

**Adaptation of white spruce to climatic risk environments in spring:
implications for management under climate change**

by
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Abstract

The timing of spring dormancy release and bud break in trees is an adaptive trait with potentially important management implications. Depending on how spring phenology is controlled, climate warming may disrupt the synchronization of bud break with the available growing season. Further, addressing climate change through human assisted migration in reforestation programs could cause additional problems if phenology triggers of source and target locations differ. Here, I assess how phenology is controlled by heat sum and chilling requirements for a widespread and commercially important boreal tree species, white spruce (*Picea glauca*) in a range-wide common garden experiment. I find significant genetic population differentiation in heat sum requirements ranging from 390 to 450 degree days among regions (± 12 average SE), and from 375 to 500 (± 16) degree days among populations within regions. The most northern populations showed the lowest heat sum requirements, which could be explained by frost avoidance or growth optimization strategies. My data favors a frost avoidance hypothesis, although the explanations are not mutually exclusive. Chilling requirements in white spruce were also found (approx. 15 degree days), but they showed no geographic population differentiation. Due to generally low chilling requirements, I do not anticipate de-synchronization of spring phenology with the growing season under climate warming in spruce. Synthesizing results from this study and other research on additional growth and adaptive traits, I conclude that assisted migration northward, compensating for approximately 2° C warming, is safe and yields higher growth rates for white spruce.

Preface

A version of this thesis has been submitted for publication as “Casmey, M., Hamann, A., Hacke U.G. 2022. Adaptation of white spruce to climatic risk environments in spring” to the journal *Forest Ecology and Management*. The study was conceived and designed by myself, AH, and UH. I performed the data collection with input from AH and UH. I conducted analysis with input from AH. I wrote the first draft of the paper with editing contributions from AH and UG to the final manuscript.

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1. Introduction

The fitness of plants is in part shaped by the compatibility of its growth and adaptive traits with local climate environments. Phenology traits are a particularly important set of population-level characteristics that synchronize plant growth with the available growing season (Chuine & Beaubien, 2001, Muffler *et al.*, 2016). Phenology times the transitions between active and dormant states that enable plants to avoid frost, take full advantage of the available growing season, and time reproduction appropriately (Chuine, 2010, Hänninen & Tanino, 2011, Lenz *et al.*, 2013). The optimal time to initiate growth in spring depends on the probability of late spring frost, given a certain amount of warming in spring (Alberto *et al.*, 2011, Lenz *et al.*, 2016), but it also depends on the need of the plant to utilize the early part of the growing season, which is essential for understory plants and mid-successional species with moderate shade tolerance such as white spruce (Richardson & O’Keefe, 2009) or if the growing season is generally short in cold regions (Dantec *et al.*, 2015, Morin *et al.*, 2007).

In temperate and boreal plant species, the timing of spring phenology is primarily controlled by temperature via genetically determined chilling and heat sum requirements (Morgenstern, 1996). A chilling requirement is a cumulative amount of chilling temperatures (experimentally measured as degree days or degree hours between 0 and 5°C) that are required before the subsequent heat sum accumulation in spring can start. The chilling requirement prevents premature dormancy release during unusually warm fall and winter conditions. Therefore, unfulfilled chilling requirements delay the timing of spring growth (Fu *et al.*, 2015, Laube *et al.*, 2014, Nanninga *et al.*, 2017). Once chilling requirements are met, then dormancy release is advanced by an accumulation of temperature (experimentally measured as growing degree days

above a threshold of 0 to 5°C). Once a specific heat sum requirement is fulfilled, apical growth begins (Hänninen & Tanino, 2011, Körner, 2006).

Because heat sum requirements track accumulated temperature in spring, the dormancy release and bud break in spring are highly plastic traits, meaning growth begins earlier during warmer springs and later in colder springs (Gričar *et al.*, 2014, Ladwig *et al.*, 2019). Warming temperatures due to climate change are therefore expected to result in earlier spring phenology across species and regions, and this has generally been found through long-term phenology observations by citizen science networks, records related to agriculture, and more recently through remote sensing (Chen *et al.*, 2019, Jeong *et al.*, 2011, Menzel *et al.*, 2001). While advances in bud break under climate warming may be unproblematic, higher climate variability can nevertheless increase the probability of frost damage for a given spring heat sum requirement (Augspurger, 2013, Beaubien & Hamann, 2011, Zohner *et al.*, 2020a) and can exacerbate dieback and mortality together with other stress factors (Kharuk *et al.*, 2015, Vanoni *et al.*, 2016, Wolken *et al.*, 2009). Under certain conditions, climate warming can also have an opposite effect on spring phenology, resulting in delayed bud break. This phenomenon may occur if plants have high chilling requirements that are no longer fulfilled under climate warming. In that case, the beginning of heat-sum accumulation is delayed, leading to a later date of dormancy release despite sufficient forcing conditions in spring (Chen *et al.*, 2019, Fu *et al.*, 2015, Heide, 2003).

