from the warmest and driest origins showing the highest drought tolerance (Eilmann et al. 2013, Bansal et al. 2015, Montwé et al. 2015). Norway spruce also shows strong adaptive genetic variance in drought responses, with populations from the central and southeastern portion of the range exhibiting high resistance (Trujillo-Moya et al. 2018).

These results have implications for seed movement as an adaptation strategy for climate change. Human assisted migration as part of regular reforestation programs has been proposed to match planting stock with anticipated new environments, as populations become progressively mismatched with the climate to which they are adapted (Peters and Darling 1985, Lenoir et al. 2008, Bertrand et al. 2011, Pedlar et al. 2011, Aitken and Bemmels 2016). As an adaptation strategy, assisted migration prescriptions are now being implemented to address maladaptation of forests in the boreal North (Ste-Marie 2014). The provinces of British Columbia, Alberta, Ontario, and Quebec updated seed transfer rules to facilitate assisted migration through seed movement in their regular reforestation programs (e.g., O'Neill et al. 2017). However, genetic differentiation among populations is a necessary requirement for assisted migration prescriptions to be effective. If no genetic differentiations can be identified in drought resilience or for maintenance of growth under drought conditions, seed movement may have not be able to improve drought tolerance in areas that are expected to have high water deficits.

To provide additional context for interpreting the results of this common garden experiment, we provide maps of moisture deficits for the species range of white spruce for the 1961-1990 normal period and projected future conditions (Fig. 3-4), generated with the same methodology as for obtaining moisture deficit estimates for the test site and provenance locations (Table 3-1). Generally, climate moisture deficits for the range of white spruce ranges from values close to zero in the northeast to values of around 250 mm in portions of its western range. Ensemble projections from CMIP5 global circulation models according to (Wang et al. 2016) show that

250 mm moisture deficits are exceed along the southern fringe of the species distribution as well as for large parts of Alberta and the Northwest Territories (Fig. 3-4, brown hues). This is substantially drier than at the test site during the growing period (152 mm). Given the observed growth response during drought years, it seems likely that white spruce growth throughout the generally drier western portion of the boreal forest may on average be reduced by a substantial amount (up to 50% observed in this experiment), without the option to adapt to climate change by selection of drought tolerant populations in reforestation programs.

While we did not observe drought-induced mortality or dieback at this specific experiment, water deficits limit the range of white spruce at the southern fringe (Chhin et al. 2004, Chhin and Wang 2008), and have caused mortality of white spruce in the west (Peng et al. 2011). In comparison to five other boreal species, (D'Orangeville et al. 2018) found that white spruce appears to be especially prone to growth reductions under all climate simulations above 2 °C warming. While white spruce did not show massive mortality in response to drought as other species have (Worrall et al. 2013), their general fitness appears compromised. Searle and Chen (2017) showed a long term trend towards reduced abundance of late successional conifers (represented by 93% white spruce), with the strongest reductions observed in western Alberta, and they attributed the trend to warming and increases in CO_2.

For the eastern half of the species range, projections up to the 2080s do not appear to exceed values of 250 mm in moisture deficits. Results from the provenance trial further show that eastern provenances generally grow well under these conditions. In the northeast, predicted climate moisture deficits are generally above 100 mm, substantially wetter than the planting site (152 mm). These results support the view that northeastern regions of Canada appear to be a likely refugium for boreal forest tree species in a warming climate (D'Orangeville et al. 2016), while the western part of the boreal forest is prone to growth reductions under warming environment because of moisture-sensitivity. For resource managers and policy makers our results suggest that planning for widespread declines of western boreal white spruce forests may be unavoidable in many parts of the species range. Specifically, moving seed sources northward in the western boreal region to counter anticipated moisture deficits may not be an effective climate change adaptation strategy.

3.6. Conclusion

The results highlight that population differentiation in adaptive capacity to climate environments can be species and trait specific, and we provide a counter example where assisted migration prescriptions may be ineffective to mitigate climate change impacts in the western boreal portion of the species range. The study also provides direct evidence that northeastern populations of white spruce may be safe from negative climate change impacts for the medium term future, with no permanent damage observed on northeastern populations when subjected to drought conditions at the test site that they would be unlikely to experience in their native region even under pessimistic climate change projections by the 2080s. In contrast, the fate of western populations is more difficult to assess based on direct evidence from this study. We observed strong growth reductions, but no permanent damage arising from droughts in a region where the average annual water deficit is around 150 mm. However, this value is predicted to be exceeded by the 2050s throughout the western half of the species distribution. Planning for widespread declines of western boreal white spruce forests may be unavoidable where water deficits limit the species productivity. This may lead to large-scale mortality as recently observed for lodgepole pine in western boreal forests. Such sub-continental scale ecosystem disruptions are likely too large to be effectively mitigated through forest management or reforestation prescriptions.

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Table 3-1. Climate conditions for the 1961-1990 normal period for the provenance origins, summarized by regions as shown in Fig. 1, with standard deviations shown in parentheses, as well as climate conditions at the Calling Lake test site in AB. The climate variables include mean annual temperature (MAT); mean warmest month temperature (MWMT); mean coldest month temperature (MCMT); temperature difference is a measure of continentality (TD); mean annual precipitation (MAP); mean summer precipitation (MSP); and climatic moisture deficit (CMD).

Location	MAT (°C)	MWMT (°C)	MCMT (°C)	TD (°C)	MAP (mm)	MSP (mm)	CMD (mm)
Calling Lake (field site)	0.6	15.6	-18.0	33.6	491	336	150
Boreal Cordillera (n = 4)	-3.3 (1.3)	13.7 (1.2)	-22.6 (3.3)	36.3 (4.3)	310 (46)	193 (19.6)	201 (43.5)
Boreal Plains (n = 9)	-0.6 (1.6)	17.0 (1.4)	-21.7 (2.5)	38.7 (2.3)	450 (66)	291 (51.3)	177 (30.4)
Boreal Shield (n = 9)	0.7 (1.0)	16.5 (0.8)	-16.9 (2.5)	33.5 (2.9)	922 (179)	468 (66.8)	66 (52.6)
Maritime Mixedwood (n = 3)	5.0 (0.5)	17.4 (0.7)	-6.2 (0.8)	23.5 (1.3)	1246 (146)	463 (31.1)	52 (16.0)
Montane Cordillera (n = 4)	1.2 (1.6)	13.4 (0.7)	-12.2 (3.5)	25.6 (3.5)	702 (250)	290 (77.1)	174 (66.0)
Temperate Mixedwood (n = 4)	5.5 (0.6)	20.1 (0.3)	-10.9 (1.6)	31.0 (1.6)	832 (11)	384 (19.2)	192 (10.7)

Table 3-2. Growth performance and drought response of white spruce provenances from six regions tested at a central provenance trial in Calling lake AB. Height and diameter at 1.3 m of six white spruce populations after 32 and 27 years of growth, respectively. Drought indicator values (larger values are better) for resistance, recovery of two drought years and resilience for overall disturbances. Best linear unbiased predictions of means (BLUEs) and standard error of the means (in parentheses) were estimated with a generalized linear mixed-effects models (GLMMs) for survival rate, and a linear mixed-effects models (LMMs) for all other traits. Different letters behind the values indicate significant differences between groups (α = 0.05).

	Growth traits			Drought tolerance traits				
Region	Height 32	DBH 27	Survival rate	Resistance 1999	Recovery 1999	Resistance 2002	Recovery 2002	Resilience
Boreal Cordillera	546(55) a	63(8) a	0.97(0.02) ab	0.69(0.04) a	1.70(0.14) a	0.64(0.06) a	1.73(0.17) ab	1.10(0.07) a
Montane Cordillera	700(56) b	84(8) b	0.84(0.07) ab	0.60(0.04) ac	1.77(0.15) ad	0.53(0.06) a	2.14(0.12) b	0.95(0.07) a
Maritime Mixedwood	767(64) b	79(9) ab	0.78(0.10) b	0.60(0.05) ac	1.85(0.16) abd	0.69(0.07) a	1.62(0.13) a	1.07(0.07) a
Boreal Plains	908(37) c	116(5) c	0.97(0.01) a	0.50(0.03) bc	2.17(0.11) bcd	0.63(0.05) a	1.72(0.09) a	1.04(0.05) a
Boreal Shield	957(37) c	117(5) c	0.95(0.02) ab	0.44(0.03) b	2.26(0.11) bc	0.55(0.05) a	1.78(0.09) a	0.96(0.05) a
Temperate Mixedwood	966(55) c	122(8) c	0.89(0.05) ab	0.44(0.04) bc	2.43(0.14) c	0.67(0.06) a	1.71(0.12) a	1.04(0.07) a

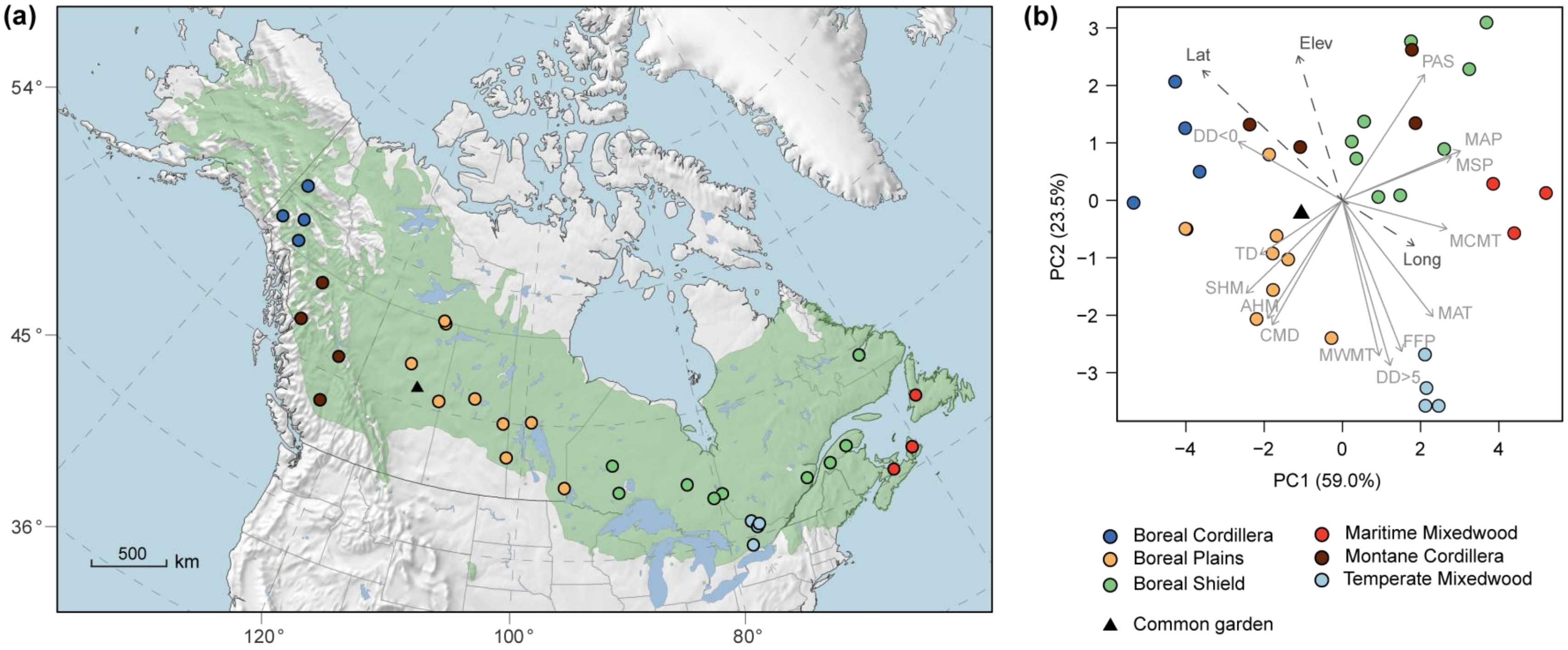

Figure 3-1. Location of white spruce provenances and test sites (**a**) and their climatic conditions (**b**). The 33 provenances are assigned to geographic regions with similar climate that approximately correspond the Canadian ecozone classification system. The vectors in the principle component analysis show how provenances and regions are associated with climate variables. Climate variables include mean annual precipitation (MAP), mean summer precipitation (MSP), precipitation as snow (PAS), mean annual temperature (MAT), mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), growing degree-days above 5 °C (DD > 5), continentality (TD), chilling degree-days (DD < 0), frost-free period (FFP), annual and summer heat-moisture index (AHM, SHM), and Hargreaves climatic moisture deficit (CMD). Geographic coordinates of provenances including Lat(itude), Long(itude), and Elev(ation) were represented in dashed arrows. The species range of white spruce is shown in green.

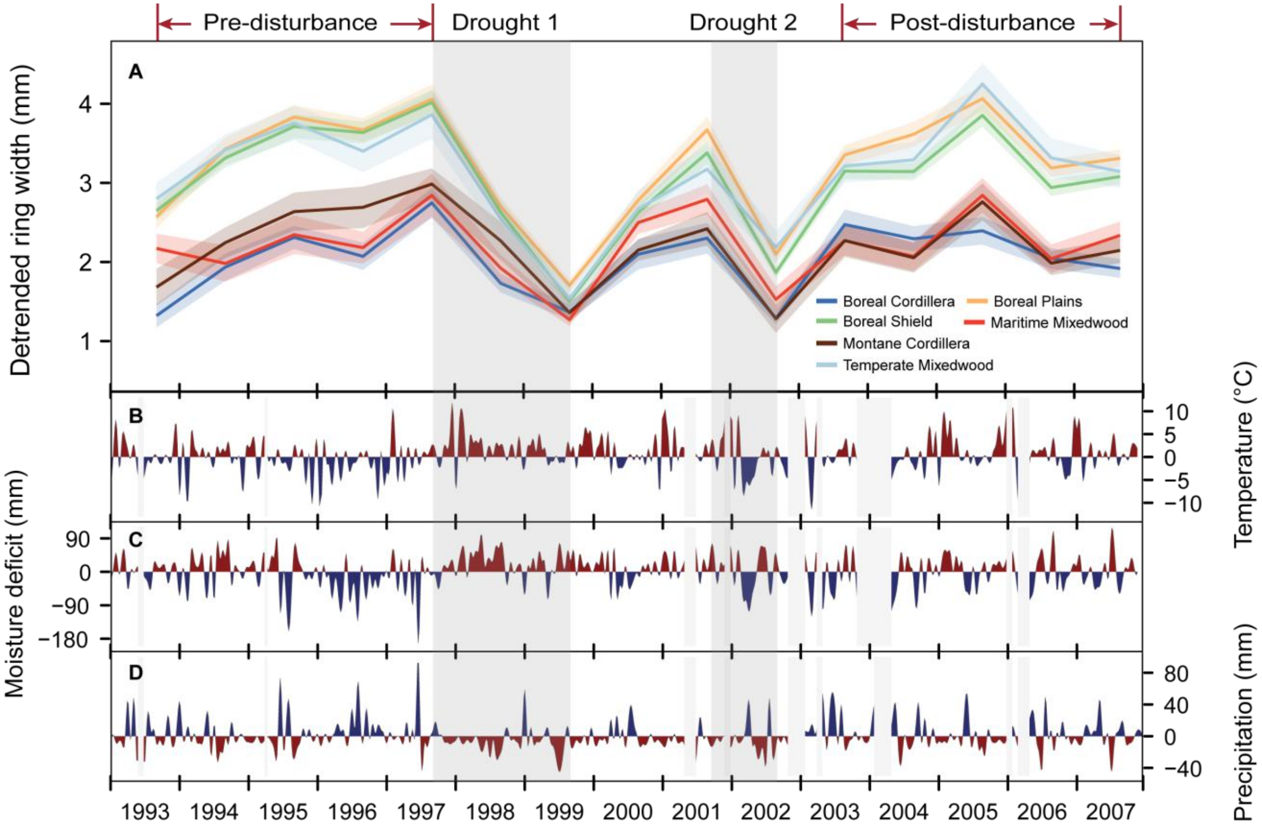

Figure 3-2. Detrended ring width increments (**A**) of provenances summarized by regions as shown in Fig. 3-1. The standard error of each group is represented by colored transparent bands. Panels **B**, **C**, and **D** show anomalies in temperature, moisture deficit, and precipitation relative to the climate normal climate conditions of the test site. The integral from the zero value shown as colored area visualizes the severity of extreme climate events, integrating the size and length of the anomaly. Two drought periods around 1998-1999 (Drought 1) and 2002 (Drought 2) were highlighted with in dark grey bars. Missing values of the weather station record at the test site were represented by light grey bars.

