Adaptation of white spruce populations to extreme climate events: implications for assisted migration practices in Western Canada

by

Jaime Sebastián Azcona

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

Doctor of Philosophy

in

Forest Biology and Management

Department of Renewable Resources
University of Alberta

Abstract

The movement of seed sources from south to north has been proposed as a tool to mitigate the effect of climate change on forest productivity and mortality. Southern provenances, coming from warmer regions are expected to better utilize the extended growing seasons expected under climate warming. But even if temperatures are warming overall, early fall frost events or late spring frost events may still occur at similar or even increased frequencies relative to the growth phenology of plants. If trees are not correctly adapted to the length of the growing season, and they release dormancy to early or stop growing too late, they will suffer frost damage.

To find the best adapted provenances I studied here different physiological adaptations to climate that should help delineate safe transfer distances of white spruce (*Picea glauca* [Moench] Voss), using a range-wide provenance trial in Central Alberta. I measured physiological and anatomical traits related to drought resistance and cold hardiness, and implemented a novel tree ring approach to detect xylem anomalies induced by past climate events.

My results showed tradeoffs between fall cold hardiness and tree growth primarily along a latitudinal cline. Southern provenances showed higher growth but a later onset of cold hardiness. Latitude of source origin was the most influential environmental variable for both tree height and cold hardiness, suggesting a strong effect of day length regimes in the control of the length of the growing season. Provenances from southern latitudes of origin and from eastern maritime climate conditions showed high productivity, but were also more susceptible to the occurrence of abnormally thin cell wall thickness and unlignified tracheids in the latewood during cold years, indicating a mismatch of growth phenology with the available growing season. Provenances from maritime and warm source environments also had higher mortality

rates despite showing good growth. In contrast, provenances from the northern part of the distribution were more vulnerable to late spring frosts when grown in at a warmer test site than their origin climate. The physiological traits related to drought resistance and anatomy measured in this study did not show any significant difference throughout the range of the species, although we found some tradeoffs between hydraulic safety and efficiency.

Based on population differentiation observed in this study, hardiness zones could also be used to limit the distance of seed transfers within the species range. The results of this study support moderate northward movement of populations to address climate trends that have already occurred over the last decades. The best performing provenances in this trial came from the southern central part of the distribution (South East Manitoba), about 500 km south and 1,500 km east of the test site and a region with warmer summers and similar winter temperatures and precipitation. These climatic conditions are consistent with expected climate change, and therefore assisted migration prescriptions northward and upward in elevation to moderately cooler temperature (–1 to –2°C difference) seem well supported by this study.

Preface

Chapter 2 of this thesis has been published as Sebastián-Azcona J, Hacke U, Hamann A (2018) Adaptations of white spruce to climate: strong intraspecific differences in cold hardiness linked to survival. Ecology and Evolution, 8, 1758-1768. The study was conceived and designed by myself, UH and AH. I conducted the field and laboratory work and analyzed the data. I wrote the first draft of the chapter, and UH and AH contributed to interpreting the results and edited the manuscript.

Chapter 3 of this thesis has been accepted as Sebastián-Azcona J, Hamann A, Hacke U, Rweyongeza D (2019). Survival, growth and cold hardiness tradeoffs in white spruce populations: implications for assisted migration. Forest Ecology and Management (in press). The study was conceived and designed by myself, AH, UH and DR. I conducted the field work with support from DR. I conducted the laboratory work, analyzed the data and wrote the first draft of the chapter. AH, UH and RT contributed to interpreting the results and edited the manuscript.

Chapter 4 of this thesis is currently prepared for submission as a journal article. The contributors are Sebastián-Azcona J, Hacke U, Hamann A, Menzel, A., Rweyongeza D. The study was conceived and designed by myself, AH and UH. I conducted the field work with support from DR. I conducted the laboratory work with support from AM. I analyzed the data and wrote the first draft of the chapter. UH, AH, DR and AM contributed to interpreting the results and edited the manuscript.

Acknowledgements

I would like to start by thanking both my supervisors Uwe Hacke and Andreas Hamann. I am lucky to have two supervisors that provided so much support from the very first day to the last. Even though I was a bit skeptical of having two supervisors at the beginning, having two mentors with different expertise have really enriched my learning experience.

Uwe, thank you for teaching me so much about plant physiology. Over the last four years I have had way too many questions and you always found the time and the patience to answer all of them, I really appreciate that. I would also like to thank you for teaching me how to work in a lab, I could not have finished all my experiments without your constant help.

Andreas, thank you for all your help with statistical analyses. You changed my view of statistics, and always encouraged me to try new methods and think outside the box. I would also like to thank you for the new career opportunities that you offered me. You introduced me to the teaching world and I am really enjoying it so far.

I would also like to thank Dr. Vic Lieffers for being the last member of my supervisory committee and for all his thoughtful comments during my PhD.

I am very grateful to The Natural Sciences and Engineering Research Council of Canada, the Faculty of Graduate Studies and Research at the University of Alberta and the University of Alberta Water Initiative for their financial support. This study would not have been possible without generous in-kind contributions and sharing of provenance trial measurements by our supporting organization, the Government of Alberta, and a especial thank you to Deogratias Rweyongeza for all his support.

A big advantage of having two supervisors is having the opportunity to be part of two labs. It would not be possible to mention all my labmates but I would like to especially thank to those that have been there from beginning to end: Dante, Rachel and Ryan. We have shared all the highs and lows of the PhD ride and I feel very fortunate it was with you.

I would like to thank all the people that helped me with my data collection, especially to those that did it voluntarily. Thank you Alan Lee, Stefan Schreiber, Rodrigo Campos and Luiz Drummond.

I finally want to thank my family and friends for all their support. Thank you to my parents, my sister and the rest of my family, I could feel your support with every single skype conversation, message, photo or video that you send me. I would like to send a huge thank you to my grandfather Vicente, your early biology lessons in "La Isla" made me reach where I am today. I want to thank all my friends who have accompanied me in this journey. Thank you to my friends back home, their daily meaningless talk was a constant reminder of where I come from and what I have back there. After spending so much time far away from home, it feels amazing to know that I have so many people back there standing behind me during my foreign adventures. My last thank you goes to my Edmonton friends for making these four years a lot more fun.

Thank you all, I could not have finished this journey without you!

Table of Contents

List of Tables

List of figures

Chapter 1. General introduction

1.1 Introduction

With 300 million hectares of forest, Canada is the country with the third largest forested area (Canadian Forest Service 2017). This vast amount of natural resources is reflected in the economy as the forestry industry employed 211,075 people and injected $23.1 billion to Canada's economy, accounting for 1.5% of the GDP in 2016 (Canadian Forest Service 2017). White spruce (*Picea glauca* [Moench] Voss) is one of the most characteristic tree species in Canada. Its distribution covers almost all of Canada from Newfoundland and Labrador in the South East to Yukon in the North West, where it reaches the arctic treeline (Nienstaedt & Zasada 1990). Although white spruce is a plastic species that can grow in a wide range of climate and soil conditions, it appears most often in well drained soils of riparian, upland or treeline sites (Nienstaedt & Zasada 1990; Abrahamson 2015). White spruce is also a very important commercial species of the boreal forest (Nienstaedt & Zasada 1990) and particularly Alberta (Rweyongeza *et al.* 2007a).

1.2 Climate trends and projections

It is still uncertain how boreal forests will react to climate change. Over the period between 1880 and 2012, the average global temperature has increased by 0.82ºC (IPCC 2014). In the boreal regions, the effect of global change in temperatures has been more evident as reflected by the 2ºC increment in average annual temperatures in Western Canada during the 1950-2003 period (Price *et al.* 2013). Future temperatures will depend on future anthropogenic emissions, but current projections for global means of the 2081-2100 period range between an increment of 0.3 and 4.8ºC relative to the 1986-2005 period (IPCC 2014). For the Boreal Plains ecozone in Canada, Price *et al.* (2013) predicted an increment of 3.4 to 4.8ºC for the 2071-2100 period respect the 1961-1990 baseline. Despite the obvious warming trend in average temperatures, climate change is also expected to increase the frequency and severity of extreme events, which have a higher potential to impact vegetation communities (Lloret *et al.* 2012). Changes in precipitation over the last decades have been more spatially heterogeneous than for temperature, with no clear trends globally (IPCC 2014). At a regional scale, Alberta experienced a reduction in precipitation of up to 20% in the 1997-2006 period compared to the 1961-1990 normal (Mbogga, Hamann & Wang 2009) and this drying trend is likely to continue according to future projections (Wang *et al.* 2014).

1.3 Impact of climate change in forests

The new environmental conditions created by climate change will directly impact forest productivity and mortality rates at a global scale. The increased temperatures and elevated CO_2 concentration have increased forests' productivity when other factors, such as drought or nitrogen availability are not limiting (Norby *et al.* 2005; Boisvenue & Running 2006; Lindner *et al.* 2010; Norby *et al.* 2010). However, the increased temperatures will also increase water demand, so forests are becoming increasingly stressed by drought, even in areas that were not previously limited by water (Williams *et al.* 2013). This increased drought stress has already caused higher mortality rates across the globe, either by drought-induced hydraulic failure or as a facilitator for other stresses (McDowell *et al.* 2008; Allen *et al.* 2010). The combination of warmer temperatures and reduced tree vigor are ideal conditions for insect outbreaks (Bentz *et al.* 2010). Drought stressed forests also provide better fuel for forest fires, which coupled with the warmer and drier weather conditions will result in more frequent and intense forest fires (Flannigan, Stocks & Wotton 2000).

In boreal forests, warmer temperatures were initially expected to have beneficial effects on forest productivity (Melillo *et al.* 1993). Several studies in treeline populations reported increased growth in response to warmer temperatures using dendrochronology methods (MacDonald *et al.* 1998; Lloyd & Fastie 2002). In an experimental warming study, Danby and Hik (2007) also observed a positive effect of temperatures on white spruce growth and photosynthetic rates. Despite these studies showing a higher productivity linked to warmer temperatures, an excessive increase in temperatures will create a water deficit that will reverse the positive effect of warmer temperatures.(D'Orangeville *et al.* 2018). In fact, drought seems to be an increasingly important limitation in boreal forests as shown by the decreased productivity of aspen (Hogg, Barr & Black 2013) and white spruce (Hogg *et al.* 2017) in Western Canada. Extreme drought events were also linked to aspen mortality in North American forests (Michaelian *et al.* 2011; Worrall *et al.* 2013).

As for white spruce, drought has been consistently reported as a main constrain for growth (Chhin, Wang & Tardif 2004; Chhin & Wang 2008; Jiang *et al.* 2016a; Alam *et al.* 2017; Chen *et al.* 2017; Hogg *et al.* 2017) and survival (Peng *et al.* 2011). In the most recent study, Hogg *et al.* (2017) observed a drastic decline of tree growth during the severe drought of 2001-2002 in Alberta and Saskatchewan, which was further intensified by the subsequent droughts until the year 2015.

1.4 Assisted migration as a tool to mitigate climate change

Due to natural selection, local populations are normally adapted to the environmental conditions of their habitat (Morgenstern 1996). Patterns of local adaptation have traditionally been accounted for by establishing seed zones, so that only seeds from within a seed zone could be used in reforestation practices. This practice would limit the maximum seed transfer distances and therefore assure that reforestation stock would be adequately adapted to that environment. However, climate change that we are experiencing is shifting the environmental conditions too fast for trees to adapt (Aitken *et al.* 2008). Besides adaptation to the new environment, tree populations may track their optimal growth environment through seed and pollen dispersal, but migration distances appear too large for migration to track predicted climate change (Davis & Shaw 2001). The inability to keep up with climate change will create an adaptational lag that has already been reported in several studies (Zhu, Woodall & Clark 2012; Corlett & Westcott 2013a). Gray and Hamann (2013) estimated an already existing average lag of 130 km in latitude or 60m in Western North America, which could increase to 590 km or 260 m by 2050.

As a potential solution to adaptational lag, human assisted migration has been proposed to mitigate the effect of climate change on forests (Pedlar *et al.* 2012; Aitken & Bemmels 2016). The idea of assisted migration in a reforestation contest consists of using seeds from areas that are already experiencing warmer conditions, instead of selecting seed sources solely based in geographical proximity. Assisted migration has also been proposed as a conservation tool to move endangered species with small habitats that are likely to disappear to areas that can support it but are too far to be reached by natural migration (McLachlan, Hellmann & Schwartz 2007). However, in a forestry context we consider assisted migration of populations within a species range or barely outside of it. This type of assisted migration is sometimes denominated as "assisted gene flow" or "assisted population migration" to differentiate it from the assisted migration performed for conservation purposes. Assisted migration used for conservation has been a continuous focus of debate due to its potential risks. Moving species outside of their natural range can create new exotic invasive species, hybridization between the introduced species and local species and a potential risk of introducing new diseases to other species. Assisted migration in forestry still has similar potential risks, but at a much lower level since the species is already present in the area (Pedlar *et al.* 2012).

The success of assisted migration practices in forestry relies on identifying seed sources that will perform better than local populations. This information is obtained from provenance trials that study differences between populations (Matyas 1996). In provenance trials, seeds from different origins, or provenances, are planted in a common garden so that genetic differences between populations can be observed. The observable characteristics of an individual, or phenotype, are the result of the interaction between its genetic information, or genotype, and the environment in which they occur (White, Adams & Neale 2007). By planting all the individuals in a single site, the environmental effect is removed and all observed differences can be attributed to genetic differences. Finding more productive provenances has been a goal of forest researchers for decades (Langlet 1971), but significantly more effort has been put recently in understanding the physiological reasons behind population differentiation (Aitken & Bemmels 2016). If we are able to identify the physiological characteristics that make some trees more successful than others, we can use that information to select the seed sources that are best adapted to the new environmental conditions, such as the expected increased drought stress.

1.5 Tree water relations and drought adaptation

Water is transported from the roots to the leaves of a tree through the xylem. The mechanism responsible for this movement is explained by the Cohesion-Tension theory. The evaporation occurring in the leaves creates a tension that is transmitted through a continuous column of water to the rest of the plant. Water ascends through the xylem in a metastable condition since the pressure inside the xylem is lower than the vapor pressure of water (Dixon & Joly 1895). The metastable condition of the water column means that if this column is broken, it will not rejoin until positive pressures occur in the xylem. The process by which air is pulled inside the conduit breaking the water conduit and filling the whole conduit is called cavitation. The two main mechanisms inducing cavitation are freezing-induced cavitation and drought-induced cavitation (Hacke & Sperry 2001). When water freezes in the xylem, dissolved gases form bubbles. If the tension in the conduit is too high when the ice thaws, then those bubbles will expand and block the conduit. The most likely mechanism inducing drought-induced cavitation is the air-seeding hypothesis. According to this hypothesis, air is aspired from a contiguous air-filled conduit when the tension within the conduit is higher than the capillary forces present in the pit connecting both conduits

(Sperry & Tyree 1988). The ability of plants to resist cavitation is usually measured with vulnerability curves. Hydraulic conductivity is measured at different water stress levels and the represented as a percentage of conductivity loss from the maximum conductivity. The water potential needed to induced a 50% loss of conductivity is commonly used to report the susceptibility of trees to cavitation (e.g. Sperry, Donnelly & Tyree 1988; Pammenter & Van der Willigen 1998).

Since drought stress is predicted to become more common in the near future due to climate change, trees with higher resistance to dry condition should be favored in reforestation practices. Anderegg *et al.* (2016) found that the hydraulic safety margin was the best predictor was the best predictor for species-specific mortality anomalies. Hydraulic safety margin is defined as the difference between the typical minimum xylem water potential and the water potential that would induce a 50% conductivity loss (Meinzer *et al.* 2009). The downside of xylem with high cavitation resistance is normally a tradeoff with xylem conductivity. Trees cannot have high resistance and high conductivity xylem at the same time, although low values of both characteristics are possible (Gleason *et al.* 2016a). Trees that are resistant to drought stress are usually associated to more robust tissues, as implied from the positive effect in drought resistance of traits such as high wood density, low specific leaf area and low leaf-to-sapwood area (Hacke *et al.* 2001b; Gleason *et al.* 2016a; Greenwood *et al.* 2017).

1.6 The importance of cold hardiness in a warming world

Even if climate warming will likely reduce the number of freezing events (IPCC 2014), the study of cold hardiness in plants is still a very relevant topic. Because assisted migration is based on moving seed sources from warmer to colder areas, frost damage becomes a serious risk for the newly introduced plants. Even after the warming period of the last few decades, severe frost damage still occurs in natural populations as reported by Gu *et al.* (2008) and Man *et al.* (2009a) after a frost spell in spring 2007 in Eastern North America.

There are two main strategies against frost damage: avoidance and tolerance of freezing (Levitt 1980). One strategy of frost damage avoidance is to prevent the formation of ice by deep supercooling. When water is supercooled, it can reach temperatures below its freezing point while remaining liquid. If water does not have contact with extracellular ice or any other nucleating agent, it can stay in liquid form until about -40ºC (Sutinen *et al.* 2001). Frost tolerant tissues on the other hand, allow the formation of extracellular ice. Since frozen water has a lower potential than liquid water, water will move from the intracellular solution to the growing ice crystals outside the cells until the potential inside the cell matches that of the ice crystals. This creates a dehydration stress similar to drought stress (Palta 1990). In the boreal species, frost tolerance is the most common strategy while freezing avoidance is often seen in temperate species (Sutinen *et al.* 2001).

Cold hardiness is not uniform during the year. While temperatures just below freezing can cause damage during the growing season, fully acclimated twigs have been reported to tolerate temperatures as low as -196ºC (Sakai & Sugawara 1973). Trees adapted to cold temperatures must stop growing and become dormant before frosts occur. This cold acclimation occurs in two or three stages (Sakai & Sugawara 1973). In the first stage, growth ceases and the tree becomes partially resistant to low temperatures. The second stage is triggered by low temperatures close to freezing, increasing cold hardiness. The third stage is only present in species living in extreme environment and occurs at temperatures between -30ºC and -50ºC. Dormancy is released after a period of temperatures slightly above freezing, and after dormancy is released, growth starts when a certain sum of growing degree days has been reached (Howe *et al.* 2003a). Even if temperatures and photoperiod are the main environmental queues for cold hardiness phenology, other factors such as water, irradiance or mineral nutrients can also affect the cold hardiness of trees (Bigras *et al.* 2001).

Because release of dormancy in spring and onset of dormancy in fall are controlled by different environmental queues, the expected climate change will affect them differently. The beginning of the growing season, which is controlled mainly by temperatures, advances to an earlier day of year as the sum of temperatures required for the onset of growth happens earlier in spring. In Europe, spring events have advanced 2.5 days/decade on average between 1971 and 2000 (Menzel *et al.* 2006). In Canada, aspen blooming advanced 2.7 days/decade between 1900 and 1997 (Beaubien & Freeland 2000). Trends in fall phenology, which is mostly regulated by photoperiod but also influenced by temperatures, are not so clear. Even though several studies report a delay of fall phenology, this delay is usually smaller than the advance in spring. For instance *Picea abies* showed ranges in population means of 4-12 days for budbreak and 17-32 days for budset (Aitken & Hannerz 2001 and literature cited therein). The same European study that reported a 2.5

days/decade in spring, found a delay in fall of 1.0 days/decade on average (Menzel *et al.* 2006).

1.7 Dendrochronological methods to study past climate events

The characteristic seasonality of tree growth in temperate and boreal forests induces the formation of tree rings. Tree rings allow identifying the xylem growth corresponding to a specific year. Measuring the width of these tree rings can be used to study growth trends over the tree's lifetime. These trends can then be attributed to climate or other environmental variables (Fritts 1976). In the case of more extreme climate events, xylem anomalies might form as a response. Frost damage caused by late spring or summer frosts while the cambium is active manifest as "frost rings" (Glerum & Farrar 1966). A frost ring will show thin and unlignified cell walls in the earlywood, followed by a zone of collapsed cells. After this layer of collapsed cells, traumatic parenchyma cells are formed followed by tracheids with lignified cell walls but abnormal shapes (Glerum & Farrar 1966). In years with low temperatures at the beginning and end of the growing season, tree rings with abnormally thin cell walls in the latewood might form. These tree rings are called "light rings" (Filion *et al.* 1986). Low temperatures at the end of the growing season might also induced the formation of unlignified cell walls in the latewood. These unlignified cells can be identified with a double stain of safranin and astra blue, so lignified cells are stained red by safranin while unlignified tracheids will show a blue stain. Tree rings with unlignified latewood cell walls are called "blue rings" (Piermattei *et al.* 2015). Another interesting xylem anomaly is formed when a very dry summer is followed by a sudden increase in precipitation at the end of the growing season. This climate event might induce the formation of latewood-like cells in the earlywood of the tree ring, giving the impression of a “double ring”.

Combining dendrochronology analyses with provenance trial experiments can be a powerful tool to understand how different populations reacted to past climate, so we can better predict the effects of climate change in the future. This approach has been used mostly to study drought susceptibility of different provenances and species (e.g. McLane, Daniels & Aitken 2011; Taeger *et al.* 2013; Montwé *et al.* 2016). Although this approach has a great potential to observe differences in cold hardiness, these studies are much scarcer (Montwé *et al.* 2018).

1.8 Thesis outline and objectives

The general objective of this thesis is to discover which anatomical or physiological adaptations to climate are present in white spruce. Identifying frost or drought resistant populations could inform proposed assisted migration practices based not only in the productivity of the provenances, but also taking into account their adaptation to regional climate conditions and climate extremes. This thesis consists of three research chapters that systematically address these overall objectives:

In my **first research chapter**, I performed an exploratory analysis trying to identify key traits that could be responsible for differences in tree performance. For that, I screened many physiological and anatomical traits in a reduced number of provenances that represented the full geographic range of the species, with clearly different climates of origin and contrasting performances in growth and survival. The objectives of this chapter were:

- Discovering genetic population differentiation among provenances from across the entire range of the species for a wide selection of hydraulic, anatomical and cold hardiness traits
- Analyzing how these traits are related to the climate of origin of the provenances
- Detecting possible relationships between resistance to climate (cold and drought), tree growth and survival

In my **second research chapter**, I investigated adaptive traits that showed strong population differentiation in my previous chapter. After finding a strong association between fall cold hardiness and tree mortality, I measured this trait in more detail, sampling more provenances from a more comprehensive range of environmental conditions and testing cold hardiness at several times during the growing season. The main objectives of this chapter were:

- Identifying possible tradeoffs between frost hardiness, growth and survival
- Analyzing the association of climate and latitude at the origin of seed sources (as a proxy for day length regime) with growth, survival and frost hardiness observed in the common garden trial

- Quantifying the impact of long distance transfers to identify seed sources with good hardiness characteristics as well as good growth performance as a recommendation for assisted migration prescriptions.

In my **third research chapter**, I used dendrochronological analyses to identify if past climate events, recorded in tree rings, compromised growth and survival. Specifically, I looked for spring and summer frost damage in earlywood (frost rings), effect of cool temperatures over the whole growing season (light and blue rings) and signatures of drought conditions (double rings). The specific objectives of this chapter were:

- Linking the presence of different tree ring anomalies to past climate events.
- Identifying differences between provenances tree ring anomalies that indicate resistance or susceptibility to past climate events.
- Quantifying the relationship between the climate of origin of the seed sources with tree ring anomalies to infer adaptation to climate conditions.
- Investigating whether the presence of the different tree rings impacted the growth and survival rates of the different provenances, and analyzing its importance in assisted migration prescriptions.

1.9 References

Abrahamson, I. (2015) Picea glauca, white spruce. *Fire Effects Information System, [Online]*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Aitken, S.N. & Bemmels, J.B. (2016) Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications,* **9,** 271-290.

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications,* **1,** 95-111.

Alam, S.A., Huang, J.-G., Stadt, K.J., Comeau, P.G., Dawson, A., Gea-Izquierdo, G., Aakala, T., Hölttä, T., Vesala, T. & Mäkelä, A. (2017) Effects of competition, drought stress and photosynthetic productivity on the radial growth of white spruce in western Canada. *Frontiers in Plant Science,* **8,** 1915.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D. & Hogg, E.H.T. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management,* **259,** 660-684.

Anderegg, W.R.L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A.F.A., Choat, B. & Jansen, S. (2016) Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences,* **113,** 5024-5029.

Barber, V.A., Juday, G.P. & Finney, B.P. (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature,* **405,** 668.

Beaubien, E.G. & Freeland, H.J. (2000) Spring phenology trends in Alberta, Canada: links to ocean temperature. *International journal of biometeorology,* **44,** 53-59.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F. & Seybold, S.J. (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *Bioscience,* **60,** 602-613.

Bigras, F.J., Ryyppö, A., Lindström, A. & Stattin, E. (2001) Cold acclimation and deacclimation of shoots and roots of conifer seedlings. *Conifer cold hardiness* (eds F.J. Bigras & S. Colombo), pp. 57-88. Springer.

Boisvenue, C. & Running, S.W. (2006) Impacts of climate change on natural forest productivity–evidence since the middle of the 20th century. *Global Change Biology,* **12,** 862-882.

Canadian Forest Service (2017) The state of Canada's forests. Annual report 2017. (ed. N.R. Canada). Ottawa.

Chen, L., Huang, J.-G., Stadt, K.J., Comeau, P.G., Zhai, L., Dawson, A. & Alam, S.A. (2017) Drought explains variation in the radial growth of white spruce in western Canada. *Agricultural and Forest Meteorology,* **233,** 133-142.

Corlett, R.T. & Westcott, D.A. (2013) Will plant movements keep up with climate change? *Trends in ecology & evolution,* **28,** 482-488.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E. & Peterson, C.J. (2001) Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *AIBS Bulletin,* **51,** 723-734.

Danby, R.K. & Hik, D.S. (2007) Responses of white spruce (Picea glauca) to experimental warming at a subarctic alpine treeline. *Global Change Biology,* **13,** 437-451.

Flannigan, M.D., Stocks, B.J. & Wotton, B.M. (2000) Climate change and forest fires. *Science of the total environment,* **262,** 221-229.

Gleason, S.M., Westoby, M., Jansen, S., Choat, B., Hacke, U.G., Pratt, R.B., Bhaskar, R., Brodribb, T.J., Bucci, S.J. & Cao, K.F. (2016) Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist,* **209,** 123-136.

Gray, L.K. & Hamann, A. (2013) Tracking suitable habitat for tree populations under climate change in western North America. *Climatic Change,* **117,** 289-303.

Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C.D., Fensham, R., Laughlin, D.C., Kattge, J. & Bönisch, G. (2017) Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters,* **20,** 539-553.

Gu, L., Hanson, P.J., Post, W.M., Kaiser, D.P., Yang, B., Nemani, R., Pallardy, S.G. & Meyers, T. (2008) The 2007 eastern US spring freeze: increased cold damage in a warming world? *AIBS Bulletin,* **58,** 253-262.

Hacke, U.G. & Sperry, J.S. (2001) Functional and ecological xylem anatomy. *Perspectives in Plant Ecology, Evolution and Systematics,* **4,** 97-115.

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloh, K.A. (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia,* **126,** 457-461.

Hogg, E.H., Michaelian, M., Hook, T.I. & Undershultz, M.E. (2017) Recent climatic drying leads to age-independent growth reductions of white spruce stands in western Canada. *Global Change Biology,* **23,** 5297-5308.

Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. & Chen, T.H.H. (2003) From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany,* **81,** 1247-1266.

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the

Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Jiang, X., Huang, J.-G., Stadt, K.J., Comeau, P.G. & Chen, H.Y.H. (2016) Spatial climate-dependent growth response of boreal mixedwood forest in western Canada. *Global and Planetary Change,* **139,** 141-150.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T. & Safranyik, L. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature,* **452,** 987.

Langlet, O. (1971) Two hundred years genecology. *Taxon***,** 653-721.

Levitt, J. (1980) Responses of plants to environmental stress. *Chilling, freezing, and high temperature stresses*. Academic Press.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P. & Kolström, M. (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management,* **259,** 698-709.

Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J. & Valladares, F. (2012) Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology,* **18,** 797-805.

Lloyd, A.H. & Fastie, C.L. (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change,* **52,** 481-509.

MacDonald, G.M., Szeicz, J.M., Claricoates, J. & Dale, K.A. (1998) Response of the central Canadian treeline to recent climatic changes. *Annals of the Association of American Geographers,* **88,** 183-208.

Man, R., Kayahara, G.J., Dang, Q.-L. & Rice, J.A. (2009) A case of severe frost damage prior to budbreak in young conifers in Northeastern Ontario: Consequence of climate change? *The Forestry Chronicle,* **85,** 453-462.

Matyas, C. (1996) Climatic adaptation of trees: rediscovering provenance tests. *Euphytica,* **92,** 45-54.

Mbogga, M.S., Hamann, A. & Wang, T. (2009) Historical and projected climate data for natural resource management in western Canada. *Agricultural and Forest Meteorology,* **149,** 881-890.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A. & Williams, D.G. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist,* **178,** 719-739.

McLachlan, J.S., Hellmann, J.J. & Schwartz, M.W. (2007) A framework for debate of assisted migration in an era of climate change. *Conservation Biology,* **21,** 297-302.

Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A. & Woodruff, D.R. (2009) Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology,* **23,** 922-930.

Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B., Vorosmarty, C.J. & Schloss, A.L. (1993) Global climate change and terrestrial net primary production. *Nature,* **363,** 234.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O.g. & Briede, A. (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology,* **12,** 1969-1976.

Morgenstern, M. (1996) *Geographic variation in forest trees: genetic basis and application of knowledge in silviculture*. UBC press, Vancouver, Canada.

Nienstaedt, H. & Zasada, J.C. (1990) White spruce. *Silvics of North America*, pp. 389-442.

Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P. & Ceulemans, R. (2005) Forest response to elevated CO2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences,* **102,** 18052-18056.

Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E. & McMurtrie, R.E. (2010) CO2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences,* **107,** 19368-19373.

Palta, J.P. (1990) Stress interactions at the cellular and membrane levels. *HortScience,* **25,** 1377-1381.

Pammenter, N.W.v. & Van der Willigen, C. (1998) A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiology,* **18,** 589-593.

Pedlar, J.H., McKenney, D.W., Aubin, I., Beardmore, T., Beaulieu, J., Iverson, L., O'Neill, G.A., Winder, R.S. & Ste-Marie, C. (2012) Placing Forestry in the Assisted Migration Debate. *Bioscience,* **62,** 835-842.

Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R.A., Hogg, E.H., Girardin, M.P., Lakusta, T., Johnston, M. & McKenney, D.W. (2013) Anticipating the consequences of climate change for Canada's boreal forest ecosystems. *Environmental Reviews,* **21,** 322-365.

Rweyongeza, D., Yang, R.-C., Dhir, N., Barnhardt, L. & Hansen, C. (2007) Genetic variation and climatic impacts on survival and growth of white spruce in Alberta, Canada. *Silvae Genetica,* **56,** 117-127.