Optimal adaptation to spring risk environments under and future climate will therefore depend on the mechanisms that govern trade-offs between avoiding frost risk in spring and fully utilising the growing season (Duputié *et al.*, 2015). High-elevation and boreal tree species often exhibit

lower heat sum requirements in the coldest environments to take maximum advantage of a short growing season (Ford *et al.*, 2016, Nienstaedt, 1967, Olson *et al.*, 2013). However, an early bud break, with higher frost risks, to take advantage of a short growing season, may not be advantageous under climate warming where growing season length may not remain a critical limiting factor. Further, population-level differentiations in chilling requirements can interact with climate warming as well. In a study with boreal populations of *Populus balsamifera*, Thibault *et al.* (2020) showed that southern populations had higher chilling requirements than northern populations, potentially leading to substantially delayed bud break in southern populations under climate warming.

Trade-off mechanisms between frost avoidance and utilizing the full length of the growing season also have implications for forest management under climate change (Cooper *et al.*, 2019, Corlett & Westcott, 2013). Synchronized timing of bud break is particularly important for undersory species that have a narrow window of sunlight to capitalize on before the overstory canopy develops (Richardson & O’Keefe, 2009). Assisted migration of southern populations northward to track changing climate can increase productivity (Etterson *et al.*, 2020, Schreiber *et al.*, 2013), but this benefit may come at the risk of frost damage, due to an onset of cold hardiness in fall that is too late (Montwé *et al.*, 2018, Sebastian-Azcona *et al.*, 2019).

Determining optimal assisted migration distances and matching source populations and target planting regions correctly, requires information on how spring phenology is controlled (Grady *et al.*, 2015).

Here, I contribute a quantitative assessment of heat sum and chilling requirements for a range-wide sample of populations of white spruce (*Picea glauca* [Moench] Voss), a widespread and commercially important boreal tree species. I use a mature common garden experiment that allows repeated sampling of genotypes from throughout the range of the species to conduct a series of forcing experiments to quantify phenology parameters. My objectives are to (1) detect if white spruce has genetic population differentiation in heat sum and chilling requirements throughout its range; (2) understand potential genetic differentiation of local populations as evolutionary adaptation to local spring risk environments; and (3) infer likely impacts of climate change on synchronization of populations with the growing season, with implications for reforestation management of the species under climate change.

2. Literature review

2.1. Geographic variation in phenology

As early as 1739, Linnaeus first made note of earlier timing of growth of foreign tobacco as opposed to local sources leading to increased hazards from early spring frosts (Langlet, 1971). Since these initial observations of genetic variation in phenology, ecologists have sought to understand spatial patterns of local adaptation in the spring phenology of plants. Similar to Linnaeus's observations on tobacco seeds from different locations growing at different times, researchers have used provenance trials of various species to study this trait. In provenance trials, seeds taken from different populations are planted at a single site, or series of sites, to investigate population level differentiation. As all trees at a provenance trial experience the same environmental conditions, researchers can conclude that observed differences in any trait are due to genetic differentiation. For the spring phenology of northern trees, researchers have to

consider possible genetic differentiation in heat sum requirements and chilling requirements. Decades of results from experiments using these provenance trials have revealed consistent geographic trends in spring phenology of populations (Alberto *et al.*, 2013, Langlet, 1971).

Variation in heat sum requirements is thought to be the result of benefits to evolutionary fitness from differentiation in the timing of budbreak (See (Alberto *et al.*, 2013)). Heat requirements are an internal mechanism that control the exact timing of growth initiation in spring. It is widely theorized that the optimal timing of spring growth depends on a trade-off between evolutionary pressure to avoid frost damage and a pressure to take advantage of the growing season (Leinonen & Hänninen, 2002). In areas with a short growing season there is evolutionary pressure for plants to initiate growth earlier in the spring so they can complete necessary growth and reproductive processes (Chuine, 2010, Chuine & Beaubien, 2001). Therefore in areas with a short growing season, this theory would anticipate plants would have low heat sum requirements that would cause them to grow earlier in the spring. In contrast, for populations in areas with a long growing season sufficient for essential life processes, there is evolutionary pressure for budbreak to be later in the season to avoid damage to new growth from spring frosts. Results from provenance trial experiments generally support this theory. Populations from higher latitudes, high elevations, and continental regions generally have lower heat sum requirements which causes them to initiate growth earlier in provenance trials than populations from lower latitudes, low elevation, and maritime regions (Ford *et al.*, 2016, Guo *et al.*, 2021, Johnsen *et al.*, 1996, Lenz *et al.*, 2016, Nienstaedt, 1967, Olson *et al.*, 2013). This spatial variation correlates well with the length of the growing season and frost conditions. Freezing temperatures persist later in the spring and fall begins earlier at higher latitudes and elevations which shortens the

amount of the year favorable to plant growth. Maritime regions also have longer growing seasons than areas further inland due to the moderating influence of oceans (Oliver, 2005).

Variation in chilling requirements is less common, but has been observed in some species (Cannell & Smith, 1983, Leinonen, 1996, Thibault *et al.*, 2020). In temperate and boreal locations, plants have chilling requirements to prevent precocious budbreak during unseasonably warm periods (characterized by temperatures above 5°C) during the late fall and winter. Plants with chilling requirements require a set amount of time at chilling temperatures (usually assumed to be temperatures between 0°C and 5°C) before they end deep winter dormancy and begin to track heat sum requirements. It is expected there is pressure for chilling requirements to be longer in locations with regular mid-winter temperature fluctuations. Maritime and lower latitude climates are characterized by these mild winter conditions and tree populations here are expected to have higher chilling requirements than interior populations (Cannell & Smith, 1983). Southern populations of *Populus balsamifera* and maritime populations of *Picea abies* and *Pinus sylvestris* have higher chilling requirements than northern and interior populations respectively (Hannerz *et al.*, 2003, Leinonen, 1996, Thibault *et al.*, 2020).