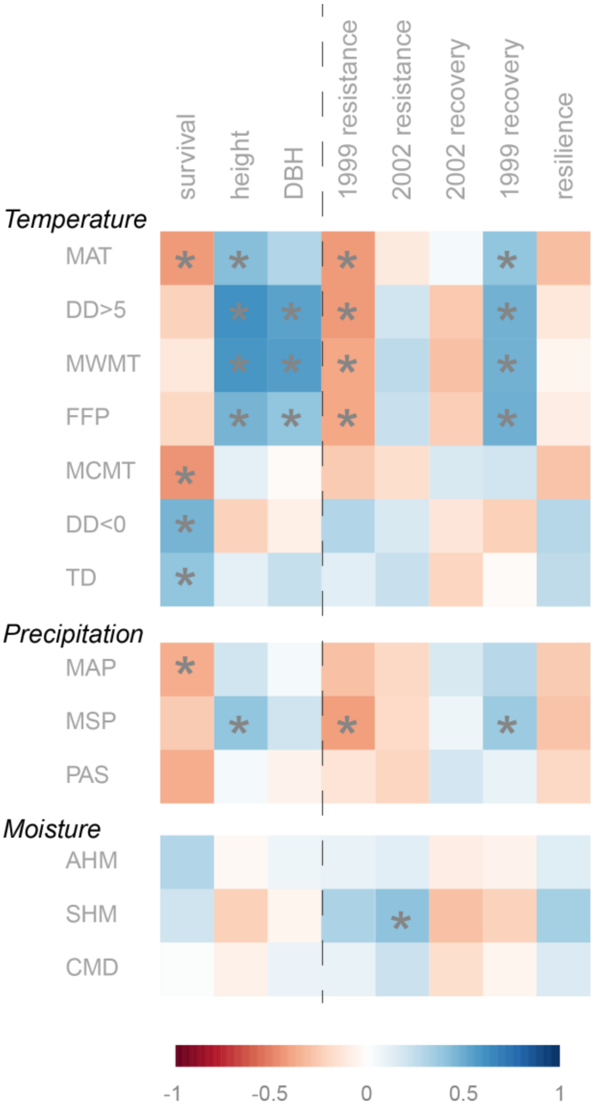

Figure 3-3. Correlation coefficient among the climate of provenance origin and growth measurements at the field site and drought metrics calculated from tree ring analysis. Significant correlations after adjustment for multiple inference are highlighted with asterisks ($p < 0.05$). Climate variables include mean annual temperature (MAT), chilling and growing degree-days (DD < 0, DD > 5), mean temperature for the warmest (MWMT) and coldest month (MCMT), frost-free period (FFP), continentality (TD), growing season precipitation (May to September) (MSP), annual precipitation (MAP), precipitation as snow (PAS), annual and summer heat-moisture index (AHM, SHM), Hargreaves climatic moisture deficit (CMD). DBH abbreviates diameter at breast height.

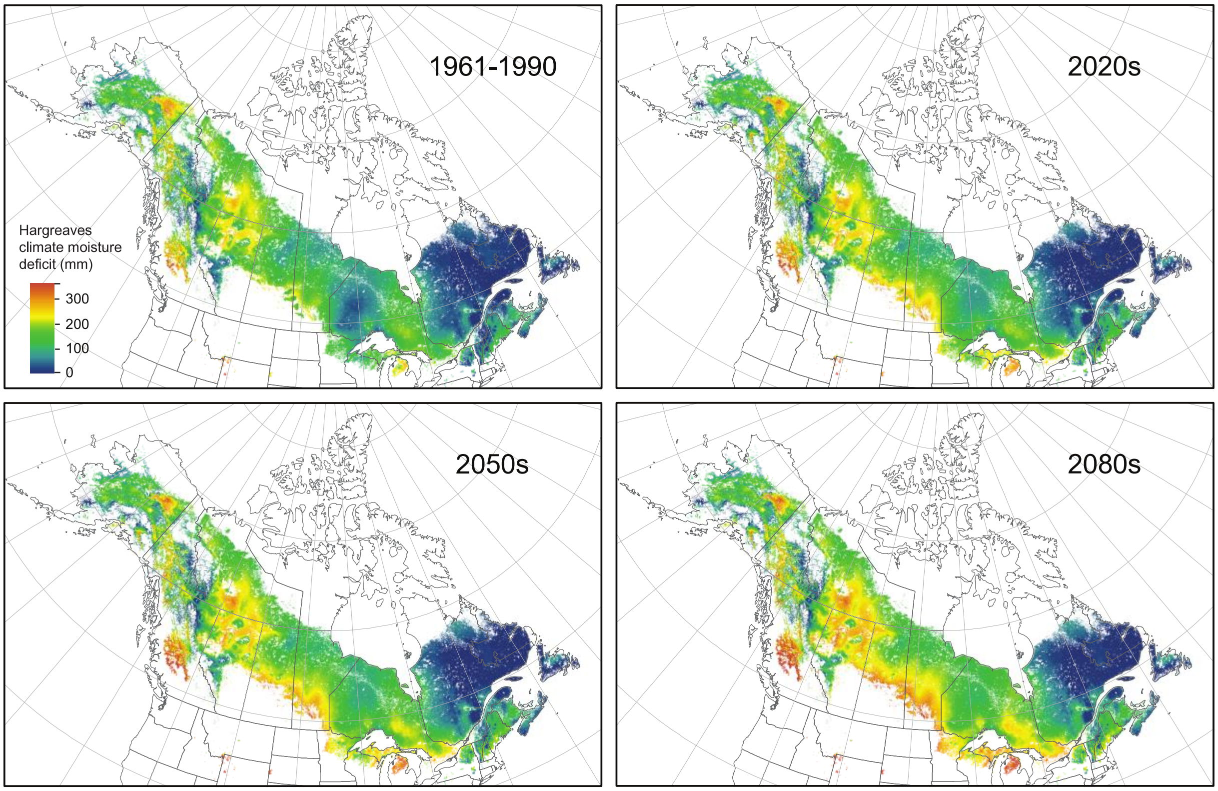

Figure 3-4. Hargreaves climatic moisture deficit (CMD) for the current distribution of white spruce. The 1961-1990 normal represents a historic reference period, and the 2020s, 2050s and 2080s are ensemble multi-model (CMIP5) projections according to (Wang et al. 2016).

Chapter 4 - Adapting reforestation programs to observed and projected climate change

4.1. Summary

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 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 feasibility as well as magnitude and direction of assisted migration prescriptions to adapt their reforestation programs to new planting environments.

4.2. 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 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., Lu et al. 2019, 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., Rehfeldt 1995, Savolainen et al. 2007, Pluess et al. 2016, Collevatti et al. 2019).

Seed transfer limits can be implemented in two ways. Allowable seed movement can be limited by geographic or climatic maximum distances from collection to planning location (e.g., Rehfeldt 1994, Parker and van Niejenhuis 1996), 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), and consider genotype by environment interactions as main criteria for seedzone delineation (e.g., Weng et al. 2019).

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 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 (Etterson et al. 2020, Bisbing et al. 2021). To address maladaptation of reforestation stock, assisted migration of locally adapted planting material has been proposed, primarily within species ranges (e.g., Peters and Darling 1985, Pedlar et al. 2011, Williams and Dumroese 2013, Aitken and Bemmels 2016, Park et al. 2018).

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. 2008, Pedlar et al. 2011, O'Neill et al. 2017, 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 adaptational lag that already exists would have the highest priority for implementation to mitigate negative impacts of climate change.

4.3. Materials and methods

4.3.1. 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 degree of latitude and an elevation range 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. 4-1a).

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 consist 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 4-1 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 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).

4.3.2. 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 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 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.

4.3.3. Analysis

Climate gradients were summarized by principal component analysis (PCA), implemented with the *princomp()* function of the R programming environment (R Core Team 2020). 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 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 components, which accounting for 90% of variation in original climate variables. The resulting one-dimensional vector in the direction of the climate change was subsequently used for the analysis of white spruce growth performance variation under projected climate change. The coordinate system rotation towards the climate vector was carried out with a linear model by predicting the climate vector as a function of two principal component scores.

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 current white spruce habitat. This division (of two moisture classes by three temperature series) created six climatic regions, covering 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.

4.4. Results

4.4.1. 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. 4-1). 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. 4-2). Red areas in the PC1 map indicate especially mild winters (c.f., Fig. 4-1, 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. 4-1b), 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. 4-1, 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. 4-1 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 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 4-2). 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. 4-1 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).

4.4.2. Observed and projected climate change

Observed climate change for the breeding regions is indicated in Fig. 4-1 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 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. 4-3). 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. 4-1b). Although precipitation is generally expected to increase under future climate change scenarios, these changes are relatively small compared to the geography of the precipitation gradients. Because of warming temperature, 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 4-3.

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. 4-3). Current white spruce frequencies are highest in the climate space where breeding regions are situated (Fig. 4-3b, 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. 4-3 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. 4-3, 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. 4-3, 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. 4-3, 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.

4.4.3. 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 out an additional rotation of PC1 and PC2 to align the climate change vector with the x-axis of the plot (Fig. 4-4). 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., Fig. 4-4 and 4-1). 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. 4-4). The lower series in the graph contains moister breeding regions (Fig. 4-4, green to blue) and the upper series represents the drier breeding regions (Fig. 4-4, 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.

4.4.4. Transfer function analysis of populations

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. 4-5). Transfers among breeding regions in the dry series (Fig. 4-5a) 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 towards the left). The transfer among breeding regions in the moist series (Fig. 4-5b) 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 differences in the growth among G1, D, and I sources compared to the variance within regions.

4.5. Discussion

4.5.1. 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. The observed and expected multivariate vector of climate change does not align with geographic gradients in latitude and topography of Alberta. The primary environmental gradients across the landscape in this example are a temperature cline along elevation and latitude, as well as a second gradient from milder more maritime (montane) conditions to continental climates in interior plains, a configuration that applies to many parts of the world. As a consequence, straight forward solutions for climate-based assisted migration prescriptions that compensate for observed and projected climate change may be difficult to derive.

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 how white spruce may respond to no-analogue climate conditions under projected climate change. However, Schneider (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 (Peng et al. 2011, Boulanger et al. 2017, Aubin et al. 2018).

The magnitude of observed and projected climate change relative to 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. 4-4). 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. 4-4) should also not increase the risks of exposing vulnerable seedlings to substantially colder planting conditions, where they may be damaged by unseasonal frosts.

4.5.2. 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 differentiation in adaptive traits does 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 differentiation of moist-series provenances in height (blue points) in panel H versus all other panels of Fig. 4-5a. While the populations of the moist series do not reveal any significant differences at most planting sites, the population with the warmest source climate (Region I) 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 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, 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. 4-5a), 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. 4-5b). Cross-over interaction among genotypes are the clearest evidence for local adaptation, and transfers among wet and dry series climates (Fig.

4-5, orange to red color ramps versus blue to green color ramps) should therefore be avoided. 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 × 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). That said, G×E interactions and implied local adaptation was not strong within the wet series or dry series, or may also not be prevalent in other portions of the species range (Lu et al. 2016, Lu et al. 2019).

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.

4.5.3. 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). In planted forests, competition between species is also routinely controlled through spacing, and measures to remove weeds and naturally regenerating trees. 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).

However, we currently have no data to quantify the climatic tolerances of spruce, or how silvicultural interventions, such as 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. Also, genetic test sites close to the species southern range limit in the grassland/parkland transition zone are lacking. Such silvicultural trials and genetic tests should be established under environmental conditions at or slightly beyond the climate space (in the direction of the climate change vector, Fig. 4-4), where forestry is currently practiced, 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.

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Table 4-1. 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	*113*	112	0	1	1	23	1	2	214
D1	3	52	*132*	7	11	4	12	34	73	39
E	4	52	119	*33*	11	14	3	2	3	38
E1	2	4	12	32	*11*	10	1	2	3	2
E2	3	77	22	0	1	*1*	21	2	3	187
G1	2	3	3	0	1	1	*74*	3	2	2
G2	4	4	41	6	11	1	76	*99*	74	2
H	1	3	37	7	12	1	28	35	*76*	2
I	8	114	111	0	2	2	27	4	3	*219*

Table 4-2. Geographic and climatic summary statistics for breeding regions of Alberta. The ranges are given from the 5th to the 95th percentile.

	Geographic characteristics			Climatic variables		
Region	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

Table 4-3. 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, ΔMAT ranges from 2.8 to 3.1 °C).

		Observed		Projected 2020s		Projected 2050s		Projected 2080s	
Code	Climate variable (unit)	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

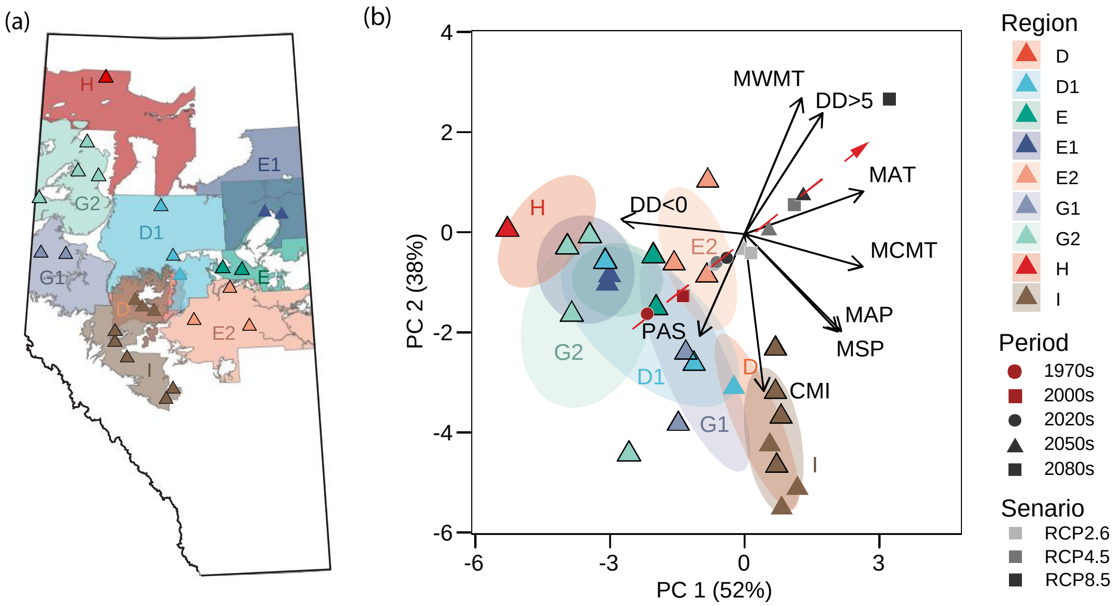


Figure 4-1. Geographic locations of nine Alberta white spruce breeding regions (a), and their climatic conditions described with nine climate variables in a principal component plot (b). For climate variable abbreviations, see Table 4-2. Test sites are indicated by triangles, and the range of climate 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.

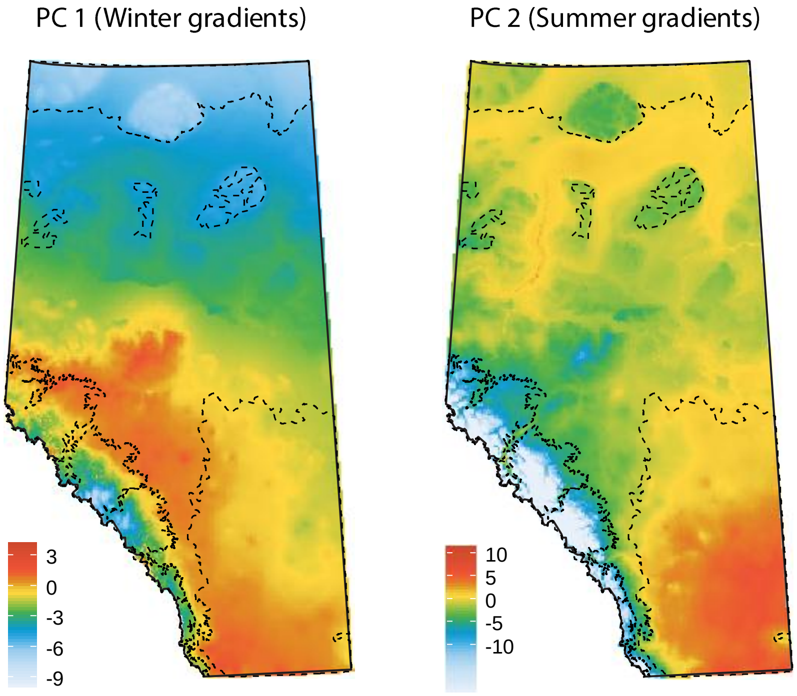


Figure 4-2. Climate gradients expressed as principal component scores for nine climate variables, explaining 90% of the total variation in original climate variables. Principal component scores of 1-km grid cells for Alberta indicate where they are located in the principal component ordination, i.e. the color legends correspond to the PC1 and PC2 values in Fig. 4-1b.