Sakai, A. & Sugawara, Y. (1973) Survival of poplar callus at super-low temperatures after cold acclimation. *Plant and cell physiology,* **14,** 1201-1204.

Sperry, J.S., Donnelly, J.R. & Tyree, M.T. (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment,* **11,** 35-40.

Sperry, J.S. & Robson, D.J. (2001) Xylem cavitation and freezing in conifers. *Conifer cold hardiness*, pp. 121-136. Springer.

Sperry, J.S. & Tyree, M.T. (1988) Mechanism of water stress-induced xylem embolism. *Plant Physiology,* **88,** 581-587.

Sutinen, M.-L., Arora, R., Wisniewski, M., Ashworth, E., Strimbeck, R. & Palta, J. (2001) Mechanisms of frost survival and freeze-damage in nature. *Conifer cold hardiness* (eds F.J. Bigras & S.J. Colombo), pp. 89-120. Springer.

Tyree, M.T. (1997) The cohesion-tension theory of sap ascent: current controversies. *Journal of experimental botany,* **48,** 1753-1765.

Tyree, M.T. & Sperry, J.S. (1989) Vulnerability of xylem to cavitation and embolism. *Annual review of plant biology,* **40,** 19-36.

Tyree, M.T. & Zimmermann, M.H. (2002) *Xylem Structure and the Ascent of Sap,* 2 edn. Springer-Verlag Berlin Heidelberg.

Wang, Y., Hogg, E.H., Price, D.T., Edwards, J. & Williamson, T. (2014) Past and projected future changes in moisture conditions in the Canadian boreal forest. *The Forestry Chronicle,* **90,** 678-691.

Way, D.A. & Montgomery, R.A. (2015) Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell & Environment,* **38,** 1725-1736.

White, T.L., Adams, W.T. & Neale, D.B. (2007) *Forest genetics*. Cabi.

Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R. & Grissino-Mayer, H.D. (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change,* **3,** 292.

Zhu, K., Woodall, C.W. & Clark, J.S. (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology,* **18,** 1042-1052.

Chapter 2. Adaptations of white spruce to climate: strong intra-specific differences in cold hardiness linked to survival

2.1 Summary

Understanding local adaptation of tree populations to climate allows the development of assisted migration guidelines as a tool for forest managers to address climate change. In this chapter, we study relationships between climate, a wide range of physiological traits, and field performance of selected white spruce provenances originating from throughout the species range. Tree height, survival, cold hardiness, hydraulic and wood anatomical traits were measured in a 32-year-old, common garden trial located in a central location of white spruce distribution. Provenance performance included all combinations of high versus low survival and growth, with the most prevalent population differentiation for adaptive traits observed in cold hardiness. Cold hardiness showed a strong association with survival and was associated with cold winter temperatures at the site of seed origin. Tree height was mostly explained by the length of the growing season at the origin of the seed source. Although population differentiation was generally weak in wood anatomical and hydraulic traits, within-population variation was substantial in some traits, and a boundary analysis revealed that efficient water transport tended to be linked to vulnerable xylem and low wood density, indicating that an optimal combination of high water transport efficiency and high cavitation resistance is not possible. Our results suggest that assisted migration prescriptions may be advantageous under warming climate conditions, but pronounced tradeoffs between survival and cold hardiness require a careful consideration of the distances of these transfers.

2.2 Introduction

Geographic patterns of local adaptation of forest trees have been studied since the 18thcentury, and most studies found that local populations were the best fit to a specific environment (Langlet 1971). This has led forest managers to develop so called “seed zones”, where areas of similar conditions were defined assuming that individuals coming from that area would have superior growth and survival when planted within the same seed zone. More recently, climate change has led to locally adapted populations lagging behind their optimal climate niche, thus challenging the assumption that “local is best” (Hacke *et al.* 2001a; Aitken *et al.* 2008). Gray and Hamann (2013) found that based on observed climate trends, forest tree species in western North America already lag behind their optimal climate niche by approximately 130 km in latitude. Furthermore, Alberta also experienced a reduction in precipitation in the past 25 years (Mbogga, Hamann & Wang 2009), and the trend toward drier conditions may continue during the 21st century (Wang *et al.* 2014). Such data implies that trees may become increasingly maladapted to new climate conditions.

One way of accommodating changes in climate is the use of seed sources from areas already adapted to warmer temperatures as part of regular reforestation programs. This usually implies selecting seeds from southern areas to be planted in a more northern region (Millar, Stephenson & Stephens 2007). Such assisted migration prescriptions depend on identifying well-adapted genotypes from matching climate regions. This can be done using provenance trials, in which seed sources collected from different geographic regions and different environments are planted in a common garden where genetic differences between populations may be observed. If promising genotypes can be identified in provenance trials, then these genotypes could be moved and planted where their characteristics match the anticipated climate. Previous work on white spruce provenances in different parts of its distribution suggests that northern transfers can increase growth rates (e.g. Li, Beaulieu & Bousquet 1997b; Lesser & Parker 2004b; Rweyongeza *et al.* 2007b; Lu *et al.* 2014b; Gray *et al.* 2016b). A recent study proposed relatively short northward transfers for Alberta, putatively limited by cold temperatures in the north of the province (Gray *et al.* 2016b). All these studies analyzed the response of tree growth to different planting environments, but there is little understanding of the physiological causes of different local adaptations.

In the boreal forest, increased temperatures may have a positive effect on tree growth as has been observed in some white spruce populations (MacDonald *et al.* 1998; Lloyd & Fastie 2002; Danby & Hik 2007). But this positive effect will only occur with adequate water availability, since the opposite effect was found in drier areas or years, showing that drought can be an important limitation for white spruce development in the future (Barber, Juday & Finney 2000; Lloyd & Fastie 2002; Danby & Hik 2007; Jiang *et al.* 2016b; Chen *et al.* 2017). Even if precipitation rates are not affected by climate change, increased temperatures will enhance drought stress in plants by increasing transpiration. With higher transpiration, water reserves will deplete faster inducing a drought stress caused by high temperatures (Breshears *et al.* 2005). Moreover, snow reserves will melt earlier reducing water availability during the growing season (Barnett, Adam & Lettenmaier 2005). Finding a productive and drought resistant genotype might be a difficult challenge since tradeoffs between growth and heat/drought resistance have been reported in white spruce (Bigras 2000; Bigras 2005). The tradeoff between hydraulic safety and efficiency of the xylem was analyzed in detail by Gleason *et al.* (2016b), arriving at the conclusion that although the correlation between both traits is not always clear, the combination of both high efficiency and high resistance is not possible. This tradeoff can be partially explained by anatomical features of the tree such as wood density, conduit size or ratio between photosynthetic and conductive tissue (Sperry, Hacke & Pittermann 2006; Gleason *et al.* 2016b).

Even though frost events are lower in frequency and severity now compared to the first half of the 20th century, extreme climate events may still occur on rare occasions, especially if overall variability in climate increases. A single unexpected frost event can cause great damage to forests if it happens during the growing season (Gu *et al.* 2008). Man *et al.* (2009b) also reported severe frost damage in a white spruce stand after a late frost spell. Since such frost events that cause dieback and mortality are very rare, it remains difficult to assess the risk involved in moving planting stock north, even with data from long-term provenance trials because mature trees may not be as susceptible to frost damage as seedlings and saplings. Generally, differences between provenances in the onset of cold hardiness in fall are greater than in the release of cold hardiness in spring, so a movement in latitude might have a bigger effect in changing susceptibility to early frosts in fall (Aitken & Hannerz 2001). Cold hardiness heavily relies on the phenology of the onset and release of cold hardiness, and a tradeoff between growth and cold hardiness is usually driven by how long trees extend their growing season in the fall (Howe *et al.* 2003b). The effect of climate change in fall usually gets less attention than other seasons even though fall events can have important ecological impact (Gallinat, Primack & Wagner 2015).

While growth performance of white spruce provenances has been well studied, there is a lack of understanding which physiological and anatomic traits are responsible for those genetic population differences. Tradeoffs between growth and cold hardiness or drought resistance pose an extra challenge for forest managers to maintain the productivity and health of our forests under climate change. We also wanted to analyze how adaptation relates to tree survival, a parameter not usually studied in classical provenance trial studies. In this study, we used ten provenances coming from five distinct climatic regions across the range of the species to assess the importance of adaptive traits that could impact tree performance under various environmental conditions. The specific goals were to 1) discover genetic population differentiation among provenances from across the entire range of the species for a wide selection of hydraulic, anatomical and cold hardiness traits, 2) detect possible relationships between resistance to climate (cold and drought), tree growth and survival and 3) analyze how these traits are related to the climate of origin of the provenances. The results of this range-wide experiment could point to key traits for climate adaptation that could serve as a reference for more geographically limited studies with higher sample densities to support regional assisted migration prescriptions.

2.3 Methods

2.3.1 Plant material

Plant material for this study came from two contiguous white spruce (*Picea glauca* [Moench] Voss) trials in a single site in central Alberta, Canada (55°17'N, 113°10'W). Both trials belong to a provenance trial experiment described in detail by Rweyongeza *et al.* (2007b). One of the trials is planted with provenances from only the province of Alberta, while the other trial has provenances covering the whole Canadian distribution of white spruce, with some provenances present in both trials. Both trials have five blocks each, with nine trees per block for the Alberta trial and five trees per block for the Canada-wide trial. They were established in 1982 with four-year-old seedlings. Height was assessed after 32 growing seasons in the field and survival was calculated as the ratio of living trees to the total planted. Diameter at breast height was also measured after 27 growing seasons, but we only use height as a performance measure in this thesis for simplification, due to the high correlation between height and diameter in the site (Pearson's $r = 0.96$, $p < 0.001$).

We selected two provenances from five distinct regions that covered most of the white spruce distribution (Fig. 2.1, Table 2.1). The regions in Alberta corresponded to the three regions that showed genetic differences in previous studies (Rweyongeza *et al.* 2007b): northern Alberta (nAB), central Alberta (cAB) and Foothills (FH). The other two provenances belong to climatically and geographically different parts of the species range: Yukon (YU) in the north and Ontario (ON) in the south. The same sample trees were used for all measurements so that an individual comparison between variables was possible. A total of seven trees (at least one from each block) were selected for each provenance, except for provenances nAB.2 and cAB.2 that were present in both trials, for which five trees from each trial and provenance were selected. The sample size was reduced for time consuming anatomic measurements (for details see notes in Table 2.2). Climate data for the provenances and study site was extracted with the software ClimateNA v5.21, available at *http://tinyurl.com/ClimateNA* (Wang *et al.* 2014). We used the standard reference normal period of 1961-1990 as a representation of the climate of origin to which populations are putatively adapted.

2.3.2 Hydraulic measurements

Samples for hydraulic measurements were collected between May 19 and June 8, 2015. Distal branches from sun-exposed parts of the tree crown were cut with a pole pruner. The branches were packed in plastic bags with wet paper towels to avoid desiccation and transported to a cold room (+4°C) the same day. All hydraulic measurements were made within one week after collection. We follow methodology described in Hacke and Jansen (2009) and Schoonmaker *et al.* (2010) for conductivity measurements. Briefly, we cut approximately 15 cm long branch segments under water and attached them to a conductivity apparatus that applied a 20 mM KCl+ 1 mM $CaCl_2$ solution under controlled pressure to the segment. The outflow was measured every 10 seconds with an electronic balance (CP225D; Sartorius, Göttingen, Germany) until it stabilized. The average of the last five measurements was used to calculate hydraulic conductivity (K_H) with the following expression:

$$\mathrm{K_H} = \frac{\text{Water flow } \times \text{segment length}}{\text{Pressure head}}$$

Hydraulic conductivity was first measured to assess the native conductivity of the segments in the field. Then, samples were subjected to a partial vacuum in the measuring solution to remove any native embolism and determine the maximum conductivity. Native embolism was calculated as the ratio of the initial to the maximum conductivity. Vulnerability to cavitation was assessed by applying a known pressure to the segment using a centrifuge and calculating the percentage loss of conductivity (*PLC*) relative to the maximum conductivity. This procedure was repeated for six pressure levels from -2 to -7 MPa and the results were fitted to two commonly used functions: the Weibull function (Cai *et al.* 2014) and the exponential sigmoidal function (Pammenter & Vander Willigen 1998). The best fitted function was selected in each individual case. From these curves, we calculated the pressure at which the xylem loses 50% of its maximum conductivity (P50). Maximum K_H was used to calculate xylem-area specific conductivity (K_S) and needle-area specific conductivity (K_L). Xylem area (A_X) was measured in the center of the segments using a stereomicroscope (MS5, Leica, Wetzlar, Germany). For the estimation of needle area (A_L), we first measured the projected area of a subset of needles, and then the same subset was weighted after drying the needles in an oven. Using the ratio of area to weight from the subset of needles, we could estimate the total area of the needles distal to the segment by drying and weighting the remaining needles. K_S and K_L were then calculated according to Tyree and Zimmermann (2002):

$$\mathrm{K_S} = \frac{\mathrm{K_H}}{\mathrm{A_X}}$$

$$\mathrm{K_L} = \frac{\mathrm{K_H}}{\mathrm{A_L}}$$

Lastly, the ratio of leaf area to xylem area (A_L:A_X) was also calculated as a measure of hydraulic efficiency.

2.3.3 Wood anatomy

The same segments used for hydraulic measurements were also used for wood anatomy analysis. Tracheid lumen diameter was measured for the most recent complete two rings of each segment using a radial file of three cells wide with images taken with a Leica DM3000 microscope at

200x. Only non-compression wood was analyzed. The hydraulically weighted mean lumen diameter (T_{diam}) was calculated using the Hagen-Poiseuille formula:

$$\mathrm{T}_{\mathrm{diam}} = \left(\frac{\sum \mathrm{d}^4}{\mathrm{n}}\right)^{1/4}$$

where *d* is tracheid diameter and n is the total number of tracheids measured. Tracheid length (T_{length}) was measured using chemical macerations following (Schoonmaker *et al.* 2010). Wood sections corresponding to the outer rings of each segment were digested in a 1:1 mixture of glacial acetic acid (80%) and hydrogen peroxide at 60°C for 48 hours. Macerated tissue was analyzed with a light microscope at 25x magnification to measure the length of 200 tracheids for each sample. All the image analyses were performed with ImagePro Premier (Media Cybernetics, Silver Spring, MD, USA) software.

2.3.4 Cold hardiness

Healthy, sun-exposed branches were collected for cold hardiness measurements from the same trees on September 22 and brought to a cold room (+4°C) in plastic bags with wet paper towels within the same day. The whole-plant freeze testing method (Burr *et al.* 2001) was used to estimate frost damage. Distal parts of the branches of approximately 20 cm length were frozen at different temperatures in a programmable freezer (85-3.1A; ScienTemp, Adrian, MI, USA). We used a cooling rate of 5°C/hour and maintained the samples at the test temperature for one hour, followed by warming up to room temperature at the same rate of 5°C/hour. Three test temperatures were used: -30°C, -40°C and -50°C. After the freezing treatment, samples were transferred to a growth chamber where they were stored in transparent plastic bags with wet paper towels. Frost damage in the needles was assessed visually two weeks after the treatment as a percentage of damaged tissue.

2.3.5 Data analysis

All statistical analyses were conducted with the R v3.2 programming environment (R Core R Core Team 2015). We used a mixed effects model to calculate the means of the provenances using the variable of interest as a fixed effect and block as a random effect with the *lme4* package (Bates *et al.* 2014). Means were calculated as least squares means with the *lsmeans* package (Lenth 2016a). Multiple comparisons of the means were done with the general linear hypothesis method of the *multcomp* package (Hothorn, Bretz & Westfall 2008). Differences among provenances in survival were tested for statistical significance with Fischer's exact *z*-test and Holm's adjustment for multiple inference, implemented with the *p.adjust* function of the R base package. We visualized the effect of the climate of origin on the performance in the field using a multivariate indirect gradient analysis. The ordination space consisted of standardized values of height and survival, defined as standard deviations from the overall experimental mean set to zero. We calculated the individual correlations of each climatic variable with this ordination space using the function *vf()* from the package *ecodist* (Goslee & Urban 2007) and plotted them as vectors in the figure. To analyze tradeoffs and relationships among specific hydraulic and anatomical traits, we conducted boundary analyses with quantile regressions using the function *rq()* from the package *quantreg* (Koenker 2013). A quantile regression can be used when a response cannot change by more than some upper limit, but may change by less when other unmeasured factors are limiting (Cade & Noon 2003). A quantile regression is similar to a linear regression but it allows for the estimation of a quantile instead of the average. In this case we calculated the 5% (P50) and 95% (wood density) quantiles. This regression can identify a region of a scatter plot where it is very rare to find points and can point to a tradeoff even if the overall correlation between variables for the majority of the sample points is weak.

2.4 Results

Provenance field testing results conformed to the expectation that “local is best”, with provenances from the vicinity of the planning site showing the highest growth and good survival (Fig. 2.2, upper right quadrant). Provenances from the Alberta Foothills represented the other extreme, with below-average growth and survival. The remaining six provenances showed a tradeoff between growth and survival, with provenances from Ontario having high growth but relatively low survival and provenances from northern regions (Yukon and Northern Alberta) exhibiting high survival but lower growth. The observed differences in growth and survival among individual provenances were statistically significant as indicated in Table 2.2, and they provide a reference to interpret the importance of physiological and anatomical adaptive traits as causes of population performance in the field.

Among the physiological and wood anatomical variables measured, we found the strongest differentiation in cold hardiness (Fig. 2.3, Table 2.2). At the time of sampling, the -50°C test temperature resulted in the greatest range of observed damage from 1% to 96% in one of the Yukon (YU.2) and one of the Foothills (FH.1) provenance samples, respectively. Provenances within the same region generally behaved similarly, except for the Alberta

Foothills, which showed a statistically significant difference between its provenances. Most of the provenances showed good resistance to -30°C temperatures at the time of assessment in mid-September, and only Ontario showed significant damage (12%). We observed no significant differences among provenances in hydraulic and anatomic variables putatively related to adaptation to drought, except for leaf-to-xylem area ratio, due to high intra-population variance (Table 2.2).

Frost hardiness was strongly related to survival (Fig. 2.4), but it did not show a significant tradeoff with tree height (Table 2.3). There was a significant correlation between height and both K_L and P50, but we did not find any relationship between survival and hydraulic variables (Table 2.3). Despite weak correlations, the boundary analysis suggested tradeoffs between xylem specific conductivity (K_S) and wood density (Fig. 2.5a), and between xylem specific conductivity (K_S) and the pressure at which the xylem loses 50% of its maximum conductivity (*P50*) (Fig. 2.5b). Using quantile regressions we are able to estimate a boundary (dashed line in Fig. 2.5) beyond which values are very rare to find. Low transport efficiency (low K_S values) was associated with a wide range of both *P50*s and xylem densities but the most efficient branches were always linked to vulnerable xylem and low densities, indicating that an ideal combination of high efficiency and high cavitation resistance is not possible (note the absence of data points in the top right in Fig. 2.5a and bottom right in Fig. 2.5b). The leaf to xylem area ratio appeared as an influential trait for hydraulic variables since it was significantly correlated to both efficiency (K_S and K_L) and cavitation resistance (*P50*; Table 2.3). Leaf specific conductivity was strongly correlated to *P50*, so that the more vulnerable branches had also a poorer ability to provide water to the needles. Wood density was the most influential among anatomic variables, as it was significantly correlated to tree survival and cold hardiness. Tracheid size was not related to any variable measured.

The climate of origin was strongly associated with the field performance of provenances. Climate vectors significantly correlated to height, survival, or a combination of both traits as per indirect gradient analysis. This is displayed in Fig. 2.2, where the vector length with respect to each axis represents the strength of the association. The variables that were most correlated with survival are, in this order, mean average precipitation, mean coldest month temperature and degree-days below 0°C, suggesting that provenances with better survival came from dry climates with cold and long winters. For growth, the most important predictor variables were frost-free period and mean annual temperature at the origin of the seed source. If we look at the beginning and end of the frost free period separately, we can see the higher influence of the latter since it is the only significant result (Table 2.4, Fig. 2.6). Annual heat-moisture index was not significantly correlated to either height or survival alone (Table 2.4), but it was associated with high combined survival and growth of central Alberta provenances (Fig. 2.2).

Cold hardiness was also associated with the climate of origin. Damage at -50°C was mostly related to day length and winter temperatures, having the highest correlations with latitude, mean coldest month temperature and degree-days below 0°C (Fig. 2.7a, Table 2.4). Damage at -30°C was more correlated to variables corresponding to annual temperatures like evapotranspiration and mean average temperature, and also to the date of the first frost event (Fig. 2.7b, Table 2.4). It is important to note that by the time of sample collection (day of year 265), the first frost event at the location of origin for an average year would have already happened for all provenances except for those originating from Ontario (Fig. 2.7b). We did not find any significant associations between climate at the origin of seed sources and hydraulic or anatomic variables (Table 2.4).

2.5 Discussion

2.5.1 Local adaptation and tradeoffs

Although this study was not designed to study local optimality or to be used to derive practical assisted migration guidelines, provenances that originated near the vicinity of the study site showed the best combination of long-term performance in growth and survival in the field. Local provenances (central Alberta) originated slightly southeast of the study site which corresponds to a short northwest transfer as was recommended by (Gray *et al.* 2016b) to account for climate change that has already occurred over the last several decades. The provenances that showed both poor growth and low survival came from the Alberta Foothills (lower left quadrant in Fig. 2.2). This area corresponds to relatively mild climate conditions both in summer and winter with short growing seasons due to the combination of high elevations and the presence of warm winds from ocean origin. Possible introgression with Engelmann spruce, native to higher elevation than white spruce, would enhance its adaptation to these mountainous conditions at the cost of lower growth (De La Torre *et al.* 2014). Liepe *et al.* (2016) also reported that high-elevation sources of spruce had short growing seasons, lacked strong cold tolerance, and tended to be poor growers. The other six provenances in our study showed a clear tradeoff between growth and survival. Northern provenances (Yukon and Northern Alberta), with the coldest winters and lowest precipitation, exhibited high survival but inferior growth. For Ontario provenances, coming from areas with more favorable conditions for plant growth where inter- and intra-species competition is presumably more important, the opposite was observed, an emphasis of growth over safety.

2.5.2 Strong population differentiation in cold hardiness

The adaptive trait with the strongest genetic population differentiation was cold hardiness, and trait values showed strong associations to latitude and the mean coldest month temperature of seed origin. Cold hardiness was measured in branches collected around mid-September and at this time of year, only provenances from Ontario exhibited some frost damage after exposure to -30°C. Ontario provenances usually do not experience any frost at this time of year at their location of origin. Hence, there is no need to develop cold hardiness so early in the fall when trees grow in their native climate. The other provenances do regularly experience mild frost events earlier in September in their native climate and exhibited no significant damage when exposed to -30°C at the test site. The fact that cold hardiness patterns could largely be explained by the native climate of the selected provenances indicates that the seasonal dynamics of cold hardiness were under strong genetic control, and that there was little potential for phenotypic plasticity. These results conform to many other studies (Howe *et al.* 2003b and literature cited therein). Of all the traits measured in this study, cold hardiness appeared as the most important adaptive trait, clearly linked to survival of provenances in the field. Despite cold hardiness not being significantly correlated to tree height, the influence of the end of the growing season at the source of the provenances suggests that the timing of growth cessation plays an important role in the growth potential of white spruce.

2.5.3 Wood anatomical and hydraulic parameters

While it seems that patterns in survival and tree height could largely be explained by cold tolerance and growing season length, respectively, we also measured a wide range of hydraulic and wood anatomical parameters, putatively related to drought resistance. Wood density emerged as a potentially influential variable as it was correlated with survival and cold resistance. Lighter wood may increase the risk of stem breakage (Spatz & Bruechert 2000), which may be important under heavy snow loads (Hlasny *et al.* 2011). High wood density also provides a stronger defense against pathogens as well as lower vulnerability to drought stress (Hacke *et al.* 2001a; Chave *et al.* 2009; Rosner *et al.* 2014; Hacke *et al.* 2015). Higher wood densities are often found in environments that are associated with stress. Positive correlations of wood density with survival and cold hardiness seem consistent with these reports.

Tree height was negatively correlated with leaf-specific conductivity (K_L), i.e., taller trees tended to show lower K_L values than shorter trees. Lower values of K_L corresponded to higher needle area distal to the section measured relative to its ability to transport water. K_L was mostly regulated by needle area rather than by a change in hydraulic conductivity as we can see from the significant correlation between K_L and A_L:A_X and the absence of a correlation between K_L and K_S (Table 2.3). Similar findings were reported from studies on pine populations sampled across climate gradients (Martínez-Vilalta *et al.* 2009; Lopez *et al.* 2016). At a particular transpiration rate (E), a branch with higher K_L will be able to maintain a smaller water potential gradient ($\Delta\Psi$) than a branch with lower K_L, because $E = K_L\,\Delta\Psi$ (Tyree & Zimmermann 2002). While having high K_L may seem conservative and advantageous from a hydraulic perspective, it comes with the disadvantage of having less photosynthetic area or having to invest more resources into non-photosynthesizing xylem tissue to increase transport capacity.

In our study, Yukon and Foothill provenances exhibited the highest K_L values. Both Yukon and Foothills have the shortest frost-free periods. Trees in these regions must deal with frozen soils for the longest time and they may also experience many freeze-thaw events in spring. Drought stress can develop in the winter when water uptake from a frozen/cold soil is impaired while needles continue to lose water (Mayr *et al.* 2006). Having a higher K_L may reduce the tension in the xylem during this period and may therefore be advantageous over a greater emphasis on leaf area and growth potential.

Hydraulic conductivity standardized by xylem area (K_S) was not correlated with growth or survival, but showed complex relationships with wood density and P50. The boundary analysis approach shown in Fig. 2.5 illustrates that high wood densities and K_S values were mutually exclusive. This points to a strength versus hydraulic efficiency trade-off and is understandable given constraints arising from the geometry of tracheid-based xylem (see detailed discussion in Pittermann *et al.* 2006; Hacke *et al.* 2015). High hydraulic conductivity (K_S) values also came at the expense of increased vulnerability to cavitation. The safety versus efficiency trade-off is complex (Gleason *et al.* 2016b), but our boundary analysis indicates that certain trait combinations are unattainable despite high within-population variation in either of these traits.

2.5.4 Conclusion

In this range-wide common garden study we identified traits that could potentially play an important role in tradeoffs between growth potential and resistance to climatic stress. We should emphasize that the growing conditions can significantly affect the tradeoffs revealed in this study. Differences in adaptive traits that did not have an effect on growth and survival either at the population or individual tree level in this study, could be consequential under different growing environments. Wood density and the leaf specific conductivity were identified as potentially important traits, but fall cold hardiness stood out as key trait for tree survival and also showed easily interpretable associations with climate of the provenance origin. Furthermore, the relation between height and the end of the growing season points to the importance of the timing of growth cessation in the growth potential of white spruce. Therefore, regional studies that make use of a higher sampling density to develop assisted migration guidelines should focus on measuring the effects of seed transfers on fall phenology and match provenances to new locations so that their synchronization of the onset of frost hardiness matches new environmental conditions under climate change.

2.6 References

Aitken, S.N. & Hannerz, M. (2001) Genecology and gene resource management strategies for conifer cold hardiness. *Conifer cold hardiness*, pp. 23-53. Springer.

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications,* **1,** 95-111.

Barber, V.A., Juday, G.P. & Finney, B.P. (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature,* **405,** 668-673.

Barnett, T.P., Adam, J.C. & Lettenmaier, D.P. (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature,* **438,** 303-309.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software,* **67,** 1-48.

Bigras, F. (2000) Selection of white spruce families in the context of climate change: heat tolerance. *Tree Physiology,* **20,** 1227-1234.

Bigras, F.J. (2005) Photosynthetic response of white spruce families to drought stress. *New Forests,* **29,** 135-148.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L. & Belnap, J. (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America,* **102,** 15144-15148.

Burr, K.E., Hawkins, C.D., L'Hirondelle, S.J., Binder, W.D., George, M.F. & Repo, T. (2001) Methods for measuring cold hardiness of conifers. *Conifer cold hardiness* (eds F.J. Bigras & S.J. Colombo), pp. 369-401. Springer.

Cade, B.S. & Noon, B.R. (2003) A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment,* **1,** 412-420.

Cai, J., Li, S., Zhang, H.X., Zhang, S.X. & Tyree, M.T. (2014) Recalcitrant vulnerability curves: methods of analysis and the concept of fibre bridges for enhanced cavitation resistance. *Plant Cell and Environment,* **37,** 35-44.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters,* **12,** 351-366.

Chen, L., Huang, J.-G., Stadt, K.J., Comeau, P.G., Zhai, L., Dawson, A. & Alam, S.A. (2017) Drought explains variation in the radial growth of white spruce in western Canada. *Agricultural and Forest Meteorology,* **233,** 133-142.

Danby, R.K. & Hik, D.S. (2007) Responses of white spruce (Picea glauca) to experimental warming at a subarctic alpine treeline. *Global Change Biology,* **13,** 437-451.

Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science,* **292,** 673-679.

De La Torre, A.R., Wang, T.L., Jaquish, B. & Aitken, S.N. (2014) Adaptation and exogenous selection in a Picea glauca x Picea engelmannii hybrid zone: implications for forest management under climate change. *New Phytologist,* **201,** 687-699.

Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015) Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution,* **30,** 169-176.

Gleason, S.M., Westoby, M., Jansen, S., Choat, B., Hacke, U.G., Pratt, R.B., Bhaskar, R., Brodribb, T.J., Bucci, S.J., Cao, K.F., Cochard, H., Delzon, S., Domec, J.C., Fan, Z.X., Feild, T.S., Jacobsen, A.L., Johnson, D.M., Lens, F., Maherali, H., Martinez-Vilalta, J., Mayr, S., McCulloh, K.A., Mencuccini, M., Mitchell, P.J., Morris, H., Nardini, A., Pittermann, J., Plavcova, L., Schreiber, S.G., Sperry, J.S., Wright, I.J. & Zanne, A.E. (2016) Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist,* **209,** 123-136.

Goslee, S.C. & Urban, D.L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software,* **22,** 1-19.

Gray, L.K. & Hamann, A. (2013) Tracking suitable habitat for tree populations under climate change in western North America. *Climatic Change,* **117,** 289-303.

Gray, L.K., Hamann, A., John, S., Rweyongeza, D., Barnhardt, L. & Thomas, B.R. (2016) Climate change risk management in tree improvement programs: selection and movement of genotypes. *Tree Genetics & Genomes,* **12,** 1-12.

Gu, L., Hanson, P.J., Post, W.M., Kaiser, D.P., Yang, B., Nemani, R., Pallardy, S.G. & Meyers, T. (2008) The 2007 eastern US spring freeze: increased cold damage in a warming world? *AIBS Bulletin,* **58,** 253-262.

Hacke, U.G. & Jansen, S. (2009) Embolism resistance of three boreal conifer species varies with pit structure. *New Phytologist,* **182,** 675-686.