2.2. Implications of climate change effects on phenology for management

As the mechanisms that determine phenology of spring growth, heat sum requirements and chilling requirements, are relatively genetically fixed and are dependent on temperature they will be affected by climate change. Some have speculated the effects of climate change could be beneficial for forest managers. Earlier initiation of spring growth due to warming temperatures in recent decades has been demonstrated with centuries of phenology observations (Bradley *et al.*,

1999, Menzel *et al.*, 2001, Primack *et al.*, 2009). For forest managers, an earlier start to season could be positive as this would, in theory, lengthen the growing season and lead to gains in forest productivity (Leinonen & Kramer, 2002). Results from provenance trials confirm that when transplanted to the south, where they experience warmer temperatures as under climate change, northern populations grow earlier than local populations (Chmura & Rozkowski, 2002, Li *et al.*, 2010a). However, whether this advance in phenology causes significant increases in growth remains unclear. Instead of the timing of spring phenology, the rate of growth (Wang *et al.*, 2003) and synchronization with population level adaptation to local environmental conditions (Thomson & Parker, 2008, Thomson *et al.*, 2009) are more correlated with population-level productivity. As a result, predictive models based population-level adaptation to local environmental conditions often predict declines in productivity under future climatic conditions (O'Neill & Nigh, 2011, Wang *et al.*, 2006). Thus despite advancing phenology due to warming spring conditions, the lengthening of the growing season is unlikely to translate to larger yields from harvested forests.

Reduced in productivity and survival due to other changes aspects to climate change ,such as drought (Breshears *et al.*, 2005, Montwé *et al.*, 2016), have caused many researchers to propose assisted migration as a strategy to mitigate the effects of climate change while maintaining productivity of planted trees by moving populations to track climatic conditions (Pedlar *et al.*, 2012, Thomas Ledig & Kitzmiller, 1992, Williams & Dumroese, 2013). For the purposes of this thesis, I consider assisted migration as the movement of populations within the range of the species to improve population survival, which has also been called assisted population migration by Williams and Dumroese (2013). This form of assisted migration would involve the

identifying seed sources with adaptations optimal to future expected climatic conditions (e.g., identify drought tolerant seed sources for regions expected to experience decreased rainfall). Provenance trials, which have been employed for decades by forest managers to identify highly productive seed sources, can additionally be used to identify populations with genotypes ideal for future climatic conditions (Matyas, 1994). The different reactions to climatic conditions at the trial location of populations originating from a variety of climates can reveal any differences in adaptive traits. For example, researchers can use tree cores and dendrology to understand the resiliency and resistance of different populations to the same natural drought conditions as in Montwé *et al.* (2016).

Results from provenance trials show that short distance movement of seed sources can improve productivity. Dozens of studies for several commercially important species, such as *Populus tremuloides* and *Pinus banksiana*, show that northward movement of southern species improves their productivity (Alberto *et al.*, 2013, Etterson *et al.*, 2020, Gray *et al.*, 2011, Thomson & Parker, 2008, Thomson *et al.*, 2009). Though this north-south geographic cline is relatively common, the relationship between productivity and provenance of origin is more likely related to climatic factors (Aitken & Bemmels, 2016) and as such can be more complicated along coastal or elevation clines (Liepe *et al.*, 2016, Vitasse *et al.*, 2009). Short distance transfers are recommended as the strong local adaptation observed in populations can decline in fitness if populations are moved outside of their adaptive niche. This is of particular importance for boreal species as bud set is more influenced by photoperiod than bud break in the spring (Way & Montgomery, 2015). Northward movement of southern populations can therefore cause desynchronization of the timing of fall bud set (Aitken & Bemmels, 2016).

Despite the benefits of assisted migration, there are several risks associated with moving populations to novel climates that have led to great controversy among researchers and forest managers (Aubin *et al.*, 2011). One major concern is unforeseen issues with populations lacking fitness to their new habitat or unexpected effects of climate change (Vitt *et al.*, 2010). As Pedlar *et al.* 2012 point out, these are risks that currently affect forest management. Continued planting using only local populations also runs the risk of maladaptation as a result of climate change. Issues arising from moved populations lacking fitness can be better mitigated through research into traits that confer fitness. For example, one issue with assisted migration would be a mismatch in the timing of bud set and frost hardening of southern populations transplanted to northern locations as this trait is essentially static as it is determined by photoperiod. Despite this, long distance northward transfers (up to 500 km) do not necessarily increase risk of frost damage and can enable managers to take advantage of best-performing seed sources (Sebastian-Azcona *et al.*, 2019). Other pressures faced by trees in novel climatic environments include drought, unprecedented extreme heat events, growing season length, northward movement of novel pest and pathogen outbreaks, and increased fire risks (Williams & Dumroese, 2013). Furthermore, assisted migration could reduce fire risks and help trees withstand pest and pathogen by increasing overall tree health due to better fitness to the future climates of recipient ecosystems. Another concern is that assisted migration of populations can detrimentally dilute the local gene pool due hybridization (Aubin *et al.*, 2011). However, this is unlikely to significantly impact tree species due to high levels of gene flow (Levin & Kerster, 1974). Furthermore, the introduction of specific genotypes for performance into natural populations already occurs in forestry, with no documented effects on genetic diversity (Krakowski & El-

Kassaby, 2004, Pedlar *et al.*, 2012). Above all, researchers note the need for the analysis of genetic differentiation in species traits to determine the feasibility of assisted migration (Hewitt *et al.*, 2011).