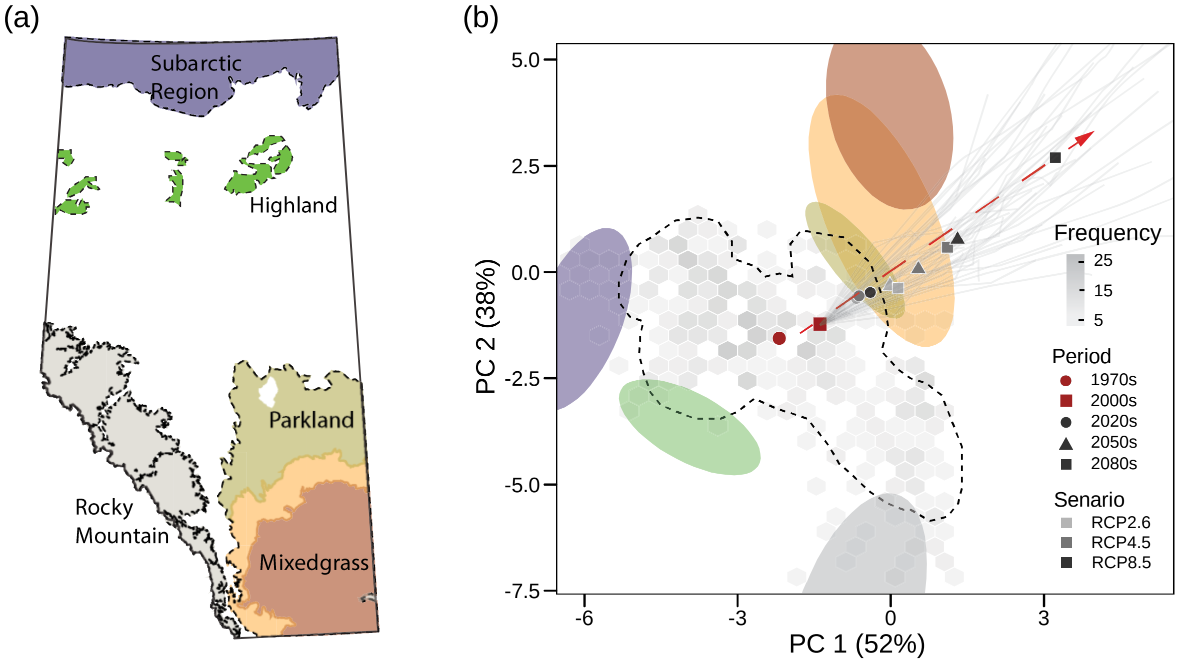


Figure 4-3. The climate space of white spruce breeding regions (dashed line), adjacent ecosystems (colored 80% ellipses), and spruce frequencies for different climatic conditions (hexagons). The ordination is otherwise identical to Fig. 4-1.

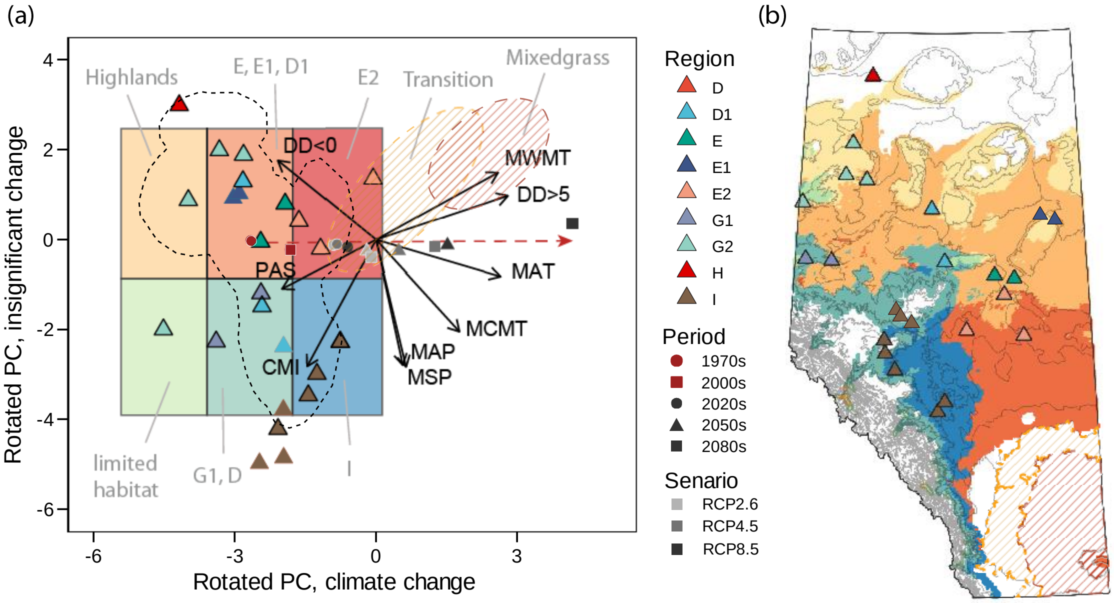
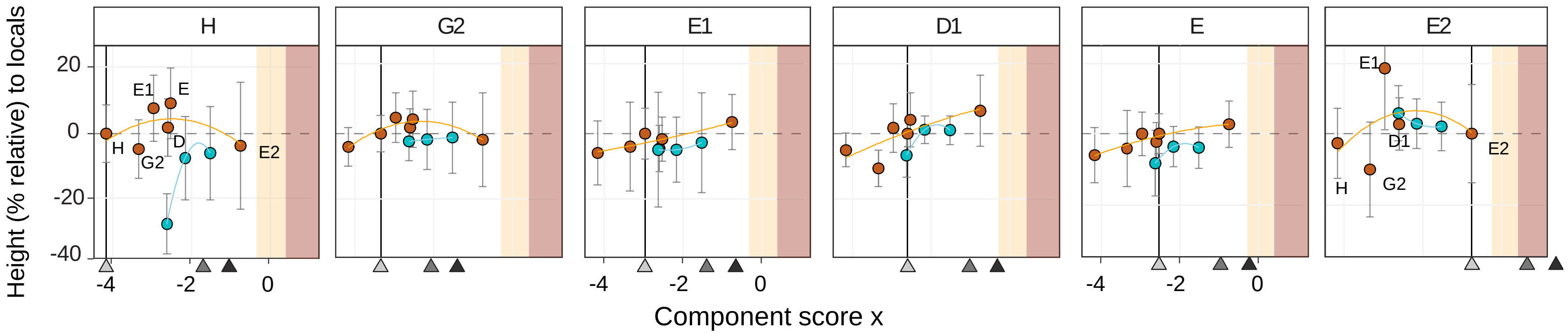


Figure 4-4. The climatic space of the principal component analysis of Fig. 4-1 rotated toward the climate change vector, so that the y-axis represents climate variables that do not change (a). Colored boxes represent a most and a dry temperature series, spatially plotted across Alberta (b). For climate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

(a) Transfer function for testing sites in dry series regions



(b) Transfer function for testing sites in moist series regions

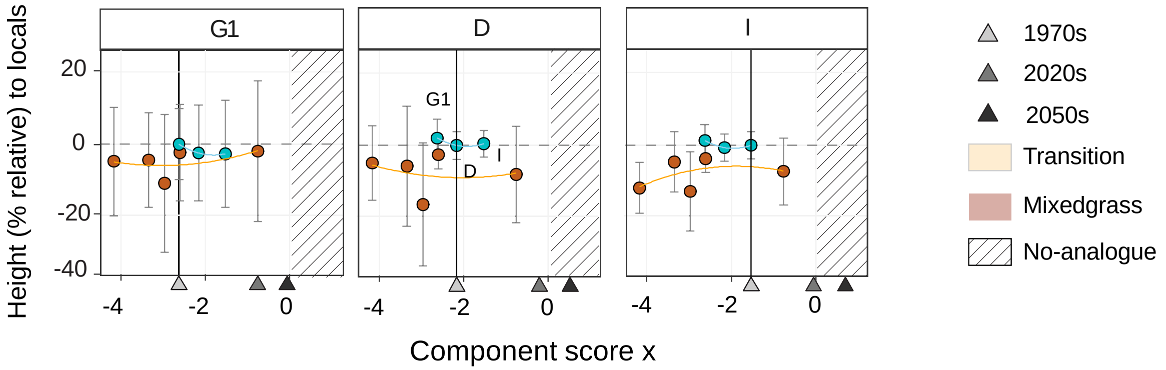


Figure 4-5. Transfer functions of white spruce growth when transferred among breeding regions. We separate transfer functions for the dry (orange) temperature series and the moist temperature series (blue) as defined by the climatic "bins" in Fig. 4-4. Each panel represents the results of testing genotypes in one breeding region, indicated by the header and the vertical line. The x-axis in this graph corresponds to the x-axis in Fig. 4-4 and represents the projected climate shift of the vertical line by the 2020s and 2050s is indicated by triangles on the x-axis.

Chapter 5 - Assisted migration poleward rather than upward in elevation minimizes frost risks in plantations

5.1. Summary

When assisted migration is used to address climate change, tree seedlings may have to be moved to substantially colder environments in anticipation of climate warming over their life span. Here, we evaluate frost risks for four economically important forest tree species of western Canada, Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine *(Pinus contorta*), interior spruce (*Picea glauca, P. engelmannii,* and their hybrids), and western larch (*Larix occidentalis*), when moved to adjacent northern and higher elevation seed zones that are cooler by approximately 2 °C. Changes to risks of damaging frosts among seed zones are evaluated during two 30-day periods, after dormancy release in spring and before onset of dormancy in fall, assuming a temperature-dominated day of bud break and a critical photoperiod-controlled onset of dormancy in fall. Based on daily interpolated climate data between 1980 and 2019, we find that late spring and early fall frost risks do not change significantly for transfers toward the north (<1 percentage point in most cases). In contrast, moving planting stock toward higher elevation generally leads to a substantial increase in exposure to unseasonal frosts (late spring frosts: 0.5% to 9.4%, early fall frosts: 0.8% to 17.1%). We conclude that transfers toward the north are preferable to transfers up in elevation in reforestation of these tree species in western Canada.

5.2. Introduction

Tree species and their populations are usually genetically adapted to the historical local climate conditions where they occur (e.g., Morgenstern 1996). In recognition of local genetic differentiation of populations, reforestation activities are typically governed by seed zones or seed transfer restrictions to minimize the risk of maladaptation, based on the assumption that local seed sources are best adapted (e.g., Campbell 1986, O'Neill and Aitken 2004). Most jurisdictions in North America have historically divided their forested land base into zones that are climatically, edaphically, and ecologically fairly homogeneous, and only seed sources that originate within these regions may be planted in the same region. Such seed transfer restrictions through seed zones govern reforestation activities in Alberta (Downing and Pettapiece 2006) and in British Columbia, Canada (MFLNRO 2018) as well.

However, fixed geographic seed zone systems no longer are a valid management approach under climate change, due to their underlying assumption that local seed sources are optimally adapted to their corresponding environments. Since the beginning of the 20th century, mean annual temperatures have increased by 1.3 °C across British Columbia and Alberta (Wang et al. 2016), which causes a mismatch between new climate conditions, and the optimal environment for current ecosystems, the climatic tolerances of the species they contain, and genetic adaptations of their populations to local environments (Gray and Hamann 2013, Etterson et al. 2020). This mismatch has already caused major disruptions to forest health and productivity in western Canada (e.g., Michaelian et al. 2011, Chen and Luo 2015, Chaste et al. 2019, Comeau et al. 2021)

To address this issue, it has been proposed that tree species and their populations be moved northward and upward in elevation, also referred to as assisted migration (Peters and Darling

1985). In the context of forestry, this can relatively easily be implemented as part of regular reforestation activities in managed forests (Gray et al. 2011, McLane and Aitken 2012, Aitken and Bemmels 2016, Pedlar et al. 2021). Moving seeds poleward and to higher elevations, where planting environments are cooler, would help to compensate for climate warming that has already occurred. This will increase the likelihood that climate conditions to which local populations are adapted match current and future growing environments, and thereby maintain forest health and productivity for the coming decades. Assisted migration prescriptions within and outside of current species ranges are already being implemented in western Canada by moving some species and their populations (e.g., western larch, *Larix occidentalis*) to more northern locations or to higher elevation bands across seed zone boundaries to compensate for observed and projected climate change (Marris 2009, O'Neill et al. 2017, MFLNRO 2018, Natural Resources Canada 2020).

However, the benefits of assisted migration prescriptions have to be balanced against the inherent risk of major changes to management practices (Hotte et al. 2016). One potential problem that arises for long-lived tree species is that they may experience substantial climate change over the course of their lifetime. In order to match their optimum climatic niche with their most productive growing period, seeds and seedlings may have to be exposed to colder than optimal environments in anticipation of climate warming over the decades or centuries of their life span. Therefore, the risk of potential frost damage to planting stock that is to be moved to colder locations needs to be balanced against the benefit of more mature trees being better adapted to warmer growing environments decades later. For example, a seedling established in central Alberta in 2020 would ideally come from a source location that is 1.3 °C warmer to account for observed climate change since the beginning of the 20th century. By the age of 20, the best matching seed source would originate from climate conditions about 2.5 °C warmer than the current planting site condition, and by the age of 50 the optimal source location would be approximately 3.5 °C warmer, according to CMIP5 multi-model climate projections (Knutti et al. 2013). It would therefore be helpful to understand how far we can move planting stock to colder environments, without exposing them to unreasonable frost risks at early life stages.

Temperate trees use environmental cues closely related to seasonal changes (e.g., photoperiod and thermal conditions) to synchronize their growing period with favorable environmental conditions (Rathcke and Lacey 1985). Local populations typically evolve timing of active growth so that evolutionary growth-survival trade-offs are optimized (Loehle 1998). A late bud break would protect young leaf tissue from late spring frosts, but would also reduce the growing season length and the competitiveness with other species or differently adapted individuals. For temperate plants, the timing of bud break is usually controlled through a mechanism that accumulates temperature exposure above a base temperature up to a species- and population-specific heat sum requirement. The timing of the onset of dormancy and development of frost hardiness in fall is primarily controlled by photoperiod in most boreal and temperate tree species, (e.g., Ekberg et al. 1979, Oleksyn et al. 1992), although temperature and internal circadian clocks can contribute of fall phenology as well (Cooke et al. 2012).

Here, we quantify frost risks for geographic seed zones of four important commercial conifer species of British Columbia and Alberta, Canada: the coastal and interior varieties of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* and var. *glauca* (Mirb.) Franco, lodgepole pine (*Pinus contorta* Douglas var. *latifolia* (Engelm.) Critchfield), interior spruce (a species complex of *Picea glauc*a (Moench) Voss, *P. englemannii* Parry ex Engelm. and their hybrids), and western larch (*Larix occidentalis* Nutt.), when moved to adjacent northern and higher elevation seed zones that are cooler by approximately 2 °C. Specifically, we evaluate the probability and severity of frost events in the 30 days following an approximated day of bud break in spring, and the probability and severity of frost events approximately 30 days before an estimated onset of dormancy in fall. The objectives of this analysis are to (1) determine the safety of assisted migration options by determining the probability of frost events in origin and target seed zones for 14 elevation and 15 latitude transfers, (2) to provide general guidance on how to minimize the risk of frost damage or plantation failure when planting stock is moved to colder environment in assisted migration prescriptions to address climate change.

5.3. Materials and methods

5.3.1. Study area

In this study, we evaluate late spring frost and early fall frost risks for four important commercial tree species of British Columbia and Alberta: Douglas-fir, lodgepole pine, interior spruce, and western larch. We evaluate changes to frost risks due to the movement of planting material to adjacent northern and higher elevation seed zones for orchard seed from tree improvement programs (Fig. 5-1). In British Columbia species-specific “seed planning zones” are divided into elevational bands which are known as “seed planning units” (O’Neill et al. 2008, British Columbia Government 2019). In Alberta, a similar system is referred to as “controlled parentage program regions”. Here, we refer to them as “seed zones” that were evaluated in this study (Fig. 5-1).

The study area has considerable latitudinal and altitudinal variation in climate, with mean annual temperature of individual 1 km² grid cells ranging from +10 °C in southern British Columbia to −15 °C in high mountains or Alberta’s north (Fig. 5-2). However, the average temperature of seed zones where trees are commercially planted in Alberta only range from −1.1 to +2.3 °C (a

3.4 °C range), representing sub-boreal and boreal forests east of the Rocky Mountains with a mild latitudinal temperature gradient (Fig. 5-2). Average temperatures of seed zones in British Columbia, with a more heterogeneous environment, span from –0.3 to +7.2 °C (a 7.5 °C range).