Hacke, U.G., Lachenbruch, B., Pittermann, J., Mayr, S., Domec, J.-C. & Schulte, P.J. (2015) The hydraulic architecture of conifers. *Functional and ecological xylem anatomy* (ed. U. Hacke), pp. 39-75. Springer.

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloch, K.A. (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia,* **126,** 457-461.

Hlasny, T., Kristek, S., Holusa, J., Trombik, J. & Urbancova, N. (2011) Snow disturbances in secondary Norway spruce forests in Central Europe: Regression modeling and its implications for forest management. *Forest Ecology and Management,* **262,** 2151-2161.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical journal,* **50,** 346-363.

Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. & Chen, T.H.H. (2003) From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany-Revue Canadienne De Botanique,* **81,** 1247-1266.

Jiang, X.Y., Huang, J.G., Stadt, K.J., Comeau, P.G. & Chen, H.Y.H. (2016) Spatial climate-dependent growth response of boreal mixedwood forest in western Canada. *Global and Planetary Change,* **139,** 141-150.

Koenker, R. (2013) quantreg: Quantile Regression. R package version 5.05. *R Foundation for Statistical Computing: Vienna*.

Langlet, O. (1971) Two hundred years genecology. *Taxon***,** 653-721.

Lenth, R.V. (2016) Least-squares means: the R package lsmeans. *Journal of Stattistical Software,* **69,** 1-33.

Lesser, M.R. & Parker, W.H. (2004) Genetic variation in Picea glauca for growth and phenological traits from provenance tests in Ontario. *Silvae Genetica,* **53,** 141-148.

Li, P., Beaulieu, J. & Bousquet, J. (1997) Genetic structure and patterns of genetic variation among populations in eastern white spruce (Picea glauca). *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* **27,** 189-198.

Liepe, K.J., Hamann, A., Smets, P., Fitzpatrick, C.R. & Aitken, S.N. (2016) Adaptation of lodgepole pine and interior spruce to climate: implications for reforestation in a warming world. *Evolutionary Applications,* **9,** 409-419.

Lloyd, A.H. & Fastie, C.L. (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change,* **52,** 481-509.

Lopez, R., Cano, F.J., Choat, B., Cochard, H. & Gil, L. (2016) Plasticity in vulnerability to cavitation of Pinus canariensis occurs only at the driest end of an aridity gradient. *Frontiers in Plant Science,* **7**.

Lu, P.X., Parker, W.H., Cherry, M., Colombo, S., Parker, W.C., Man, R.Z. & Roubal, N. (2014) Survival and growth patterns of white spruce (Picea glauca Moench Voss) rangewide provenances and their implications for climate change adaptation. *Ecology and Evolution,* **4,** 2360-2374.

MacDonald, G.M., Szeicz, J.M., Claricoates, J. & Dale, K.A. (1998) Response of the central Canadian treeline to recent climatic changes. *Annals of the Association of American Geographers,* **88,** 183-208.

Man, R.Z., Kayahara, G.J., Dang, Q.L. & Rice, J.A. (2009) A case of severe frost damage prior to budbreak in young conifers in Northeastern Ontario: Consequence of climate change? *Forestry Chronicle,* **85,** 453-462.

Martínez-Vilalta, J., Cochard, H., Mencuccini, M., Sterck, F., Herrero, A., Korhonen, J., Llorens, P., Nikinmaa, E., Nole, A. & Poyatos, R. (2009) Hydraulic adjustment of Scots pine across Europe. *New Phytologist,* **184,** 353-364.

Mayr, S., Hacke, U., Schmid, P., Schwienbacher, F. & Gruber, A. (2006) Frost drought in conifers at the alpine timberline: Xylem dysfunction and adaptations. *Ecology,* **87,** 3175-3185.

Mbogga, M.S., Hamann, A. & Wang, T. (2009) Historical and projected climate data for natural resource management in western Canada. *Agricultural and Forest Meteorology,* **149,** 881-890.

Millar, C.I., Stephenson, N.L. & Stephens, S.L. (2007) Climate change and forests of the future: managing in the face of uncertainty. *Ecological applications,* **17,** 2145-2151.

Pammenter, N.W. & Vander Willigen, C. (1998) A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiology,* **18,** 589-593.

Pittermann, J., Sperry, J.S., Hacke, U.G., Wheeler, J.K. & Sikkema, E.H. (2006) Inter-tracheid pitting and the hydraulic efficiency of conifer wood: the role of tracheid allometry and cavitation protection. *American Journal of Botany,* **93,** 1265-1273.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosner, S., Svetlik, J., Andreassen, K., Borja, I., Dalsgaard, L., Evans, R., Karlsson, B., Tollefsrud, M.M. & Solberg, S. (2014) Wood density as a screening trait for drought sensitivity in Norway spruce. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* **44,** 154-161.

Rweyongeza, D.M., Yang, R.C., Dhir, N.K., Barnhardt, L.K. & Hansen, C. (2007) Genetic variation and climatic impacts on survival and growth of white spruce in Alberta, Canada. *Silvae Genetica,* **56,** 117-127.

Schoonmaker, A.L., Hacke, U.G., Landhausser, S.M., Lieffers, V.J. & Tyree, M.T. (2010) Hydraulic acclimation to shading in boreal conifers of varying shade tolerance. *Plant Cell and Environment,* **33,** 382-393.

Spatz, H.C. & Bruechert, F. (2000) Basic biomechanics of self-supporting plants: wind loads and gravitational loads on a Norway spruce tree. *Forest Ecology and Management,* **135,** 33-44.

Sperry, J.S., Hacke, U.G. & Pittermann, J. (2006) Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany,* **93,** 1490-1500.

Tyree, M.T. & Zimmermann, M.H. (2002) Xylem structure and the ascent of sap. *Xylem structure and the ascent of sap*, pp. i. Springer-Verlag, Berlin, Germany.

Wang, Y., Hogg, E.H., Price, D.T., Edwards, J. & Williamson, T. (2014) Past and projected future changes in moisture conditions in the Canadian boreal forest. *The Forestry Chronicle,* **90,** 678-691.

Table 2.1. Geographic location of the provenance origins and the common garden test site used in this study.

Location	Latitude	Longitude	Elevation (m)
nAB.1	58.73	-111.25	235
nAB.2	59.88	-111.72	813
cAB.1	54.37	-110.75	396
cAB.2	54.63	-110.22	610
FH.1	51.40	-115.22	1750
FH.2	49.65	-114.62	1585
ON.1	45.97	-77.43	170
ON.2	45.50	-77.02	121
YU.1	61.35	-139.00	792
YU.2	64.02	-139.00	609
Site	55.27	-113.16	635

Table 2.2. Least squares means of field performance, anatomy, hydraulic and cold hardiness traits. Individual provenances that have the same letter (in columns) are not significantly different at $p<0.05$. Absence of letters for a trait indicates that there were no significant differences among provenances after an experiment-wise α-level adjustment for 45 pairwise comparisons.

Provenance	Height	Survival	Cold30	Cold50	A_L:A_X	K_L	K_S	P50	Emb_{Nat}	Density	Tr_{Diam}	Tr_{Length}
nAB.1	7.9 **a**	97 **ab**	0	19 **ab**	37.4 **ab**	0.0136	0.478	-4.09	3.8	0.569	10.3	1.44
nAB.2	7.9 **abc**	97 **a**	0	19 **ab**	32.9 **ab**	0.0157	0.449	-4.25	7.4	0.581	11.4	1.29
cAB.1	10.9 **d**	98 **ab**	4	24 **ab**	37.0 **ab**	0.0120	0.420	-4.04	6.8	0.577	11.0	1.38
cAB.2	9.9 **d**	93 **abc**	2	49 **ac**	35.3 **ab**	0.0174	0.520	-4.28	1.9	0.544	10.7	1.46
FH.1	7.2 **a**	89 **abc**	2	44**ac**	29.1 **ab**	0.0188	0.490	-4.34	12.1	0.552	10.5	1.24
FH.2	7.6 **a**	75 **c**	3	96 **d**	21.2 **a**	0.0180	0.336	-4.31	6.9	0.538	11.2	1.28
ON.1	10.3 **d**	76 **bc**	11	82 **cd**	45.9 **b**	0.0108	0.534	-3.91	26.3	0.551	11.0	1.38
ON.2	9.6 **cd**	84 **abc**	14	91**d**	35.5 **ab**	0.0154	0.520	-4.14	3.3	0.547	10.3	1.46
YU.1	5.0 **b**	96 **abc**	0	16**ab**	33.9 **ab**	0.0180	0.537	-4.20	4.2	0.555	10.4	1.30
YU.2	4.4 **b**	92 **abc**	0	1**b**	30.5 **ab**	0.0186	0.461	-4.42	16.6	0.556	12.3	1.55

Tree height (m) and survival (%, N = 70 for nAB.2 and cAB.2; N = 45 for nAB.1, cAB.1, FH.1 and FH.2; N = 25 for ON.1, ON.2, YU.1 and YU.2); Tr_{Length} = Tracheid length (mm, N = 1 tree/provenance; 200 tracheids/tree); Tr_{Diam} = Tracheid diameter (µm, N = 2); Density = wood density (g/cm^3, N = 7); A_L:A_X = leaf to xylem area ratio (cm^2/ mm^2, N = 4); Emb_{Nat} = native embolism (%, N = 7); K_S = xylem specific maximum conductivity (mg mm^{-1} s^{-1} kPa^{-1}, N = 7); K_L = leaf specific maximum conductivity (mg mm^{-1} s^{-1} kPa^{-1}, N = 4); P50 = pressure at which 50% of the conductivity is lost (MPa, N = 7); Cold30 and Cold50 = frost damage at -30 and -50 °C respectively (%, N = 7)

Table 2.3. Pearson's correlation coefficients for the mean values of provenances for anatomy, hydraulic, cold hardiness and performance variables. Statistically significant correlations at $p<0.05$ are highlighted in bold.

	Height	Survival	Cold30	Cold50	A_L:A_X	K_L	K_S	P50	Density	Tr_{Diam}
Survival	-0.19									
Cold30	0.61	-0.61								
Cold50	0.49	**-0.88**	**0.75**							
A_L:A_X	0.50	0.12	0.44	-0.05						
K_L	**-0.71**	0.05	-0.49	-0.15	**-0.79**					
K_S	0.03	0.17	0.29	-0.10	**0.68**	-0.12				
P50	**0.67**	-0.12	0.56	0.26	**0.82**	**-0.94**	0.30			
Density	0.07	**0.72**	-0.34	**-0.67**	0.30	-0.43	-0.08	0.26		
Tr_{Diam}	-0.39	-0.06	-0.31	-0.30	-0.29	0.20	-0.44	-0.44	0.13	
Tr_{Length}	0.03	0.15	0.17	-0.18	0.33	-0.15	0.24	0.02	-0.05	0.30

Cold30 and Cold50 = frost damage at -30 and -50 °C respectively, A_L:A_X = leaf area to xylem area, K_L = leaf specific conductivity, K_S = xylem specific conductivity, P50 = vulnerability to cavitation expressed as the pressure at which 50% of the maximum conductivity is lost, Density = wood density, Tr_{Diam} = tracheid diameter, Tr_{Length} = tracheid length.

Table 2.4. Pearson's correlation coefficients for the relationship between climate variables and anatomy, hydraulic, cold hardiness and performance variables. Statistically significant correlations at $p<0.05$ are highlighted in bold.

	Height	Survival	Cold30	Cold50	A_L:A_X	K_L	K_S	P50	Density	T_{Diam}	T_{Length}
Latitude	-0.68	-0.76	**-0.85**	**-0.92**	-0.17	0.35	-0.03	-0.44	0.49	0.42	0.19
MAT	0.78	-0.67	**0.91**	**0.87**	0.31	-0.47	0.09	0.54	-0.41	-0.41	-0.02
MWMT	0.69	-0.20	0.77	0.37	0.70	-0.74	0.30	0.68	0.11	-0.13	0.51
MCMT	0.46	**-0.81**	0.69	**0.90**	-0.13	-0.07	-0.13	0.19	-0.65	-0.34	-0.33
TD	-0.14	0.70	-0.33	-0.71	0.43	-0.25	0.26	0.11	0.68	0.27	0.54
MAP	0.47	**-0.85**	**0.84**	**0.88**	0.12	-0.23	0.07	0.30	-0.56	-0.24	-0.11
MSP	0.58	-0.65	0.75	0.74	0.22	-0.24	0.21	0.31	-0.49	-0.36	-0.15
AHM	0.54	0.53	-0.06	-0.20	0.33	-0.44	0.01	0.45	0.43	-0.38	0.05
SHM	-0.24	0.61	-0.36	-0.62	0.21	-0.18	0.01	0.05	0.66	0.32	0.42
DD<0	-0.65	0.74	-0.76	**-0.91**	-0.04	0.24	0.06	-0.35	0.55	0.43	0.26
DD>5	0.76	-0.34	**0.88**	0.53	0.67	-0.71	0.31	0.70	-0.04	-0.25	0.40
bFFP	-0.74	0.01	-0.61	-0.22	-0.67	0.73	-0.22	-0.61	-0.22	0.07	-0.59
eFFP	**0.81**	-0.49	**0.89**	0.71	0.51	-0.67	0.16	0.66	-0.13	-0.35	0.17
FFP	**0.82**	-0.27	**0.80**	0.50	0.62	-0.74	0.20	0.67	0.05	-0.23	0.40

Cold30 and Cold50 = frost damage at -30 and -50 °C respectively , A_L:A_X = leaf area to xylem area, K_L = leaf specific conductivity, K_S = xylem specific conductivity, P50 = vulnerability to cavitation expressed as the pressure at which 50% of the maximum conductivity is lost, Density = wood density, T_{Diam} = tracheid diameter, T_{Length} = tracheid length. MAT= mean annual temperature, MWMT = mean warmest month temperature, MCMT = mean coldest month temperature, TD = continentality or temperature difference between MWMT and MCMT, MAP = mean annual precipitation, MSP = May to September precipitation, AHM = annual heat-moisture index (MAT+10)/(MAP/1000), SHM = summer heat-moisture index MWMT/(MSP/1000), DD<0 = degree-days below 0°C, DD>5 = degree-days above 5°C, bFFP = the day of the year on which FFP begins, eFFP = the day of the year on which FFP ends, FFP = frost free period.

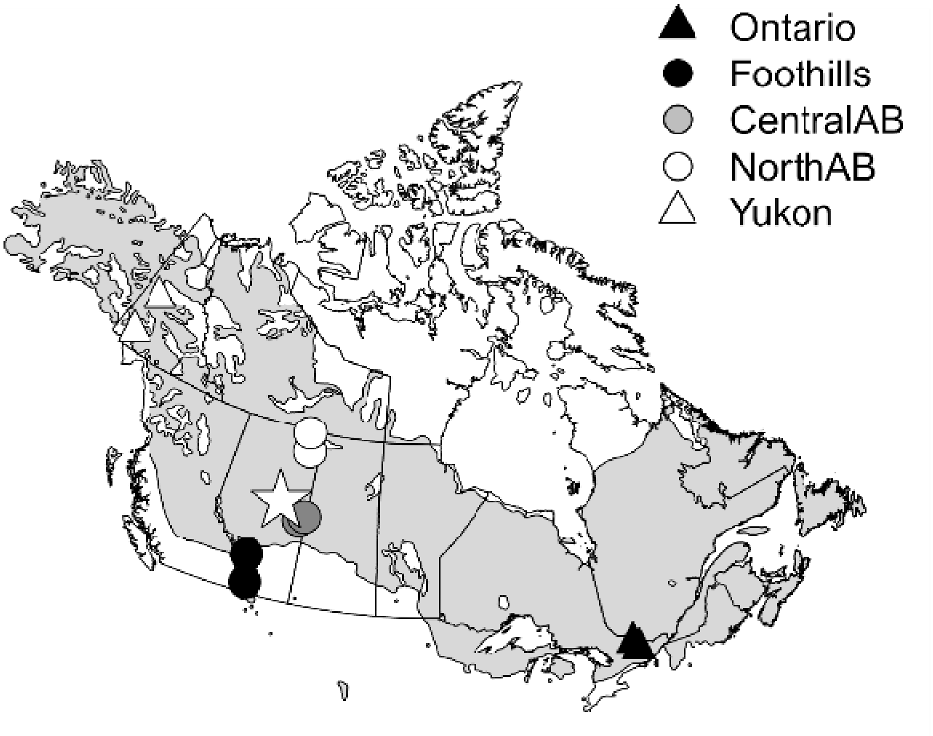

Figure 2.1. Locations of origin of provenances and the common garden test site where they were grown. The area in grey delineates the species range of white spruce.

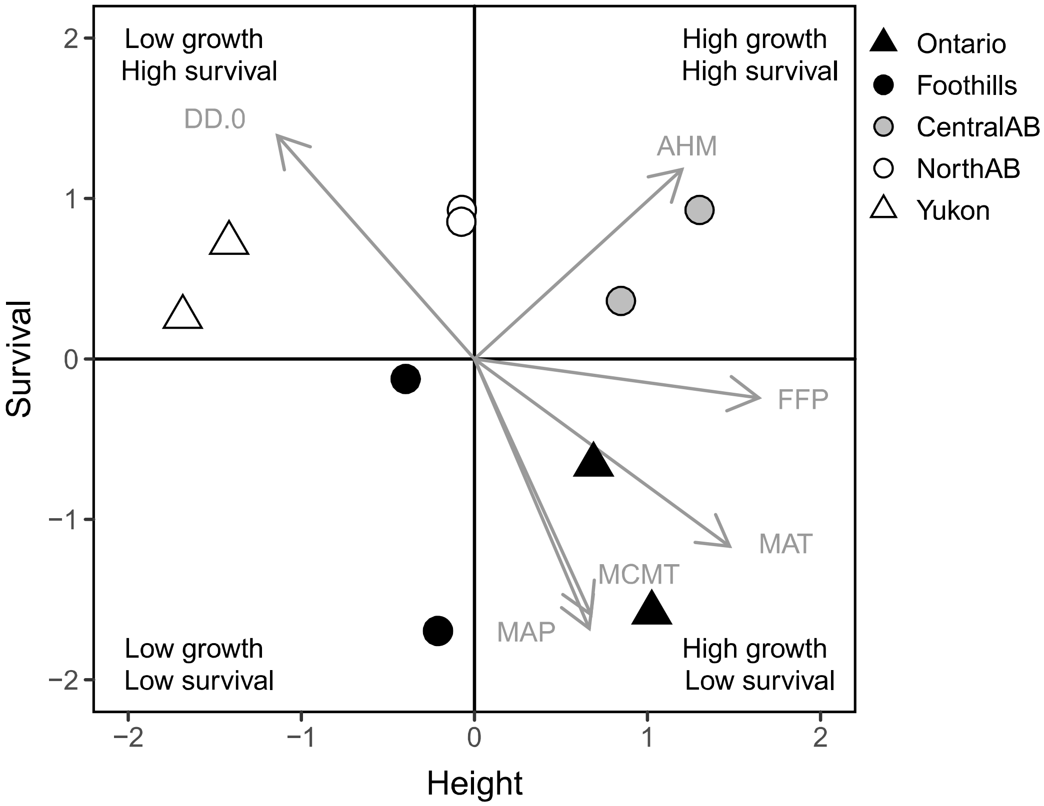

Figure 2.2. Performance of the provenances at the study site. Height and survival are expressed in units of standard deviations from an overall mean of zero. The vectors represent significant associations of the climate of the provenance origin with growth and survival in an indirect gradient analysis, where DD.0 = degree-days below 0°C, AHM = annual heat-moisture index, FFP = frost-free period, MAT = mean annual temperature, MCMT = mean coldest month temperature and MAP = mean annual precipitation.

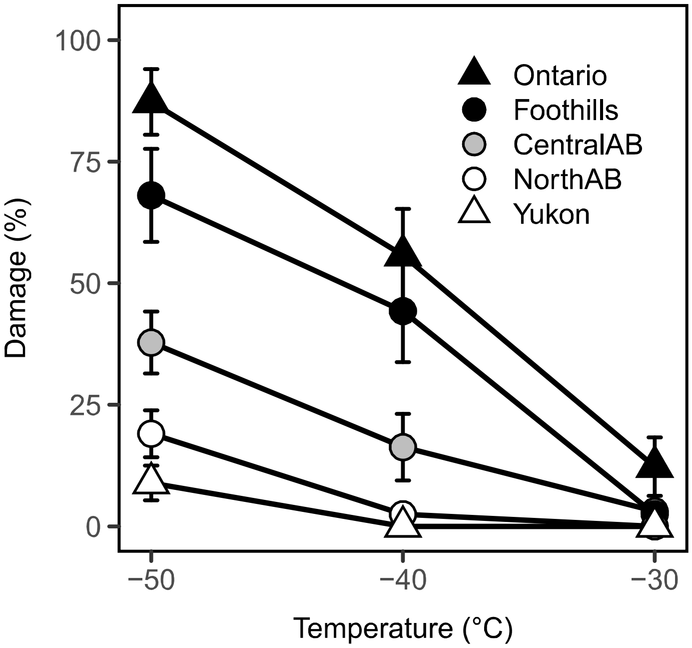

Figure 2.3. Percentage of damaged tissue shown by the different regions at three experimental freezing temperatures. Error bars represent standard errors of the mean. Samples were collected on September 22nd.

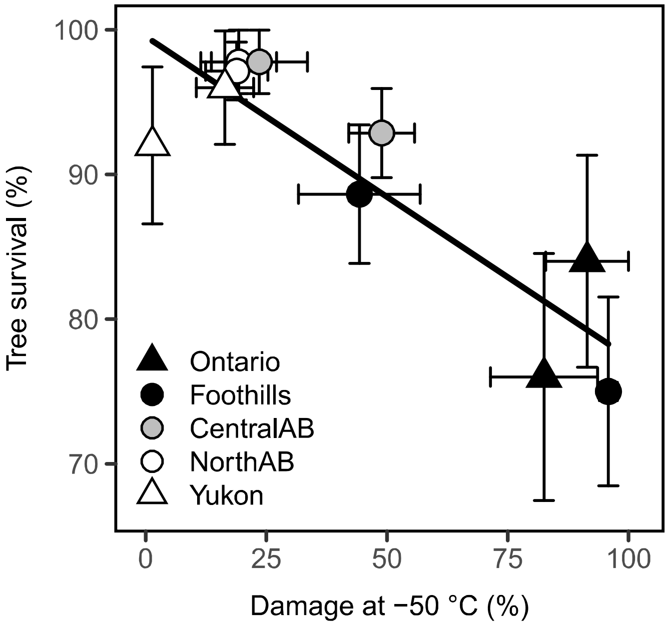

Figure 2.4. Tree survival was correlated to cold damage at a test temperature of -50°C ($R^2 = 0.746$, $p < 0.001$). Error bars correspond to one standard error.

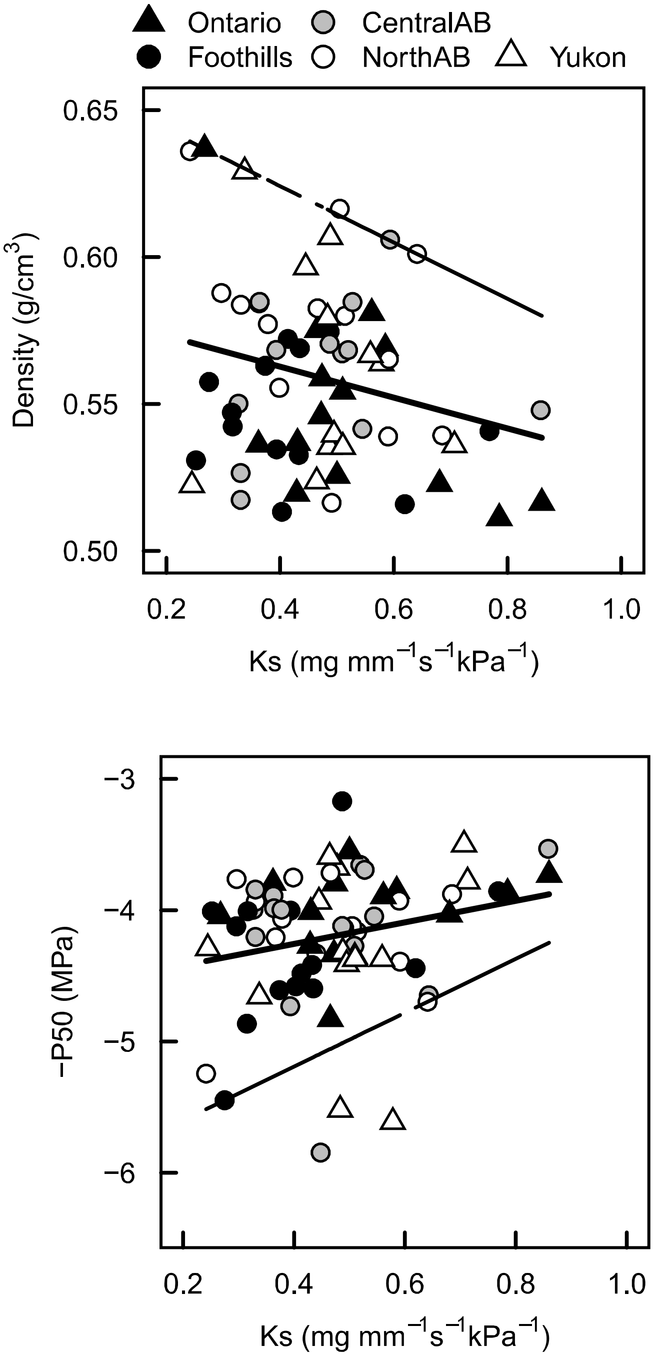

Figure 2.5. Relationship of individual values of xylem specific conductivity (K_S) and (a) wood density ($R^2 = 0.077$, $p = 0.013$) and (b) vulnerability to cavitation expressed as P50, the xylem pressure inducing 50% loss of hydraulic conductivity ($R^2 = 0.048$, $p = 0.042$). The dashed lines represent the 95% (a) and 5% (b) quantile regression lines to illustrate the scarcity/absence of data points in the upper right (a) and lower right (b) corner.

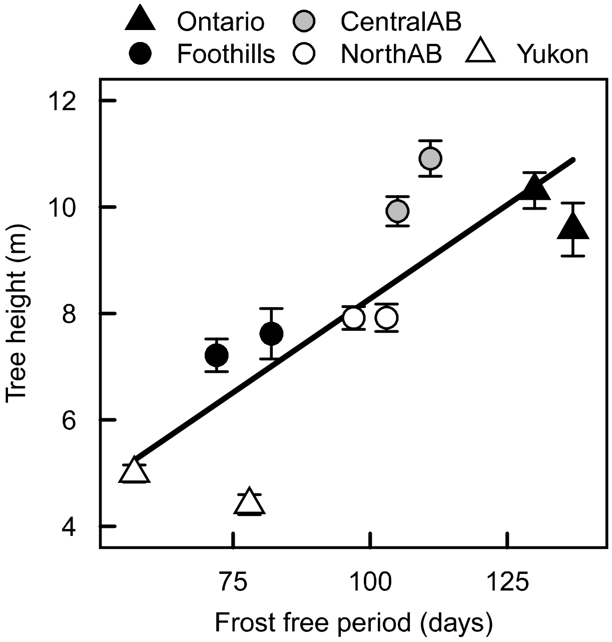

Figure 2.6. Relationship between tree height and the average date of the first frost event at the source of the provenances ($R^2 = 0.616$, $p = 0.004$), showing the effect of the end of the growing season on tree growth. Error bars represent the standard error of the mean.

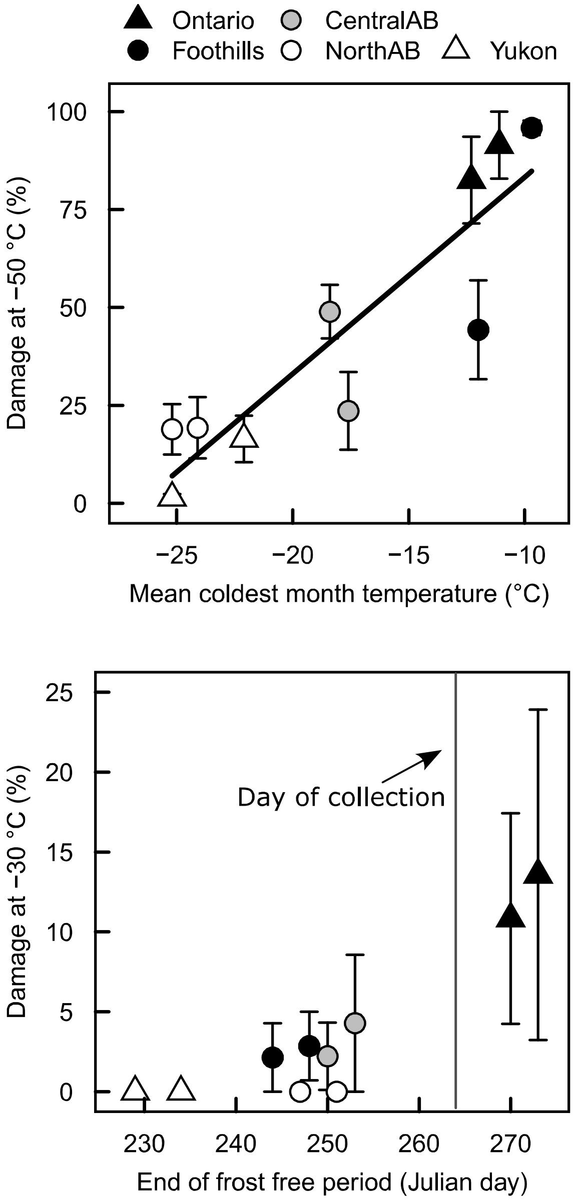

Figure 2.7. Relationship between cold hardiness (on the y-axis) and source climate (on the x-axis). (a) Cold damage at -50°C showed a high correlation to the mean coldest month temperature ($R^2 = 0.784$, $p < 0.001$). (b) Cold damage at -30°C as a function of the average day of the year when the first frost event occurs. Samples were collected on day 265 (September 22nd, dashed line). Only Ontario provenances (closed triangles) showed damage significantly greater than 0, consistent with the absence of frost at their native environment at that time of year. Error bars correspond to one standard error.

Chapter 3. Survival, growth and cold hardiness tradeoffs in white spruce populations: implications for assisted migration

3.1 Summary

Human assisted movement of reforestation stock poleward or upward in elevation has been proposed as a tool to address climate change in regular reforestation programs. However, moving warm adapted seed sources to colder environments could carry the risk of frost damage if seed sources are moved too far. Here, we assess genetic differentiation in growth potential, survival and cold hardiness of wide-ranging tree species, white spruce (*Picea glauca* [Moench] Voss). We use data from a 34-year-old common garden experiment planted in the approximate center of the species range. Cold hardiness was negatively related to growth and positively to survival. Generalized additive models identified mean coldest month temperature and latitude (as a proxy for the day length regime) as an exceptionally good predictor for the onset of cold hardiness (R^2_{adj}=0.91). The results suggest that day length, an environmental factor that is not influenced by climate change, is an important factor controlling the timing of the onset of hardiness. Survival was only moderately well predicted, primarily by precipitation of the provenance origin (R^2_{adj}=0.43) indicating that other adaptive traits besides cold hardiness should be considered in assisted migration prescriptions. Survival of seed sources appears primarily compromised when transplanting sources from wet origins to a dry location. Nevertheless, acceptable migration distances without significant tradeoffs were up to 500km north and 1,500km west towards a central planting location.