This study contributes an assessment of how spring phenology is determined by heat sum and chilling requirements for white spruce (*Picea glauca* [Moench] Voss), a widespread and commercially important boreal tree species. For data collection, I use a mature common garden experiment that allows repeated sampling of genotypes from throughout the range of the species to conduct a series of forcing experiments to quantify phenology parameters. The objectives of this study are to (1) detect if white spruce has genetic population differentiation in heat sum and chilling requirements throughout its range; (2) understand potential genetic differentiation of local populations as evolutionary adaptation to local spring risk environments; and (3) infer likely impacts of climate change on synchronization of populations with the growing season, with implications for reforestation management of the species under climate change.

3. Methods

3.1. Plant material and experimental design

Plant material was sampled at a common garden experiment, where 43 seed sources from throughout the range of white spruce were planted in central Alberta, Canada at 55° 17' N, 113° 10' W (Fig. 1). This test plantation was established in 1982 with four-year-old seedlings from open-pollinated natural stands, and at the time of sampling, the trees were 43 years old. The trial was laid out as a randomized complete block design with five blocks containing five-tree rows plots planted with a 2.5 × 2.5 m spacing with two border rows to minimize edge effects

(Rweyongeza *et al.*, 2007). Branches were sampled with pole pruners for forcing experiments at different times of the year to examine heat sum requirements and chilling requirements.

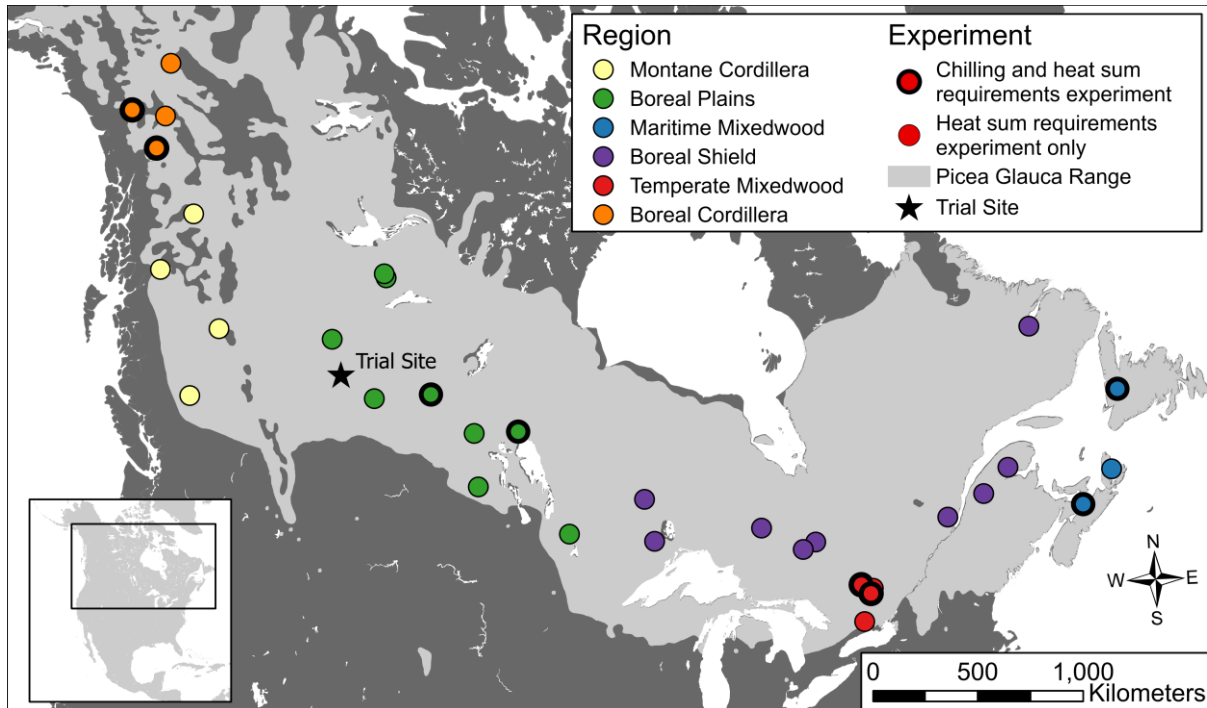


Fig. 1. Locations of 33 provenances collections used in this study to estimate heat sum requirements, and a subset of 8 provenances to assess chilling requirements. Colors indicate ecozones of provenance origins, according to the Canadian ecozone classification system.

The sampling design for the heat sum versus chilling experiments differed due to logistical constraints as the trial was located 200km away from the nearest lab facilities. For estimating heat sum requirements, a larger set of 33 provenances were sampled over the course of two weeks to comprehensively sample the species range (Fig. 1). Since chilling experiments require repeated sampling trips, eight provenances were included that could be sampled in approximately bi-weekly intervals within two consecutive days of sampling (Fig. 1). This sub-sampling strategy still captured much of the geographic and climatic range of the species, with two provenances selected from each major ecological region.