5.3.2. Frost risk metrics

We evaluate risks of late spring frost and early fall frosts that may damage living tissue during periods where the plant is not fully hardened in winter dormancy. In boreal and sub-boreal ecosystems, bud break in spring typically occurs during April and May (e.g., Glerum 1973), which is preceded by a dormancy release and dehardening process. However, the timing can vary substantially from year to year and also depends on the microclimate of specific locations. In general, the timing of bud break correlates well with accumulated growing degree days (also referred to as a heat sum), which is calculated as cumulative value of the daily average temperature (in units of °C) above a given base temperature. Usually, a base temperature of 0 to 5 °C best predicts bud break for boreal and temperate trees (e.g., Rathcke and Lacey 1985). Daily temperature values above the base temperature are added cumulatively over time, normally starting with zero value on January 1st, to describe the heat sum for any day of the year.

To arrive at heat sum metrics that can be used to describe subsequent spring frost risks, we make the assumption that trees need to avoid a certain severity of late spring frost events that may vary among species. To cover a range of late spring frost events that may damage plants at different de-hardening stages, we used the frost event severities of −5, −10, and −15 °C. Note that these frost event severities were observed at standard weather station locations that are situated in open field conditions and would only serve as a proxy for actually damaging frost event values at the microsite where a plant is situated. Because our analysis relies on a relative comparison of frost risks of a warmer source region (where seeds are collected) to a cooler target region (where planting stock may be used for reforestation), specific biotic and environmental factors that contribute to frost damage do not need to be explicitly modeled, as they are assumed to be comparable between the source and target seed zones.

For each of the −5, −10, and −15 °C frost event severities, we screened for heat sum values across the study area, using both a base temperature of 0 °C and 5 °C, where frost risks are just above zero for the subsequent 30 days (i.e., implying a bud break timing where frost risks are just avoided at the beginning of the available growing season). The heat-sum value that leads to a low but non-zero frost risk differs for different base temperatures and different frost severity values. A search was carried out for 10-degree-day value increments of candidate heat sum values. For each candidate heat sum value an empirical probability of a subsequent frost event below −5, −10, and −15 °C was calculated based on a 40-year daily minimum temperature record of interpolated weather station data (see below for details on climate data). Empirical probabilities of late spring frost risks for a 30-day window following estimated bud break were calculated for all seed zones at a 1 km^2 grid cell resolution, using interpolated daily climate data for the last 40 years. A 30-day window was sufficient to capture virtually all late spring-frost events after the predicted bud break. The following heat sum values were chosen, so that no seed zone was free of the risk of experiencing a frost event by a large margin for the purpose of comparing frost risks among seed zones: (1) 40 degree days above a base temperature of 0 °C to avoid −15 °C frost events, (2) 40 degree days above a base temperature of 0 °C to avoid −10 °C frost events, (3) 20 degree days above a base temperature of 5 °C to avoid −10 °C frost events, (4) 100 degree days above a base temperature of 5 °C to avoid −5 °C frost events.

To assess fall frost risks, we have to assume that different species may respond to different photoperiod cues to initiate the onset of hardening in fall (Rathcke and Lacey 1985). Although temperature plays a modifying role in the onset of hardening, day length and temperature are confounded and cannot be separately modeled outside of experimental situations. We calculated fall frost probabilities during 30-day periods after night length exceeded 9, 10, and 11 hours for each seed zone in our study area. The implied frost risk severity that would be avoided was similarly determined as for spring frost risks based on a 40-year daily minimum temperature record of interpolated weather station data, choosing a frost severity for which no seed zone was risk-free by a large margin (implying a timing of the onset of dormancy so that frost risks are just avoided at the end of the available growing season). The value was −5 °C for a night length of 9 hours, −8 °C for a night length of 10 hours, and −10 °C for a night length of 11 hours. Subsequently, probabilities of experiencing these frost severities in the 30-day period following the critical night length were calculated for each 1 km^2 grid cell of a seed zone based on a 40-year daily minimum temperature record of interpolated weather station data.

5.3.3. Climate data

We calculated frost risks based on interpolated daily climate data obtained from the U.S. Department of Energy's Office of Science (*https://daymet.ornl.gov*). The DAYMET database includes approximately 15,000 daily climate grids per climate variable since 1980 for North America at 1-km resolution in Lambert Conformal Conic projection (Thornton et al. 2014). We used automated batch downloading supported by the Daymet Single Pixel Extraction Web Service API (*https://daymet.ornl.gov/web_services*) to extract 1.6 million 1 km^2 gridded cells for the study area of British Columbia and Alberta in Universal Transverse Mercator (Zone 11) projection. The climate variables we used were daily maximum and minimum temperatures for 40 years from January 1, 1980 to December 31, 2019. All degree day-related calculations were performed based on average daily temperatures. Frost events were parsed based on minimum night-time temperatures. Sample scripts for calculating probability of late spring frost and early fall frost events for the R programming environment (R Core Team 2020) are provided as Appendix C.

Seed zones were also characterized for longer-term climate normal periods to compare their average temperatures. For this purpose, we calculated the 1961-1990 normal temperature by averaging values of gridded climate data points for each seed zone, estimated with the ClimateNA database and software package (http://tinyurl.com/ClimateNA, Wang et al. 2016). Adjacent seeds zones with approximate differences of 2 °C in mean annual temperature were evaluated for frost risk changes under potential assisted migration prescriptions, but the analysis is based on a historical frost risk comparison. We do not estimate the change of frost risks under climate change in this study, which would also have to include estimations of plant phenology response under climate change.

As a check for the validity of our conclusions, we also directly evaluated daily weather station data obtained by the Government of Canada (*http://climate.weather.gc.ca*). While forestry seed zones are generally not well represented by weather station coverage, we wanted to confirm that general frost risk patterns associated with latitude and elevation that we inferred from interpolated data products used in this study are consistent with those observed in raw weather station data. This validation is provided as Appendix D, and shows that weather stations located at higher elevations have greater temperature variance in spring and fall than low elevation stations, and northern Alberta has a lower temperature variance than southern Alberta.

5.4. Results & Discussion

5.4.1. Frost probability landscapes

We describe frost risks with an emphasis on the latest spring frost and earliest fall frost events, i.e., the avoidance of –5 °C frost events, because results of our analysis indicated that avoidance of –8 °C, –10 °C, and –15 °C events generally showed similar patterns. The analysis for the latter thresholds is provided as supplemental information (Appendix E to Appendix H). Based on 40 years of daily temperature records, the landscapes of probabilities for late spring frost risks and early fall frost risks are broadly similar, primarily following elevational gradients (Fig. 5-3). For early fall frost risks, the expectation is that higher elevation locations at the same latitude should have higher frost risks because they are colder than lower locations for a given day length. In contrast, comparing northern versus southern locations at similar elevations, the expectation would be no change in risks. The 9-hour night length threshold that defines the start of our fall frost time interval would occur later at more northern locations, but at the time of identical night length, frost risks should be comparable at different latitudes. We find, in fact, no latitudinal gradient in early fall frost risk for the 30-day period subsequent to a 9-hour critical night length to initiate dormancy, as can be seen for low-elevation areas of British Columbia and Alberta (Fig. 5-3, right panel). The observed fall frost risk pattern appears to be largely determined by altitude differences across the study area.

The landscape of spring frost probabilities is slightly different. First, elevational differences are not as pronounced as for fall frosts (less red in Fig. 5-3, left panel). In addition, there is a slight decline in spring frost risks from south to north in low-elevation areas of Alberta (yellow to gray in Fig. 5-3 left panel). The expectation of geographic patterns for the spring frost risk map is uniform with no elevational or latitudinal trends, except at very high elevation where the frost-free period is less than our 30-day monitoring period (Fig. 5-3, dark red). This is because we calculate the frost risks for varying time intervals after a 100 growing degree day threshold is reached. Thus, for a colder northern or higher elevation location, the time interval that we screen for frost events occurs later, because the heat sum value is reached later. In principle, screening a later time period for late spring frosts may compensates for generally colder climate conditions with respect to changes in frost risks.

We do, however, find clear elevational changes in late spring frost risks, with a similar pattern albeit less pronounced than in fall (Fig. 5-3). The observed latitudinal and altitudinal gradients in spring frost risks could be driven by differences in daily temperature variability in different geographic regions or elevations. We find this interpretation confirmed in raw weather station observations. Higher elevation weather stations show greater temperature variance than low elevation stations in spring, and northern Alberta has a lower temperature variance than southern Alberta in spring (Appendix D).

5.4.2. Frost exposure changes under assisted migration

Data shown in Fig. 5-3 could in principle allow assessing risk of seed movement for assisted migration prescriptions. A point-to-point comparison of frost risks may, for example, be appropriate to evaluate changes from a source to target location for an endangered species in a conservation context. However, for practical purposes, transfer recommendations are often summarized into larger spatial units, such as ecosystem delineations or forestry seed zones. Because planting forest trees is usually organized around seed zone delineations, this is an obvious choice with practical benefits for this case study that could be used as a template elsewhere using other types of management delineations. In the following, we summarize frost risks shown in Fig. 5-3 for operational seed zones mapped in Fig. 5-1.

As a detailed example for a seed zone transfer, we evaluate lodgepole pine seeds originating from a southern, low elevation seed zone (NE low) to be moved to a more northern low elevation seed zone (PG low). The transfer represents an assisted migration prescription to an approximately 2 °C colder zone, about 300 km further north in British Columbia (Fig. 5-1). The frequency of daily coldest temperature values in the 30-day time intervals in spring and fall can be displayed as frost probability distributions for different seed zones (Fig. 5-4). Assuming no future climate warming and simply comparing two zones for the same 40-year data period, we can ask how spring and fall frost risks would change under this assisted migration prescriptions. We find that the risk of late spring frosts remains low. The southern low-elevation zone of lodgepole pine (NE low; Fig. 5-4 green solid line) has very low frost probabilities, as has the next zone to the north (PG low; Fig. 5-4 blue solid line) during the late-spring periods (Fig. 5-4, upper left panel). Similarly, fall frost risks for both low-elevation seed zones are close to zero (Fig. 5-4, upper right panel).

In contrast to latitudinal transfers, elevational transfers result in substantial changes to the probabilities of potentially damaging below-freezing events, when comparing low and high elevation zones in the same area. The probabilities of cold events (we highlight the area under the curve below –5 °C in Fig. 5-4) increases substantially both in spring and fall if seed sources are moved to higher elevation zone that is approximately 2 °C colder. Higher elevation seed zones have a wider range of freezing temperatures in both spring and fall, with wider distributions and lower peaks of the distributions. For example, the NE high seed zone (Fig. 5-4, green dashed line) has much higher frost risks than the low-elevation seed zone from the same region (Fig. 5-4, green solid line). With elevation, the probability of frost risk increases, as well as the occurrence of more extreme frosts (e.g., −10 °C or lower) in both spring and fall (Fig. 5-4, bottom row).

The minimum temperature distribution differences for latitude transfers also exist but are less obvious. Comparing low-elevation bands, northern seed zones have slightly less variation in cold events in spring and fall. For example, the more northern seed zone PG low has a narrower distribution with shorter tails, implying the same low risks of damaging cold events, despite generally colder climates with the distribution shifted to the left of the more southern NE low zone (Fig. 5-4, top row). In contrast, increased variability in cold events is a contributor to frost risks at high elevations (Fig. 5-4, bottom row). The probability distribution of the NE high seed zone is wider and has a lower maximum temperature in addition to being shifted to the left, compared to the generally warmer NE low zone. Both a downward shift in means and increased variance leads to considerably higher frost exposure at higher elevations in both the spring and fall 30-day windows that we evaluated.

5.4.3. Summary statistics for all potential seed transfers

To expand this analysis to all plausible transfers to adjacent seed zones at higher elevation or further north for all four species across British Columbia and Alberta, we report the changes in frost probabilities, represented by colored areas under the curve in Fig. 5-4 as numerical values in Tables 5-1 and 5-2. The magnitude of changes in frost risks due to the possible seed transfers are highlighted with a gray scale. Similar to the example highlighted in Fig. 5-4, we find that the risk of a late spring frost or early fall frost does not change substantially in most cases when planting stock is moved to adjacent seed zones toward the north, while the average elevation remains constant or is slightly decreased (Table 5-1). In contrast, moving planting stock toward higher elevation, while the average latitude remains largely constant, generally leads to a substantial increase in exposure to both late spring frosts and early fall frosts (Table 5-2). On average, the probability of experiencing a late spring frost ≤ −5 °C following bud burst increases from 0.5% to 9.4% across all seed zones. The change for fall frosts as a consequence of elevation transfers is 16% (from an average 0.8% at lower seed zones to an average 17% at adjacent high elevation seed zones).

This general result that movement of seed to adjacent northern seed zones is less risky than movements to a higher elevation seed zone also holds true for earlier and more severe frost events in spring (–10 °C, and –15 °C following lower heat sum accumulation), and later and more severe frost events in fall (–8 °C, and –10 °C following longer critical night lengths). To see this pattern, compare the late spring frost risk changes highlighted with colors in Appendix E for latitudinal transfers versus Appendix F for elevation transfers. Large increases in frost risks are indicated by red colors. Similarly, for early fall frost risk changes, compare Appendix G for latitudinal transfers versus Appendix H for elevation transfers. Also for risks of early fall frosts, latitudinal transfers are preferable to elevation transfers.

The transfers that we evaluate in this study, both in elevation and in latitude are typically around 2 °C in mean annual temperature (last row in Tables 5-1 and 5-2). This 2 °C difference appears inherent in the design of Alberta’s and British Columbia’s seed zone system, and is the result of empirical research on what geographic seed transfer distances lead to loss of forest productivity and forest health. We note that this value corresponds to a perceived “tipping point” where negative consequences of climate warming of more than 2 °C are anticipated for natural and managed ecological systems (IPCC 2018). Assisted migration prescriptions to cooler environments by about 2 °C would therefore seem to be of an appropriate magnitude to make a difference in addressing negative impacts due to climate change. On average, such transfers would correspond to movements of planting stock of about 300-400 km northward given the approximately same elevation (Table 5-1, last row) or 500-600 m upward, given the same latitude, or a combination of both with an approximate conversion factor of a 100 m elevation change being equivalent to a 60 km latitude movement in Alberta and British Columbia.

It is important to note that the above generalizations for western Canada should be qualified for specific regions and species. Elevation movements in some areas have almost no changes to frost exposure as a consequence, for example, in the EK and NE seed zones of Douglas-fir in the southeast corner of British Columbia (Fig. 5-1, Table 5-2). The most pronounced increases in frost exposure are located in northwestern British Columbia for the BV, CP and NS seed zones (Fig. 5-1, Table 5-2). We did not make an attempt in this study to formally analyze the reasons for the variation in changes to frost risks associated with geographic movements. However, minimal changes to fall frost risks due to elevation transfers appear to be strongly associated with maritime climates of coastal rainforests (M seed zones) and interior rainforests represented by the NE, EK seed zones (Table 5-2 and Appendix H). Minimal changes to spring frost risk do not appear associated with maritime climates (Table 5-1, Appendix F). A logical next step would be a global analysis of the type we present here to generally quantify under which circumstances elevation transfers may not be associated with substantially increased frost risks, as was generally observed in this study.

5.4.4. Response of planting stock to relocation and climate change

Our analysis asks: if we move locally adapted planting stock to colder locations at higher elevations and latitudes in anticipation of future climate change that has not yet occurred, what are the changes to frost risk? However, climate has already warmed by about +1.3 to +1.5 °C since the beginning of the 20th century across the interior forests of Alberta and British Columbia, and by about +0.8 °C for coastal forests of British Columbia. We can therefore assume that tree species and their populations already lag behind their optimal climate niche by a considerable amount today.

Responding to this climate warming signal, plants would break buds earlier due to reaching the heat sum requirement for dormancy release earlier as long as they have met their chilling requirement (Bailey and Harrington 2006). There is good evidence that leaf unfolding and flowering dates of plants have advanced by up to a week in spring (e.g., Schwartz and Reiter 2000, Anderson et al. 2012), but that may not necessarily cause changes to late spring frost risks when the temperature increase is primarily driven by increases in minimum temperature during periods of leaf unfolding (Bigler and Bugmann 2018, Vitasse et al. 2018). Other research has found that under climate warming, earlier bud break timing could reduce the safety margin between the date of bud break and the date of the last spring frost event, and therefore potentially increase frost risks (e.g., Beaubien and Hamann 2011, Bigler and Bugmann 2018).