3.2 Introduction

In widely distributed tree species, natural selection usually leads to populations that are genetically adapted to specific climate conditions or other environmental factors (Morgenstern, 1996). This local adaptation is the basis for forest management rules that allow only locally adapted genetic material to be used for reforestation purposes. These rules are typically implemented by seed zone systems or seed transfer guidelines that limit the movement of planting stock (Holst 1962a; Ying & Yanchuk 2006; Bower, Clair & Erickson 2014). Under climate change, however, local adaptation of provenances is expected to lag behind new climate conditions due to the long life cycle of trees (Aitken *et al.* 2008; McKenney, Pedlar & O'Neill 2009). Several studies have documented this adaptational lag between the optimal and current habitats, and this lag is expected to increase under projected climate (Zhu, Woodall & Clark 2012; Corlett & Westcott 2013b).

One approach that has been proposed to mitigate the effect of climate change on survival and growth performance of future forests is human assisted migration that can be implemented as part of normal reforestation programs. Here, we refer to assisted migration as the transfer of locally adapted planting stock to locations with colder climate within or somewhat beyond a natural species range, following Gray and Hamann (2011). As a consequence of moving warm adapted seed sources to colder environments, assisted migration prescriptions could carry the risk of frost damage if seed sources are moved too far or if expected warmer climate conditions have not yet materialized. Severe frost damage can even be observed in natural populations that have not been moved (Gu *et al.* 2008; Man *et al.* 2009a). This implies the need to quantify local adaptation in cold hardiness to avoid maladaptation of planted forests.

Population differentiation in growth and adaptive traits can be studied with common garden experiments, usually referred to as provenance trials in a forestry context. Historically, provenance trials have been established for many commercial forestry species to identify fast growing seed sources, and they have now also become ideal climate change laboratories, where we can observe how exposure of populations to different climatic conditions can influence tree growth and survival (Mátyás 1994). Generally, provenance trials have shown that population survival is limited by low temperatures for sources that originate from the cold edge of the species range (Woodward 1990) and by a combination of biotic and abiotic factors for populations from the warm edge of the species range (Cahill *et al.* 2014). These limitations suggest a tradeoff between growth potential and cold hardiness (Loehle 1998; Howe *et al.* 2003a). Northern populations limit their growth by adapting to a shorter growing season and spending their resources into thicker and more rigid cell walls that give structural stability to the leaf tissues and by producing cryoprotectant substances, such as lipids, proteins or carbohydrates, which protect the cell structures from frost damage (Sakai & Larcher 1987; Zwiazek *et al.* 2001).

Frost hardiness can be evaluated through various protocols, including experimental freeze testing and evaluation of cellular damage (Burr *et al.* 2001), as well as morphological properties of needles and hydraulic tissue (Schreiber *et al.* 2013; Montwé *et al.* 2018). The amount of resources invested in the needles can be estimated with the ratio of projected leaf area to dry mass, or specific leaf area. Specific leaf area is lower in plants growing under more adverse conditions which have a slower growth and invest more resources to produce persistent leaves (Poorter *et al.* 2009).

White spruce (*Picea glauca* [Moench] Voss) is one of the most important commercial species in Canada and significant efforts have been made to understand how climate change might impact its growth and survival. An artificial warming experiment with open-top chambers showed that a warmer climate can enhance white spruce growth under subartic climate conditions (Danby & Hik 2007). Increased growth rates were also observed in a dendrochronology study in Alberta for the last part of the 20th century, but the unusually dry conditions experienced after 2001 induced a decrease in growth (Hogg *et al.* 2017). Several provenance trial experiments have been conducted to study genetic population differentiation. Seedling experiments in eastern Canada observed that southern provenances had a higher growth potential (Li, Beaulieu & Bousquet 1997a; Lesser & Parker 2004a; Prud'homme *et al.* 2017). Similar results were obtained in mature, range-wide provenance trials (Rweyyongeza, Barnhardt & Hansen 2011a; Lu *et al.* 2014a), showing that southern sources had the fastest growth. Based on a large set of provenance and progeny trials 7 to 32 years of age, Gray *et al.* (2016b) concluded that short northward transfers are generally beneficial in a regional study for the province of Alberta. Most of these authors cautioned against long distance transfers because of the risk of maladaptation to cold temperatures.

In this paper we contribute a comprehensive cold hardiness assessment for white spruce that covers provenance from throughout the species distribution, including a wide range of source climate conditions. Cold hardiness assessments include experimental freeze testing as well as morphological characteristics of needles. These data are evaluated in the context of long-term growth and survival observed in a 35-year-old field trial. Cold hardiness is measured experimentally through freeze tests. Specifically, we (1) investigate geographic patterns of genetic differentiation among provenances; (2) identify possible tradeoffs between frost hardiness, growth and survival; (3) analyze the association of climate and latitude at the origin of seed sources (as a proxy for day length regime) with growth, survival and frost hardiness observed in the common garden trial; and (4) quantify the impact of long distance transfers to identify seed sources with good hardiness characteristics as well as good growth performance as a recommendation for assisted migration prescriptions.

3.3 Methods

3.3.1 Field trial and measurements

The common garden experiment includes bulk seed collections from 43 natural stands of white spruce across the Canadian distribution of the species (Fig. 3.1). Seeds were collected between 1959 and 1976, and planted in 1982 as four-year-old seedlings in central Alberta, Canada (55°17'N, 113°10'W). The experimental layout of the provenance trial was a randomized complete block design of five blocks with five trees per provenance planted in each block in a row plot with 2.5×2.5m spacing. Provenances were grouped by Canadian ecoregions to calculate summary statistics for this analysis, indicated by different colors in Fig. 3.1. Height and survival of all trees was assessed in 2014 after 32 growing seasons in the field trial.

Cold hardiness measurements were performed once in spring (May 12-14, 2016) and at four dates in fall (August 25-27, September 9-11, September 23-25 and October 7-9, 2016). Because of limitations on processing and freeze testing within a given time, we sampled only 28 of the 43 provenances for cold hardiness assessments (Fig. 3.1, circles). Six trees per provenance and date were chosen at each date (one from each block, and one block sampled twice). To avoid excessive damage to trees, a different tree was chosen from each 5-tree row plot within each block for different sampling dates. During each of the three-day field visits, we collected healthy, sun-exposed branches from the upper part of the crown, approximately 60cm long to provide enough material for freeze testing at multiple temperatures. Branches were labeled and stored in plastic bags with wet paper towels to maintain humidity, and transferred to a cold room (+4ºC) on the same day.

Freeze testing was carried out generally following the protocol described by Burr *et al.* (2001). Cold hardiness assessments were made with 20cm branch sections at two temperatures (-25° and -40°C) in spring, and different sets of test temperatures for different dates in fall, starting with a measurement series of -20°, -25°, -30° and -40°C in August, and ending with measurement series of -30°, -40°, -50° and -60°C in October (Fig. 3.S1). A programmable freezer (Model 85-3.1A; ScienTemp, Adrian, MI, USA) was used for a gradual ramp-down from the +4ºC storage temperature to the test temperature at a cooling rate of 5ºC/hour. The test temperature was held constant for one hour before bringing the branches to room temperature at a warming rate of 5ºC/hour. To let cold damaged tissue develop discoloration, we then stored the samples in partially open clear plastic bags with wet paper towels in a growth chamber. Paper towels were re-wetted as needed. The percentage of damaged (brown) needles was visually assessed 14 days after the freezing treatment. Needles from the most recent growing season were the most vulnerable to freeze damage, and we therefore only used scores for recent needles in the analysis. A more precise and time consuming method, the electrolyte leakage method (Burr *et al,* 2001), was also considered. We compared both methods with a few samples in spring of 2016 and, after getting similar results with both methods, we decided to continue using the visual assessment which allowed the analysis of a higher sample size.

For the samples collected in October, we also assessed the ratio of leaf area to leaf dry mass to assess whether some provenances differed in producing morphologically more robust needles relative to the leaf area. For this purpose, approximately 150 needles from the current year were removed. To calculate the specific leaf area, we first scanned fresh needles from branches and measured their projected area using ImagePro Premier software (Media Cybernetics, Silver Spring, MD, USA). The same needles were then oven-dried at 60ºC for 48 hours and weighed. The specific leaf area was calculated as the ratio of needle area to dry mass.

3.3.2 Climate data

Climate data of the provenance origin locations and the study site were estimated with the software ClimateNA v5.21 (Wang *et al.* 2016). We used the standard reference normal period of 1961-1990 to represent the climate of origin to which populations are adapted. The 1961-1990 period is largely prior to a strong anthropogenic warming signal, and weather station coverage prior to this period becomes increasingly sparse. The climate variables considered in this study as putatively biologically relevant were: mean annual temperature (MAT), mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), continentality (TD) measured as the temperature difference between MCMT and MWMT, mean annual precipitation (MAP), mean summer precipitation from May to September (MSP), an annual heat-moisture index (AHM) calculated as (MAT+10)/MAP*1000, summer heat-moisture index (SHM) calculated as MWMT/MSP*1000, chilling degree-days below 0ºC (DD0), growing degree-days above 5ºC

(DD5), frost-free period (FFP), day of year at which the frost-free period begins (FFPB) and ends (FFPE), and Hargreaves' climatic moisture deficit (CMD).

3.3.3 Statistical analysis

To determine the onset of cold hardiness, we calculated the date at which 50% of the needles of freeze-tested samples suffered damage as follows. The damage scores for the two temperatures that were tested in all four dates in fall (-30ºC and -40ºC) were used to fit a Weibull function (similar to a sigmoidal function), using a non-linear regression function *nls* of the R base package (R Core Team 2017). These regressions were then used to calculate the date at which 50% of the needles were damaged by each temperature ($D50_{-30}$ and $D50_{-40}$ describing the date of 50% damage at a test temperature of -30ºC and -40ºC, respectively). For spring measurements, where hardiness was only assessed for one date, we fit a linear regression with the two temperatures tested and then calculated the temperature at which 50% of the needles were damaged (T50). No linear extrapolation was required at the provenance level to determinate T50.

Because different trees were sampled at each date for the assessment of the onset of fall cold hardiness, only provenance averages were used for calculating the values of $D50_{-30}$ and $D50_{-40}$. However, for all other measurements (height, mortality, specific leaf area and spring cold hardiness), we took advantage of the experimental design to reduce the error of the estimate, using linear mixed-effect models, treating block and rowplot within block as random effects. To estimate mortality of provenances, we used a generalized linear mixed-effect with the logit link function for a binomial distribution. The general linear mixed model was implemented with the *lmer* function, and the generalized logit model were implemented with the *glmer* function of the *lme4* package (Bates *et al.* 2014) for the R programming environment (R Core Team 2017).

Subsequently, best linear unbiased estimates with their standard errors of provenance means for fixed effects (height, mortality, specific leaf area and spring cold hardiness) were extracted from *lmer* and *glmer* objects with the *lsmeans* package (Lenth 2016b). We tested for statistically significant differences among regions using a Tukey adjustment for multiple inference with the *cld* function of the *lsmeans* package.

To test associations between the climate condition at the provenance source locations and hardiness, height and mortality assessments, we used generalized additive models (GAM) using the *gam* function of the package *mgcv* (Wood 2017) for the R programming environment (R Core Team 2017). GAMs are flexible in that they fit cumulative curves for each independent variable, without assuming any prior shape by fitting splines. We specified the Gaussian identity link function as an option in the GAM model for normally distributed errors in height and hardiness variables, and the logit function for the binomial distributed error of mortality. We used a low basis dimension (k=3) to restrict the shape of the splines to straight lines or simple curves, to avoid overfitting the data. Statistically significant variables for each model were determined with the *select* option of the *gam* function, which can completely remove terms from the model by assigning penalties to smoothing parameter estimation of individual predictor variables. If the smoothing parameter is set to zero (i.e. the model term is removed), the individual variable penalty is also set to zero, thereby avoiding overfitting not only by restricting the number of basis dimensions, but also by restricting the number of predictor variables. The contribution of each predictor variable was further quantified by an effect size measure, calculated as the difference between the maximum and minimum value of individual splines across the range of the predictor variable.

3.4 Results

3.4.1 Population differentiation in cold hardiness

We found significant population differentiation in the onset of cold hardiness for the main test temperatures (-30 and -40°C) that were evaluated at all four assessment dates (Fig. 3.2, Table 3.1). When plotting damage scores over test temperature separately for each measurement date, the September and October dates at colder temperatures (-50 and -60°C) also showed pronounced differentiation among provenances in the absolute cold hardiness values in fall (Fig 3.S1). In all cases, we observed a similar genetic cline, with the most northern region (Boreal Cordillera) showing the earliest resistance to frost damage and the highest absolute resistance values, followed by the two regions from central latitudes (Montane Cordillera and Boreal Plains). The provenances in the south and east of the distribution (Boreal Shield, Temperate Mixedwood and Maritime Mixedwood) were the most vulnerable for both absolute hardiness values and the timing of onset in the last measurement (Fig. 3.2, Fig. 3.S1).

The observed regional differences were statistically significant for the fall hardiness assessments, but not for spring cold hardiness (Table 3.1, indicated by letters). Provenance variation of hardiness within regions was relatively homogeneous, with standard deviation of the onset of cold hardiness typically around ± 4 days (data not shown). The most resistant provenances, from the northern edge of the distribution were resistant to 50% damage in the needles as early as August 27th for a test temperature of -30ºC, and at September 3rd for a temperature of -40ºC. The least resistant provenances on the other hand had a much later onset of cold hardiness, becoming 50% resistant to -30ºC in September 18th and to -40ºC in October 13th (data not shown).

3.4.2 Correlation with growth and survival

We also observed significant differences between regions in growth and survival (Table 3.1). For tree height, we found three groups that were clearly differentiated, with differences between their means of about 2 m each. The superior growing group was comprised of the central and southern regions, followed by the two coastal regions that showed intermediate growth. The lowest tree growth was found in the most northern region. The region with the best survival was the Boreal Plains from the central part of the distribution, which recorded less than 5% mortality in all its provenances except for one source (16%). The region with the highest mortality was the Atlantic coast (Maritime Mixedwood), where provenances showed mortality rates between 16 and 28% when grown at a central location. There were no significant differences among regions for specific leaf area due to high within-region and within-provenance variability.

When evaluating associations between growth and adaptive traits, we found correlations that could indicate tradeoffs. The populations that were most vulnerable to cold damage in fall ($D50_{-40}$) also showed the best growth (Fig 3.3a). The same result was obtained for the $D50_{-30}$ measurement with a Pearson's R of 0.54 ($p = 0.003$). Trees that became resistant to low temperatures later in the fall also showed higher mortality than those that started its cold adaptation earlier (Fig. 3.3b). However, mortality was not linearly correlated, but showed a significant curved response after fitting a GAM ($R^2 = 0.18$, $p < 0.001$). Spring cold hardiness, measured as the temperature causing 50% damage, showed weak associations with growth and survival (Pearson's R of -0.23 with height and –0.18 with mortality), meaning a tendency of hardier provenances having better growth and lower survival. However, these relationships were not statistically significant.

Specific leaf area was not significantly correlated to height or mortality and it was not correlated to any cold hardiness variables either (data not shown).

3.4.3 Association with the climate of provenance origin

We analyzed relationships of traits with the climate of origin of the provenances to infer genetic adaptation of white spruce populations to climate. The climate of provenance origin explained a large proportion of the variance in height, mortality and fall cold hardiness observed in the common garden experiment. For both cold hardiness models, latitude was the best predictor variable (Table 3.2). The best model for the onset of cold hardiness represented by the $D50_{-40}$ measurement included the predictor variables latitude and mean coldest month temperature, and were able to explain 90.5% of the among provenance variance (Table 3.2, Fig 3.4). For the $D50_{-30}$ measurement, only latitude was included as a significant predictor variable with a lower proportion of the variance explained. We used the $D50_{-40}$ model to make spatial prediction from gridded climate data for the onset of cold hardiness across Canada (Fig. 3.5). Using an interval size of one week difference in the onset of cold hardiness, we obtain five fall hardiness zones for areas covered by the sampled provenances, plus two extrapolated zones north and south of our data coverage for the range of the species.

The best model for tree height included latitude, mean annual temperature, mean annual precipitation and frost free period, and explained 83.1% of the variance (Table 3.2). Latitude was the most important predictor variable with the highest variance explained and the largest effect size of all four variables (5.9 m), with southern provenances growing significantly better than northern provenances (Figure 3.S2). Precipitation had a negative effect with provenances from wetter origins growing worse than provenances from drier origins after other effects have been accounted for. Annual temperature was optimal at levels close to the study site, with provenances from warmer or colder origins performing worse after other effects have been accounted for by the GAM. Provenances with longer growing seasons in their climate of origin also performed better than provenances with shorter ones, but this variable had the lowest effect size (Table 3.2, Fig. 3.S2).

The climate variables that best explained tree mortality were mean annual precipitation and mean annual temperature, although tree mortality was much less related to the climate of origin than tree height and cold hardiness with an R^2 of 0.43 for this model (Table 3.2, Figure 3S3). Mean annual precipitation was the most important variable of the model, with an effect size of 6.8 % ($p<0.001$). As for the height model, provenances with mean annual temperature similar to that of the test site were optimal for tree survival. Precipitation had a negative effect, with provenances with high precipitation in the environment where they originated showing higher mortality.

3.5 Discussion

3.5.1 Tradeoffs between growth and adaptive traits

The timing of phenological events is often associated with tradeoffs between growth and survival. Full utilization of the available growing season may come at the expense of risks of frost damage due to early fall frosts or late spring frosts (Aitken & Hannerz 2001; Howe *et al.* 2003a). This tradeoff seems to apply for our fall hardiness measurements. Provenances from southern locations that hardened later grew better but had lower survival rates, indicating that the onset of frost hardiness needs to strike a balance between survival and growth. In contrast, we did not observe strong genetic differentiation in spring cold hardiness.

Secondly, we tested the hypothesis that there may be a tradeoff between investment in hardier tissues to morphologically adapt to cold environments and growth. We used specific leaf area as a proxy for more resistant needle tissues. Although differences in specific leaf area can be due to many chemical or anatomical components, a higher specific leaf area (i.e. a higher ratio of leaf area to leaf dry weight) is usually related to faster growing species while species coming from harsher environments tend to show lower specific leaf area. (Lambers & Poorter 1992). The lack of correlation between specific leaf area and both height and cold hardiness observed in this study does not support the hypothesis of a higher investment in more resistant needles of northern provenances. We also failed to detect anatomical features in needle sections from different provenances that could be linked with cold hardiness.

There are few studies that measure cold hardiness directly, and they are either limited in sample size (Simpson 1994) or range (e.g., Hamilton *et al.* 2016). However, tradeoffs between phenology and tree growth can also be estimated by observations of bud set and bud break, which are often closely related to the timing of the onset and release of cold hardiness. For a seedling study of eastern white spruce provenances, Li *et al.* (1993) reported strong population differences in the timing of bud set, which was correlated with tree height, but no differences in the timing of bud break, which conforms well to our results for cold hardiness testing. Other studies reporting bud set got similar conclusions with northern provenances showing an earlier bud set timing and lower growth in white spruce seedlings of eastern Canada (Li, Beaulieu & Bousquet 1997a; Lesser & Parker 2004a). With respect to the timing of bud break, the same two studies in eastern Canada reported a latitudinal cline with northern provenances flushing earlier, but most of the variance (~90%) was within populations (Li, Beaulieu & Bousquet 1997a; Lesser & Parker 2004a). In a similar study covering the same range of white spruce in Ontario and Quebeck, Lu and Man (2011) did not find a cline in budbreak.

3.5.2 Environmental drivers of population differentiation

The environmental regulation of the onset and release of cold hardiness can explain the different degree of genetic differentiation observed in fall and spring cold hardiness timing. Bud flush and the release of cold hardiness in spring is mainly regulated by temperatures (Nienstaedt 1966; Saxe *et al.* 2001). First, a certain amount of time with temperatures between 0ºC and 5°C is needed to satisfy chilling requirements. Subsequently, growth initiation occurs in response to accumulation of degree days above a certain threshold. As a result release of dormancy is a highly plastic trait that strongly responds to year to year variation in spring temperature, and may therefore not require the same degree of genetic differentiation as the onset of fall hardiness.

The environmental cue for bud set and the onset of cold hardiness in fall is usually determined by day length (Hänninen *et al.* 1990; Saxe *et al.* 2001). This makes fall phenology a much less plastic trait with relatively little inter-annual variation. Therefore, trees must adapt genetically to different day length cues corresponding to local fall frost regimes. Temperature plays a secondary role in the speed of cold acclimation. Unusually warm fall temperatures may lead to a delay in the onset of dormancy in fall, but the opposite effect has also been observed: higher photosynthetic rates under warmer tempertature can provide the resources necessary to produce the cryoprotectant substances that lead to increases in cold hardiness at an earlier date (Hamilton *et al.* 2016).

The type of environmental control of tree phenology will dictate the vulnerability to climate change. Even though frost events are expected to be less frequent in the near future (Thornton *et al.* 2014), populations must adapt their phenology to take advantage of the longer growing seasons without increasing the risk to early or late frost events. Assisted migration can be used for this purpose to find the best compromise between the use of the growing season and vulnerability to frost. In spring, warmer temperatures will advance the timing of bud flush and growth initiation of tree populations (Menzel *et al.* 2006). If this advance of the beginning of the growing season is too fast, frost damage can occur following a late spring frost. Although this study as well as previous results point to small differences in spring cold hardiness between provenances, northward transfers could reduce the risk of such damage because southern populations flush later (Li, Beaulieu & Bousquet 1997a; Lesser & Parker 2004a). Another concern with warmer temperatures is whether the chilling requirement will be met. This should not be a concern in boreal regions, where temperatures close to freezing will still occur every year and where chilling requirements are usually low or nonexistent. However, under more maritime conditions, if temperatures remain too high during winter, growth start could be delayed and subsequent growth rates may be reduced (Luedeling *et al.* 2011).

Because day length regimes are not affected by climate change, a mismatch between climate and photoperiod is likely to occur in natural populations. However, this issue is not associated with a risk of fall cold injury but rather with a missed opportunity to take advantage of suitable growing conditions in fall. This mismatch should therefore be considered in tree breeding programs and assisted migration prescriptions. If southern provenances with late growth cessation are moved northwards, the change in the photoperiod regime will result in an even later cessation at their new location (Way & Montgomery 2015). The latitudinal effect observed in both fall cold hardiness and tree height models in our study (Table 3.2) conforms to a strong influence of photoperiod on the timing of growth cessation and onset of cold hardiness. Our freezing tests showed that all provenances were already resistant to -30ºC in early October, long before the first fall frosts are expected to occur.

3.5.3 Other tradeoff mechanisms

Besides latitude, we found significant relationships of tree height and mortality with mean annual precipitation and temperature. Both mortality and height models had similar patterns for temperature and precipitation, with an optimal temperature of source origin close to that of the study site and a negative effect of precipitation in both cases. These results suggest that adaptation to drought may explain this relationship. Specifically the eastern maritime provenances (and to some degree the most southern provenances from Ontario) lack drought adaptations that lead to higher mortality and lower growth when transplanted to a central boreal site. That said, other provenances from Ontario and Quebec, often with origin climates that were much wetter than the central test site, did not appear to be compromised in growth or mortality (Table 3.1).

In a physiological experiment with six of the provenances that were also evaluated in the present study a tradeoff between drought resistance and growth potential was observed (Sebastian-Azcona, Hacke & Hamann 2018). Taller trees showed lower leaf-specific conductivity, which corresponds to a higher leaf area standardized by its ability to transport water. On the one hand, low leaf-specific conductivity represents a relatively greater investment in photosynthesis relative to water supply. On the other hand, it will induce more negative water potentials (more water stress) for the same transpiration rate (Sebastian-Azcona, Hacke & Hamann 2018). Bigras (2005) also found a relation between drought resistance and growth in white spruce because slow growing families were able to maintain photosynthetic levels under a higher water stress. Although warmer temperatures are expected to generally increase productivity of boreal forests, water limitation can hamper this positive effect by reducing photosynthesis during drought events.

3.5.4 Management implications

An important application of adaptation to cold is the delineation of plant hardiness zones. These hardiness zones are developed to predict areas where a plant can survive and have been traditionally used in horticulture to safely introduce non-native ornamental species (McKenney *et al.* 2007). With data of population differentiation from common garden experiments, hardiness zones could also be used to limit the distance of seed transfers within the species range (Figure 3.5).

In the context of climate change, the results of this study support moderate northward movement of populations to address climate trends that have already occurred over the last decades. Superior growth of southern populations has been continuously reported in white spruce provenance trial studies, but extreme cold events are perceived as potentially compromising survival in northern transfers. However, our freezing tests suggest that all provenances are already resistant to -30ºC in early October, long before cold snaps of this magnitude occurs in the study site.

The best performing provenances in this trial came from the southern central part of the distribution (South East Manitoba), about 500 km south and 1,500 km east of the study site and a region with warmer summers and similar winter temperatures and precipitation. These climatic conditions are consistent with the expected climate change at the test site, and therefore assisted migration prescriptions of moderate distance or temperature (+1 to +2°C difference in the source climate compared to the planting site) seem well supported by this study.

3.6 References

Aitken, S.N. & Hannerz, M. (2001) Genecology and gene resource management strategies for conifer cold hardiness. *Conifer cold hardiness* (eds F.J. Bigras & S. Colombo), pp. 23-53. Springer, Netherlands.

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications,* **1,** 95-111.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014) Fitting linear mixed-effects models using *lme4*. *Journal of Statistical Software,* **67,** 1-48.

Bigras, F.J. (2005) Photosynthetic response of white spruce families to drought stress. *New Forests,* **29,** 135-148.

Bower, A.D., Clair, J.B.S. & Erickson, V. (2014) Generalized provisional seed zones for native plants. *Ecological Applications,* **24,** 913-919.

Burr, K.E., Hawkins, C.D., L'Hirondelle, S.J., Binder, W.D., George, M.F. & Repo, T. (2001) Methods for measuring cold hardiness of conifers. *Conifer cold hardiness* (eds F.J. Bigras & S. Colombo), pp. 369-401. Springer, Netherlands.

Cahill, A.E., Aiello-Lammens, M.E., Caitlin Fisher-Reid, M., Hua, X., Karanewsky, C.J., Ryu, H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B. & Wiens, J.J. (2014) Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. *Journal of Biogeography,* **41,** 429-442.

Corlett, R.T. & Westcott, D.A. (2013) Will plant movements keep up with climate change? *Trends in Ecology and Evolution,* **28,** 482-488.

Danby, R.K. & Hik, D.S. (2007) Responses of white spruce (*Picea glauca*) to experimental warming at a subarctic alpine treeline. *Global Change Biology,* **13,** 437-451.

Gray, L.K. & Hamann, A. (2011) Strategies for reforestation under uncertain future climates: guidelines for Alberta, Canada. *PLoS One,* **6,** e22977.

Gray, L.K., Hamann, A., John, S., Rweyongeza, D., Barnhardt, L. & Thomas, B.R. (2016) Climate change risk management in tree improvement programs: selection and movement of genotypes. *Tree Genetics & Genomes,* **12,** 1-12.

Gu, L., Hanson, P.J., Post, W.M., Kaiser, D.P., Yang, B., Nemani, R., Pallardy, S.G. & Meyers, T. (2008) The 2007 eastern US spring freeze: increased cold damage in a warming world? *AIBS Bulletin,* **58,** 253-262.

Hamilton, J.A., El Kayal, W., Hart, A.T., Runcie, D.E., Arango-Velez, A. & Cooke, J.E.K. (2016) The joint influence of photoperiod and temperature during growth cessation and development of dormancy in white spruce (*Picea glauca*). *Tree Physiology,* **36,** 1432-1448.

Hänninen, H., Häkkinen, R., Hari, P. & Koski, V. (1990) Timing of growth cessation in relation to climatic adaptation of northern woody plants. *Tree Physiology,* **6,** 29-39.

Hogg, E.H., Michaelian, M., Hook, T.I. & Undershultz, M.E. (2017) Recent climatic drying leads to age-independent growth reductions of white spruce stands in western Canada. *Global Change Biology,* **23,** 5297-5308.

Holst, M. (1962) Seed selection and tree breeding in Canada. *Technical Note No. 115.* Department of Forestry, Ottawa, Canada.

Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. & Chen, T.H.H. (2003) From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany,* **81,** 1247-1266.

Lambers, H. & Poorter, H. (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in ecological research,* **23,** 187-261.

Lenth, R.V. (2016) Least-squares means: the R package *lsmeans*. *Journal of Statistical Software,* **69,** 1-33.

Lesser, M.R. & Parker, W.H. (2004) Genetic variation in *Picea glauca* for growth and phenological traits from provenance tests in Ontario. *Silvae Genetica,* **53,** 141-148.

Li, P., Beaulieu, J. & Bousquet, J. (1997) Genetic structure and patterns of genetic variation among populations in eastern white spruce (*Picea glauca*). *Canadian Journal of Forest Research,* **27,** 189-198.

Li, P., Beaulieu, J., Corriveau, A. & Bousquet, J. (1993) Genetic variation in juvenile growth and phenology of white spruce provenance-progeny test. *Silvae Genetica,* **42,** 52-60.

Loehle, C. (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography,* **25,** 735-742.

Lu, P. & Man, R. (2011) Assessment of assisted migration effects on spring bud flush in white spruce (*Picea glauca* [Moench] Voss) seedlings. *The Forestry Chronicle,* **87,** 391-397.

Lu, P., Parker, W.H., Cherry, M., Colombo, S., Parker, W.C., Man, R. & Roubal, N. (2014) Survival and growth patterns of white spruce (*Picea glauca* [Moench] Voss) rangewide provenances and their implications for climate change adaptation. *Ecology and Evolution,* **4,** 2360-2374.

Luedeling, E., Girvetz, E.H., Semenov, M.A. & Brown, P.H. (2011) Climate change affects winter chill for temperate fruit and nut trees. *PLoS One,* **6,** e20155.

Man, R., Kayahara, G.J., Dang, Q.-L. & Rice, J.A. (2009) A case of severe frost damage prior to budbreak in young conifers in Northeastern Ontario: Consequence of climate change? *The Forestry Chronicle,* **85,** 453-462.

Mátyás, C. (1994) Modeling climate change effects with provenance test data. *Tree Physiology,* **14,** 797-804.