For heat sum experiments, two branches were collected from a randomly selected tree within each of the five blocks of the experimental design. Collection occurred between April 29 and May 15, 2021 before any visible swelling of buds, but with any chilling requirements likely fulfilled. A total of 496 branches were collected, based on sampling 2 branches per tree \times 2 trees per block \times 5 blocks \times 33 provenances, with the reduced total number due to mortality in the plantation. For the chilling requirement assessments a ramp of naturally occurring accumulated chilling degree days were obtained through a series of consecutive sampling dates: by Sept. 18 only 2 chilling degree days (cdd) had been accumulated, followed by sampling on Oct. 22/23 (approx. 5 cdd), Oct. 16/17 (approx. 16 cdd) and Oct. 20/31 (approx. 26 cdd), 2021. In total, 556 branches were collected where each branch on a sampling date was collected from a separate block, to take advantage of the original randomized complete block design.

Harvested branches were transferred on the same day to a laboratory for forcing experiments and observations of the timing of bud break every other day. Branches were placed in glass jars filled with water that was refreshed once a week. Indoor heat sums were monitored using an Elitech RC-4HC Temperature and Humidity Data Logger. There was minimal variation in temperature and humidity with an average temperature of 23°C ($\pm 1^\circ\text{C}$ stdev) and average humidity of 37% ($\pm 6\%$ stdev). On observation days, buds on individual branches were rated using a standardized scale (1-initial swelling of buds, through 6-complete bud break) following protocols developed by Dhont *et al.* (2010). Branches that did not progress in bud stage after initial development were kept for continued observations, but were removed if they did not reach later stages of bud development. For the chilling requirements experiment, branches were subjected to an artificial

16 hours day length regime with a light intensity of $\sim 45 \mu\text{molm}^{-2}\text{s}^{-1}$ (units of number of photons) in order to not inhibit bud break in the absence of complete chilling, following recommendations by Nienstaedt (1966).

3.2. Climate data and degree day calculations

This analysis makes use of different types of climate data for different purposes. To calculate the field-portion of heat sum and chilling degree days prior to sampling, hourly temperature data was obtained from a weather station through the Alberta Climate Informative Service (2021), located 20km from the genetic trial site (Rock Island Lake auto weather station, ID: 3065515, located at 55.3264, -113.4604). Field growing degree days were calculated with a start date of January 1 and ending on the date of branch collection. Indoor growing degree days were calculated using measurements from a temperature logger. Heat sum requirements reported in this study correspond to the total of indoor and outdoor growing degree days at the first observation of each developmental stage. Growing degree days were calculated using a model where heat accumulates uniformly above 0 °C (Man & Lu, 2010). Chilling degree days were calculated using the same approach, where degree days accumulated uniformly for temperatures between 0 °C and 5 °C beginning September 1 until the sampling date. Chilling requirements to quantify the increase in heat sum requirements associated with insufficient chilling was calculated as the difference between the averages of the heat sum requirements to reach stage 3 bud break for the first two collecting trips and the last two collecting trips.

While it is possible and common practice to determine heat sum and chilling degree metrics at an hourly scale (e.g. chilling hours), outdoor measurements from weather stations were only

available on a daily basis, and indoor temperatures were essentially constant. As such, hourly units that could be obtained through a simulated diurnal curve were almost perfectly correlated with daily metrics. Therefore, I choose to use heat sum and chilling degree days as units for this study, which represents the temporal accuracy of the measurements best.

The second set of monthly interpolated climate data at 1km resolution was obtained to characterize long-term climate conditions to which local populations are adapted. For this purpose, I used a 1961-1990 long-term climate normal average. This period represents a compromise between good weather station coverage across Canada and only a relatively small anthropogenic warming signal during this period. Annual averages of twenty-five climatic variables derived from monthly data were obtained with the software package ClimateNA (Wang *et al.*, 2016) available at <http://climatena.ca>. An initial exploratory analysis revealed three variables from this dataset, date of the beginning of frost free period (bFFP), frost free period (FFP), and the number of frost-free days (NFFD), to have a strong relationship with heat sum requirements, which were chosen for subsequent reporting.

A third set of daily interpolated climate data at 1km resolution was used to better describe frost risk environments. This data, obtained from <http://daymet.ornl.gov>, covers the years 1980 to 2020 and was accessed with the *Daymetr* package for the R programming language (Thornton *et al.*, 2020). I calculated variables that describe spring climate environments found to be relevant for other species (Wang *et al.*, 2014, Wang *et al.*, 2019) This included the standard deviation of daily spring temperatures (SDST) 40 days prior to bud break, the spring mean temperature (SMT) 60 days prior to bud break, and number of spring frost days (SFD) prior to 80 days bud

break. In addition, I developed a metric that describes length of the spring frost period (SFP) after temperatures first reach 0°C, calculated as accumulated growing degree days between the first day with temperatures above 0 °C and the last day with temperatures below 0 °C. Both the length of the spring frost period and accumulated heat are accounted for in this variable, which is best interpreted as the rapidity of the transition from winter to suitable growing conditions during the critical spring frost period. High values indicate a slow transition, and low values a rapid transition during the time when spring frost events occur.