The situation may be more straight forward for the effect of climate warming on early fall frost exposure. Since bud set and the onset of dormancy in fall is primarily triggered by lengthening nights, which are not affected by climate change, it would imply that frost exposure distributions (such as those shown in Fig. 5-4) would be uniformly shifted to the right toward lower frost risks under climate warming. However, the beneficial effect of reduced frost risks due to a shift in distributions due to climate warming is relatively small, even when allowing for stronger local warming signals at higher elevation. For the example shown for fall frost risks distribution (Fig. 5-4, lower right panel) a 1.5 to 2.5 °C shift toward the right due to observed climate warming could not compensate for the increased exposure to frost risks due to movements to a higher elevation seed zones with higher daily temperature variability.

The empirical probability distributions developed for seed zones in this study suggest that changes to temperature variability could be key in determining future risks of frost exposure. However, future projections or historical evidence for changes in minimum temperature variability are not easy to obtain (e.g., Meehl et al. 2000, Zwiers et al. 2013). We also did not find any statistical evidence or even visual trends for changes in temperature variability within the 1980-2019 period, when plotting probability distributions of interpolated daily temperature data in the four consecutive decades of the 1980s to 2010s (data not shown).

Another consideration in assisted migration prescriptions is that populations are often locally adapted to a combination of biotic and abiotic factors. Local populations of tree species situated at high elevation or at far northern locations tend to evolve lower heat sum requirements leading to an earlier bud break relative to late spring frost risks, and similarly a later growth cessation relative to early fall frost risks. This leads to reduced safety margins against frost damage, but allows local populations to take full advantage of a short growing season in cold environments (Dantec et al. 2015, Bigler and Bugmann 2018, Vitasse et al. 2018). Under more temperate conditions, the climate-phenology relationships can be reversed, with relatively longer growing season utilizations in common garden experiments observed in sources from warm, competitive environments (e.g., Mimura and Aitken 2010). Also, populations from warmer southern locations tend to have lower levels cold hardiness (Sebastian-Azcona et al. 2019), more frost damage (Montwé et al. 2018), and respond less sensitively to shortening day length (e.g., Li et al. 2010, Liepe et al. 2016, Silvestro et al. 2019). Therefore, Silvestro et al. (2019) concluded that latitudinal transfer of southern, warm provenances northward would increase early fall frost risks relative to local populations should generally apply, except for the most northern and high elevation environments, where low safety margins have evolved to take advantage of a restricted growing season.

5.5. Conclusion

Compensating for observed and anticipated climate change may require movement of planting stock to colder environments further north or at higher elevation. At the same time, we must ensure that transferred planting stock does not suffer frost damage that would compromise their survival at the time of plantation establishment. The climatic risk analysis presented here suggests that transfers toward the north are preferable to transfers towards higher elevation, although this general observation does have some exceptions (e.g. transfers to higher elevation do not appear associated with increased fall frost risks under maritime climate conditions). For northward transfers of approximately 300-400 km, there are virtually no changes to late spring and early fall frost risks compared to the status quo of not moving seed sources. In contrast, an approximately 500-600 m transfer to higher elevation was associated with a substantial increase in frost risks. The reason for the observed latitudinal and altitudinal changes in spring frost risks is the increased variability in daily temperatures. Temperature variability and associated frost risks increase with elevation but not with latitude. Assuming a temperature-controlled day of bud burst, late spring frost risks of northwards transfers should remain near identical to historic probabilities. Assuming a day-length controlled onset of dormancy and climate warms as projected, early fall frost risks may decrease overall compared to historical probabilities for northward transfers but not under transfers to higher elevation.

5.6. Literature cited

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Table 5-1. Changes to frost risks with northward latitudinal transfers that represent a transfer to environments approximately 2 °C colder in mean annual temperature (MAT). Late spring frost events are defined as nights ≤ −5 °C in a 30-day window following the day of year where growing degree days reach 100 (proxy for bud break). Early fall frost events are nights ≤ −5 °C in a 30-day window after the day of 9-hour night length (proxy for onset of dormancy). Examples provided for comparisons of movements among seed zones for 3 species.

Species	Transfer difference			Spring risk change		Fall risk change	
Seed zone transfer	MAT (°C)	Elev (m)	Lat (km)	Probability (≤ -5 °C)		Probability (≤ -5 °C)	
Douglas-fir							
CT low to PG low	-1.2	-113	**+261**	0.1 to 0%	0%	0% to 1%	+1%
EK low to PG low	-1.2	-245	**+466**	0.1 to 0%	0%	0% to 1%	+1%
Lodgepole pine							
c to j	-2.8	-219	**+ 300**	0.2 to 0.7%	+1%	1% to 11%	+11%
EK low to CP low	-1.9	-252	**+ 580**	0.1 to 0.1%	+0%	0% to 2%	+2%
NE low to PG low	-1.2	-49	**+ 301**	0.7 to 0%	-1%	0% to 0%	0%
PG low to CP low	-1.4	-75	**+ 285**	0 to 0.1%	0%	0% to 2%	+2%
TO low to BV low	-2.8	-48	**+ 449**	0.7 to 0.2%	0%	0% to 1%	+1%
Interior spruce							
d to g2	-2.3	-149	**+ 269**	0.2 to 0.6%	0%	0% to 8%	+8%
d1 to e1	-1.5	-229	**+ 170**	1.2 to 2.4%	+1%	1% to 1%	0%
e to e1	-1	-129	**+ 149**	3.4 to 2.4%	-1%	1% to 1%	0%
e2 to d1	-1.3	-19	**+ 199**	3.4 to 1.2%	-2%	0% to 1%	+1%
g1 to g2	-2	-67	**+ 214**	0.5 to 0.6%	0%	0% to 8%	+8%
NE low to PG low	-1.8	-22	**+ 395**	0 to 0.1%	0%	0% to 1%	+1%
PG low to PR low	-2.5	-257	**+ 413**	0.1 to 0%	0%	1% to 4%	+3%
TO low to BV low	-1.8	-55	**+ 389**	2.2 to 0.6%	-2%	2% to 3%	0%
Average change	-1.9	-129	**+ 323**		0%		+3%

Table 5-2. Changes to frost risks for transfers upwards in elevation to environments approximately 2 °C colder in mean annual temperature (MAT). Late spring frost events are defined as nights ≤ −5 °C in a 30-day window following the day of year where growing degree days reach 100 (proxy for bud break). Early fall frost events are nights ≤ −5 °C in a 30-day window after the day of 9-hour night length (proxy for onset of dormancy). Examples of risk provided for movements among seed zones for 4 species.

Species	Transfer difference			Spring risk change		Fall risk change	
Seed zone transfer	MAT (°C)	Elev (m)	Lat (km)	Probability (≤ -5 °C)		Probability (≤ -5 °C)	
Douglas-fir:							
M low to M high	-1.8	**+ 654**	+23	0.3 to 11%	+11%	0% to 1%	+1%
NE low to NE high	-2.1	**+ 547**	-25	0 to 3%	+3%	0% to 1%	+1%
Lodgepole pine:							
BV low to BV high	-1.1	**+ 359**	-3	0.2 to 14%	+13%	1% to 37%	+35%
CP low to CP high	-1.6	**+ 494**	+38	0.1 to 14%	+13%	2% to 46%	+44%
EK low to EK high	-2.7	**+ 631**	-1	0.1 to 1%	+1%	0% to 4%	+4%
NE low to NE high	-2.8	**+ 689**	-1	0.7 to 11%	+10%	0% to 7%	+7%
NS low to NS high	-2.7	**+ 752**	+4	1.1 to 22%	+21%	3% to 49%	+46%
PG low to PG high	-1.9	**+ 529**	-15	0 to 8%	+8%	0% to 18%	+18%
TO low to TO high	-2.4	**+ 617**	-10	0.7 to 7%	+6%	0% to 5%	+5%
Western larch:							
NE low to NE high	-2.5	**+ 638**	-23	1.1 to 10%	+9%	0% to 7%	+7%
Interior spruce:							
BV low to BV high	-1.2	**+ 431**	-23	0.6 to 8%	+7%	3% to 19%	+17%
NE low to NE high	-2.3	**+ 558**	+7	0 to 4%	+4%	0% to 2%	+2%
PG low to PG high	-1.4	**+ 492**	+20	0.1 to 2%	+2%	1% to 12%	+11%
TO low to TO high	-2.2	**+ 511**	-6	2.2 to 17%	+15%	2% to 24%	+21%
Average change	-2	**+ 564**	-1		+9%		+16%

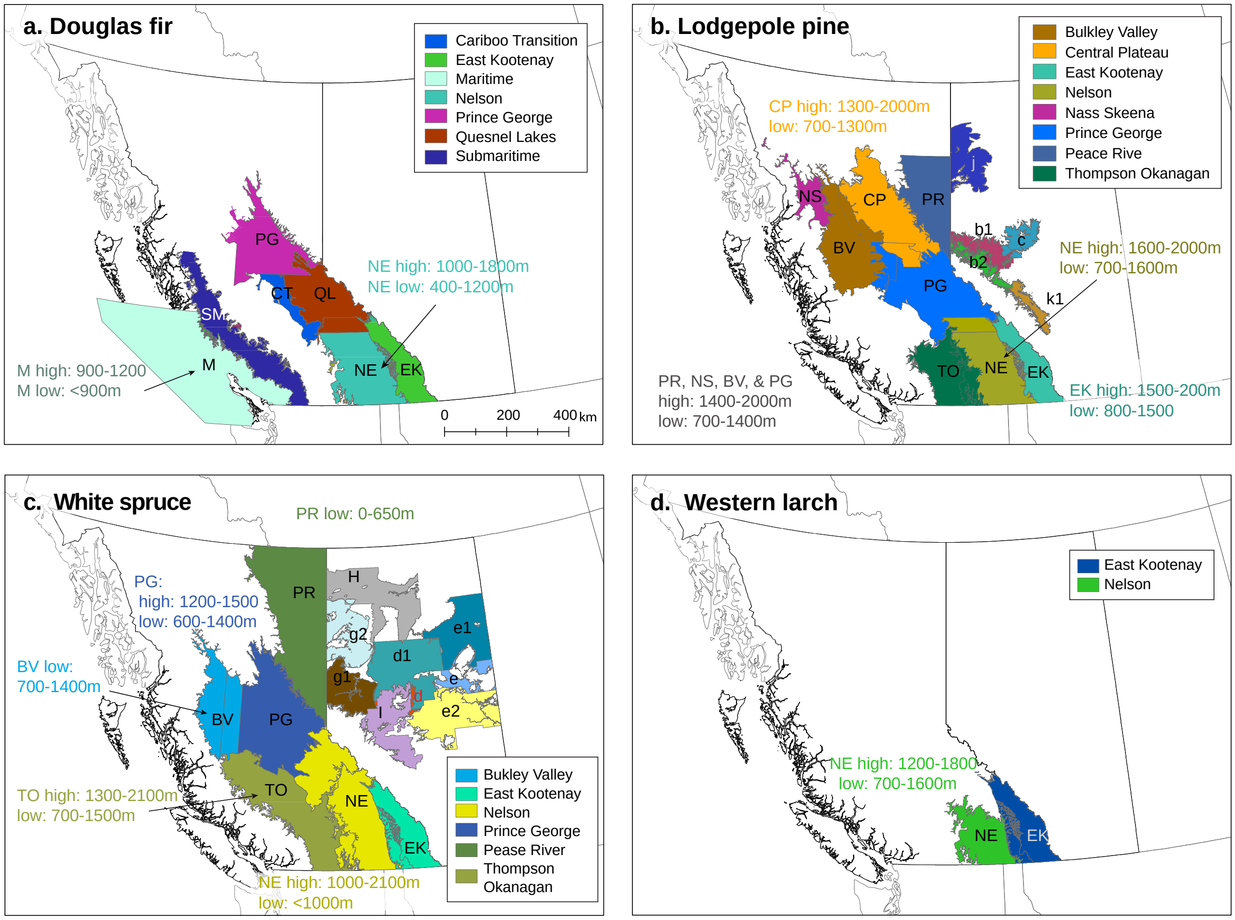

Figure 5-1. Seed zones of four economically important forestry species of the Canadian provinces British Columbia and Alberta evaluated in this analysis.

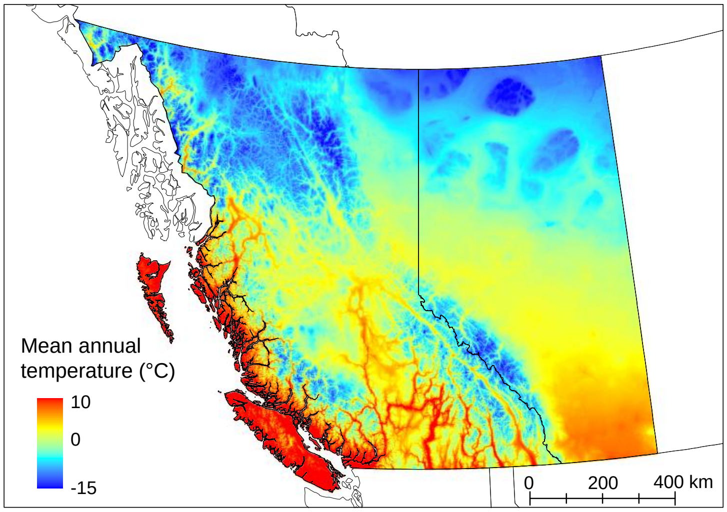

Figure 5-2. Mean annual temperature for the 1961 to 1990 normal period across the Canadian provinces British Columbia (left) and Alberta (right).

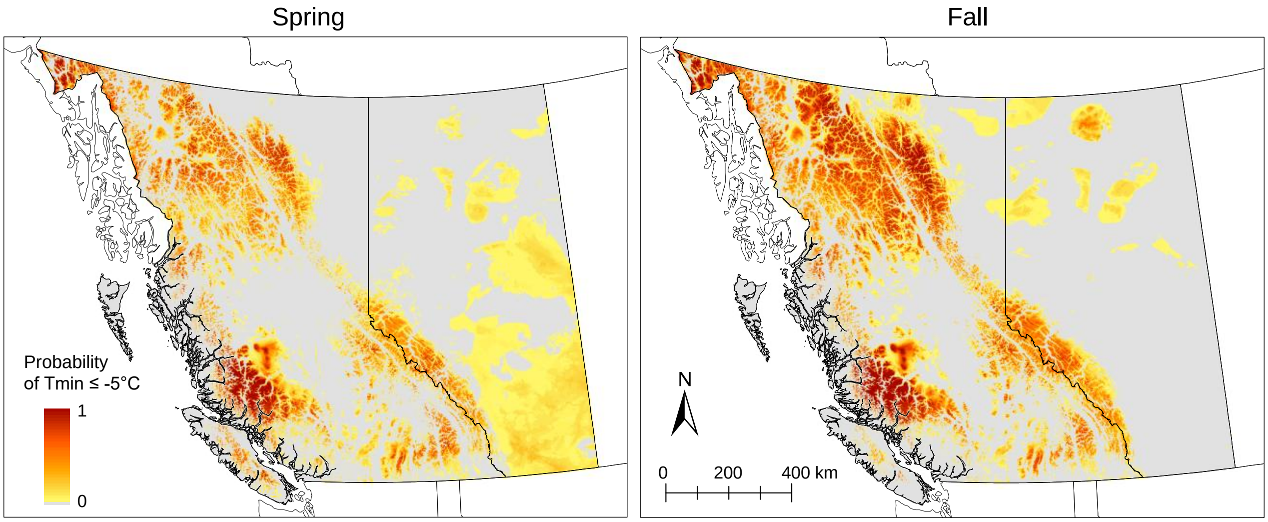

Figure 5-3. Probability of experiencing a late spring frost or an early fall frost in any given year. Late spring frost events are defined as nights ≤ −5 °C in a 30-day window following the day of year where growing degree days reach 100 (proxy for bud burst). Early fall frost events are nights ≤ −5 °C in a 30-day window after the day with 9-hour night length (proxy for onset of dormancy).