Mayr, S., Gruber, A. & Bauer, H. (2003) Repeated freeze–thaw cycles induce embolism in drought stressed conifers (Norway spruce, stone pine). *Planta,* **217,** 436-441.

McKenney, D., Pedlar, J. & O'Neill, G. (2009) Climate change and forest seed zones: Past trends, future prospects and challenges to ponder. *The Forestry Chronicle,* **85,** 258-266.

McKenney, D.W., Pedlar, J.H., Lawrence, K., Campbell, K. & Hutchinson, M.F. (2007) Beyond traditional hardiness zones: using climate envelopes to map plant range limits. *Bioscience,* **57,** 929-937.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O.g. & Briede, A. (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology,* **12,** 1969-1976.

Montwé, D., Isaac-Renton, M., Hamann, A. & Spiecker, H. (2018) Cold adaptation recorded in tree rings highlights risks associated with climate change and assisted migration. *Nature Communications,* **9,** 1574.

Nienstaedt, H. (1966) Dormancy and dormancy release in white spruce. *Forest Science,* **12,** 374-384.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist,* **182,** 565-588.

Prud'homme, G.O., Lamhamedi, M.S., Benomar, L., Rainville, A., DeBlois, J., Bousquet, J. & Beaulieu, J. (2017) Ecophysiology and growth of white spruce seedlings from various seed sources along a climatic gradient support the need for assisted migration. *Frontiers in Plant Science,* **8,** 2214.

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rweyyongeza, D.M., Barnhardt, L.K. & Hansen, C. (2011) Patterns of optimal growth for white spruce provenances in Alberta. *Ref. T/255 ISBN No. 978-0-7785-9796-4*. Alberta Tree Improvement & Seed Centre, Government of Alberta, Alberta, Canada.

Sakai, A. & Larcher, W. (1987) *Frost survival of plants: responses and adaptation to freezing stress*. Springer, Berlin, Germany.

Saxe, H., Cannell, M.G., Johnsen, Ø., Ryan, M.G. & Vourlitis, G. (2001) Tree and forest functioning in response to global warming. *New Phytologist,* **149,** 369-399.

Schreiber, S.G., Hamann, A., Hacke, U.G. & Thomas, B.R. (2013) Sixteen years of winter stress: an assessment of cold hardiness, growth performance and survival of hybrid poplar clones at a boreal planting site. *Plant, Cell & Environment,* **36,** 419-428.

Sebastian-Azcona, J., Hacke, U.G. & Hamann, A. (2018) Adaptations of white spruce to climate: strong intraspecific differences in cold hardiness linked to survival. *Ecology and Evolution,* **8,** 1758-1768.

Simpson, D.G. (1994) Seasonal and geographic origin effects on cold hardiness of white spruce buds, foliage, and stems. *Canadian Journal of Forest Research,* **24,** 1066-1070.

Thornton, P.K., Ericksen, P.J., Herrero, M. & Challinor, A.J. (2014) Climate variability and vulnerability to climate change: a review. *Global Change Biology,* **20,** 3313-3328.

Wang, T., Hamann, A., Spittlehouse, D. & Carroll, C. (2016) Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One,* **11,** e0156720.

Wang, W., Vinocur, B. & Altman, A. (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta,* **218,** 1-14.

Way, D.A. & Montgomery, R.A. (2015) Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell & Environment,* **38,** 1725-1736.

Wood, S.N. (2017) *Generalized additive models: an introduction with R*. CRC press, Boca Taton, FL.

Woodward, F.I. (1990) The impact of low temperatures in controlling the geographical distribution of plants. *Philosophical Transactions of the Royal Society of London B,* **326,** 585-593.

Ying, C.C. & Yanchuk, A.D. (2006) The development of British Columbia's tree seed transfer guidelines: purpose, concept, methodology, and implementation. *Forest Ecology and Management,* **227,** 1-13.

Zhu, K., Woodall, C.W. & Clark, J.S. (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology,* **18,** 1042-1052.

Zwiazek, J.J., Renault, S., Croser, C., Hansen, J. & Beck, E. (2001) Biochemical and biophysical changes in relation to cold hardiness. *Conifer cold hardiness* (eds F.J. Bigras & S. Colombo), pp. 165-186. Springer, Netherlands.

Table 3.1. Best linear unbiased estimates of mixed-effect models for regional means of tree height, mortality, cold hardiness and specific leaf area. Standard errors of the estimates are given in parenthesis. Mean estimates for regions with the same letter were not significantly different at $p < 0.05$, using a Tukey adjustment for multiple comparisons. The number of provenances per region for lab assessments were a subsample of the number of provenances in the field trial, and the number of trees was 25 per provenance for field assessments (height and mortality) and 6 per provenance for lab assessments (specific leaf area and cold hardiness variables).

Region	Number of provenances for field assessments	Number of provenances for lab assessments	Height (m)	Mortality (%)	Temperature causing 50% damage in spring (ºC)	Date at which -30ºC caused 50% damage (Days)	Date at which -40ºC caused 50% damage (Days)	Specific Leaf Area (cm^2/g)
Boreal Cordillera	4	3	5.4 (2.3) a	3.9 (2.0) ab	-27.1 (0.7) a	28 Aug (2.6) a	9 Sep (3.3) a	44.2 (4.2) a
Montane Cordillera	6	4	8.0 (2.1) b	5.5 (2.1) ab	-27.9 (0.4) a	2 Sep (2.2) ab	29 Sep (2.9) bc	51.1 (3.9) a
Boreal Plains	12	7	9.5 (1.7) c	2.9 (1.0) a	-27.2 (0.4) a	3 Sep (1.7) ab	25 Sep (2.0) b	41.7 (3.2) a
Boreal Shield	13	8	9.6 (1.6) c	7.5 (1.6) ab	-27.0 (0.8) a	10 Sep (1.6) c	2 Oct (2.2) bc	43.8 (3.0) a
Temperate Mixedwood	4	3	9.6 (2.2) c	12.6 (3.2) bc	-26.7 (0.6) a	9 Sep (2.6) bc	6 Oct (3.3) bc	49.5 (4.3) a
Maritime Mixedwood	3	3	7.7 (2.9) b	22.4 (5.2) c	-28.0 (0.6) a	13 Sep (2.6) c	9 Oct (3.3) c	48.7 (4.4) a

Table 3.2. Generalized additive models for mean height, mortality and fall cold hardiness as a function of climate variables and latitude as a proxy for the day length regime. Effect size is the difference between the maximum and minimum predicted value by the individual splines across the range of the predictor variable. Sample size was 43 provenances for height and mortality and 28 for cold hardiness.

Model	R^2	Variables	Cumulative R^2	Effect size	P-value
Height	0.83	Latitude	0.647	5.87 (m)	<0.0001
		MAP	0.116	2.81 (m)	<0.0001
		MAT	0.046	3.16 (m)	<0.0001
		FFP	0.022	1.83 (m)	0.0256
Mortality	0.43	MAP	0.310	6.76 (%)	<0.0001
		MAT	0.129	3.57 (%)	0.0051
$D50_{-30}$	0.64	Latitude	0.640	20.01 (days)	<0.0001
$D50_{-40}$	0.91	Latitude	0.832	23.08 (days)	<0.0001
		MCMT	0.073	13.01 (days)	<0.0001

$D50_{-30}$ = date at which a -30ºC freeze treatment caused 50% damage, $D50_{-40}$ = date at which a -40ºC freeze treatment caused 50% damage.

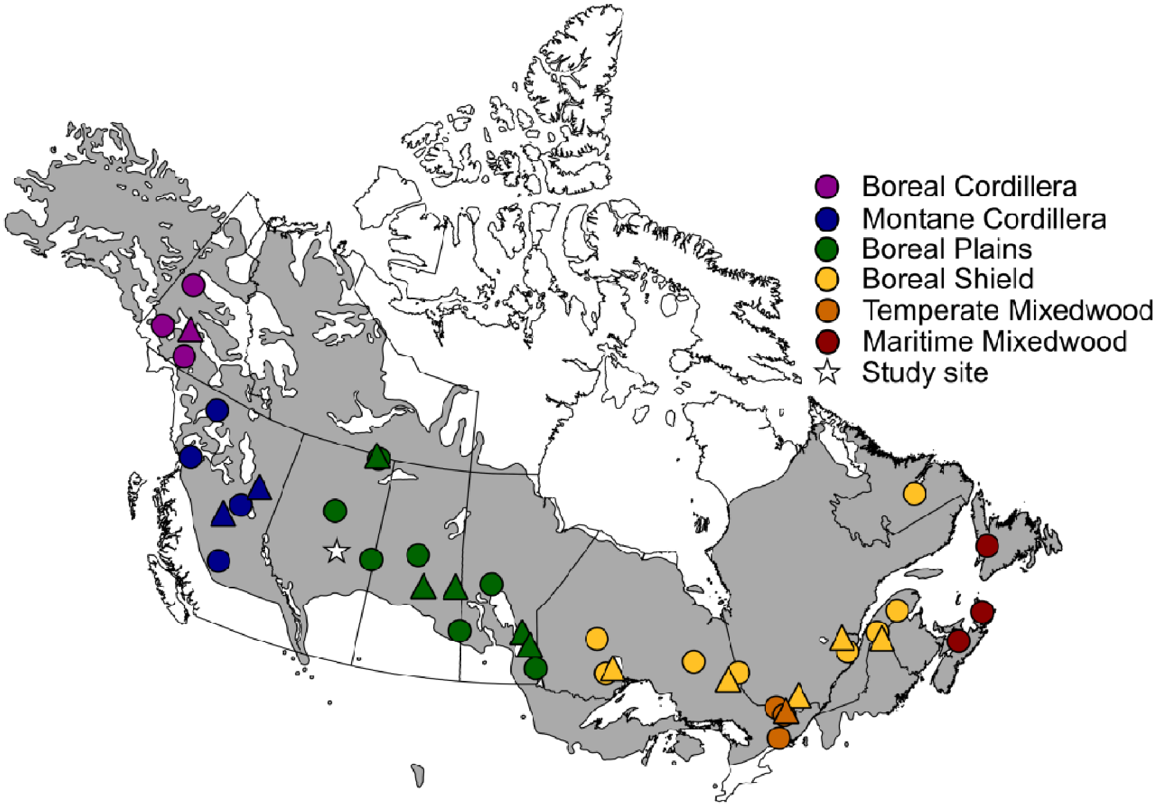

Figure 3.1. Location of the common garden experiment (star) and the origin of seedlots used in this study. The number of provenances for lab assessments (circles) were a subsample of the provenances in the field trial (circles and triangles). The area in grey delineates the species range of white spruce.

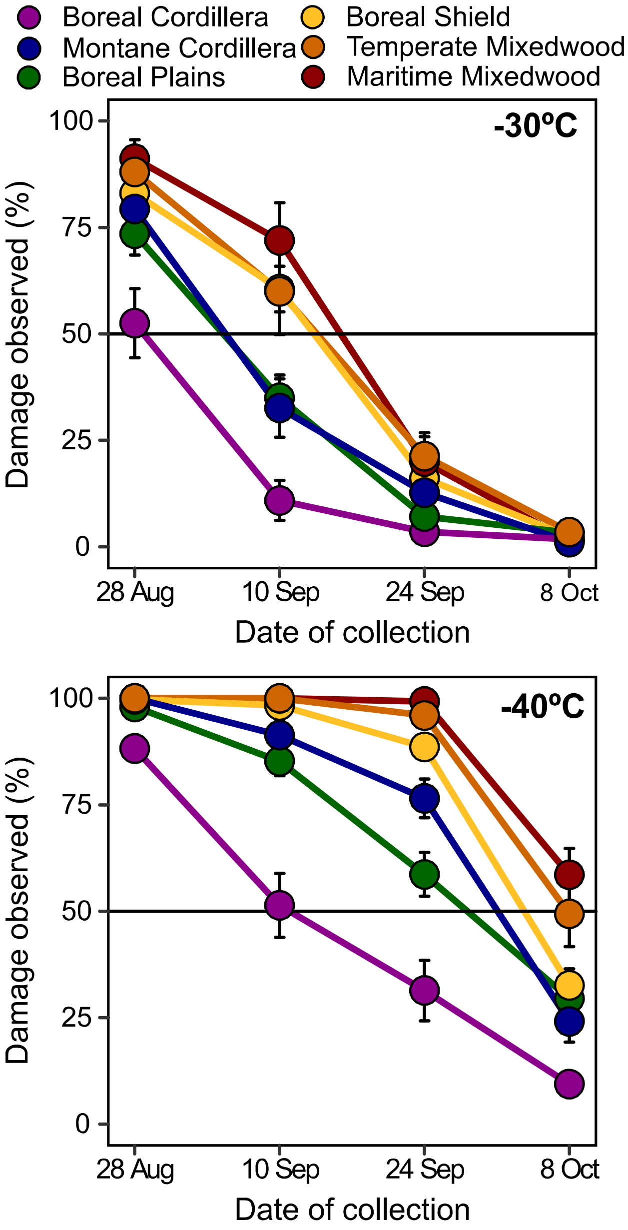

Figure 3.2. Percentage of observed damage in needle tissue at each collection date for the two freeze test temperatures (-30 and -40ºC). Error bars represent the standard error of the means.

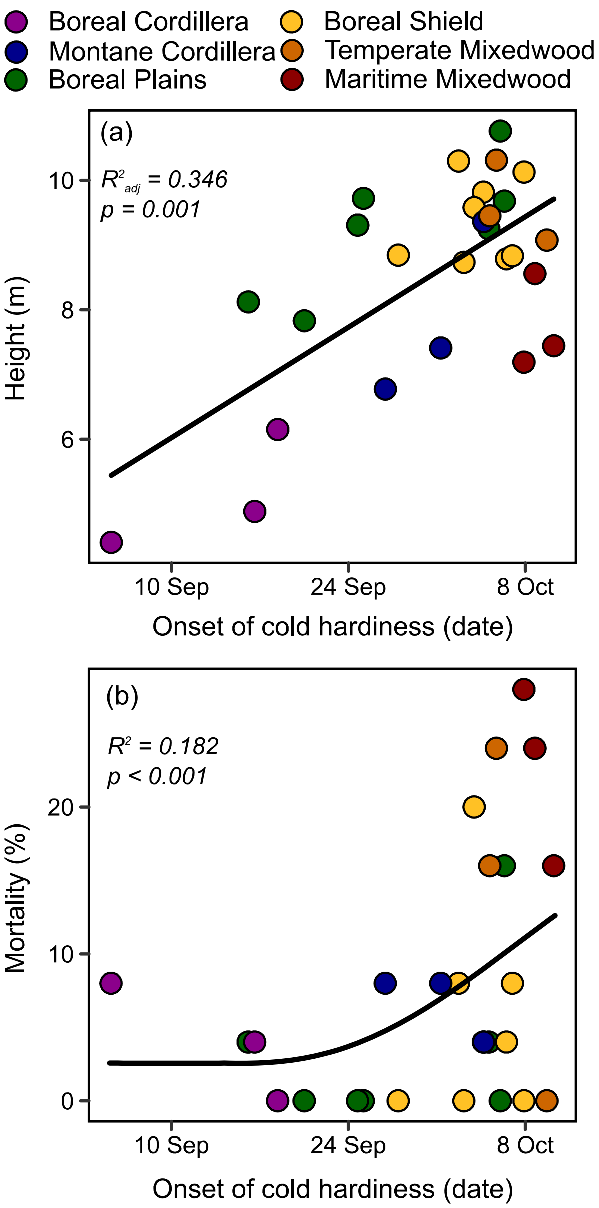

Figure 3.3. Association of height (a) and mortality (b) with the onset of frost hardiness, measured as the date at which 50% of the needles were damaged at a test temperature of -40ºC. A later date indicates that the provenance is more vulnerable to frost damage.

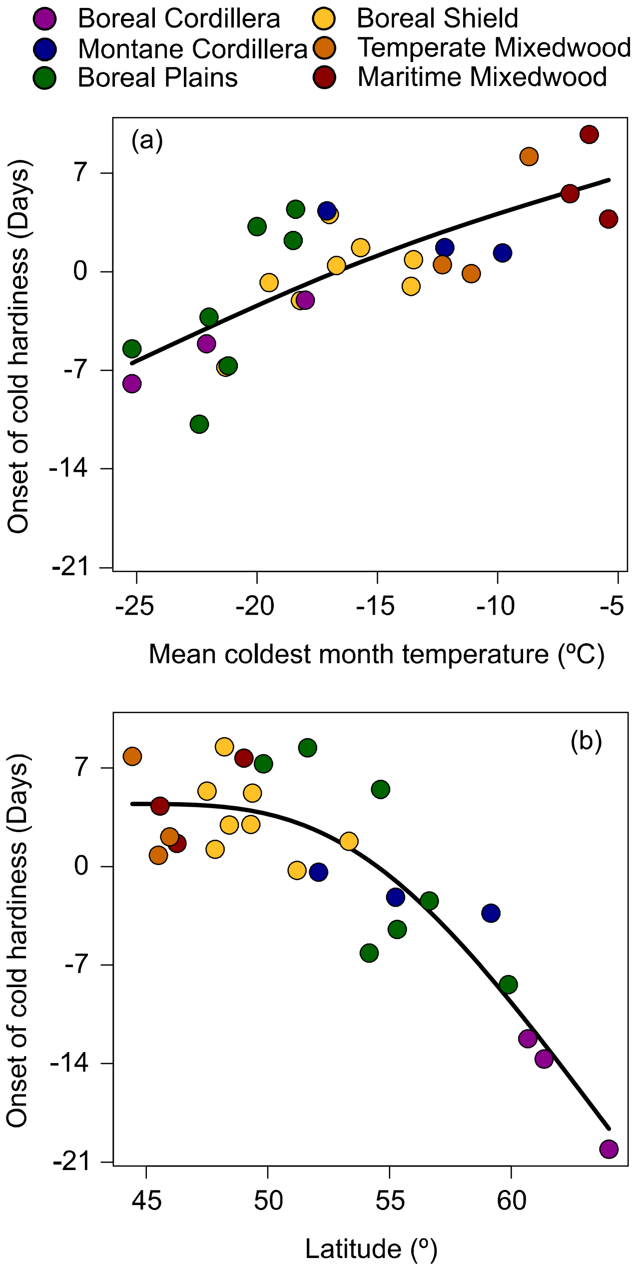

Figure 3.4. Visualization of the individual predictor variable effects in the generalized additive for the onset of cold hardiness (Table 3.2, $R^2 = 0.91$). The onset of frost hardiness was measured as the date at which 50% of the needles were damaged at a test temperature of -40ºC. A later date indicates that the provenance is more vulnerable to frost damage. Climate variables are represented in the X-axes and their individual model effects on tree height are shown in the Y-axis.

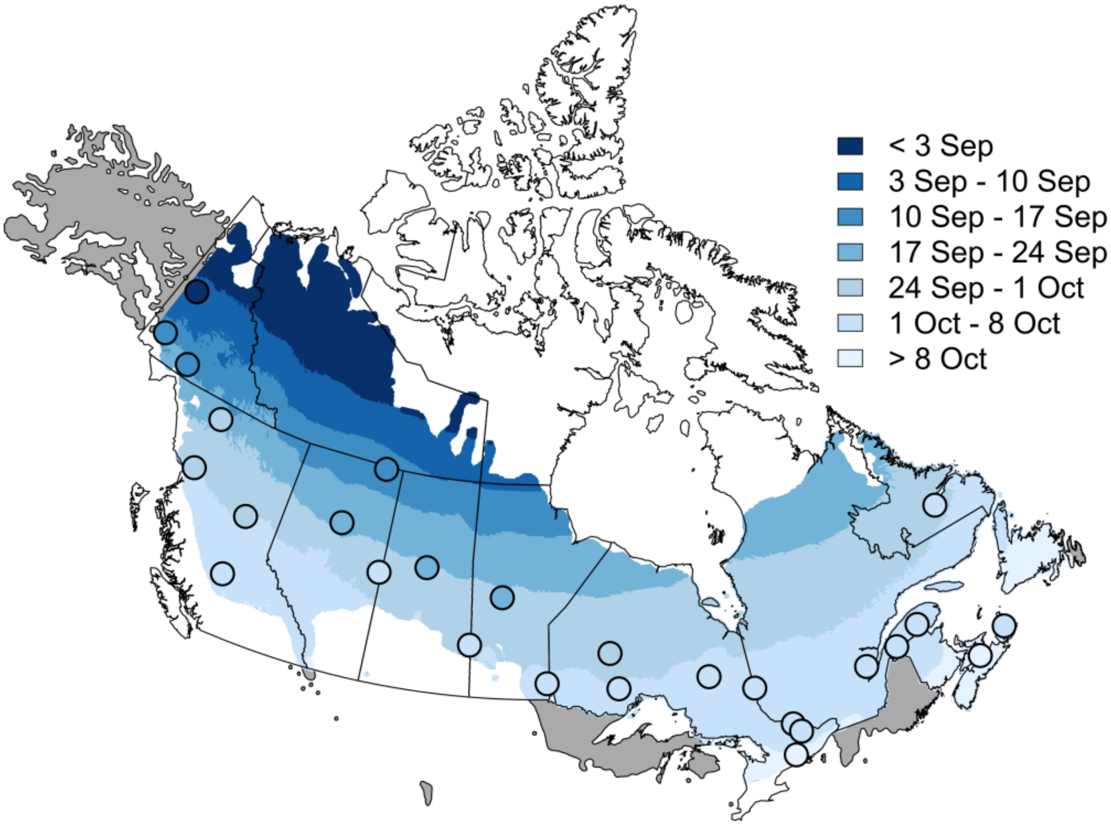

Figure 3.5. Cold hardiness zones inferred by one week intervals in the onset of frost hardiness. The onset of cold hardiness observed for provenances (circles) was predicted by a generalized additive model using latitude and mean coldest month temperature as the best predictor variables (Table 3.2, $R^2 = 0.91$). The dates represent the time at which 50% of needles were damaged at a test temperature of -40ºC.

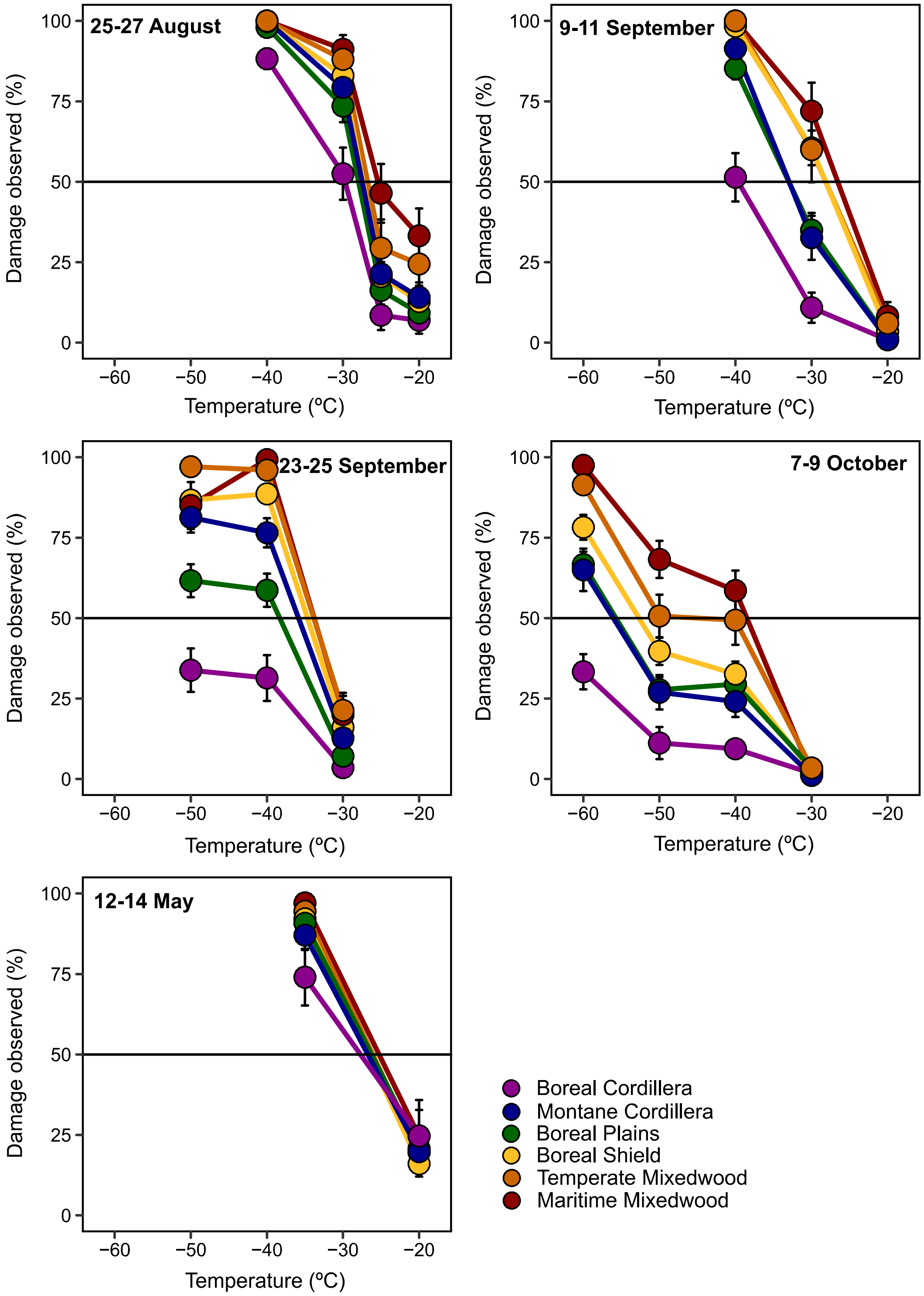

Figure 3.S1. Percentage of observed damage in needle tissue (Y-axes) at each test temperature (X-axes) for every collection date (indicated in bold). Error bars represent the standard error of the means.

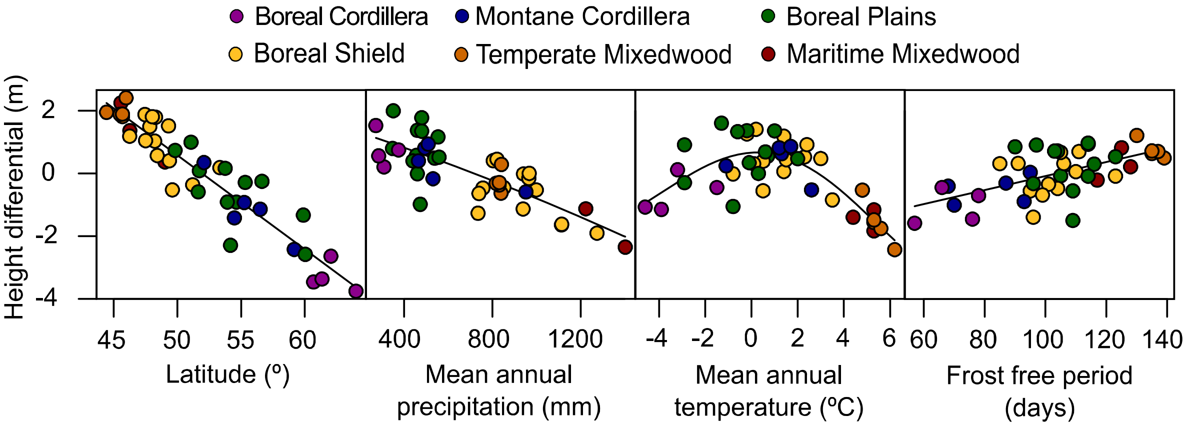

Figure 3.S2. Visualization of the individual predictor variable effects in the generalized additive for tree height explained by the generalized additive model (Table 3.2, $R^2 = 0.83$). Climate variables are represented in the X-axes and their individual model effects on tree height are shown in the Y-axis.

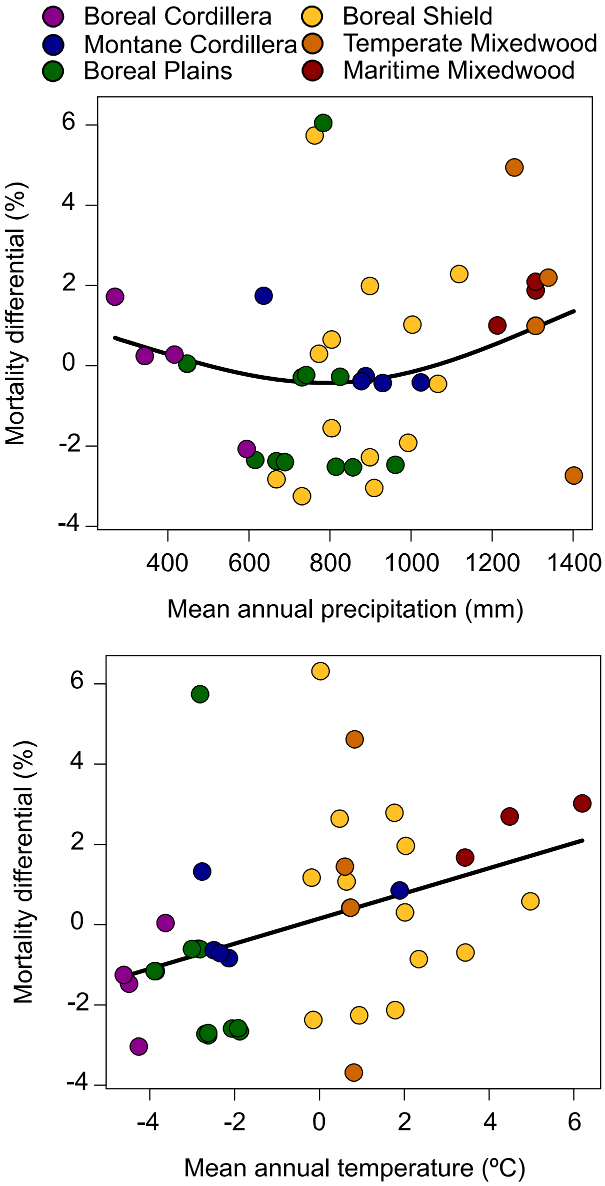

Figure 3.S3. Visualization of the individual predictor variable effects in the generalized additive for tree mortality explained by the generalized additive model (Table 3.2, $R^2 = 0.43$). Climate variables are represented in the X-axes and their individual model effects on tree height are shown in the Y-axis.

Chapter 4. Effect of temperature in the formation of xylem: risks of maladaptation to low temperatures in long distance seed transfers

4.1 Summary

The movement of seed sources from warmer to colder areas has been proposed as a tool to adapt to climate change. Provenances from southern regions are expected to take better advantage of the available growing season under climate warming when transferred northward or to higher elevations. However, susceptibility to cold temperatures may still be an important risk for such seed transfers. Here, we study xylem anomalies (frost, light, blue and double rings) caused by climate events in the tree rings of white spruce trees that were transferred to new environments in a range-wide provenance trial. Frost rings caused by low temperatures in spring and early summer were common in all the provenances during the first years, and became progressively less common in larger trees. Light rings, caused by low temperatures at the beginning and end of the growing season, were more common in southern provenances with high growth potential. Trees that are able to extend their growing season later into fall might take advantage of the warmer temperatures expected under climate change but can produce unlignified tracheids with low cell wall thickness in years with lower temperatures. Our results suggest that, although frost damage was not a direct limitation for growth performance, a mismatch of plant phenology with the beginning or end of the growing season was associated with lower survival, and caused xylem anomalies that can compromise wood quality.