3.3. Statistical analysis

To estimate the heat sum requirement for each provenance, a sigmoidal function was fitted with the *nls* functions for the R programming environment version 3.5 (R Core Team, 2020), predicting heat-sum requirements from an ordinal predictor variable (stage 1: initial bud swelling, stage 2: vertical bud swelling, stage 3: horizontal bud swelling, stage 4: bud shoot visible through bud scale, stage 5: bud scales torn, stage 6: bud scales fallen off). Provenance differentiation was best quantified at intermediate scores, so I chose stage 4 to determine heat sum requirements. For chilling requirements, where the accuracy of estimates was limited by sample size, stage 3 was chosen because it had the highest number of branches with bud break activity across the four dates of sample collection.

Differences among regional provenance means for heat sum and chilling requirements were tested with the *emmeans* function for the R programming environment version 3.5 (R Core Team, 2020). After visual confirmation of approximately linear relationships, I used Pearson correlation coefficients to test significant associations between provenance phenology and

climatic variables at the origin location. Variance components in heat sum and chilling requirements, explained by source climate variables, were quantified using a commonality analysis implemented with the *varpart* function of the *vegan* library for R (Oksanen *et al.*, 2020).

4. Results

4.1. Climatology of white spruce provenances

Multivariate climate environments across the range of white spruce were summarized with a principal component analysis (Fig. 2). The first principal component primarily represents mean annual temperature (MAT), number of frost free days (NFFD), and the length of the frost free period (FFP) among others, explaining approximately 48% of the total variance in climate variables among provenance samples. This component contrasts eastern populations with warm and long growing seasons (Fig 2, right side), with cold northern boreal populations (left). Populations with dry, continental climates, i.e. high seasonal temperature differences (TD) and low values of mean annual precipitation (MAP) are positioned toward the upper left, also partially represented by the second principal component (explaining 26% of the variance). Their climatic opposites are the maritime mixedwood provenances (lower right) with wet and maritime climate environments. Boreal shield populations represent the average climate conditions within the range of white spruce (Fig 2, center).

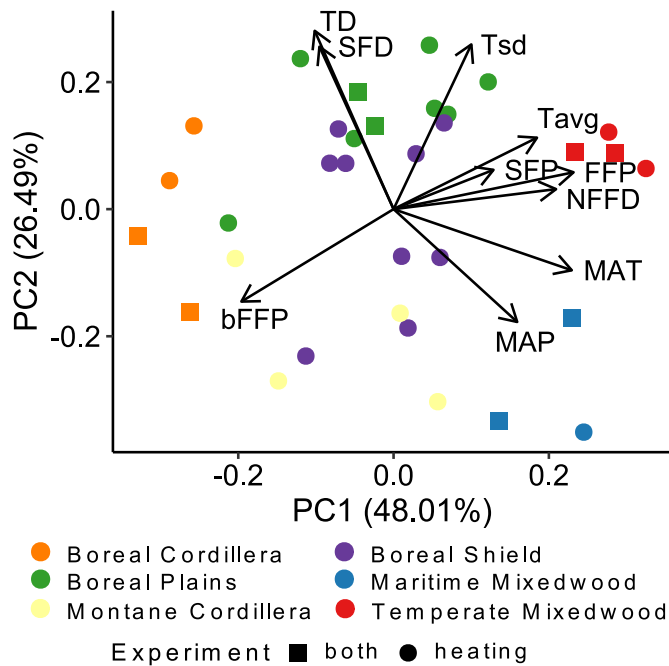


Fig. 2. Principle component analysis of the origin climates of 33 provenances as shown in Fig 1. Variables include mean annual temperature (MAT); mean annual precipitation (MAP); number of frost free days (NFFD); beginning of frost free period (bFFP); length of frost free period (FFP); temperature difference (TD); spring mean temperature prior to budbreak (SMT); the standard deviation of spring temperatures prior to budbreak (SDST); the number of frost days in spring prior to budbreak (SFD); and the length of the spring frost period after temperatures first reach 0°C (SFP).

With regards to variables derived from daily climate data that describe spring risk environments, a third principal component, representing an independent dimension, explains 12% of the total variance and uniquely represents the spring frost period metric (SFP). This variable, representing the rate of spring warming, is a short vector in Fig 2, but can be visualized as pointing primarily in a third dimension. While not visible in this plot, the SFP principal component has a fast rate of spring warming for populations at the northern edge of the species distribution, and a slow rate of spring warming at the southern edge of the distribution. Other variables describing spring risk environments include the standard deviation of spring temperatures before bud break (SDST), with boreal plains populations having the greatest variance in spring temperatures. The number

of spring frost days before bud break (SFD) correlates highly with the previously discussed diagonal gradient from dry continental to wet maritime populations (Fig 2). Lastly, spring mean temperature before bud break (SMT) correlates highly with first principal component.

4.2. Genetic differentiation in heat sum and chilling requirements

I find significant genetic population differentiation in heat sum requirements ranging from 390 to 450 degree days among region means with typical standard errors around ± 12 (Table 1).

Provenance means of heat sum requirements range from 375 to 500 with typical standard errors around ± 16 (Table S1). Provenances from the boreal cordillera had heat sum requirements significantly less than provenances from the boreal plains, and temperate mixedwood ecoregions for stage 4 bud break. In general, provenances from the northern edge of the species distribution had lower heat sum requirements than populations from the southern edge. This represents a primarily latitudinal cline that is somewhat diagonally tilted (Fig. 3, left panel). There were no apparent regional differentiations along the southern edge of the species distribution along an east-west direction.