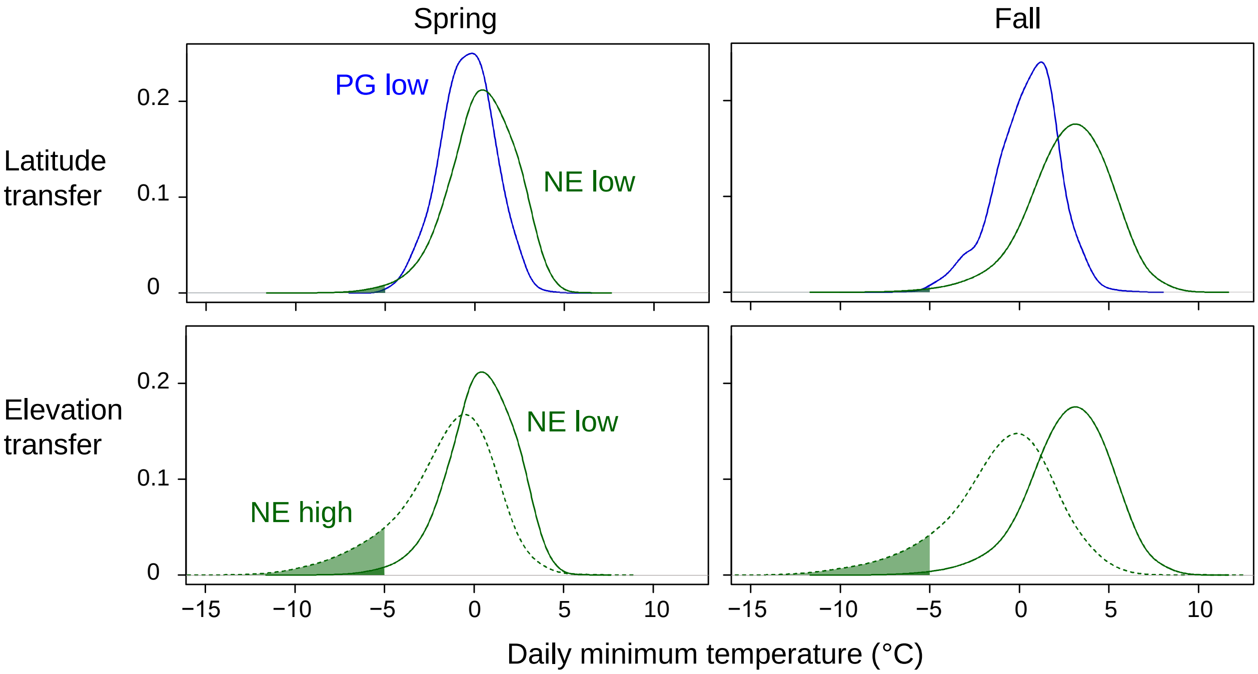

Figure 5-4. Example of the probability distribution of the coldest late spring frost event (left panel) or the coldest early fall frost event (right panel) exceeding a threshold of ≤ −5 °C (highlighted by a colored area) for three lodgepole pine seed zones. The seed zone pairs represent a 350 km northward transfer (NE low to PG low) and a 550 m upward elevation transfer (NE low to high). Distributions in all cases are for daily temperatures from 1980 to 2019.

Chapter 6 - Conclusions

The objective of this PhD thesis was to quantify the sensitivity of forest tree populations to climate variability and climate change at different scales, to aid reforestation activities under climate change, and to contribute scientific knowledge for economic, social, and ecological benefits. In the following, I am trying to address five more general questions, drawing on results from all thesis chapters: (1) What are the threats to future forestry under climate change? (2) Does climate change create opportunities for forestry? (3) What can we say about white spruce adaptive capacity, distinguishing plastic vs genetic response? (4) What can be recommended for seed movement and tree improvement in Alberta to address climate change? and (5) How should assisted migration be implemented in Alberta?

6.1. What are the threats to future forestry under climate change?

Both the remote-sensing based response function analysis (Chapter 2) and the dendrochronology analysis in response to an extreme event (Chapter 3) suggest that drought plays an important role in limiting growth of forested ecosystems, and white spruce specifically. Climate change impacts for high latitudes of North America, where the warming signal is strongest have already been well documented through remote sensing, especially in western Canada and Alaska (de Jong et al. 2011, Ju and Masek 2016, Pan et al. 2018). Similarly, previous tree ring studies revealed drought-limitations in the western boreal of Alaska (Barber et al. 2000, Trugman et al. 2018) and western Canada (Girardin et al. 2016, Hogg et al. 2017). Results from this thesis add to this body of research, identifying drought-limited forest stands across the western boreal forest.

Further, results from Chapter 4 suggest that for white spruce, southern breeding regions of Alberta that are not part of the moist foothills are expected to become unsuitable for forestry with white spruce because of moisture deficits. Projected climate conditions would only support grassland ecosystems. Other studies 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 (Peng et al. 2011, Boulanger et al. 2017, Aubin et al. 2018). For the moist southern foothills region, there is no test sites that would allow for inferences how white spruce may respond to no-analogue climate conditions under projected climate change. However, Schneider (2013) mentioned that these warm and moist foothill regions would still support forest ecosystems by the 2080s.

6.2. Does climate change create opportunities for forestry?

High-latitude boreal ecosystems are generally expected to benefit from warming trends with respect to remotely-sensed vegetation response (Chapter 2), although there are exceptions in western Canada and Alaska, where time series analysis of remote sensing data indicate local browning trends or a reversal of initial greening to browning trends in the most recent decade (Phoenix and Bjerke 2016). Projected warmer climate benefits the expansion of woody species distribution (e.g., Brodie et al. 2019). The general opportunity offered by longer and warmer growing seasons in the North could be further enhanced by moving climatically adapted, and high-performing provenances in this direction through human assisted migration as part of regular reforestation programs. This recommendation is supported by an analysis of white spruce provenance trials predicted an increase in productivity for several breeding regions through northward transfers relative to local sources (Chapter 4). Specifically for breeding regions D1, E and E2, transfers from warmer sources to these cooler environments resulted in better growth based on both historical data and projected growth response under future climate change. Migrating seed sources to northern and colder regions could mitigate the climatic lag and keep forest health and productive. 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).

For Canadian boreal forests as a whole, Chapter 2 suggests the most favorable growth response to higher temperatures in the eastern boreal forest, similar to other studies that suggest forest productivity could benefit from up to 2 °C warming, and the Northeast might serve as a climate refugia for boreal forest species (D'Orangeville et al. 2016, D'Orangeville et al. 2018). This view is supported by results from Chapter 3 for eastern populations of white spruce. Eastern provenances generally performed well when tested under substantially drier conditions in western Canada. Populations from Ontario and Quebec actually showed increased growth relative to western provenances despite originating from source locations with double the annual precipitation compared to the test site in western Canada. Further, the results showed no reduction of survival rates for Ontario and Quebec provenances. The optimistic outlook for white spruce populations of the eastern boreal is, however, only based on growth performance in this research and other studies cited above. A warming climate could bring other disturbances for white spruce in the east, for example pest and diseases that are enabled by warmer winters and longer potential growing seasons.

6.3. Recommendations for seed movement and tree breeding in Alberta

The underlying premise of assisted migration of species populations within their current range is genetic differentiation of populations. The general expectation for widespread forest trees that occur over a wide range of environmental conditions is that local sources are expected to have the highest fitness, and often also the highest growth rates where they originate (Morgenstern 1996). The data for white spruce partially conforms to these expectations in both range-wide and Alberta-specific analyses. Local sources from the Boreal Plains ecoregion were among the top performers (Chapter 3) when compared in a range-wide provenance trial. However, a more fine-grained local study with more provenances and more test sites in Alberta showed that sources from within the same breeding regions were good performers, but almost never the best choice (Chapter 4). Instead, seed sources from slightly warmer source locations performed best. This result generally conforms to other research that also showed populations from the southern fringe of the boreal forest have the highest growth potential, when transferred to northern test sites (e.g., Lu et al. 2014).

The magnitude of observed and projected climate change relative to climatic scale of breeding regions suggest that assisted migration prescriptions can often be implemented with minimal risk. With a rotation age of 60 – 100 years, assisted migration prescriptions to address climate change could safely target 2050s climate for choosing reforestation stocks (i.e. 30 years from present), especially given that observed climate change conforms in direction and magnitude to model projections, and thus partially compensating for climate change that has already occurred. Mapping these shifts for Alberta revels that assisted migration for the dry series of test sites (breeding regions E2 to E E1 and D1, and I to G1 and D) would correspond to an approximately

300-500 km movement northward. Such a general prescription would likely enhance or maintain growth, while improving the match between climate conditions to which planting stock is adapted.

A movement of this magnitude is also supported by a climatic frost risk analysis for current planting units across four major forestry species in Alberta and British Columbia, including white spruce (Chapter 5). Movement of planting stock to colder environments further north or at higher elevation may entail risks of frost damage to seedlings that would compromise their survival at the time of plantation establishment. However, the analysis shows that for northward transfers of approximately 300-400 km, there are virtually no changes to late spring and early fall frost risks compared to the status quo of not moving seed sources. In contrast, an approximately 500-600 m transfer to higher elevation was associated with a substantial increase in frost risks. The reason for the observed altitudinal changes in spring frost risks is the high variability in daily temperatures in mountainous environments with high topographic and climatic complexity. Therefore, high-elevation planting sites should source their seed from comparable elevations further south.

6.4. White spruce plastic versus genetic adaptive capacity

Two of the research chapters (chapter 3 and 4) allow inferences on plastic response versus genetic adaptation in white spruce through different approaches. In Chapter 3 genetic differentiation can be inferred by comparing different provenances at the same test site, and plastic response is observed in response to interannual climate variation over time. In Chapter 4 provenances planted on multiple test sites along multivariate climate gradients could further quantify genetic differentiation and plastic response. The most notable result from the range-wide provenance experiment (Chapter 3) was that no obvious adaptations to drought extremes were observed. While resistance and recovery metrics significantly varied among populations, no crossover interactions were observed where a provenance with lower growth under favorable moisture conditions exceeds productive provenances under drought conditions. No population was able to maintain a substantially higher level of productivity under drought constraints. This implies that the species as a whole may lack genetic variation and adaptive capacity to maintain growth under drought. That said, our sampling design did not cover a sufficient amount of samples from isolated or marginal populations at the southern boreal fringe, where such adaptation may still be found.

The multi-site trial series for Alberta seed sources (Chapter 4) could not reveal populations resilient to drought conditions either. The seed sources from multiple provenances share similar growth (height) performance comparing with local seeds. There was a similar lack of provenances originating from the most southern fringe of the species distribution in Alberta, and also test sites were not located in very dry and warm sites in Alberta's south, which could better reveal genetic differentiation for drought adaptation. Currently there is no data to quantify the climatic tolerances of spruce, or how silvicultural interventions, such as 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 should be established under environmental conditions at or slightly beyond the climate space, where forestry is currently practiced, 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.

6.5. How should assisted migration be implemented in Alberta

While the recommendations outlined above in general terms should generally be useful for developing policies and best practices for climate change adaptation, they do not directly support the selection of optimal seed sources based on multiple criteria. With the data available through this thesis research, specific seed source recommendations are, however, possible. While not fully developed as part of this thesis, I programmed an on-line seed selection tool that takes in multiple criteria of growth performance and multivariate climate match under past, current, and projected climate conditions to find the optimal seed sources with respect to growth and adaptation (Fig. 6-1 and http://ualberta.ca/~zihaohan/alberta3st).

The on-line tool allows selection of a planting region and then makes suggestions for suitable seed sources based on multiple criteria, which can interactively modified with sliders and check-boxes, e.g. (1) narrowing or widening the required climate match to the target environment, (2) setting an acceptable growth performance, (3) limiting the geographic transfer distance, (4) setting additional latitudinal and elevation transfer restrictions. As a result of these interactive modifications with data entries of all currently available seed sources from the Alberta Tree improvement and Seed Centre (ATISC) gets dynamically updated and mapped. This tool allows policy makers to test the realism of policy prescriptions. If criteria are too stringent, no seed sources may be available for some regions. If set too broad, unsuitable planting stock may be included as reforestation options without need. For some regions, it is clear that collections are adequate to ensure reforestation stock suitable for future climate, for other regions, additional collections may be necessary. This on-line tool, once fully developed can help to set regional priorities for seed collections and transfers.

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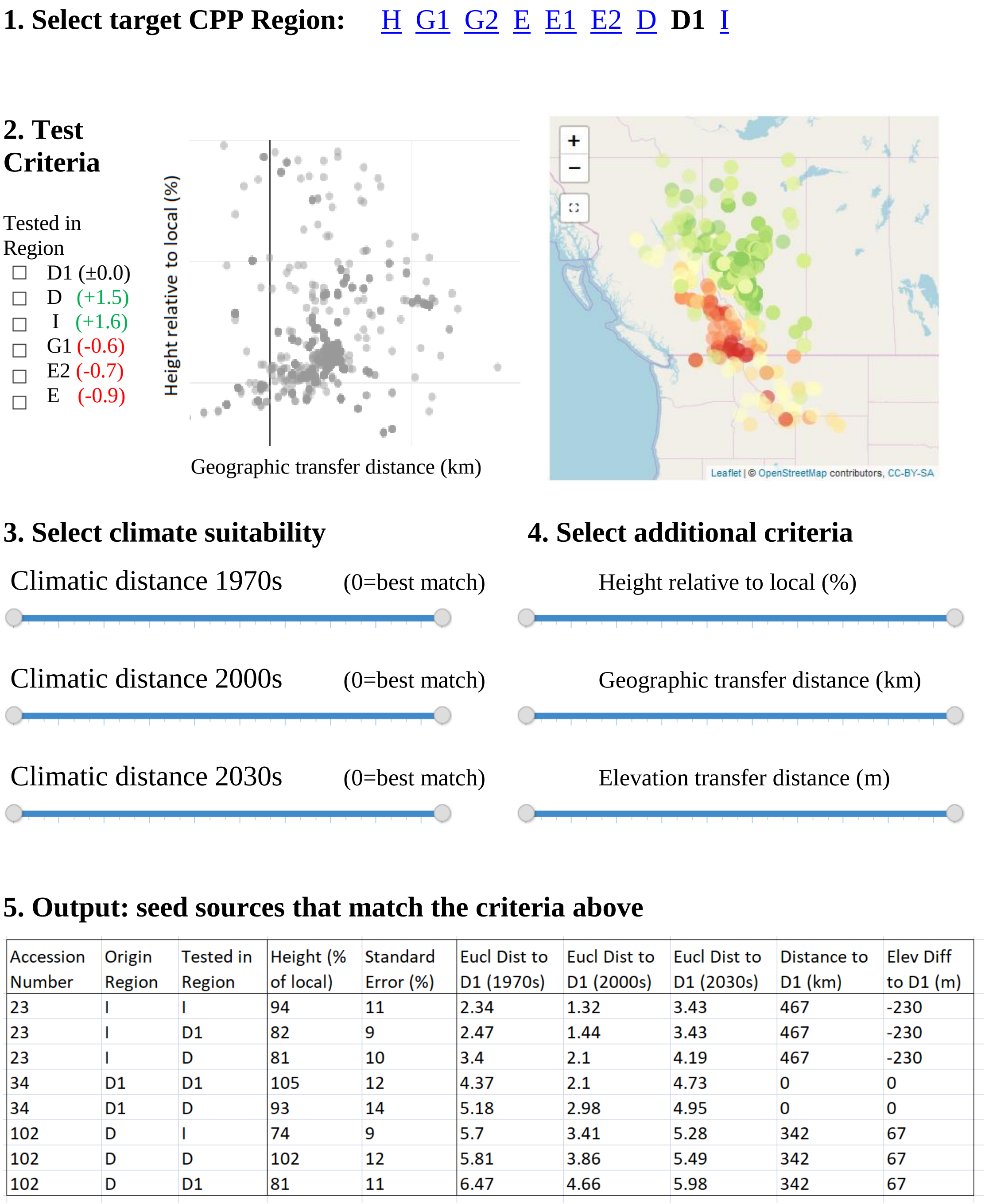

1. Select target CPP Region: H G1 G2 E E1 E2 D **D1** I

2. Test Criteria

Tested in Region

- ☐ D1 (±0.0)
- ☐ D (+1.5)
- ☐ I (+1.6)
- ☐ G1 (-0.6)
- ☐ E2 (-0.7)
- ☐ E (-0.9)

3. Select climate suitability

Climatic distance 1970s (0=best match)

Climatic distance 2000s (0=best match)

Climatic distance 2030s (0=best match)

4. Select additional criteria

Height relative to local (%)

Geographic transfer distance (km)

Elevation transfer distance (m)

5. Output: seed sources that match the criteria above

Accession Number	Origin Region	Tested in Region	Height (% of local)	Standard Error (%)	Eucl Dist to D1 (1970s)	Eucl Dist to D1 (2000s)	Eucl Dist to D1 (2030s)	Distance to D1 (km)	Elev Diff to D1 (m)
23	I	I	94	11	2.34	1.32	3.43	467	-230
23	I	D1	82	9	2.47	1.44	3.43	467	-230
23	I	D	81	10	3.4	2.1	4.19	467	-230
34	D1	D1	105	12	4.37	2.1	4.73	0	0
34	D1	D	93	14	5.18	2.98	4.95	0	0
102	D	I	74	9	5.7	3.41	5.28	342	67
102	D	D	102	12	5.81	3.86	5.49	342	67
102	D	D1	81	11	6.47	4.66	5.98	342	67

Figure 6-1. Alberta Seed Source selection tool. The on-line tool is functional for all breeding regions of Alberta and accessible here: http://ualberta.ca/~zihaohan/alberta3st