4.2 Introduction

In widely distributed tree species, local populations may differ in terms of cold hardiness and other adaptive traits. Local adaptation is the basis for the choice of seed sources in forestry. Seed zones and seed transfer rules are used to preserve local adaptations by limiting the distance with which a population can be displaced from its native location with a minimum risk of maladaptation (Holst 1962b; Ying & Yanchuk 2006; Bower, Clair & Erickson 2014).

Evolution by natural selection occurs over many generations; a pace that may not match the projected rate of climate change (Aitken *et al.* 2008; McKenney, Pedlar & O'Neill 2009). Climate change, especially warming, could reduce the growth of forest trees if local populations are intolerant of new climatic conditions such as drought. Even in the absence of adverse effects, local populations may not be able to take advantage of longer growing seasons. A potential solution to this problem is the northward translocation of populations that are already adapted to warmer conditions and longer growing seasons, usually referred to as assisted migration (e.g. Gray & Hamann 2011; O'Neill, Stoehr & Jaquish 2014). This practice could not only mitigate the negative effect of climate change but could also improve current growing rates. Provenance trials enable us to study the relationship between biological traits of tree populations and climatic variables to better manage seed transfer for reforestation in a changing climate (Mátyás 1994).

The climate experienced by a tree throughout its lifetime affects its growth pattern and can be reconstructed with dendrochronology tools (Fritts 1976). In addition to causing changes in tree ring width, unusual climate events can induce different xylem anomalies (Schweingruber, Börner & Schulze 2006). The timing of these climate factors can be linked with the stages of xylem formation, and the location of the anatomical anomaly in the tree ring. For instance, if there is a period of freezing temperatures while the cambium is active and the development of newly formed tracheids is not yet completed, a frost ring can form (Glerum & Farrar 1966; Fritts 1976). A severe frost ring shows tracheids with thin and unlignified cell walls in the earlywood, followed by a zone of collapsed cells. After this layer of collapsed cells, traumatic parenchyma cells are formed followed by tracheids with lignified cell walls but abnormal shapes (Glerum & Farrar 1966). Frost rings can be present in different parts of the tree ring depending on when the frost event took place. If the frost event damaged the cambium before the start of the growing season, the damaged cells will show at the beginning of the tree ring. If the frost event occurred during the growing season, the position will depend on whether it was a late spring or a mid-summer frost (Glerum & Farrar 1966, Schweingruber, Börner & Schulze 2006).

Light rings are another type of xylem anomaly (Filion *et al.* 1986; Wang, Payette & Bégin 2000). They are characterized by thin cell walls in the latewood (Filion *et al.* 1986) and are formed in years with low temperatures at the beginning and end of the growing season (Castagneri *et al.* 2017). A more extreme case of low temperatures at the end of the growing season can induce the formation of "blue rings" (Piermattei *et al.* 2015). A sudden drop in temperatures can interrupt the lignification process in the last few rows of the latewood. Using a double stain of safranin and astra blue, lignified cells are stained red by safranin while unlignified tracheids will show a blue stain (Piermattei *et al.* 2015). Partially unlignified tracheids will show a blue secondary cell wall in the inner part of the cell and a red primary cell wall. This occurs because the lignifications process start in the primary cell wall and follows an inward direction.

Finally, intra-annual density fluctuations, also known as double rings, can appear when latewood-like cells appear within the earlywood in years with dry summer conditions followed by high precipitation at the end of the growing season (Rigling *et al.* 2001).

In this study, we recorded the occurrence of these four types of xylem anomalies in a boreal white spruce plantation. Trees represent 24 provenances covering the entire species range in Canada. We took tree cores from 120 trees and used light microscopy to analyze thin sections stained with safranin and astra blue. We linked the occurrence of the different xylem anomalies to past climate events. We also analyzed whether provenances from different ecozones differed in their susceptibility to each of the tree ring disturbances. Finally, we evaluated whether the observed patterns of xylem anomalies correlated with trends in tree growth and survival.

4.3 Methods

4.3.1Plant material

Samples were collected in a white spruce provenance trial in central Alberta, Canada (55°17'N, 113°10'W; Sebastian-Azcona *et al.* 2018; Sebastian-Azcona, Hacke & Hamann 2018). Trees from 43 provenances across the Canadian species range were planted in 1982 as 4-year-old seedlings (Fig. 4.1). The experimental setup is a randomized complete block design with five blocks and five trees per provenance planted in each block with a 2.5 x 2.5 m spacing. Height and survival of all the trees were assessed 32 years after planting and DBH was measured 27 years after planting. We selected a subset of 24 provenances for anatomical analyses corresponding to six different Canadian ecozones (Fig. 4.1). One tree of average height and DBH was selected from each provenance and block, for a total of five trees per provenance. When the quality of a whole sample or part of it was not good enough for an adequate analysis, it was discarded.

4.3.2 Section preparation

Tree cores of 5 mm width were taken from each selected tree approximately 50 cm above ground with an increment borer, in a north-south direction. Samples were collected during the summer of 2017, so 2016 is the last complete year used for analyses. Tree cores were first dried and sanded, and then 15-20 μm sections were taken with a GSL-1 microtome (Gärtner, Lucchinetti & Schweingruber 2014). Sections of the southern half of the core, from pith (if available) to bark, were stained using a 1:1 mix of safranin and astra blue solutions (Gärtner & Schweingruber 2013). Safranin solution contained 0.8 g of safranin powder in 100 ml of distilled water. Astra blue solution consisted of 0.5 g of astra blue powder dissolved in 100 ml of distilled water and 2 ml acetic acid. The double stain was applied for 5 min. Samples were then washed with distilled water, followed by 70% and 99% ethanol. Finally, the stained samples were mounted in glycerol.

4.3.3 Tree ring analyses

The presence of frost, light, blue and double rings was recorded using a light microscope (Leica DM3000) at 100 x and 200 x magnifications. Frost rings were classified according to their intensity (low, medium and severe) and position in the ring (A, B and C; Fig. 4.2). Low intensity rings consisted of only a few rows of tracheids that were slightly deformed (Fig. 4.2a), while medium intensity frost rings had several rows with clearly damaged tracheids that did not meet the requisites for the severe category. Severe frost rings showed extremely distorted tracheids usually preceded by unlignified (blue) cells and a clear zone of collapsed cells (Fig. 4.2b). The position depended whether the frost ring occurred right at the beginning of the growing season (up until the third tracheid row, position A; Fig. 4.2a), in the early part of the growing season (between tracheid rows 3 and 15, position B; Fig. 4.2b) or at a later stage (beyond row 15, position C).

Blue rings also had three intensity categories: low intensity rings consisted of patches of unlignified cells in the last few tracheid rows, medium intensity rings had their last one or two rows of tracheids completely unlignified and the severe blue rings had three or more unlignified tracheid rows (Fig. 4.2d). For light and double rings, we assigned either low or severe intensity categories according to how easy they were to detect by the observer. Only one person (the first author) performed these analyses for consistency. The total number of tree rings analyzed each year is shown in Fig. 4.3.

4.3.4 Climate data

All the climate data used in this study was generated by the software ClimateNA v5.21 (Wang *et al.* 2016). To explore the relationship between the occurrence of the different ring anomalies and the climate of that year, monthly, seasonal and yearly variables were extracted from 1982 to 2016. To test the influence of the climate of origin of the different provenances, we used normal data for the 1961-1990 period. We selected this period because it is representative of the climate prior to recent warming trends. The climate variables considered in this study were: mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), mean annual precipitation (MAP), the length of the frost-free period (FFP), day of year at which the frost-free period begins (bFFB) and ends (eFFP). We also considered latitude as a proxy for the day length regime.

4.3.5 Statistical analyses

We performed all statistical analysis with the R programming environment (R Core Team 2017). We used generalized linear mixed models to calculate the average presence ratio and intensity of the different xylem anomalies for each provenance and ecoregion. We chose the binomial family to represent the error distribution of the presence ratio and the Poisson family to represent the error distribution of the intensity data. We treated presence and intensity of xylem anomalies as fixed effects and blocks as random effects for these models. Average provenance mortality was also calculated with generalized linear mixed models using the logit link function for a binomial distribution. Linear mixed models were used for height and diameter models, in all cases treating blocks as random effects. We used the functions *glmer and lmer* from the package *lme4* (Bates et al. 2014) to run these models and then calculated the least-squared means with the *lsmean* function and the pairwise comparisons with the *cld* function, both from the package *lsmeans* (Lenth 2016b). We also used generalized linear mixed models to estimate the effect of monthly climate variables in the intensity of tree ring disturbances. For these models we treated block and provenance as random effects. To facilitate the interpretation of these models, we calculated the marginal R^2 that represents the variance explained by the fixed effects of the model, which in this case are the monthly climate variables. We calculated the marginal R^2 using the function *r.squaredGLMM* from the package *MuMIn* (Barton 2018). We analyzed the relationships between the average intensity of the tree ring disturbances for the different provenances with the average climate of origin for the 1961-1990 period and their performance in the field calculating

Pearson correlations and fitting linear regressions. Correction for multiple comparisons was performed using the Holms method and square root or logarithmic transformations were performed when necessary to fix non-normality problems.

4.4 Results

All four types of xylem anomalies were found in our samples. Frost rings were the most common of these phenomena, present in 13.7% of the rings. Light rings were detected in 7.6% of the rings, followed by double rings with a 4.2% occurrence rate. Blue rings were only found in 1.6% of the rings. As illustrated in Fig 4.3, frost rings were common in young trees until 9 years after planting; after that they progressively became less frequent. Almost no frost rings were found after 1998. Blue rings were also more common in very young trees. Blue rings only appeared in rings formed before the year 2001. Note, however, that our sample size of the early years was lower due to our occasional failure to drive the corer toward the pith and the earliest xylem rings. By contrast, light and double rings appeared throughout the entire lifetime of the trees.

4.4.1 Xylem disturbances and monthly climate

Next, we asked whether the occurrence of the different ring features was linked to monthly climate variables of the year when the ring feature was formed. Frost rings were mostly linked to spring temperatures. The different frost ring positions were correlated to monthly minimum temperatures that would explain its earlier or later presence in the tree ring. Frost rings in position A were only weakly related to minimum temperatures in March ($R^2 = 0.12$, $p < 0.001$). The occurrence of frost rings in position B was correlated with minimum temperatures in April

($R^2 = 0.38$, $p < 0.001$); frost rings in position C were caused by low temperatures in June ($R^2 = 0.31$, $p < 0.001$).

Light rings were found throughout the entire lifetime of trees (Fig. 4.3). Their formation was triggered by low temperatures at the beginning and end of the growing season (Fig. 4.4). The monthly variables that were most related to the presence of light rings were average temperatures in April ($R^2 = 0.30$, $p < 0.001$), May ($R^2 = 0.31$, $p < 0.001$) and September ($R^2 = 0.19$, $p < 0.001$). This relationship can be observed in Fig 4.4. A high percentage of light rings (represented by circles) was found in years that were characterized by cold temperatures in both April/May and September. Years with low temperatures in only one of the two periods did not show a high number of light rings.

The conditions that favored the formation of double rings were warm and dry summers characterized by highly negative climate moisture indices and a sudden increase in precipitation in September. The highest percentage of double rings was observed in 2015; a year with a very dry summer followed by a sudden increase in precipitation in September (Fig. 4.5). Finally, blue rings were triggered by low temperatures in September ($R^2 = 0.17$, $p < 0.001$); dry conditions in August also contributed to their formation ($R^2 = 0.12$, $p < 0.001$).

4.4.2 Differences between ecozones

We next studied whether the four xylem anomalies were equally present in provenances representing contrasting climate zones (Table 4.1). Provenances coming from the same ecozone of the study site (Continental Boreal) showed a high resistance to all types of anomalies. All other regions showed contrasting vulnerabilities to the different anomalies. Provenances from the most northern region (Northern Boreal) were the most vulnerable to mid-summer frosts, but were relatively resistant to frost rings in other positions and the most resistant provenances to anomalies related to the later stages of the growing season. Provenances from warmer regions showed a relatively low percentage of frost rings, but were the most susceptible to the other three anomalies. More specifically, provenances from the Temperate and the Mild Boreal ecozones showed the highest vulnerability to light rings, while trees from the humid Maritime region had the highest occurrence of blue and double rings (Table 4.1).

4.4.3 Effect of climate of origin

We next analyzed whether the climate of origin of the provenances was correlated with the type of tree ring anomaly (Table 4.2). The latitude of the origin of the provenances was negatively correlated with the percentage of light, double, and blue rings. These anomalies all occur in the second half of the growing season. In all cases, provenances from southern origins (relative to the planting site in Alberta) were more susceptible to the occurrence of these disturbances. The formation of light rings was also related to mean annual temperature and the end of the growing season, meaning that provenances from regions with warm and long growing seasons tended to have more light rings. The percentage of blue rings was correlated with multiple climate factors, including the end of the growing season. Provenances that showed a higher percentage of blue rings usually came from areas with a late end of the growing season, relatively mild winters and high precipitation levels (e.g., Maritime region).

Frost rings showed no significant correlation to the climate of origin of the provenances, but a few correlations appeared when the different frost ring positions were analyzed separately. Frost rings in position A were negatively correlated with continentality, i.e., the difference between the mean warmest and coldest month temperatures. Provenances from areas with cold winters and warm summers showed a higher resistance to this type of damage. The presence of frost rings in position C was correlated with the length of the frost-free period. Trees from provenances with longer growing seasons suffered more frost rings in this position. Frost rings in position B were not significantly correlated with any of the variables analyzed.

4.4.4 Impact of xylem disturbances in tree performance

We finally investigated whether the presence or absence of the different tree ring anomalies was related to the performance of the trees in terms of growth and survival (Table 4.3, Fig. 4.6). Height and diameter were both positively correlated to the presence of light rings, and negatively correlated to the presence of frost rings. All three frost ring positions were negatively correlated with tree height (Table 4.3), but combining frost rings in positions B and C showed the highest correlation with tree height. Mortality, on the other hand, showed a positive correlation to the presence of blue and double rings.

4.5 Discussion

We studied four tree ring anomalies in the context of when they occurred in the life of trees. We identified the climate factors that were associated with these xylem anomalies, and we linked the occurrence of these four xylem disturbances with the provenances' climate of origin. In a broader sense, our data provide new insights on xylem formation and how it is influenced by unusual climate events. Such knowledge will become increasingly important as forest managers weight benefits and risks of assisted migration.

Our findings can be discussed within the framework of the four stages of xylem formation: 1) cell differentiation and expansion, 2) secondary cell wall formation, 3) cell wall lignification, and 4) programmed cell death (Plomion, Leprovost & Stokes 2001; Bollhöner, Prestele & Tuominen 2012). In the boreal forest, these four stages occur approximately from May to early October (Rossi *et al.* 2011), and are affected by different environmental variables such as temperature, photoperiod, precipitation, snowmelt or health status (Chmielewski & Rötzer 2001; Marion, Gričar & Oven 2007; Rossi, Morin & Deslauriers 2011; Swidrak *et al.* 2011; Zohner *et al.* 2016).

4.5.1 First stage, cell differentiation and frost rings

The onset of xylem formation has been reported to be related to heat accumulation in spring, which is needed to break winter dormancy (Howe *et al.* 2003a). For the formation of a frost ring, a frost event needs to take place while the cambium is active (Glerum & Farrar 1966). Our results show that frost rings were mostly related to temperatures between March and June, depending on the position of the frost ring. Frost rings that appeared right at the beginning of the tree ring were apparently caused by low temperatures in March. This indicates that the cambium can be damaged by a severe frost early in spring, so the very first cells produced by the tree will be damaged.

In addition, the presence of frost rings in position A may be related to the conditions at the end of the growing season of the previous year (Montwé *et al.* 2018). Low temperatures in the later part of the growing season and the presence of blue rings were found to correlate with damaged cambial initials, and this contributed to the formation of frost rings in position A. Although these relationships were statistically significant in our study, the observed damage appeared to be caused mainly by frost events right before the beginning of the growing season. Frost rings in position B on the other hand were related to high temperatures in April. Although this correlation might seem counter intuitive, higher temperatures in April will advance the start of the growing season for that year, making trees more vulnerable to a late spring frost. Finally, frost rings in position C were related to minimum temperatures in June, showing the effect of summer frosts.

Frost rings appeared almost exclusively in the first 15 years after planting although favorable climate conditions for their formation persisted in subsequent decades. We found that taller (Fig. 4.6) and older (Fig. 4.3) trees were less prone to the formation of frost rings. This agrees with previous reports that frost rings are often restricted to smaller trees (Waito et al 2013, Gurskaya 2006, Payette 2010, Arco et al 2016). A possible explanation for the higher resistance of bigger trees to frost damage is that thicker stems, especially if accompanied by a thicker bark, are able to accumulate more heat so that they can maintain temperatures above freezing in the stem even if outside temperatures drop below 0ºC (Arco et al 2016).

4.5.2 Second stage, secondary wall formation, light and double rings

Light rings are related to the second stage of xylem formation, cell wall formation and thickening. We found that these rings with abnormally thin cell walls in the latewood were associated with low temperatures both at the beginning (May and June) and end (September) of the growing season (Fig. 4.4). In the boreal forest, temperature is the main limiting factor for photsynthesis at the beginning and end of the growing season (Man & Lieffers 1997). Similar results were obtained by Castagneri *et al.* (2017) in high elevation populations of Norway spruce. They attributed the impact of spring temperatures on cell wall thickness to higher carbon assimilation during the most favorable conditions for photosynthetic activity, while low temperatures in late summer constrain carbon mobilization and deposition rates.

The fact that light rings were more frequent in southern provenances is consistent with a more extensive use of the growing season and a later onset of cold hardiness in these trees at our study site (Sebastian-Azcona *et al.* 2018). These factors also translated into greater height growth (Sebastian-Azcona *et al.* 2018, Fig 3 there). We therefore conclude that the trend shown in Fig. 4.6b is an indirect expression of the causal relationship between tree height and growing season length.

Interestingly, the variable that showed the strongest correlation with the presence of light rings was latitude, which corresponds to different photoperiod regimes. In contrast to the onset of growth, which is linked to temperatures, maximum growth rates (Rossi, 2006) and growth cessation (Jackson 2009) are linked to day length.

Drought conditions during summer can also affect tracheid size and cell wall thickness as reflected by the presence of double rings. Warm and dry conditions between May and August followed by high precipitation in September induced fluctuations in cell size and cell wall thickness. Intra-annual density fluctuations are commonly associated with dry years and environments (De Micco *et al.* 2016). Latitude was again the environmental variable of the origin of the provenances that showed the strongest correlation with double rings. This suggests that provenances that end their growing season too early cannot take advantage of the favorable growing conditions provided by a high precipitation in fall.

4.5.3 Third stage, lignification and blue rings

The formation of blue rings is linked to the third stage of xylem formation, lignification. The occurrence of blue rings was correlated with low temperatures in September and low precipitation in August. Piermattei *et al.* (2015) observed a high proportion of blue rings in years with low temperatures at the end of the growing season and severe drought was also related to abnormally lignified cell walls in radiata pine (Donaldson 2002). Although the lignification process can be carried on during winter in temperate species (Donaldson 2001), this is not usually the case in boreal regions (Gričar *et al.* 2005). The percentage of blue rings in this study was much lower than in other similar studies where the number of blue rings was recorded in pine species (Piermattei *et al.* 2015; Montwé *et al.* 2018). This could be related to a more “intensive strategy” of spruce species that have a shorter growing season but higher growth rates that pines which have an “extensive strategy” and expand their growing season later in the year (Cuny *et al.* 2012; Jyske *et al.* 2014). Similar to light rings, blue rings were more common in provenances from southern latitudes with a late end of the growing season. However, blue rings were also more frequent in provenances coming from wetter regions, so a lack of adaptation to drought might favor the formation of blue rings.

4.5.4 Recommendations for assisted migration

Even though we do not think that the presence of xylem anomalies had a direct impact in tree performance, we can extract some useful conclusions for assisted migration recommendations. Although frost rings tended to be more frequent in some northern provenances with low growth, frost rings were not restricted to these trees. We found frost rings in all provenances, suggesting that their formation is relatively common among smaller white spruce trees. Furthermore, since the frequency of frost rings was not correlated with mortality (Table 4.3), we cannot conclude that frost rings have a negative effect on tree performance. It is possible, however, that the severe xylem phenotypes caused by frost damage contribute to the structural weakening of the growth ring. Frost rings may also facilitate the spreading of pathogens and the formation of xylem embolism in the earlywood.

A potentially important trade-off was observed between growth potential and the formation of light rings. Trees that utilize the growing season more aggressively may benefit from higher growth rates, but this may come at the cost of lower wood densities in the latewood. Blue rings and double rings that were a consequence for utilizing a longer growing season were also correlated with higher mortality rates, prevalent in the provenances from maritime and temperate regions. Much research has been devoted to studying the trade-offs associated with wood density (Hacke *et al.* 2001b; Rosner *et al.* 2007; Chave *et al.* 2009). For instance, Rosner *et al.* (2007) found greater resistance to bending in Norway spruce trees with high density. High wood density is also associated with higher resistance to hydraulic failure (Hacke *et al.* 2001b). A more severe consequence of extending the growing season too late into fall is the lack of lignin in the cell walls, which is an important component of tree resistance to several biotic and abiotic stresses (Moura *et al.* 2010).

4.6 References

Aitken, S.N. & Hannerz, M. (2001) Genecology and gene resource management strategies for conifer cold hardiness. *Conifer cold hardiness*, pp. 23-53. Springer.

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications,* **1,** 95-111.

Barton, K. (2018) MuMIn: Multi-Model Inference.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software,* **67,** 1-48.

Bower, A.D., Clair, J.B.S. & Erickson, V. (2014) Generalized provisional seed zones for native plants. *Ecological Applications,* **24,** 913-919.

Castagneri, D., Fonti, P., von Arx, G. & Carrer, M. (2017) How does climate influence xylem morphogenesis over the growing season? Insights from long-term intra-ring anatomy in Picea abies. *Annals of Botany,* **119,** 1011-1020.

Chmielewski, F.-M. & Rötzer, T. (2001) Response of tree phenology to climate change across Europe. *Agricultural and Forest Meteorology,* **108,** 101-112.

Cuny, H.E., Rathgeber, C.B.K., Lebourgeois, F., Fortin, M. & Fournier, M. (2012) Life strategies in intra-annual dynamics of wood formation: example of three conifer species in a temperate forest in north-east France. *Tree Physiology,* **32,** 612-625.

De Micco, V., Campelo, F., De Luis, M., Bräuning, A., Grabner, M., Battipaglia, G. & Cherubini, P. (2016) Intra-annual density fluctuations in tree rings: how, when, where, and why? *IAWA Journal,* **37,** 232-259.

Deslauriers, A., Morin, H. & Begin, Y. (2003) Cellular phenology of annual ring formation of Abies balsamea in the Quebec boreal forest (Canada). *Canadian Journal of Forest Research,* **33,** 190-200.

Donaldson, L.A. (2001) Lignification and lignin topochemistry—an ultrastructural view. *Phytochemistry,* **57,** 859-873.

Donaldson, L.A. (2002) Abnormal lignin distribution in wood from severely drought stressed Pinus radiata trees. *IAWA Journal,* **23,** 161-178.

Filion, L., Payette, S., Gauthier, L. & Boutin, Y. (1986) Light rings in subarctic conifers as a dendrochronological tool. *Quaternary Research,* **26,** 272-279.

Fritts, H. (2012) *Tree rings and climate*. Elsevier.

Gärtner, H., Lucchinetti, S. & Schweingruber, F.H. (2014) New perspectives for wood anatomical analysis in dendrosciences: the GSL1-microtome. *Dendrochronologia,* **32,** 47-51.

Gärtner, H. & Schweingruber, F.H. (2013) *Microscopic preparation techniques for plant stem analysis*. Verlag Dr. Kessel.

Glerum, C. & Farrar, J.L. (1966) Frost ring formation in the stems of some coniferous species. *Canadian Journal of Botany,* **44,** 879-886.

Gray, L.K. & Hamann, A. (2011) Strategies for reforestation under uncertain future climates: guidelines for Alberta, Canada. *PLoS One,* **6,** e22977.

Gričar, J., Čufar, K., Oven, P. & Schmitt, U. (2005) Differentiation of terminal latewood tracheids in silver fir trees during autumn. *Annals of Botany,* **95,** 959-965.

Gricar, J., Prislan, P., De Luis, M., Gryc, V., Hacurová, J., Vavrčík, H. & Čufar, K. (2015) Plasticity in variation of xylem and phloem cell characteristics of Norway spruce under different local conditions. *Frontiers in Plant Science,* **6,** 730.

Hartl, D.L. & Clark, A.G. (1997) *Principles of population genetics*. Sinauer associates Sunderland.

Holst, M. (1962) Seed selection and tree breeding in Canada. Department of Forestry, Ottawa, Canada.

Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. & Chen, T.H.H. (2003) From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany,* **81,** 1247-1266.

Jackson, S.D. (2009) Plant responses to photoperiod. *New Phytologist,* **181,** 517-531.

Lenth, R.V. (2016) Least-squares means: the R package lsmeans. *Journal of Statistical Software,* **69,** 1-33.

Lesser, M.R. & Parker, W.H. (2004) Genetic variation in Picea glauca for growth and phenological traits from provenance tests in Ontario. *Silvae Genetica,* **53,** 141-148.

Li, P., Beaulieu, J. & Bousquet, J. (1997) Genetic structure and patterns of genetic variation among populations in eastern white spruce (Picea glauca). *Canadian Journal of Forest Research,* **27,** 189-198.

Linhart, Y.B. & Grant, M.C. (1996) Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics,* **27,** 237-277.

Lu, P. & Man, R. (2011) Assessment of assisted migration effects on spring bud flush in white spruce (Picea glauca [Moench] Voss) seedlings. *The Forestry Chronicle,* **87**.

Lupi, C., Morin, H., Deslauriers, A. & Rossi, S. (2010) Xylem phenology and wood production: resolving the chicken-or-egg dilemma. *Plant, Cell & Environment,* **33,** 1721-1730.

Mangold, R.D. & Libby, W.J. (1978) A model for reforestation with optimal and suboptimal tree populations. *Silvae Genetica (Germany, FR).*

Marion, L., Gričar, J. & Oven, P. (2007) Wood formation in urban Norway maple trees studied by the micro-coring method. *Dendrochronologia,* **25,** 97-102.

Mátyás, C. (1994) Modeling climate change effects with provenance test data. *Tree Physiology,* **14,** 797-804.

McKenney, D., Pedlar, J. & O'Neill, G. (2009) Climate change and forest seed zones: Past trends, future prospects and challenges to ponder. *The Forestry Chronicle,* **85,** 258-266.

Montwé, D., Isaac-Renton, M., Hamann, A. & Spiecker, H. (2018) Cold adaptation recorded in tree rings highlights risks associated with climate change and assisted migration. *Nature communications,* **9,** 1574.

Morgenstern, M. (1996) *Geographic variation in forest trees: genetic basis and application of knowledge in silviculture*. UBC press, Vancouver, Canada.

Moura, J.C.M.S., Bonine, C.A.V., de Oliveira Fernandes Viana, J., Dornelas, M.C. & Mazzafera, P. (2010) Abiotic and biotic stresses and changes in the lignin content and composition in plants. *Journal of integrative plant biology,* **52,** 360-376.

O'Neill, G.A., Stoehr, M. & Jaquish, B. (2014) Quantifying safe seed transfer distance and impacts of tree breeding on adaptation. *Forest Ecology and Management,* **328,** 122-130.

Piermattei, A., Crivellaro, A., Carrer, M. & Urbinati, C. (2015) The "blue ring": anatomy and formation hypothesis of a new tree-ring anomaly in conifers. *Trees,* **29,** 613-620.

Plomion, C., Leprovost, G. & Stokes, A. (2001) Wood formation in trees. *Plant Physiology,* **127,** 1513-1523.

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rigling, A., Waldner, P.O., Forster, T., Bräker, O.U. & Pouttu, A. (2001) Ecological interpretation of tree-ring width and intraannual density fluctuations in Pinus sylvestris on dry sites in the central Alps and Siberia. *Canadian Journal of Forest Research,* **31,** 18-31.

Rossi, S., Anfodillo, T., Čufar, K., Cuny, H.E., Deslauriers, A., Fonti, P., Frank, D., Gričar, J., Gruber, A. & King, G.M. (2013) A meta-analysis of cambium phenology and growth: linear and non-linear patterns in conifers of the northern hemisphere. *Annals of Botany,* **112,** 1911-1920.

Rossi, S., Deslauriers, A., Anfodillo, T. & Carrer, M. (2008) Age-dependent xylogenesis in timberline conifers. *New Phytologist,* **177,** 199-208.

Rossi, S., Deslauriers, A., Anfodillo, T., Morin, H., Saracino, A., Motta, R. & Borghetti, M. (2006) Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. *New Phytologist,* **170,** 301-310.

Rossi, S., Morin, H. & Deslauriers, A. (2011a) Causes and correlations in cambium phenology: towards an integrated framework of xylogenesis. *Journal of experimental botany,* **63,** 2117-2126.

Rossi, S., Morin, H. & Deslauriers, A. (2011b) Multi-scale influence of snowmelt on xylogenesis of black spruce. *Arctic, Antarctic, and Alpine Research,* **43,** 457-464.

Rossi, S., Morin, H., Deslauriers, A. & Plourde, P.Y. (2011) Predicting xylem phenology in black spruce under climate warming. *Global Change Biology,* **17,** 614-625.

Schweingruber, F. H., Börner, A., & Schulze, E. D. (2006). Atlas of Woody Plant Stems: Evolution. *Structure, and Environmental Modifications.* Springer, Berlin

Swidrak, I., Gruber, A., Kofler, W. & Oberhuber, W. (2011) Effects of environmental conditions on onset of xylem growth in Pinus sylvestris under drought. *Tree Physiology,* **31,** 483-493.

Vieira, J., Campelo, F. & Nabais, C. (2009) Age-dependent responses of tree-ring growth and intra-annual density fluctuations of Pinus pinaster to Mediterranean climate. *Trees,* **23,** 257-265.

Wang, T., Hamann, A., Spittlehouse, D. & Carroll, C. (2016) Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One,* **11,** e0156720.

Wright, J. (1976) *Introduction to forest genetics*. Academic Press Inc, New York.

Ying, C.C. & Yanchuk, A.D. (2006) The development of British Columbia's tree seed transfer guidelines: purpose, concept, methodology, and implementation. *Forest Ecology and Management,* **227,** 1-13.