Table 1. Regional means of heat sum requirements in units of growing degree days for stage 4 bud break (new bud visible through bud scales). Standard errors are given in parentheses, and letters indicate statistically significant differences among regional means at an α -level of 0.05. Regions that share the same letter are not statistically significantly different at $p < 0.05$.

| Region | <i>n</i> | Heat sum requirement (gdd) |
|---------------------|----------|----------------------------|
| Boreal Cordillera | 4 | 390 (13) ^a |
| Montane Cordillera | 4 | 429 (13) ^{ab} |
| Maritime Mixedwood | 3 | 444 (16) ^{ab} |
| Boreal Shield | 9 | 445 (9) ^b |
| Boreal Plains | 9 | 447 (13) ^{ab} |
| Temperate Mixedwood | 4 | 450 (9) ^b |

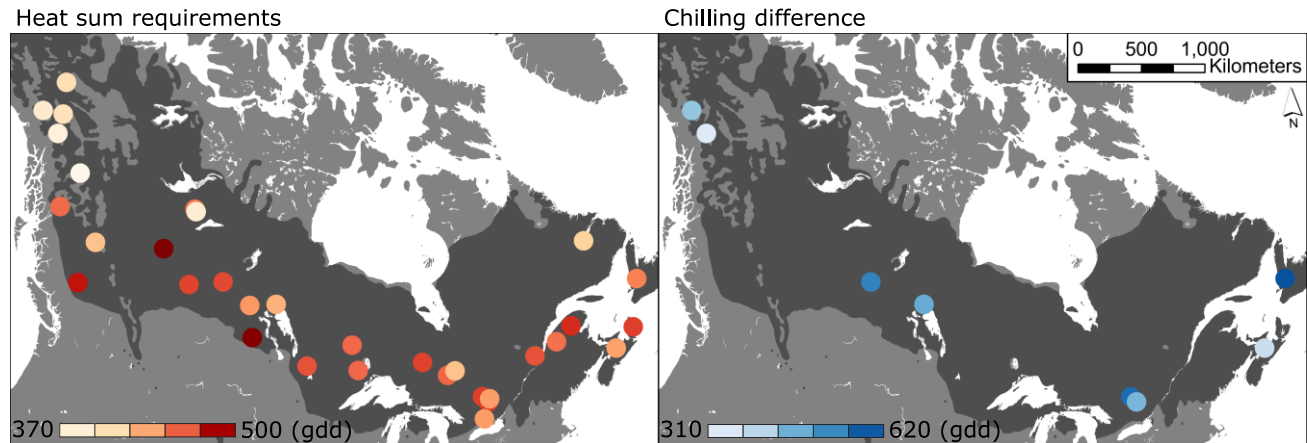


Fig. 3. Genetic population differentiation in heat sum requirements (left panel) and chilling requirements (right panel) in units of growing degree days (gdd). The estimated values with their standard error are reported in supplementary Tables S1 and S2, respectively.

Trends in chilling requirements varied slightly among provenances, but did not show patterns of regional differentiation (Fig. 3, right panel). All provenances exhibited a comparable chilling requirement as indicated by a rapid increase in heat sum requirements when samples had not been previously exposed to chilling temperatures in fall (Fig. 4). The inflection point where heat sum requirements approach a horizontal asymptote is approximately 15 chilling degree days for most provenances, representing the third sampling date. This indicates a moderate chilling requirement that, in boreal central Alberta, near the study site, is reached by the end of October. The maritime mixedwood provenances may reach this inflection point later, at around 20 chilling degree days (Fig. 4, second panel), but the limited temporal sampling resolution of this experiment did not allow for detection of statistically significant differences among regions.

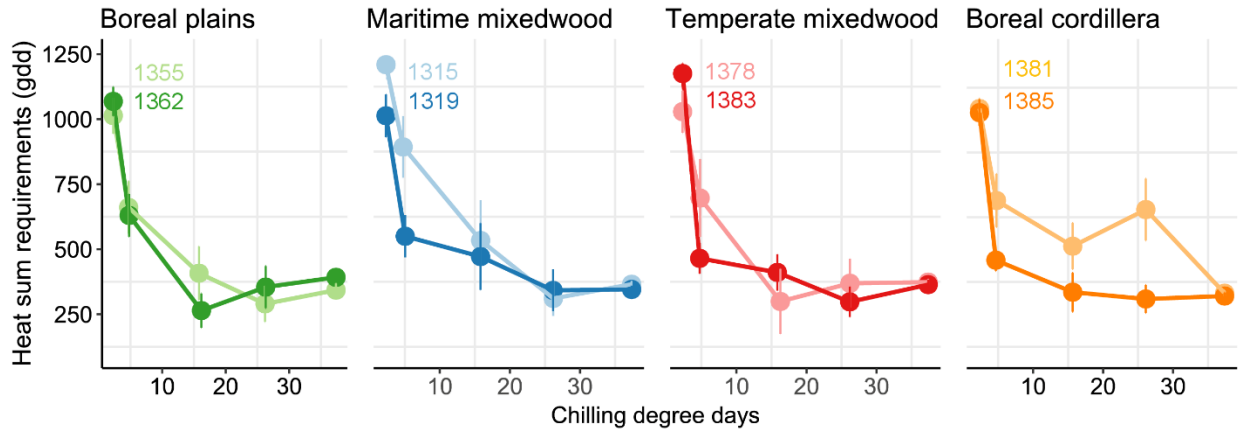


Fig. 4. Chilling requirements illustrated as plots of heat sum requirements for bud break observed in forcing experiments, after provenances were exposed to five different amounts of chilling degree days in the field at consecutive sampling dates in fall and spring (last measurement). Two provenances were sampled for each region, and each line represents a provenance corresponding to supplementary Table S2.