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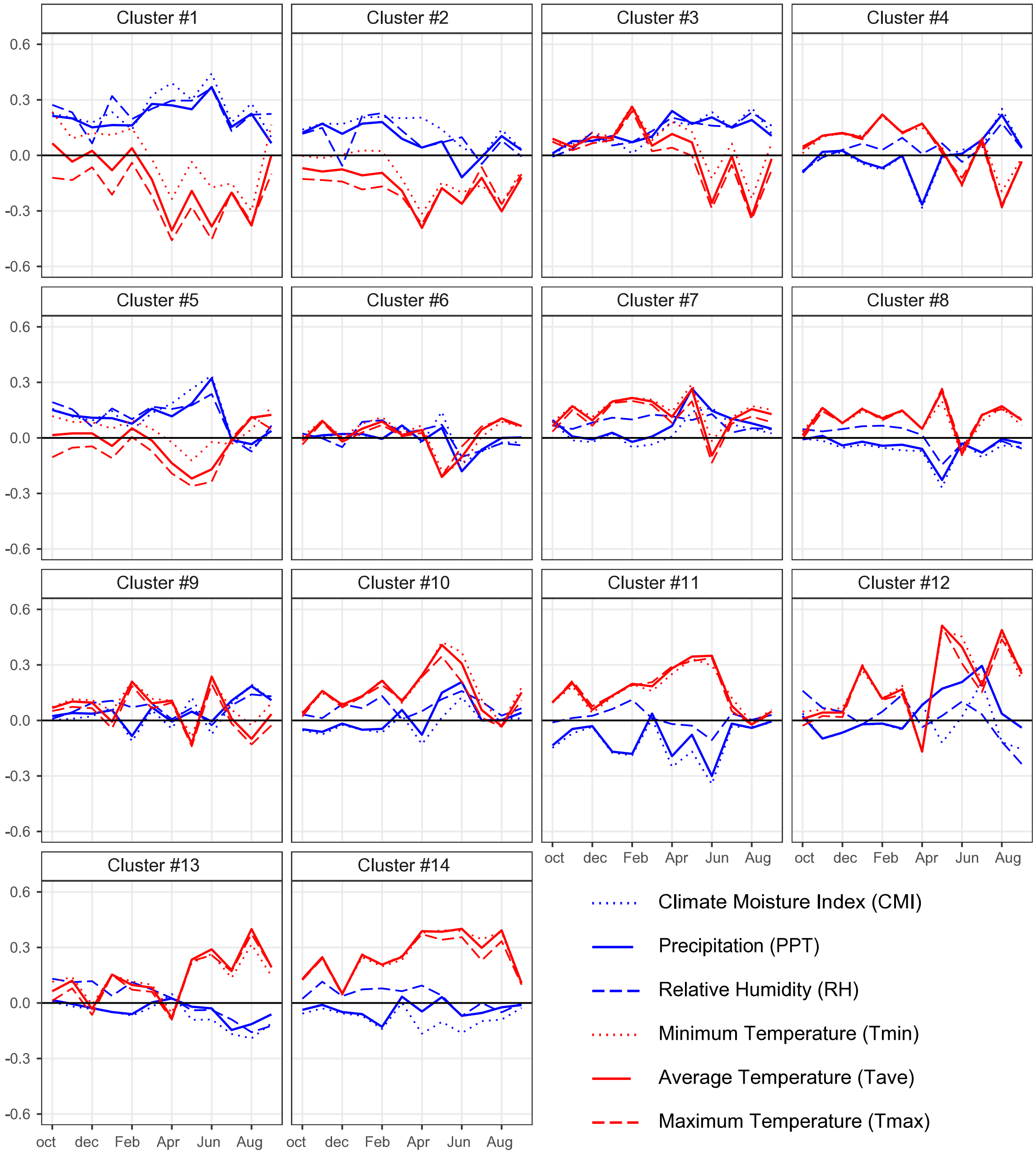
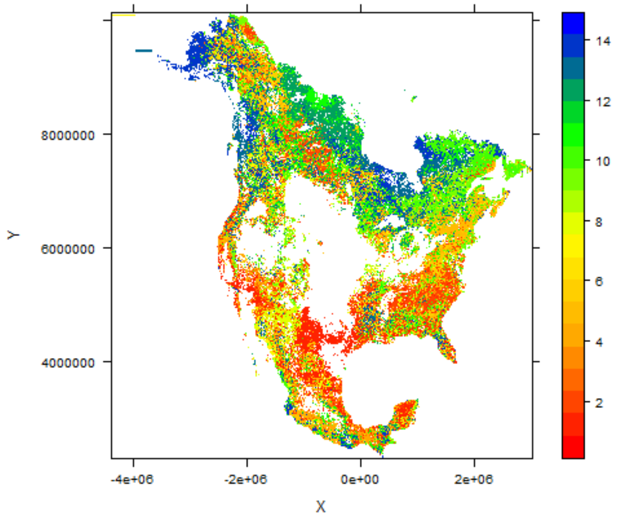
Appendix A - Average continental response functions for all 14 clusters used in this analysis. Graphs show the correlation of monthly climate variables with cumulative annual EVI values.



Appendix B - R-code used for response function analysis and clustering of grid cells with similar response coefficients. The full EVI dataset with 3 million grid cells, as well as a 30,000 grid cell sub-sampled dataset to explore the code below without significant wait times are available as open-access datasets at: https://figshare.com/s/bfec5c6944eba8227925.

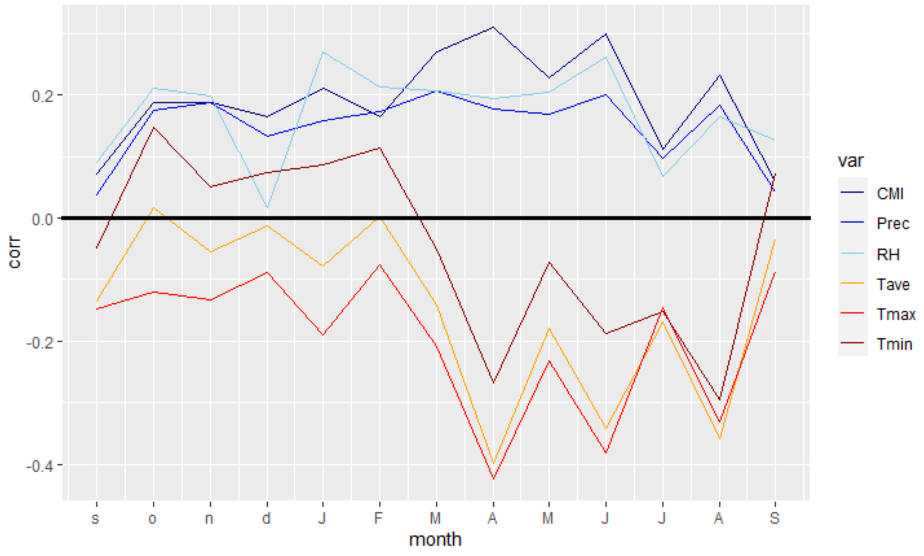
```
### Importing and re-arranging EVI and climate data:

evi <- read.csv("evi_subsample.csv");
clim <- read.csv("clim_subsample.csv")

library(tidyr); library(dplyr)
evi_long <- pivot_longer(evi, cols = EVI_2003:EVI_2019, names_to = 'YEAR',
            names_prefix = 'EVI_', values_to = 'EVI', names_transform =
            list(YEAR = as.integer))

### Calculating response coefficients for current year's Jan to Sep:

library(data.table)
current <- as.data.table(inner_join(evi_long, clim, on = c('ID20', 'YEAR')))
current <- select(current, X, Y, YEAR, EVI, ID20,
            num_range('Tmax', 1:9, width = 2),
            num_range('Tmin', 1:9, width = 2),
            num_range('Tave', 1:9, width = 2),
            num_range('Prec', 1:9, width = 2),
            num_range('RH',   1:9, width = 2),
            num_range('CMI',  1:9, width = 2))
current_coef <- current[, -c('YEAR', 'LAT', 'LONG','pYEAR')][, lapply(.SD,
            cor, .SD$EVI), by = .(ID20, X, Y)]

### Calculating response coefficients for previous year's Sep to Dec:

clim$YEAR <- clim$YEAR + 1
previous <- as.data.table(inner_join(evi_long, clim, on = c('ID20', 'YEAR')))
previous <- select(previous, X, Y, YEAR, EVI, ID20,
            num_range('Tmax', 9:12, width = 2),
            num_range('Tmin', 9:12, width = 2),
            num_range('Tave', 9:12, width = 2),
            num_range('Prec', 9:12, width = 2),
            num_range('RH',   9:12, width = 2),
            num_range('CMI',  9:12, width = 2))
previous_coef <- previous[, -c('YEAR', 'LAT', 'LONG')][, lapply(.SD,
            cor, .SD$EVI), by = .(ID20, X, Y)]

### Creating a combined table of response coefficients

names(previous_coef)[-(1:4)] <- paste('prev', names(previous_coef)[-(1:4)],
            sep = '_')
coef <- cbind(previous_coef[, -'EVI'], current_coef[, -c(1:4)])

### Generating a reduced dataset of current year's April to August for fast
### clustering
```

```
growingseason <- na.omit(select(coef, X, Y, ID20,
       num_range('Prec', 4:8, width = 2), num_range('Tave', 4:8, width = 2)))
growingseason_cor <- as.matrix(growingseason[,-c('X','Y', 'ID20')])

### Clustering via multivariate recursive partitioning:

library(mvpart)
output <- mvpart(growingseason_cor~., growingseason[,-c('X', 'Y', 'ID20')] ,
              xv="p", all.leaves=T, control = rpart.control(xval = 10,
minbucket = 2, cp = 0.007))
# click on the number "14" of the graph to proceed with 14 groups,
# a lower cp value will offer more groups


### Mapping the resulting clusters:

display <- data.frame(cluster = as.numeric(factor(output$where)),
      X = growingseason$X, Y = growingseason$Y)

library(lattice)
pccol <- colorRampPalette(c('red', 'orange', 'yellow', 'green', 'blue'))(20)

levelplot(cluster~X*Y, aspect="iso", cuts=19, col.regions=pccol,
      data=display)
```



```
### Example for a response function graph corresponding to Cluster #1 as
shown in Fig. 2-2a and Appendix A (internally coded as cluster 4)

clust4_id <- growingseason$ID20[output$where == 4]
clust4_avg <- data.frame(apply(coef[coef$ID20 %in% clust4_id, -c('X' ,'Y',
```

```
                  'ID20')], 2, mean))
clust4_dt <- mutate(clust4_avg, orig = rownames(clust4_avg),
             month = as.numeric(substr(orig, nchar(orig)-1,    nchar(orig))),
             variables = substr(orig, 1, nchar(orig)-2),
             curr_prev = stringr::str_split_fixed(variables, '_', 2)[,1],
             var = gsub('prev_','',variables),
             month2 = ifelse(curr_prev == 'prev', month-12, month))

library(ggplot2)
ggplot(clust4_dt, aes(x = month2, y = clust4_avg, color = var))
      + geom_line()
      + labs(x = '', y = 'corr')
      + scale_color_manual(values = c('navy', 'blue','skyblue', 'orange',
            'red','darkred'))
      + scale_x_continuous(breaks = (-3):9, labels =
            c('s','o','n','d','J','F','M','A','M','J','J','A','S'))
```



Appendix C - R code to estimate the probability of late spring frosts after bud break, and early fall frosts before onset of dormancy. The code process files downloaded with the Daymet Single Pixel Extraction Web Service API (https://daymet.ornl.gov/web_services).

```
library(data.table)
d <- fread('daymet.csv', skip=6,
           col.names=c('yr','doy','dl','pre','srad','swe','tx','tn','vp'))
head(d)

# Daymet variables used below
# yr  = year
# doy = day of year
# dl  = day length (seconds)
# tx  = daily maximum temperature (degree C)
# tn  = daily minimum temperature (degree C)


# Estimate probabilities of late spring frost events
b   <- 5   # set base temperature (b) for growing degree day calculation here
hsr <- 100 # set heat sum requirement (hsr) for budbreak here
spl <- 30  # set spring period length (spl) for late spring frost screening
sft <- -5  # set spring frost threshold (sft) here

s <- d[, t := (tn + tx)/2]                 # daily average temperature (t) calculation
s <- s[, gdd := ifelse(t >= b, t-b, 0)]    # growing degree day (gdd) calculation
s <- s[, hs := cumsum(gdd), keyby = yr]    # heatsum (hs) calculation
s <- s[hs>=hsr, head(.SD,spl), keyby = yr] # retain data for period following bud break
s <- s[, .(min = min(tn)), by = yr]        # retain coldest late spring frost in each year
s[,.(prob_lsf = mean(min < sft))]          # probability of a late spring frost < sft


# Estimate probabilities of early fall frost events
dlt <- 15  # set day length threshold (dlt) to represent estimated onset of dormancy
fpl <- 30  # set fall period length (spl) for early fall frost screening
fft <- -5  # set fall frost threshold (fft) here

eod <- d[(doy > 180), which.min(abs(dl - dlt*60*60)) + 180]  # estimated onset of dormancy
f <- d[doy %between% c(eod, eod+fpl-1)]    # retain data for period after onset of dormancy
f <- f[, .(min = min(tn)), by = yr]        # retain coldest early fall frost in each year
f[,.(prob_eff = mean(min < fft ))]         # probability of an early fall frost < fft
```

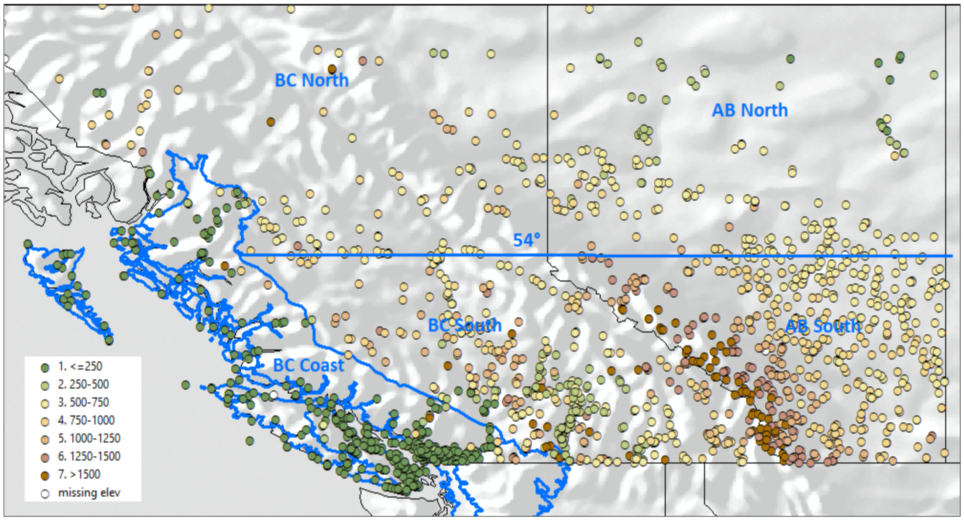
The code above represents the key algorithms for the following multi-step analysis:

- Download individual daily climate time series using the Dayment single-pixel extraction tool for the area covered by seedzone at 1km resolution (the native resolution of Dayment interpolations)
- Process single pixels with the code above, yielding grids, such those shown in Fig. 5-3. Similar grids were obtained for other values of minimum temperature thresholds (variables `sft` and `fft` above), other heat sum requirement values (`hsr`), other thresholds to calculate degree days (`b`) and other daylength thresholds (`dlt`). More parameters can be modified if desired, e.g. the window for screening late spring frost and early fall frost events (`spl` and `fpl`)
- To assess spring risks we chose the following parameters: (1) Degree days above 5 °C with (1a) Risk of -5 °C after 100 degree days and (1b) Risk of -10 °C after 20 degree days, (2) Degree days above 0 °C with (2a) Risk of -10 °C after 70 degree days and (2b) Risk of -15 °C after 40 degree days. To assess fall frost risks we chose (1) Risk of -5 °C after 9-hour night length, (2) Risk of -8 °C after 10-hour night length, and (3) Risk of -10 °C after 11-hour night length. This tests the sensitivity of parameter choices over a wide range of potentially relevant biological parameter values.
- Aggregate the individual grids (as shown in Fig. 5-3 for the first parameter combination: Degree days above 5 °C, evaluating a Risk of -5 °C after 100 degree days) by seedzones (as shown in Fig. 5-1). This is the basis for the numerical summaries of Tables 5-1 and 5-2 as well as Appendices E to H.

Appendix D - Variability in daily weather station data expressed in standard deviations of daily minimum temperature within a month (green = low variability, red = high variability). The reference map below the table shows the regions and elevation bands within the Canadian provinces of British Columbia (BC) and Alberta (AB) evaluated here.