Zobel, B. & Talbert, J. (1984) *Applied forest tree improvement*. John Wiley & Sons.

Zohner, C.M., Benito, B.M., Svenning, J.-C. & Renner, S.S. (2016) Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change,* **6,** 1120.

Table 4.1. Regional least square means of the proportion of tree ring anomalies. Standard errors of the estimates are given in parenthesis. Mean estimates for regions with the same letter were not significantly different at $p < 0.05$, using a Tukey adjustment for multiple comparisons.

Group	Frost A	Frost B	Frost C	Light	Blue	Double
Northern Boreal	6.2 (1.4) ab	8.8 (1.7) a	4.0 (1.2) a	1.8 (0.8) a	0.0 (0.0) abc	1.1 (0.6) a
Continental Boreal	3.2 (0.6) a	6.8 (0.8) a	1.1 (0.3) b	5.7 (0.8) ab	0.3 (0.2) a	3.3 (0.6) a
Mild Boreal	4.7 (0.7) a	7.0 (0.8) a	1.2 (0.4) b	9.7 (1.1) c	1.6 (0.4) ab	4.5 (0.6) ab
Maritime	5.8 (1.2) ab	8.9 (1.5) a	1.7 (0.7) ab	7.2 (1.4) bc	4.7 (1.1) c	7.0 (1.3) b
Montane	10.3 (2.0) b	6.0 (1.6) a	2.6 (1.0) ab	6.4 (1.6) abc	0.9 (0.6) abc	2.5 (1.0) ab
Temperate	5.6 (1.1) ab	6.2 (1.1) a	1.1 (0.5) ab	11.0 (1.6) c	3.1 (0.8) bc	5.2 (1.0) ab

Table 4.2. Pearson correlation between the different tree ring disturbances and the climate of origin of the seed sources. Significant correlations with $p < 0.05$ after a Holms adjustment for multiple comparisons are indicated in bold.

	Frost A	Frost B	Frost C	Light	Blue	Double
Latitude	-0.13	0.17	0.43	**-0.72**	**-0.63**	**-0.60**
MAT	0.24	-0.09	-0.33	**0.55**	**0.66**	0.50
MWMT	-0.32	-0.12	-0.47	0.53	0.40	0.47
MCMT	0.44	0.02	-0.14	0.35	**0.65**	0.38
MAP	0.30	0.16	-0.33	0.51	**0.61**	-0.28
TD	**-0.56**	-0.07	-0.02	-0.18	-0.53	-0.23
bFFP	0.29	0.21	0.49	-0.35	-0.36	-0.34
eFFP	0.02	-0.03	-0.54	**0.57**	**0.61**	0.52
FFP	-0.12	-0.12	**-0.56**	0.51	0.54	0.48

MAT = mean annual temperature, *MWMT* = mean warmest month temperature, *MCMT* = mean coldest month temperature, *MAP* = mean annual precipitation, *TD* = continentality, b*FFP* = beginning of the frost-free period, e*FFP* = end of the frost-free period, *FFP* = frost-free period

Table 4.3. Pearson correlation between the different tree ring disturbances and tree performance. Significant correlations with $p < 0.05$ after a Holms adjustment for multiple comparisons are indicated in bold.

	HT32	DBH27	Mortality
Frost A	-0.23	-0.33	0.25
Frost B	-0.45	-0.44	-0.03
Frost C	**-0.57**	**-0.54**	0.01
Light	**0.66**	**0.59**	0.21
Blue	0.11	-0.03	**0.61**
Double	0.39	0.24	**0.59**

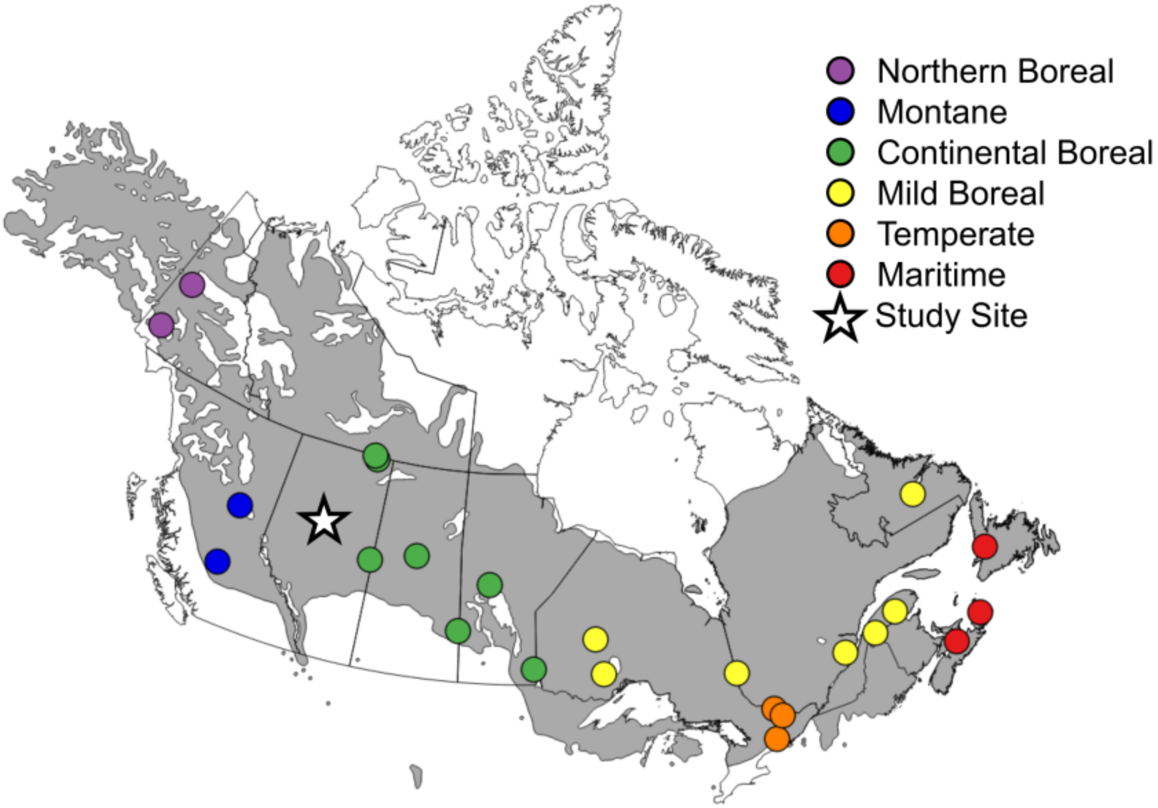

Figure 4.1. Locations of origin of the different provenances included in this study (circles) and plantation site (star). White spruce range is displayed in grey.

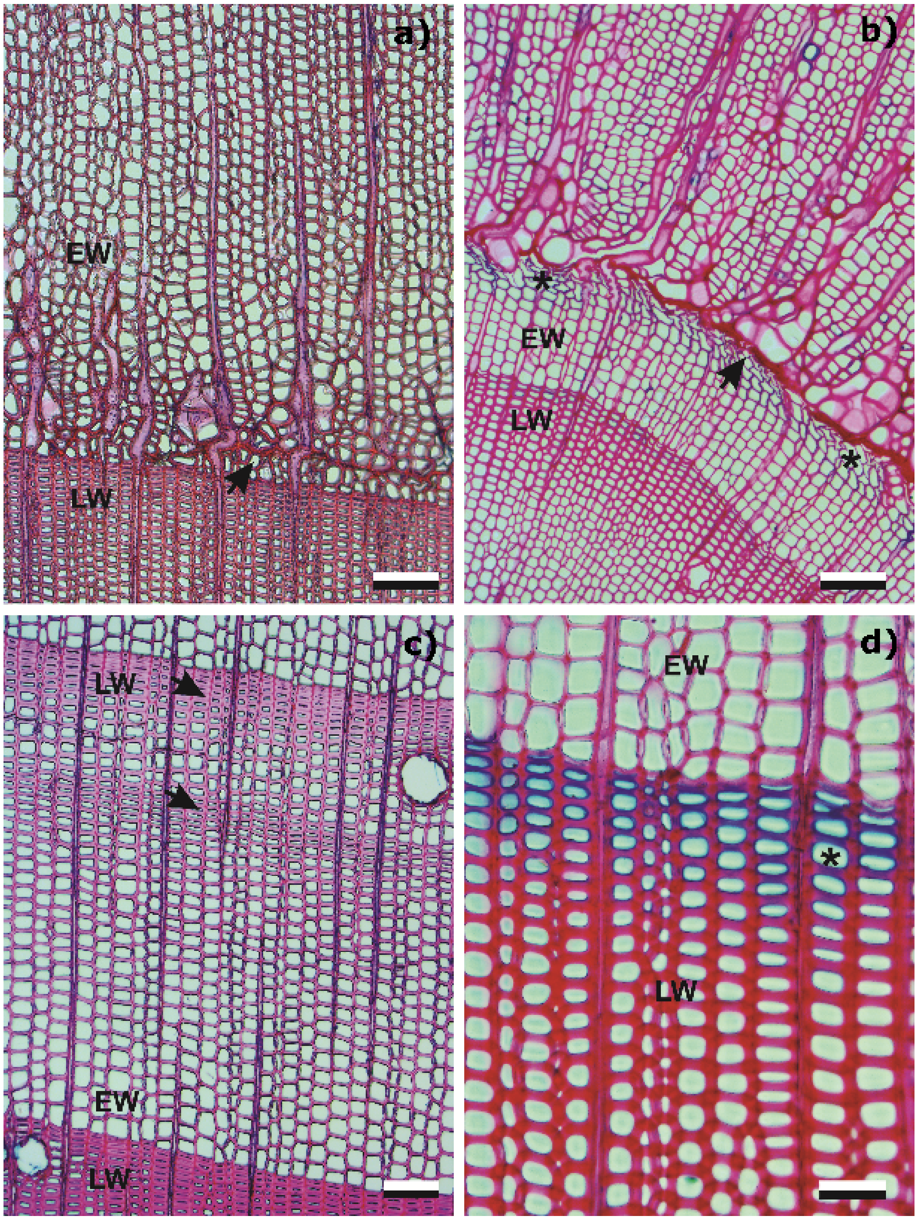

Figure 4.2. Sections of tree rings showing different xylem anomalies. The safranin-astra blue double stain distinguishes between lignified (red) and unlignified cells (blue). (a) The arrow points to a low intensity frost ring right at the start of the tree ring (position A), showing tracheids and ray parenchyma cells with abnormal shapes in the early wood. (b) The arrow points to a high intensity frost ring in position B. The severe spring frost damage stopped the lignification of some tracheids (stars) and induced the collapse and malformation of tracheids and parenchyma cells. (c) Double ring with two bands of latewood-like tracheids (labeled by arrows) caused by dry conditions in late summer and a subsequent spike in precipitation. (d) Blue ring showing unlignified cells in the latewood of a tree ring due to low temperatures. Scale bars in (a)-(c) are 100 µm and 50 µm in (d).

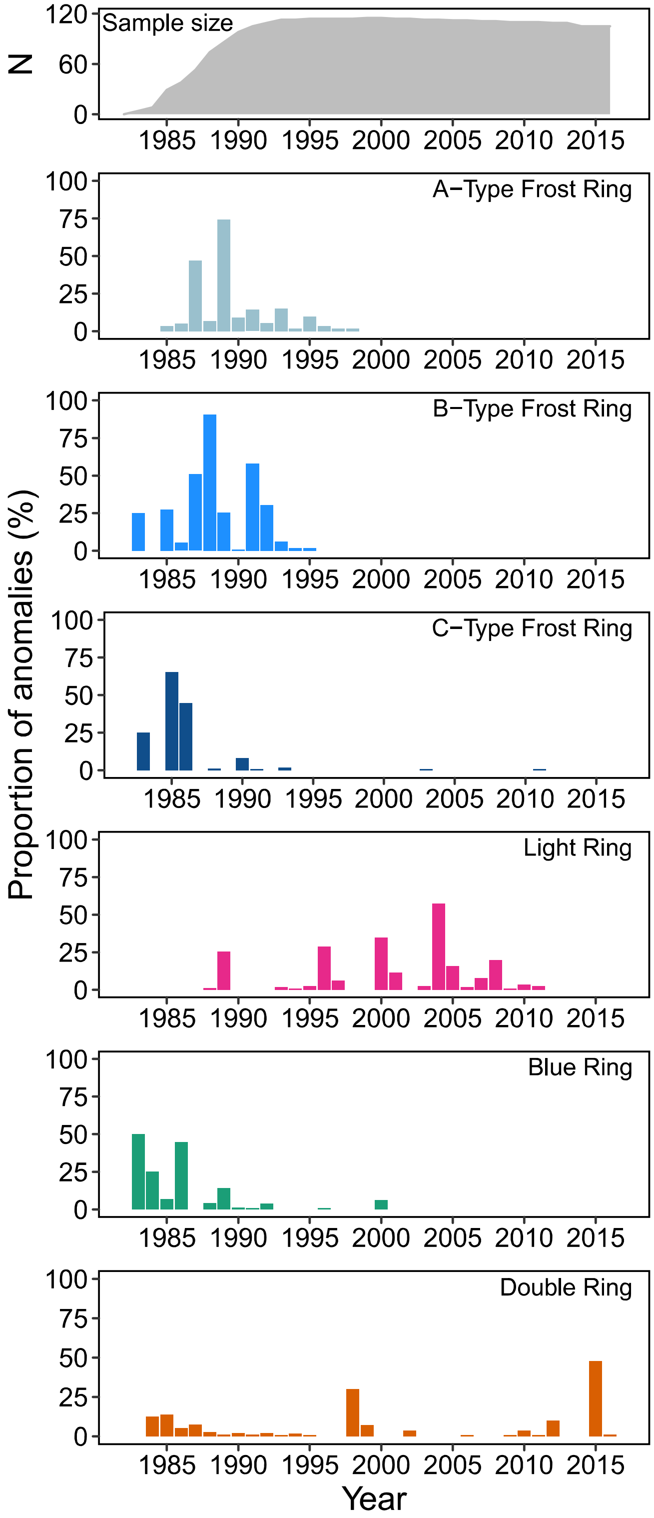

Figure 4.3. Proportion of tree ring anomalies (frost rings types A, B and C, light rings, blue rings and double rings) over the total sample size. The top figure shows the sample size for each year, showing a decreasing number of samples closer to the pith.

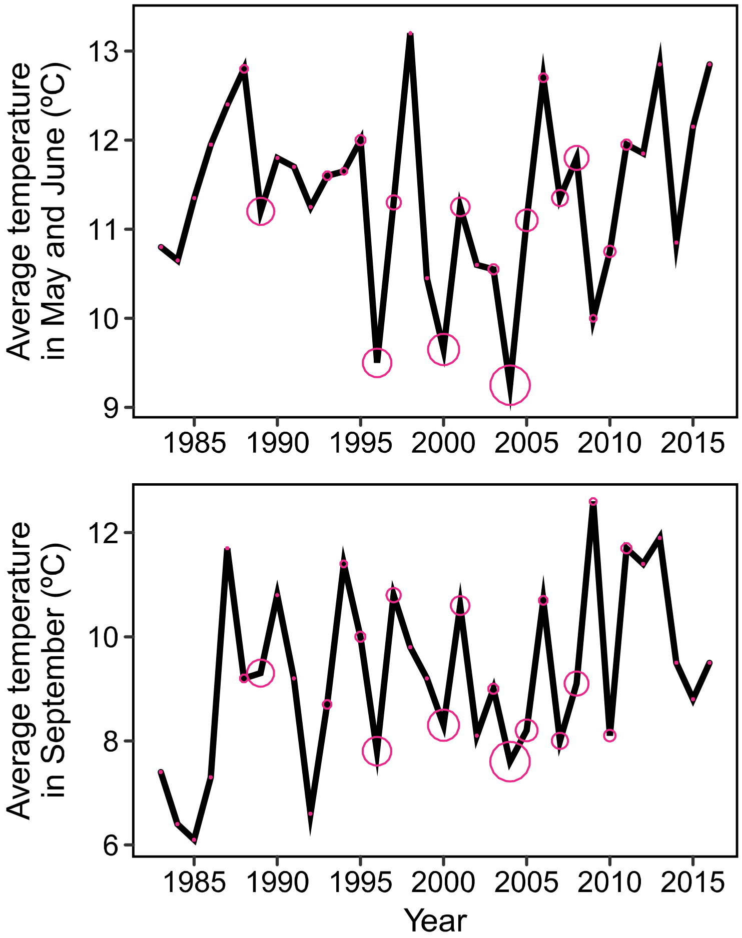

Figure 4.4. Annual average temperature in May and June (**a**) and September (**b**). Pink circles represent the proportion of light rings in each year, from 0% (e.g. 1985) to 58% (2004). The three years with the highest presence of light rings (1996, 2000 and 2004, indicated by arrows) correspond to the three coldest May and June temperatures of the study period and below average September temperatures. The red asterisk in 2009 represents a year with low temperatures in spring that did not induce light rings thanks to the warmer temperatures in September.

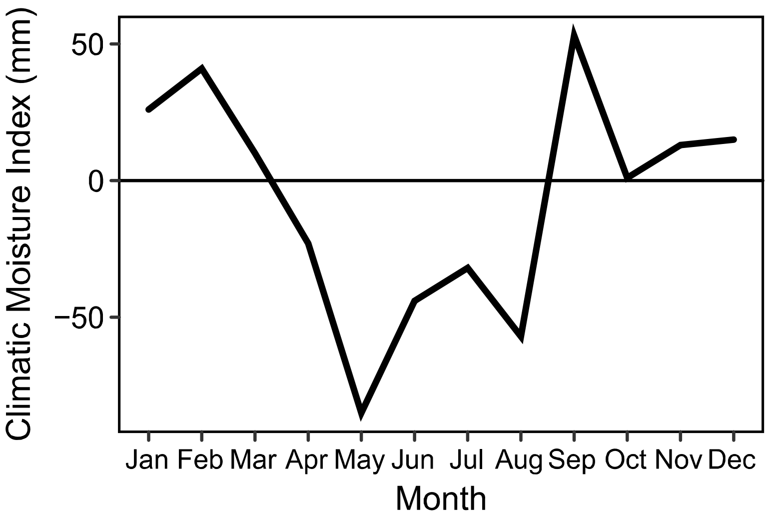

Figure 4.5. Monthly climate moisture index of the year with the highest proportion of double rings (2015). Climate moisture index is calculated as the difference between monthly precipitation and potential evapotransporation, so negative values indicate dry conditions. This year experienced a very dry spring and summer, with a sudden increase in precipitation in September.

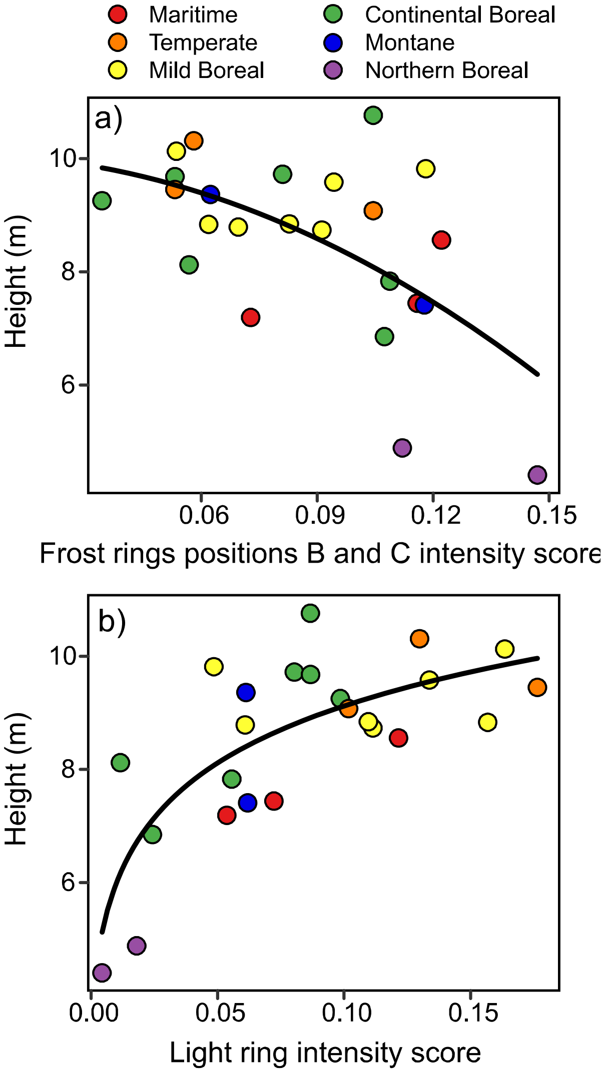

Figure 4.6. Relation between average tree height measured after 32 years and the average intensity scores of frost rings in positions B and C (**a**, $R^2 = 0.41$, $p < 0.001$) and light rings (**b**, $R^2 = 0.57$, $p < 0.001$) of the different provenances analyzed in this study. Trees with superior growth had a lower presence of frost rings but a higher presence of light rings overall.

Chapter 5. Synthesis and conclusions

5.1 Should we care about frost damage in a warming climate?

Most of the work of this thesis has focused on white spruce adaptation to cold temperatures. Many studies of white spruce provenance trials have consistently reported superior growth of southern provenances planted in different parts of its range (Li, Beaulieu & Bousquet 1997a; Rweyyongeza, Barnhardt & Hansen 2011b; Lu *et al.* 2014a; Gray *et al.* 2016a). In most of these studies, the authors recommend moderate northern transfers of seed sources but caution against long distance transfers because of the lower cold hardiness of southern provenances that could increase the risk of frost damage. Although some studies have reported differences in cold hardiness for white spruce populations, these studies were limited in number of provenances (Hamilton *et al.* 2016) or sample size (Simpson 1994). The complete description of the variation of cold hardiness within the whole range of white spruce distribution can be used to correctly assess the risks of long-distance seed transfers.

The most complete description of intraspecific differences in cold hardiness was done in *Chapter 3*, showing clear differentiation between provenances. The main tradeoff observed in this study was between fall cold hardiness and tree growth. Trees from the northern part of white spruce distribution, that are adapted to an early growth cessation to avoid early fall frost, were very resistant to low temperatures even in late August but that premature end of the growing season implicated a lower growth than other provenances. An early growth cessation corresponds to a missed opportunity of the good growing conditions happening at the end of summer. Provenances from the southern edge of the distribution showed an opposite result as they became resistant to low temperatures weeks later, which allowed them to fully utilize the extent of the growing season and acquire a higher growth. I also measured cold hardiness in spring which reported no significant differences between provenances. The lower differentiation in spring hardiness compared to fall hardiness is common in several conifer species (Aitken & Hannerz 2001).

Knowing the negative implications of a high cold hardiness, the question is how important is for white spruce trees to achieve an adequate cold hardiness. Fall cold hardiness was significantly correlated to tree mortality in both *Chapter 2* and *Chapter 3*. Despite the statistical significance of the relation between fall cold hardiness and tree mortality in *Chapter 3*, the most complete analysis of both traits, the variance of tree mortality explained by cold hardiness was relatively low. Furthermore, although there were clear differences in fall cold hardiness between the different provenances, all the provenances were fairly resistant to freezing temperatures. When compared to the climate of origin, the variables that best explained tree mortality were mean annual temperature and mean annual precipitation. Moreover, the region with the highest tree mortality was the Maritime Mixedwood, which is the wettest region within white spruce distribution. These results point to maladaptation to drought as the main cause of tree mortality in the study site. I also investigated the frost damage recorded in the xylem of the trees in *Chapter 4*. Most of the frost damage observed was recorded in the earlywood of the tree rings, corresponding to low temperatures in spring. Interestingly all the provenances showed a high presence of frost damage in the first years of their life, and a higher presence of frost rings was not correlated to tree mortality. These results suggest that, although there are clear differences in cold hardiness between white spruce populations adapted to the different environmental conditions where they evolved, having a superior cold hardiness did not show any clear advantage in their performance in Central Alberta.

5.2 Photoperiod effect on white spruce phenology

In all the chapters of this thesis, the environmental variable that has consistently reported the strongest correlations has been the latitude of origin of the provenances. Here, I use latitude as a proxy for the photoperiod regimes at the provenances' origin. Contrary to the beginning of the growing season, which is controlled by temperature, fall phenology is mostly controlled by short photoperiods (Howe *et al.* 2003a). The photoperiod control of the end of the growing season is of great interest for assisted migration practices since local populations might not be able to adapt to the extended period of warm temperatures caused by climate change. If trees keep relying on a constant photoperiod signal, they will not fully utilize the growing conditions and seed transfers might be necessary to take advantage of these new favorable conditions (Way & Montgomery 2015).

In *Chapter 3*, latitude was the environmental variable that was most highly correlated to tree height and cold hardiness. Southern provenances that are adapted to longer growing seasons showed a later cold hardening and a higher growth. Trees from warm, southern origins are already adapted to longer growing seasons. When moved northward, the critical day length that they use as signal to end the growing season will happen even later than at their site of origin. Therefor southern provenances should be able to fully utilize the new extended growing season provided by climate change. Nevertheless, this extended growing season might come at a cost in wood quality. As observed in *Chapter 4*, southern provenances had a higher frequency of tree rings with unlignified or abnormally thin cell walls in years with low temperatures.

5.3 Drought adaptations of white spruce populations

The main concern of the effect of climate change in forest ecosystems is the increase in drought stress induced by higher temperatures. In Central Alberta the recent dry periods in the beginning of the 21st century have already caused a reduced growth in white spruce populations (Hogg *et al.* 2017). Planting trees that are better adapted to drier conditions is the main goal of assisted migration. Therefore, one of the goals of this thesis was to find differences in physiological adaptations to drought and hydraulic efficiency between different white spruce provenances. Surprisingly, I did not find any differences in either cavitation resistance, xylem conductivity or other anatomical variables between the different provenances analyzed in *Chapter 2*. Despite this negative result in xylem traits, I cannot confirm that there are no drought adaptation differences in white spruce. Bigras (2005) observed that white spruce begin to close their stomata at tensions that would not result in hydraulic failure according to my results. Although I did not find physiological differences between populations, the precipitation of origin of the provenances was a significant explanatory variable for several other traits measured in this thesis. Provenances from wet origins showed higher mortality, lower growth, and a higher presence of blue rings in the xylem showing a clear maladaptation to the dry climate of Central Alberta. Therefore, drought adaptation in white spruce can be more related to stomatal control than it is to xylem hydraulic characteristics.

5.4 Implications for assisted migration

The results of this thesis can provide important information about the benefits and risks of assisted migration in white spruce. A particularly interesting feature of this study is that it explored provenances from the full range of white spruce, which provides some new information about long-distance seed transfers. The main tradeoff that I was able to detect was between tree height and fall cold hardiness, which clearly followed a latitudinal cline. Planting more productive seed sources from the southern parts of the distribution will come at a cost of lower resistance to early frosts in fall. Even though a late onset of cold hardiness was weakly associated to higher mortality rates, cold hardiness did not appeared to be an important cause of tree death. Nevertheless, planting southern provenances too far north might cause some wood quality problems. Extending the growing season too long into fall might come at a cost of wood quality with lower cell wall thickness and unlignified tracheids in the latewood. These results can be used to limit seed transfer distances, maximizing tree growth without encountering problems due to a mismatch between cold temperatures and tree phenology. My suggestion based on the result of my thesis is that, for a white spruce site located in the Central Alberta, the best provenances based on tree height, survival and cold hardiness come from about 500 km south. This recommendation is substantially higher than previous recommendations of white spruce seed transfers that generally recommended a maximum latitudinal transfer of about 300 km (Li, Beaulieu & Bousquet 1997a; Lu *et al.* 2014a; Gray *et al.* 2016a).

5.5 References

Aitken, S.N. & Hannerz, M. (2001) Genecology and gene resource management strategies for conifer cold hardiness. *Conifer cold hardiness*, pp. 23-53. Springer.

Bigras, F.J. (2005) Photosynthetic response of white spruce families to drought stress. *New Forests,* **29,** 135-148.

Gray, L.K., Hamann, A., John, S., Rweyongeza, D., Barnhardt, L. & Thomas, B.R. (2016) Climate change risk management in tree improvement programs: selection and movement of genotypes. *Tree genetics & genomes,* **12,** 23.

Hamilton, J.A., El Kayal, W., Hart, A.T., Runcie, D.E., Arango-Velez, A. & Cooke, J.E.K. (2016) The joint influence of photoperiod and temperature during growth cessation and development of dormancy in white spruce (Picea glauca). *Tree Physiology,* **36,** 1432-1448.

Hogg, E.H., Michaelian, M., Hook, T.I. & Undershultz, M.E. (2017) Recent climatic drying leads to age-independent growth reductions of white spruce stands in western Canada. *Global Change Biology,* **23,** 5297-5308.

Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. & Chen, T.H.H. (2003) From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany,* **81,** 1247-1266.

Li, P., Beaulieu, J. & Bousquet, J. (1997) Genetic structure and patterns of genetic variation among populations in eastern white spruce (Picea glauca). *Canadian Journal of Forest Research,* **27,** 189-198.

Lu, P., Parker, W.H., Cherry, M., Colombo, S., Parker, W.C., Man, R. & Roubal, N. (2014) Survival and growth patterns of white spruce (Picea glauca [Moench] Voss) rangewide provenances and their implications for climate change adaptation. *Ecology and Evolution,* **4,** 2360-2374.

Rweyyongeza, D.M., Barnhardt, L.K. & Hansen, C. (2011) Patterns of optimal growth for white spruce provenances in Alberta.

Simpson, D.G. (1994) Seasonal and geographic origin effects on cold hardiness of white spruce buds, foliage, and stems. *Canadian Journal of Forest Research,* **24,** 1066-1070.

Way, D.A. & Montgomery, R.A. (2015) Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell & Environment,* **38,** 1725-1736.

Bibliography

Abrahamson, I. (2015) *Picea glauca*, white spruce. *Fire Effects Information System, [Online]*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Aitken, S.N. & Bemmels, J.B. (2016) Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications,* **9,** 271-290.

Aitken, S.N. & Hannerz, M. (2001) Genecology and gene resource management strategies for conifer cold hardiness. *Conifer cold hardiness*, pp. 23-53. Springer.

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications,* **1,** 95-111.

Alam, S.A., Huang, J.-G., Stadt, K.J., Comeau, P.G., Dawson, A., Gea-Izquierdo, G., Aakala, T., Hölttä, T., Vesala, T. & Mäkelä, A. (2017) Effects of competition, drought stress and photosynthetic productivity on the radial growth of white spruce in western Canada. *Frontiers in Plant Science,* **8,** 1915.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D. & Hogg, E.H.T. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management,* **259,** 660-684.

Anderegg, W.R.L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A.F.A., Choat, B. & Jansen, S. (2016) Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences,* **113,** 5024-5029.

Barber, V.A., Juday, G.P. & Finney, B.P. (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature,* **405,** 668-673.

Barnett, T.P., Adam, J.C. & Lettenmaier, D.P. (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature,* **438,** 303-309.