Region & Elev	**Month**			**Spring**				**Fall**				**No of**
BC South	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**Stations**
<=250	7.1	5.6	3.9	3.2	3.1	2.9	2.8	2.8	3.4	3.8	5.2	5.8	12
250-500	7.5	6.3	4.4	3.7	3.7	3.4	3.4	3.4	3.8	4	4.9	6.2	122
500-750	8.6	7.1	5.1	3.8	3.8	3.4	3.3	3.5	4	4.2	5.7	7.4	124
750-1000	9.3	7.9	6	3.8	3.8	3.6	3.4	3.6	4	4.4	6.4	8.1	90
1000-1250	8.8	7.7	6.1	4	3.8	3.7	3.7	3.7	4.1	4.4	6.5	7.8	78
1250-1500	8.3	7.1	5.9	4	3.1	3.2	3.1	3.2	3.6	4.1	6.5	7.3	15
>1500	7.5	6.5	5.5	4.4	3.8	3.8	3.8	4	4.3	4.8	6.2	6.9	19
BC North													
<=250	8.0	7	4.9	3	3	2.8	2.4	2.8	3.1	3.6	5.3	7.1	10
250-500	11.2	10	8.4	4.9	3.7	3.4	3	3.2	3.8	5.2	8.7	11	9
500-750	11.1	9.8	8	4.5	3.8	3.5	3.2	3.6	4	4.8	7.9	9.8	69
750-1000	11.0	9.7	8.2	5	3.6	3.4	3.1	3.5	3.9	5	8.3	10	39
1000-1250	10.3	9.9	7.9	5.7	3.5	3.2	2.9	3.7	4.1	5.2	8.6	10	9
BC Coast													
<=250	5.0	4.1	3.2	2.9	2.9	2.6	2.4	2.5	2.9	3.3	3.9	4.4	422
250-500	8.7	7.1	4.8	3.6	3.7	3.4	3.1	3.4	4.1	4.2	5.6	7.4	20
500-750	7.9	6.6	4.4	3.1	3.1	2.9	2.8	2.9	3.6	3.9	4.8	6.4	13
750-1000	7.6	6.9	5.3	3.6	3.4	3.5	3.3	3.2	3.6	3.8	5.3	6.6	7
AB South													
500-750	10.1	9.3	8.4	5.2	4.3	3.5	3.2	3.6	4.1	5	7.4	9.2	155
750-1000	10.2	9.3	8.1	5	4.1	3.5	3.3	3.6	4.2	5.2	7.5	9.3	187
1000-1250	10.5	9.2	7.8	5	4	3.5	3.3	3.5	4.2	5.4	7.7	9.4	85
1250-1500	10.8	9.4	8.2	5.4	4	3.7	3.5	3.7	4.3	5.7	7.9	9.7	75
>1500	9.8	8.1	7.7	5	3.9	3.4	3.7	3.9	4.1	5.3	7.6	8.9	52
AB North													
<=250	9.5	9.5	9.6	7.7	5.2	4.3	3.7	4.3	4.5	5.3	8.4	9.3	7
250-500	10.4	10	9.6	6.6	4.5	3.8	3.4	3.9	4.4	5.4	8.6	9.8	40
500-750	10.7	9.9	8.8	5.5	4.2	3.5	3.2	3.6	4.2	5.1	8	9.7	140
750-1000	11.0	9.4	8.3	5	4.1	3.3	3.3	3.6	4	5	7.5	9.8	14
1000-1250	9.7	9.2	7.7	5.3	4.1	3.3	3.1	3.7	3.9	5.1	7	9.1	5

Reference map for weather stations by region and elevation band



Appendix E - Sensitivity analysis for late spring frost events for assisted migration towards the north. Source DoY and target DoY are the days of the year where critical heat sums are met. The changes in probabilities of late spring frost risks due to the seed transfer are highlighted by a color scheme that is consistently applied across Appendix E and F for direct comparison of elevation versus latitude transfers. Examples of risk comparisons among seed zones for 4 species are exhibited in the table (Df: Douglas-fir; Lp: lodgepole pine; Wl: western larch; Is: Interior spruce).

		Degree days above 5 °C								Degree days above 0 °C							
		Risk of -5 °C after 100 degree days				Risk of -10 °C after 20 degree days				Risk of -10 °C after 70 degree days				Risk of -15 °C after 40 degree days			
Spec.	Seed zone transfer	Source DoY	Target DoY	Change in probability	Prob. Diff.	Source DoY	Target DoY	Change in probability	Prob. Diff.	Source DoY	Target DoY	Change in probability	Prob. Diff.	Source DoY	Target DoY	Change in probability	Prob. Diff.
Df	CT low to PG low	144	148	0% to 0%	0%	118	127	1% to 0%	-1%	96	107	12% to 7%	-5%	83	96	9% to 6%	-3%
Df	EK low to PG low	137	148	0% to 0%	0%	113	127	1% to 0%	-1%	92	107	9% to 7%	-2%	80	96	8% to 6%	-2%
Lp	c to j	143	146	0% to 1%	+1%	120	125	3% to 0%	-2%	107	116	11% to 4%	-7%	96	108	16% to 3%	-13%
Lp	EK low to CP low	139	149	0% to 0%	0%	114	129	1% to 0%	-1%	93	111	9% to 5%	-3%	82	100	7% to 5%	-2%
Lp	NE low to PG low	140	143	1% to 0%	-1%	116	119	0% to 1%	0%	96	97	1% to 10%	+9%	85	85	1% to 8%	+7%
Lp	PG low to CP low	143	149	0% to 0%	0%	119	129	1% to 0%	0%	97	111	10% to 5%	-5%	85	100	8% to 5%	-3%
Lp	TO low to BV low	140	154	1% to 0%	0%	113	132	0% to 0%	0%	91	111	8% to 4%	-4%	78	100	5% to 2%	-3%
Is	d to g2	140	144	0% to 1%	0%	118	123	3% to 0%	-2%	104	114	12% to 4%	-8%	93	106	17% to 4%	-14%
Is	d1 to e1	139	143	1% to 2%	+1%	118	122	3% to 1%	-1%	107	115	10% to 6%	-4%	98	108	9% to 4%	-5%
Is	e to e1	140	143	3% to 2%	-1%	119	122	0% to 1%	+1%	110	115	4% to 6%	+2%	102	108	11% to 4%	-7%
Is	e2 to d1	135	139	3% to 1%	-1%	113	118	3% to 1%	-2%	104	107	11% to 10%	-1%	95	98	15% to 9%	-5%
Is	g1 to g2	139	144	1% to 1%	0%	116	123	4% to 0%	-4%	103	114	15% to 4%	-11%	92	106	18% to 4%	-15%
Is	NE low to PG low	130	147	0% to 0%	0%	106	125	0% to 0%	0%	83	105	2% to 8%	+6%	72	93	2% to 6%	+4%
Is	PG low to PR low	147	145	0% to 0%	0%	125	125	0% to 1%	0%	105	116	8% to 5%	-3%	93	108	6% to 5%	-2%
Is	TO low to BV low	145	157	2% to 1%	-2%	119	134	0% to 0%	0%	97	114	11% to 2%	-9%	85	102	6% to 1%	-4%
Average		**140**	**147**		**0%**	**116**	**125**		**-1%**	**99**	**111**		**-3%**	**88**	**101**		**-4%**

Appendix F - Sensitivity analysis for late spring frost events for assisted migration towards higher elevations. Source DoY and target DoY are the days of the year where critical heat sums occur. The changes in probabilities of late spring frost risks due to the seed transfer are highlighted by a color scheme that is consistently applied across Appendix E and F for direct comparison of elevation versus latitude transfers. Examples of risk comparisons among seed zones for 4 species are exhibited in the table (Df: Douglas-fir; Lp: lodgepole pine; Wl: western larch; Is: Interior spruce).

		Degree days above 5 °C								Degree days above 0 °C							
		Risk of -5 °C after 100 degree days				Risk of -10 °C after 20 degree days				Risk of -10 °C after 70 degree days				Risk of -15 °C after 40 degree days			
Spec.	Seed zone transfer	Source DoY	Target DoY	Change in probability	Prob. Diff.	Source DoY	Target DoY	Change in probability	Prob. Diff.	Source DoY	Target DoY	Change in probability	Prob. Diff.	Source DoY	Target DoY	Change in probability	Prob. Diff.
Df	M low to M high	113	148	0% to 11%	+11%	67	115	1% to 7%	+6%	32	81	7% to 25%	+18%	21	63	1% to 6%	+5%
Df	NE low to NE high	128	146	0% to 3%	+3%	104	121	0% to 1%	+1%	82	103	2% to 4%	+2%	70	93	2% to 1%	-2%
Lp	BV low to BV high	154	181	0% to 14%	+13%	132	151	0% to 3%	+3%	111	137	4% to 8%	+5%	100	126	2% to 2%	0%
Lp	CP low to CP high	149	173	0% to 13%	+13%	129	146	0% to 4%	+4%	111	134	5% to 9%	+3%	100	124	5% to 3%	-2%
Lp	EK low to EK high	139	164	0% to 1%	+1%	114	136	1% to 0%	0%	93	121	9% to 6%	-3%	82	110	7% to 3%	-4%
Lp	NE low to NE high	140	162	1% to 11%	+10%	116	132	1% to 11%	+10%	96	119	1% to 11%	+10%	85	108	1% to 1%	0%
Lp	NS low to NS high	156	177	1% to 21%	+20%	133	148	0% to 10%	+10%	112	133	2% to 21%	+19%	100	120	1% to 4%	+3%
Lp	PG low to PG high	143	171	0% to 8%	+8%	119	143	1% to 1%	+1%	97	127	10% to 7%	-3%	85	115	8% to 6%	-2%
Lp	TO low to TO high	140	161	1% to 7%	+6%	113	132	0% to 1%	+1%	91	115	8% to 8%	+1%	75	102	5% to 2%	-2%
Wl	NE low to NE high	137	153	1% to 10%	+9%	112	126	0% to 2%	+2%	92	110	2% to 8%	+6%	81	99	1% to 1%	0%
Is	BV low to BV high	157	175	1% to 7%	+7%	134	146	0% to 2%	+2%	114	131	2% to 4%	+2%	102	120	1% to 2%	+1%
Is	NE low to NE high	130	155	0% to 4%	+4%	106	129	0% to 1%	+1%	83	114	2% to 4%	+3%	72	103	2% to 0%	-2%
Is	PG low to PG high	147	163	0% to 2%	+2%	125	138	0% to 0%	0%	105	123	8% to 4%	-4%	93	112	6% to 4%	-2%
Is	TO low to TO high	145	166	2% to 17%	+15%	119	137	0% to 3%	+3%	97	120	11% to 14%	+3%	85	107	6% to 4%	-2%
Average		**141**	**164**		**+9%**	**116**	**136**		**+3%**	**94**	**119**		**+4%**	**82**	**107**		**-1%**

Appendix G - Sensitivity analysis for early fall frost events for assisted migration towards the north. Source DoY and target DoY are the days of the year where critical photoperiods occur. The changes in probabilities of early fall frost risks due to the seed transfer are highlighted by a color scheme that is consistently applied across Appendix G and H for direct comparison of elevation versus latitude transfers. Examples of risk comparisons among seed zones for 4 species are exhibited in the table (Df: Douglas-fir; Lp: lodgepole pine; Wl: western larch; Is: Interior spruce).

		Risk of -5 °C after 9-hour night length				Risk of -8 °C after 10-hour night length				Risk of -10 °C after 11-hour night length			
Spec.	Seed zone transfer	Source DoY	Target DoY	Change in probability	Prob. Diff.	Source DoY	Target DoY	Change in probability	Prob. Diff.	Source DoY	Target DoY	Change in probability	Prob. Diff.
Df	CT low to PG low	218	222	0% to 1%	+1%	234	236	0% to 1%	0%	249	251	2% to 1%	-1%
Df	EK low to PG low	214	222	0% to 1%	+1%	231	236	0% to 1%	+1%	248	251	0% to 1%	+1%
Lp	c to j	223	227	1% to 11%	+11%	236	239	0% to 7%	+7%	251	252	1% to 13%	+12%
Lp	EK low to CP low	214	224	0% to 2%	+2%	231	237	0% to 1%	+1%	248	251	0% to 1%	+1%
Lp	NE low to PG low	214	219	0% to 0%	0%	231	234	0% to 0%	0%	248	250	0% to 2%	+2%
Lp	PG low to CP low	219	224	0% to 2%	+2%	234	237	0% to 1%	+1%	250	251	2% to 1%	-1%
Lp	TO low to BV low	214	222	0% to 1%	+1%	231	236	0% to 1%	+1%	248	250	1% to 1%	0%
Is	d to g2	223	227	0% to 8%	+8%	236	239	0% to 5%	+5%	251	252	1% to 10%	+8%
Is	d1 to e1	225	227	1% to 1%	0%	238	239	1% to 2%	+1%	251	252	4% to 4%	0%
Is	e to e1	225	227	1% to 1%	0%	238	239	1% to 2%	+1%	251	252	5% to 4%	-2%
Is	e2 to d1	222	225	0% to 1%	+1%	236	238	1% to 1%	0%	250	251	3% to 4%	0%
Is	g1 to g2	224	227	0% to 8%	+8%	237	239	0% to 5%	+5%	251	252	3% to 10%	+6%
Is	NE low to PG low	215	222	0% to 1%	+1%	232	236	0% to 1%	+1%	249	250	0% to 2%	+2%
Is	PG low to PR low	222	229	1% to 4%	+3%	236	241	1% to 2%	+1%	250	253	2% to 4%	+2%
Is	TO low to BV low	216	223	2% to 3%	0%	233	236	2% to 1%	0%	249	251	4% to 1%	-3%
Average		**219**	**224**		**+3%**	**234**	**237**		**+2%**	**250**	**251**		**+2%**

Appendix H - Sensitivity analysis for early fall frost events for assisted migration towards higher elevations. Source DoY and target DoY are the days of the year where critical photoperiods occur. The changes in probabilities of early fall frost risks due to the seed transfer are highlighted by a color scheme that is consistently applied across Appendix G and H for direct comparison of elevation versus latitude transfers. Examples of risk comparisons among seed zones for 4 species are exhibited in the table (Df: Douglas-fir; Lp: lodgepole pine; Wl: western larch; Is: Interior spruce).

		Risk of -5 °C after 9-hour night length				Risk of -8 °C after 10-hour night length				Risk of -10 °C after 11-hour night length			
Spec.	Seed zone transfer	Source DoY	Target DoY	Change in probability	Prob. Diff.	Source DoY	Target DoY	Change in probability	Prob. Diff.	Source DoY	Target DoY	Change in probability	Prob. Diff.
Df	M low to M high	213	214	0% to 1%	+1%	231	231	0% to 0%	0%	248	248	0% to 1%	+1%
Df	NE low to NE high	214	214	0% to 1%	+1%	231	231	0% to 1%	+1%	248	248	0% to 2%	+2%
Lp	BV low to BV high	222	223	1% to 37%	+35%	236	237	1% to 22%	+21%	250	251	1% to 21%	+20%
Lp	CP low to CP high	224	225	2% to 46%	+44%	237	238	1% to 30%	+29%	251	251	1% to 31%	+30%
Lp	EK low to EK high	214	214	0% to 4%	+4%	231	231	0% to 1%	+1%	248	248	0% to 7%	+7%
Lp	NE low to NE high	214	214	0% to 7%	+7%	231	231	0% to 7%	+7%	248	248	0% to 8%	+8%
Lp	NS low to NS high	225	225	3% to 49%	+46%	238	238	1% to 29%	+28%	251	251	1% to 24%	+24%
Lp	PG low to PG high	219	219	0% to 18%	+18%	234	234	0% to 12%	+12%	250	250	2% to 17%	+15%
Lp	TO low to TO high	214	214	0% to 5%	+5%	231	231	0% to 4%	+4%	248	248	1% to 7%	+6%
Wl	NE low to NE high	213	213	0% to 7%	+7%	231	231	0% to 6%	+5%	248	248	1% to 9%	+8%
Is	BV low to BV high	223	222	3% to 19%	+17%	236	236	1% to 11%	+10%	251	251	1% to 11%	+10%
Is	NE low to NE high	215	215	0% to 2%	+2%	232	232	0% to 2%	+2%	249	249	0% to 4%	+4%
Is	PG low to PG high	222	222	1% to 12%	+11%	236	236	1% to 8%	+8%	250	250	2% to 11%	+10%
Is	TO low to TO high	216	216	2% to 24%	+21%	232	232	2% to 18%	+16%	249	249	4% to 23%	+19%
Average		**218**	**218**		**+16%**	**233**	**234**		**+10%**	**249**	**249**		**+12%**

The End