Barton, K. (2018) MuMIn: Multi-Model Inference. R package version 1.42.1.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014) Fitting linear mixed-effects models using *lme4*. *Journal of Statistical Software,* **67,** 1-48.

Beaubien, E.G. & Freeland, H.J. (2000) Spring phenology trends in Alberta, Canada: links to ocean temperature. *International journal of biometeorology,* **44,** 53-59.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F. & Seybold, S.J. (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *Bioscience,* **60,** 602-613.

Bigras, F. (2000) Selection of white spruce families in the context of climate change: heat tolerance. *Tree Physiology,* **20,** 1227-1234.

Bigras, F.J. (2005) Photosynthetic response of white spruce families to drought stress. *New Forests,* **29,** 135-148.

Bigras, F.J., Ryyppö, A., Lindström, A. & Stattin, E. (2001) Cold acclimation and deacclimation of shoots and roots of conifer seedlings. *Conifer cold hardiness* (eds F.J. Bigras & S. Colombo), pp. 57-88. Springer.

Boisvenue, C. & Running, S.W. (2006) Impacts of climate change on natural forest productivity–evidence since the middle of the 20th century. *Global Change Biology,* **12,** 862-882.

Bollhöner, B., Prestele, J. & Tuominen, H. (2012) Xylem cell death: emerging understanding of regulation and function. *Journal of experimental botany,* **63,** 1081-1094.

Bower, A.D., Clair, J.B.S. & Erickson, V. (2014) Generalized provisional seed zones for native plants. *Ecological Applications,* **24,** 913-919.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L. & Belnap, J. (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America,* **102,** 15144-15148.

Burr, K.E., Hawkins, C.D., L'Hirondelle, S.J., Binder, W.D., George, M.F. & Repo, T. (2001) Methods for measuring cold hardiness of conifers. *Conifer cold hardiness* (eds F.J. Bigras & S. Colombo), pp. 369-401. Springer, Netherlands.

Cade, B.S. & Noon, B.R. (2003) A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment,* **1,** 412-420.

Cahill, A.E., Aiello-Lammens, M.E., Caitlin Fisher-Reid, M., Hua, X., Karanewsky, C.J., Ryu, H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B. & Wiens, J.J. (2014) Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. *Journal of Biogeography,* **41,** 429-442.

Cai, J., Li, S., Zhang, H.X., Zhang, S.X. & Tyree, M.T. (2014) Recalcitrant vulnerability curves: methods of analysis and the concept of fibre bridges for enhanced cavitation resistance. *Plant Cell and Environment,* **37,** 35-44.

Canadian Forest Service (2017) The state of Canada's forests. Annual report 2017. (ed. N.R. Canada). Ottawa.

Castagneri, D., Fonti, P., von Arx, G. & Carrer, M. (2017) How does climate influence xylem morphogenesis over the growing season? Insights from long-term intra-ring anatomy in *Picea abies*. *Annals of Botany,* **119,** 1011-1020.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters,* **12,** 351-366.

Chen, L., Huang, J.-G., Stadt, K.J., Comeau, P.G., Zhai, L., Dawson, A. & Alam, S.A. (2017) Drought explains variation in the radial growth of white spruce in western Canada. *Agricultural and Forest Meteorology,* **233,** 133-142.

Chhin, S. & Wang, G.G. (2008) Climatic response of *Picea glauca* seedlings in a forest-prairie ecotone of western Canada. *Annals of forest science,* **65,** 1-8.

Chhin, S., Wang, G.G. & Tardif, J. (2004) Dendroclimatic analysis of white spruce at its southern limit of distribution in the Spruce Woods Provincial Park, Manitoba, Canada. *Tree-Ring Research,* **60,** 31-43.

Chmielewski, F.-M. & Rötzer, T. (2001) Response of tree phenology to climate change across Europe. *Agricultural and Forest Meteorology,* **108,** 101-112.

Corlett, R.T. & Westcott, D.A. (2013a) Will plant movements keep up with climate change? *Trends in ecology & evolution,* **28,** 482-488.

Corlett, R.T. & Westcott, D.A. (2013b) Will plant movements keep up with climate change? *Trends in Ecology and Evolution,* **28,** 482-488.

Cuny, H.E., Rathgeber, C.B.K., Lebourgeois, F., Fortin, M. & Fournier, M. (2012) Life strategies in intra-annual dynamics of wood formation: example of three conifer species in a temperate forest in north-east France. *Tree Physiology,* **32,** 612-625.

D'Orangeville, L., Houle, D., Duchesne, L., Phillips, R.P., Bergeron, Y. & Kneeshaw, D. (2018) Beneficial effects of climate warming on boreal tree growth may be transitory. *Nature communications,* **9,** 3213.

Danby, R.K. & Hik, D.S. (2007) Responses of white spruce (*Picea glauca*) to experimental warming at a subarctic alpine treeline. *Global Change Biology,* **13,** 437-451.

Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science,* **292,** 673-679.

De La Torre, A.R., Wang, T.L., Jaquish, B. & Aitken, S.N. (2014) Adaptation and exogenous selection in a Picea glauca x Picea engelmannii hybrid zone: implications for forest management under climate change. *New Phytologist,* **201,** 687-699.

De Micco, V., Campelo, F., De Luis, M., Bräuning, A., Grabner, M., Battipaglia, G. & Cherubini, P. (2016) Intra-annual density fluctuations in tree rings: how, when, where, and why? *IAWA Journal,* **37,** 232-259.

Dixon, H.H. & Joly, J. (1895) On the ascent of sap. *Philosophical Transactions of the Royal Society of London. B,* **186,** 563-576.

Donaldson, L.A. (2001) Lignification and lignin topochemistry—an ultrastructural view. *Phytochemistry,* **57,** 859-873.

Donaldson, L.A. (2002) Abnormal lignin distribution in wood from severely drought stressed *Pinus radiata* trees. *IAWA Journal,* **23,** 161-178.

Filion, L., Payette, S., Gauthier, L. & Boutin, Y. (1986) Light rings in subarctic conifers as a dendrochronological tool. *Quaternary Research,* **26,** 272-279.

Flannigan, M.D., Stocks, B.J. & Wotton, B.M. (2000) Climate change and forest fires. *Science of the total environment,* **262,** 221-229.

Fritts, H. (1976) *Tree rings and climate*. Academic Press, London, UK.

Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015) Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution,* **30,** 169-176.

Gärtner, H., Lucchinetti, S. & Schweingruber, F.H. (2014) New perspectives for wood anatomical analysis in dendrosciences: the GSL1-microtome. *Dendrochronologia,* **32,** 47-51.

Gärtner, H. & Schweingruber, F.H. (2013) *Microscopic preparation techniques for plant stem analysis*. Verlag Dr. Kessel, Remagen, Germany.

Gleason, S.M., Westoby, M., Jansen, S., Choat, B., Hacke, U.G., Pratt, R.B., Bhaskar, R., Brodribb, T.J., Bucci, S.J. & Cao, K.F. (2016a) Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist,* **209,** 123-136.

Gleason, S.M., Westoby, M., Jansen, S., Choat, B., Hacke, U.G., Pratt, R.B., Bhaskar, R., Brodribb, T.J., Bucci, S.J., Cao, K.F., Cochard, H., Delzon, S., Domec, J.C., Fan, Z.X., Feild, T.S., Jacobsen, A.L., Johnson, D.M., Lens, F., Maherali, H., Martinez-Vilalta, J., Mayr, S., McCulloh, K.A., Mencuccini, M., Mitchell, P.J., Morris, H., Nardini, A., Pittermann, J., Plavcova, L., Schreiber, S.G., Sperry, J.S., Wright, I.J. & Zanne, A.E. (2016b) Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist,* **209,** 123-136.

Glerum, C. & Farrar, J.L. (1966) Frost ring formation in the stems of some coniferous species. *Canadian Journal of Botany,* **44,** 879-886.

Goslee, S.C. & Urban, D.L. (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software,* **22,** 1-19.

Gray, L.K. & Hamann, A. (2011) Strategies for reforestation under uncertain future climates: guidelines for Alberta, Canada. *PLoS One,* **6,** e22977.

Gray, L.K. & Hamann, A. (2013) Tracking suitable habitat for tree populations under climate change in western North America. *Climatic Change,* **117,** 289-303.

Gray, L.K., Hamann, A., John, S., Rweyongeza, D., Barnhardt, L. & Thomas, B.R. (2016a) Climate change risk management in tree improvement programs: selection and movement of genotypes. *Tree genetics & genomes,* **12,** 23.

Gray, L.K., Hamann, A., John, S., Rweyongeza, D., Barnhardt, L. & Thomas, B.R. (2016b) Climate change risk management in tree improvement programs: selection and movement of genotypes. *Tree Genetics & Genomes,* **12,** 1-12.

Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C.D., Fensham, R., Laughlin, D.C., Kattge, J. & Bönisch, G. (2017) Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters,* **20,** 539-553.

Gričar, J., Čufar, K., Oven, P. & Schmitt, U. (2005) Differentiation of terminal latewood tracheids in silver fir trees during autumn. *Annals of Botany,* **95,** 959-965.

Gu, L., Hanson, P.J., Post, W.M., Kaiser, D.P., Yang, B., Nemani, R., Pallardy, S.G. & Meyers, T. (2008) The 2007 eastern US spring freeze: increased cold damage in a warming world? *AIBS Bulletin,* **58,** 253-262.

Hacke, U.G. & Jansen, S. (2009) Embolism resistance of three boreal conifer species varies with pit structure. *New Phytologist,* **182,** 675-686.

Hacke, U.G., Lachenbruch, B., Pittermann, J., Mayr, S., Domec, J.-C. & Schulte, P.J. (2015) The hydraulic architecture of conifers. *Functional and ecological xylem anatomy* (ed. U. Hacke), pp. 39-75. Springer.

Hacke, U.G. & Sperry, J.S. (2001) Functional and ecological xylem anatomy. *Perspectives in Plant Ecology, Evolution and Systematics,* **4,** 97-115.

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloch, K.A. (2001a) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia,* **126,** 457-461.

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloh, K.A. (2001b) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia,* **126,** 457-461.

Hamilton, J.A., El Kayal, W., Hart, A.T., Runcie, D.E., Arango-Velez, A. & Cooke, J.E.K. (2016) The joint influence of photoperiod and temperature during growth cessation and development of dormancy in white spruce (*Picea glauca*). *Tree Physiology,* **36,** 1432-1448.

Hänninen, H., Häkkinen, R., Hari, P. & Koski, V. (1990) Timing of growth cessation in relation to climatic adaptation of northern woody plants. *Tree Physiology,* **6,** 29-39.

Hlasny, T., Kristek, S., Holusa, J., Trombik, J. & Urbancova, N. (2011) Snow disturbances in secondary Norway spruce forests in Central Europe: Regression modeling and its implications for forest management. *Forest Ecology and Management,* **262,** 2151-2161.

Hogg, E., Barr, A. & Black, T. (2013) A simple soil moisture index for representing multi-year drought impacts on aspen productivity in the western Canadian interior. *Agricultural and Forest Meteorology,* **178,** 173-182.

Hogg, E.H., Michaelian, M., Hook, T.I. & Undershultz, M.E. (2017) Recent climatic drying leads to age-independent growth reductions of white spruce stands in western Canada. *Global Change Biology,* **23,** 5297-5308.

Holst, M. (1962a) Seed selection and tree breeding in Canada. Department of Forestry, Ottawa, Canada.

Holst, M. (1962b) Seed selection and tree breeding in Canada. Department of Forestry, Ottawa, Canada.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometrical journal,* **50,** 346-363.

Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. & Chen, T.H.H. (2003a) From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany,* **81,** 1247-1266.

Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C. & Chen, T.H.H. (2003b) From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany-Revue Canadienne De Botanique,* **81,** 1247-1266.

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the

Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Jackson, S.D. (2009) Plant responses to photoperiod. *New Phytologist,* **181,** 517-531.

Jiang, X., Huang, J.-G., Stadt, K.J., Comeau, P.G. & Chen, H.Y.H. (2016a) Spatial climate-dependent growth response of boreal mixedwood forest in western Canada. *Global and Planetary Change,* **139,** 141-150.

Jiang, X.Y., Huang, J.G., Stadt, K.J., Comeau, P.G. & Chen, H.Y.H. (2016b) Spatial climate-dependent growth response of boreal mixedwood forest in western Canada. *Global and Planetary Change,* **139,** 141-150.

Jyske, T., Mäkinen, H., Kalliokoski, T. & Nöjd, P. (2014) Intra-annual tracheid production of Norway spruce and Scots pine across a latitudinal gradient in Finland. *Agricultural and Forest Meteorology,* **194,** 241-254.

Koenker, R. (2013) quantreg: Quantile Regression. R package version 5.05. *R Foundation for Statistical Computing: Vienna*.

Lambers, H. & Poorter, H. (1992) Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in ecological research,* **23,** 187-261.

Langlet, O. (1971) Two hundred years genecology. *Taxon***,** 653-721.

Lenth, R.V. (2016a) Least-squares means: the R package lsmeans. *Journal of Stattistical Software,* **69,** 1-33.

Lenth, R.V. (2016b) Least-squares means: the R package *lsmeans*. *Journal of Statistical Software,* **69,** 1-33.

Lesser, M.R. & Parker, W.H. (2004a) Genetic variation in *Picea glauca* for growth and phenological traits from provenance tests in Ontario. *Silvae Genetica,* **53,** 141-148.

Lesser, M.R. & Parker, W.H. (2004b) Genetic variation in Picea glauca for growth and phenological traits from provenance tests in Ontario. *Silvae Genetica,* **53,** 141-148.

Levitt, J. (1980) Responses of plants to environmental stress. *Chilling, freezing, and high temperature stresses*. Academic Press.

Li, P., Beaulieu, J. & Bousquet, J. (1997a) Genetic structure and patterns of genetic variation among populations in eastern white spruce (*Picea glauca*). *Canadian Journal of Forest Research,* **27,** 189-198.

Li, P., Beaulieu, J. & Bousquet, J. (1997b) Genetic structure and patterns of genetic variation among populations in eastern white spruce (Picea glauca). *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* **27,** 189-198.

Li, P., Beaulieu, J., Corriveau, A. & Bousquet, J. (1993) Genetic variation in juvenile growth and phenology of white spruce provenance-progeny test. *Silvae Genetica,* **42,** 52-60.

Liepe, K.J., Hamann, A., Smets, P., Fitzpatrick, C.R. & Aitken, S.N. (2016) Adaptation of lodgepole pine and interior spruce to climate: implications for reforestation in a warming world. *Evolutionary Applications,* **9,** 409-419.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P. & Kolström, M. (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management,* **259,** 698-709.

Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J. & Valladares, F. (2012) Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology,* **18,** 797-805.

Lloyd, A.H. & Fastie, C.L. (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change,* **52,** 481-509.

Loehle, C. (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography,* **25,** 735-742.

Lopez, R., Cano, F.J., Choat, B., Cochard, H. & Gil, L. (2016) Plasticity in Vulnerability to Cavitation of Pinus canariensis Occurs Only at the Driest End of an Aridity Gradient. *Frontiers in Plant Science,* **7**.

Lu, P. & Man, R. (2011) Assessment of assisted migration effects on spring bud flush in white spruce (*Picea glauca* [Moench] Voss) seedlings. *The Forestry Chronicle,* **87,** 391-397.

Lu, P., Parker, W.H., Cherry, M., Colombo, S., Parker, W.C., Man, R. & Roubal, N. (2014a) Survival and growth patterns of white spruce (*Picea glauca* [Moench] Voss) rangewide provenances and their implications for climate change adaptation. *Ecology and Evolution,* **4,** 2360-2374.

Lu, P.X., Parker, W.H., Cherry, M., Colombo, S., Parker, W.C., Man, R.Z. & Roubal, N. (2014b) Survival and growth patterns of white spruce (Picea glauca Moench Voss) rangewide provenances and their implications for climate change adaptation. *Ecology and Evolution,* **4,** 2360-2374.

Luedeling, E., Girvetz, E.H., Semenov, M.A. & Brown, P.H. (2011) Climate change affects winter chill for temperate fruit and nut trees. *PLoS One,* **6,** e20155.

MacDonald, G.M., Szeicz, J.M., Claricoates, J. & Dale, K.A. (1998) Response of the central Canadian treeline to recent climatic changes. *Annals of the Association of American Geographers,* **88,** 183-208.

Man, R., Kayahara, G.J., Dang, Q.-L. & Rice, J.A. (2009a) A case of severe frost damage prior to budbreak in young conifers in Northeastern Ontario: Consequence of climate change? *The Forestry Chronicle,* **85,** 453-462.

Man, R. & Lieffers, V.J. (1997) Seasonal variations of photosynthetic capacities of white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*) saplings. *Canadian Journal of Botany,* **75,** 1766-1771.

Man, R.Z., Kayahara, G.J., Dang, Q.L. & Rice, J.A. (2009b) A case of severe frost damage prior to budbreak in young conifers in Northeastern Ontario: Consequence of climate change? *Forestry Chronicle,* **85,** 453-462.

Marion, L., Gričar, J. & Oven, P. (2007) Wood formation in urban Norway maple trees studied by the micro-coring method. *Dendrochronologia,* **25,** 97-102.

Martínez-Vilalta, J., Cochard, H., Mencuccini, M., Sterck, F., Herrero, A., Korhonen, J., Llorens, P., Nikinmaa, E., Nole, A. & Poyatos, R. (2009) Hydraulic adjustment of Scots pine across Europe. *New Phytologist,* **184,** 353-364.

Matyas, C. (1996) Climatic adaptation of trees: rediscovering provenance tests. *Euphytica,* **92,** 45-54.

Mátyás, C. (1994) Modeling climate change effects with provenance test data. *Tree Physiology,* **14,** 797-804.

Mayr, S., Hacke, U., Schmid, P., Schwienbacher, F. & Gruber, A. (2006) Frost drought in conifers at the alpine timberline: Xylem dysfunction and adaptations. *Ecology,* **87,** 3175-3185.

Mbogga, M.S., Hamann, A. & Wang, T. (2009) Historical and projected climate data for natural resource management in western Canada. *Agricultural and Forest Meteorology,* **149,** 881-890.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A. & Williams, D.G. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist,* **178,** 719-739.

McKenney, D., Pedlar, J. & O'Neill, G. (2009) Climate change and forest seed zones: Past trends, future prospects and challenges to ponder. *The Forestry Chronicle,* **85,** 258-266.

McKenney, D.W., Pedlar, J.H., Lawrence, K., Campbell, K. & Hutchinson, M.F. (2007) Beyond traditional hardiness zones: using climate envelopes to map plant range limits. *Bioscience,* **57,** 929-937.

McLachlan, J.S., Hellmann, J.J. & Schwartz, M.W. (2007) A framework for debate of assisted migration in an era of climate change. *Conservation Biology,* **21,** 297-302.

McLane, S.C., Daniels, L.D. & Aitken, S.N. (2011) Climate impacts on lodgepole pine (*Pinus contorta*) radial growth in a provenance experiment. *Forest Ecology and Management,* **262,** 115-123.

Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A. & Woodruff, D.R. (2009) Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. *Functional Ecology,* **23,** 922-930.

Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B., Vorosmarty, C.J. & Schloss, A.L. (1993) Global climate change and terrestrial net primary production. *Nature,* **363,** 234.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O.g. & Briede, A. (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology,* **12,** 1969-1976.

Michaelian, M., Hogg, E.H., Hall, R.J. & Arsenault, E. (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology,* **17,** 2084-2094.

Millar, C.I., Stephenson, N.L. & Stephens, S.L. (2007) Climate change and forests of the future: managing in the face of uncertainty. *Ecological applications,* **17,** 2145-2151.

Montwé, D., Isaac-Renton, M., Hamann, A. & Spiecker, H. (2018) Cold adaptation recorded in tree rings highlights risks associated with climate change and assisted migration. *Nature communications,* **9,** 1574.

Montwé, D., Isaac-Renton, M., Hamann, A. & Spiecker, H. (2016) Drought tolerance and growth in populations of a wide-ranging tree species indicate climate change risks for the boreal north. *Global Change Biology,* **22,** 806-815.

Morgenstern, M. (1996) *Geographic variation in forest trees: genetic basis and application of knowledge in silviculture*. UBC press, Vancouver, Canada.

Moura, J.C.M.S., Bonine, C.A.V., de Oliveira Fernandes Viana, J., Dornelas, M.C. & Mazzafera, P. (2010) Abiotic and biotic stresses and changes in the lignin content and composition in plants. *Journal of integrative plant biology,* **52,** 360-376.

Nienstaedt, H. (1966) Dormancy and dormancy release in white spruce. *Forest Science,* **12,** 374-384.

Nienstaedt, H. & Zasada, J.C. (1990) White spruce. *Silvics of North America*, pp. 389-442.

Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P. & Ceulemans, R. (2005) Forest response to elevated CO2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences,* **102,** 18052-18056.

Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E. & McMurtrie, R.E. (2010) CO2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences,* **107,** 19368-19373.

O'Neill, G.A., Stoehr, M. & Jaquish, B. (2014) Quantifying safe seed transfer distance and impacts of tree breeding on adaptation. *Forest Ecology and Management,* **328,** 122-130.

Palta, J.P. (1990) Stress interactions at the cellular and membrane levels. *HortScience,* **25,** 1377-1381.

Pammenter, N.W. & Vander Willigen, C. (1998) A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiology,* **18,** 589-593.

Pammenter, N.W.v. & Van der Willigen, C. (1998) A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiology,* **18,** 589-593.

Pedlar, J.H., McKenney, D.W., Aubin, I., Beardmore, T., Beaulieu, J., Iverson, L., O'Neill, G.A., Winder, R.S. & Ste-Marie, C. (2012) Placing forestry in the assisted migration debate. *Bioscience,* **62,** 835-842.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X. & Zhou, X. (2011) A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change,* **1,** 467.

Piermattei, A., Crivellaro, A., Carrer, M. & Urbinati, C. (2015) The “blue ring”: anatomy and formation hypothesis of a new tree-ring anomaly in conifers. *Trees,* **29,** 613-620.

Pittermann, J., Sperry, J.S., Hacke, U.G., Wheeler, J.K. & Sikkema, E.H. (2006) Inter-tracheid pitting and the hydraulic efficiency of conifer wood: the role of tracheid allometry and cavitation protection. *American Journal of Botany,* **93,** 1265-1273.

Plomion, C., Leprovost, G. & Stokes, A. (2001) Wood formation in trees. *Plant Physiology,* **127,** 1513-1523.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist,* **182,** 565-588.

Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R.A., Hogg, E.H., Girardin, M.P., Lakusta, T., Johnston, M. & McKenney, D.W. (2013) Anticipating the consequences of climate change for Canada's boreal forest ecosystems. *Environmental Reviews,* **21,** 322-365.

Prud'homme, G.O., Lamhamedi, M.S., Benomar, L., Rainville, A., DeBlois, J., Bousquet, J. & Beaulieu, J. (2017) Ecophysiology and growth of white spruce seedlings from various seed sources along a climatic gradient support the need for assisted migration. *Frontiers in Plant Science,* **8,** 2214.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rigling, A., Waldner, P.O., Forster, T., Bräker, O.U. & Pouttu, A. (2001) Ecological interpretation of tree-ring width and intraannual density fluctuations in *Pinus sylvestris* on dry sites in the central Alps and Siberia. *Canadian Journal of Forest Research,* **31,** 18-31.

Rosner, S., Klein, A., Müller, U. & Karlsson, B. (2007) Hydraulic and mechanical properties of young Norway spruce clones related to growth and wood structure. *Tree Physiology,* **27,** 1165-1178.

Rosner, S., Svetlik, J., Andreassen, K., Borja, I., Dalsgaard, L., Evans, R., Karlsson, B., Tollefsrud, M.M. & Solberg, S. (2014) Wood density as a screening trait for drought sensitivity in Norway spruce. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* **44,** 154-161.

Rossi, S., Morin, H. & Deslauriers, A. (2011) Multi-scale influence of snowmelt on xylogenesis of black spruce. *Arctic, Antarctic, and Alpine Research,* **43,** 457-464.

Rossi, S., Morin, H., Deslauriers, A. & Plourde, P.Y. (2011) Predicting xylem phenology in black spruce under climate warming. *Global Change Biology,* **17,** 614-625.

Rweyongeza, D., Yang, R.-C., Dhir, N., Barnhardt, L. & Hansen, C. (2007a) Genetic variation and climatic impacts on survival and growth of white spruce in Alberta, Canada. *Silvae Genetica,* **56,** 117-127.

Rweyongeza, D.M., Yang, R.C., Dhir, N.K., Barnhardt, L.K. & Hansen, C. (2007b) Genetic variation and climatic impacts on survival and growth of white spruce in Alberta, Canada. *Silvae Genetica,* **56,** 117-127.

Rweyyongeza, D.M., Barnhardt, L.K. & Hansen, C. (2011a) Patterns of optimal growth for white spruce provenances in Alberta. Alberta Tree Improvement & Seed Centre, Government of Alberta, Alberta, Canada.

Rweyyongeza, D.M., Barnhardt, L.K. & Hansen, C. (2011b) Patterns of optimal growth for white spruce provenances in Alberta.

Sakai, A. & Larcher, W. (1987) *Frost survival of plants: responses and adaptation to freezing stress*. Springer-Verlag Berlin Heidelberg.

Sakai, A. & Sugawara, Y. (1973) Survival of poplar callus at super-low temperatures after cold acclimation. *Plant and cell physiology,* **14,** 1201-1204.

Saxe, H., Cannell, M.G., Johnsen, Ø., Ryan, M.G. & Vourlitis, G. (2001) Tree and forest functioning in response to global warming. *New Phytologist,* **149,** 369-399.

Schweingruber, F. H., Börner, A., & Schulze, E. D. (2006). Atlas of Woody Plant Stems: Evolution. *Structure, and Environmental Modifications.* Springer, Berlin

Schoonmaker, A.L., Hacke, U.G., Landhausser, S.M., Lieffers, V.J. & Tyree, M.T. (2010) Hydraulic acclimation to shading in boreal conifers of varying shade tolerance. *Plant Cell and Environment,* **33,** 382-393.

Schreiber, S.G., Hamann, A., Hacke, U.G. & Thomas, B.R. (2013) Sixteen years of winter stress: an assessment of cold hardiness, growth performance and survival of hybrid poplar clones at a boreal planting site. *Plant, Cell & Environment,* **36,** 419-428.

Sebastian-Azcona, J., Hamann, A., Hacke, U.G. & Rweyongeza, D. (2018) Survival, growth and cold hardiness tradeoffs in white spruce populations: Implications for assisted migration. *Forest Ecology and Management*.

Sebastian-Azcona, J., Hacke, U.G. & Hamann, A. (2018) Adaptations of white spruce to climate: strong intraspecific differences in cold hardiness linked to survival. *Ecology and Evolution,* **8,** 1758-1768.

Simpson, D.G. (1994) Seasonal and geographic origin effects on cold hardiness of white spruce buds, foliage, and stems. *Canadian Journal of Forest Research,* **24,** 1066-1070.

Spatz, H.C. & Bruechert, F. (2000) Basic biomechanics of self-supporting plants: wind loads and gravitational loads on a Norway spruce tree. *Forest Ecology and Management,* **135,** 33-44.

Sperry, J.S., Donnelly, J.R. & Tyree, M.T. (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment,* **11,** 35-40.

Sperry, J.S., Hacke, U.G. & Pittermann, J. (2006) Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany,* **93,** 1490-1500.

Sperry, J.S. & Tyree, M.T. (1988) Mechanism of water stress-induced xylem embolism. *Plant Physiology,* **88,** 581-587.

Sutinen, M.-L., Arora, R., Wisniewski, M., Ashworth, E., Strimbeck, R. & Palta, J. (2001) Mechanisms of frost survival and freeze-damage in nature. *Conifer cold hardiness* (eds F.J. Bigras & S.J. Colombo), pp. 89-120. Springer.

Swidrak, I., Gruber, A., Kofler, W. & Oberhuber, W. (2011) Effects of environmental conditions on onset of xylem growth in *Pinus sylvestris* under drought. *Tree Physiology,* **31,** 483-493.

Taeger, S., Zang, C., Liesebach, M., Schneck, V. & Menzel, A. (2013) Impact of climate and drought events on the growth of Scots pine (*Pinus sylvestris* L.) provenances. *Forest Ecology and Management,* **307,** 30-42.

Thornton, P.K., Ericksen, P.J., Herrero, M. & Challinor, A.J. (2014) Climate variability and vulnerability to climate change: a review. *Global Change Biology,* **20,** 3313-3328.

Tyree, M.T. & Zimmermann, M.H. (2002) Xylem structure and the ascent of sap. *Xylem structure and the ascent of sap*, pp. i. Springer-Verlag New York Inc., 175 Fifth Avenue, New York, NY, 10010-7858, USA; Springer-Verlag GmbH & Co. KG, Heidelberger Platz 3, D-14197, Berlin, Germany.

Wang, L., Payette, S. & Bégin, Y. (2000) A quantitative definition of light rings in black spruce (*Picea mariana*) at the arctic treeline in northern Québec, Canada. *Arctic, Antarctic, and Alpine Research,* **32,** 324-330.

Wang, T., Hamann, A., Spittlehouse, D. & Carroll, C. (2016) Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One,* **11,** e0156720.

Wang, Y., Hogg, E.H., Price, D.T., Edwards, J. & Williamson, T. (2014) Past and projected future changes in moisture conditions in the Canadian boreal forest. *The Forestry Chronicle,* **90,** 678-691.

Way, D.A. & Montgomery, R.A. (2015) Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell & Environment,* **38,** 1725-1736.

White, T.L., Adams, W.T. & Neale, D.B. (2007) *Forest genetics*. Cabi.

Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R. & Grissino-Mayer, H.D. (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change,* **3,** 292.

Wood, S.N. (2017) *Generalized additive models: an introduction with R*. CRC press.

Woodward, F.I. (1990) The impact of low temperatures in controlling the geographical distribution of plants. *Philosophical Transactions of the Royal Society of London B,* **326,** 585-593.

Worrall, J.J., Rehfeldt, G.E., Hamann, A., Hogg, E.H., Marchetti, S.B., Michaelian, M. & Gray, L.K. (2013) Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology and Management,* **299,** 35-51.

Ying, C.C. & Yanchuk, A.D. (2006) The development of British Columbia's tree seed transfer guidelines: purpose, concept, methodology, and implementation. *Forest Ecology and Management,* **227,** 1-13.

Zhu, K., Woodall, C.W. & Clark, J.S. (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology,* **18,** 1042-1052.

Zohner, C.M., Benito, B.M., Svenning, J.-C. & Renner, S.S. (2016) Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change,* **6,** 1120.

Zwiazek, J.J., Renault, S., Croser, C., Hansen, J. & Beck, E. (2001) Biochemical and biophysical changes in relation to cold hardiness. *Conifer cold hardiness*, pp. 165-186. Springer.