4.3. Correlation with climate of population origins

The spring frost period (SFP) climate metric, representing the speed of the transition from winter to suitable growing conditions, had the highest correlation with provenance heat sum requirements for any of the observed stages, with the highest values observed for stage 4 (Table 2). Other variables that describe the growing season, or spring climate descriptors show some significant associations, but variance partitioning reveals that they explain less than half of the variance compared to SFP, and have only small or zero unique variance components. For example, the number of frost free days (NFFD) explain no unique variance in genetic differentiation of required heat sums, when analyzed in conjunction with SFP and Region (Fig. 5). A second variable that describes the growing season, growing degree days above 5°C (GDD5) as well as other spring climate descriptors (Table 2) also explain little or no unique variance when SFP is included in the variance partitioning analysis (data not shown). A spatial variable Region (as shown in Fig. 1) was included in the variance component analysis to

potentially represent variance explained by gene flow, which is quantified in this analysis as 6% unique variance component that could not be explained by climate variables.

Table 2. Pearson correlation coefficients among different stages of bud break and spring climate variables at population origins. Variables include beginning of frost free period (bFFP), frost free period (FFP), number of frost free days (NFFD), growing degree days above 5°C (GDD5), spring frost period (SFP), number of frost days in spring before bud break (spring frost days, SFD), average spring temperatures before bud break (SMT), standard deviation of spring temperatures (SDST). Levels of significance: * = p<0.05, ** = p<0.01, *** = p<0.001

| Bud break stage | Growing season descriptors | | | | Frost risk descriptors | | | |
|-----------------|----------------------------|-------|------|-------|------------------------|--------|------|-------|
| | bFFP | FFP | NFFD | GDD5 | SFP | SFD | SMT | SDST |
| 1 | -0.02 | 0.1 | 0.13 | 0.06 | 0.43* | -0.28 | 0.01 | 0.11 |
| 2 | -0.03 | 0.13 | 0.15 | 0.09 | 0.41* | -0.31* | 0.03 | 0.11 |
| 3 | -0.2 | 0.28 | 0.24 | 0.23 | 0.50** | -0.35* | 0.11 | 0.22 |
| 4 | -0.38* | 0.41* | 0.32 | 0.37* | 0.57*** | -0.31* | 0.19 | 0.36* |
| 5 | -0.43* | 0.42* | 0.32 | 0.39* | 0.53** | -0.23 | 0.2 | 0.40* |
| 6 | -0.43* | 0.40* | 0.31 | 0.38* | 0.50** | -0.19 | 0.2 | 0.40* |

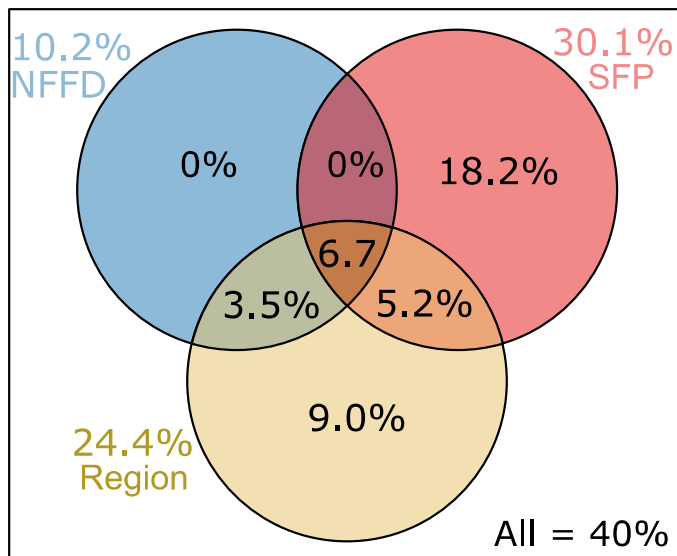


Fig. 5. Variance explained in required heatsum of populations by three predictor variables: beginning of frost-free period (bFFP), spring frost period in growing degree days (SFP), and region of the provenance of origin. Autocorrelations among predictors lead to overlap in the variance components explained, illustrated with a Venn diagram.

Mapping variables describing spring climatic conditions (Fig. 6) reveals a distinct spatial pattern for the spring frost period (SFP) metric, which shows the lowest values at the northern edge (fastest winter to summer transition during the time when frosts occur), and the highest values at the southern edge of the distribution of white spruce (slowest transitions). The beginning of the frost free period (bFFP) shows a pattern with high elevation and northern regions having the largest values, and correlated variable length of the frost free period (FFP) shows a comparable pattern (data not shown). The standard deviation of spring temperatures prior to bud break (SDST) reflects maritime influences in the east and west, with mean spring temperature (SMT) showing similar patterns (data not shown). The fourth unique geographic pattern is found in spring frost days prior bud break (SFD), again with maritime influence in the east and west similar to SDST, but with less pronounced montane and coastal influences.

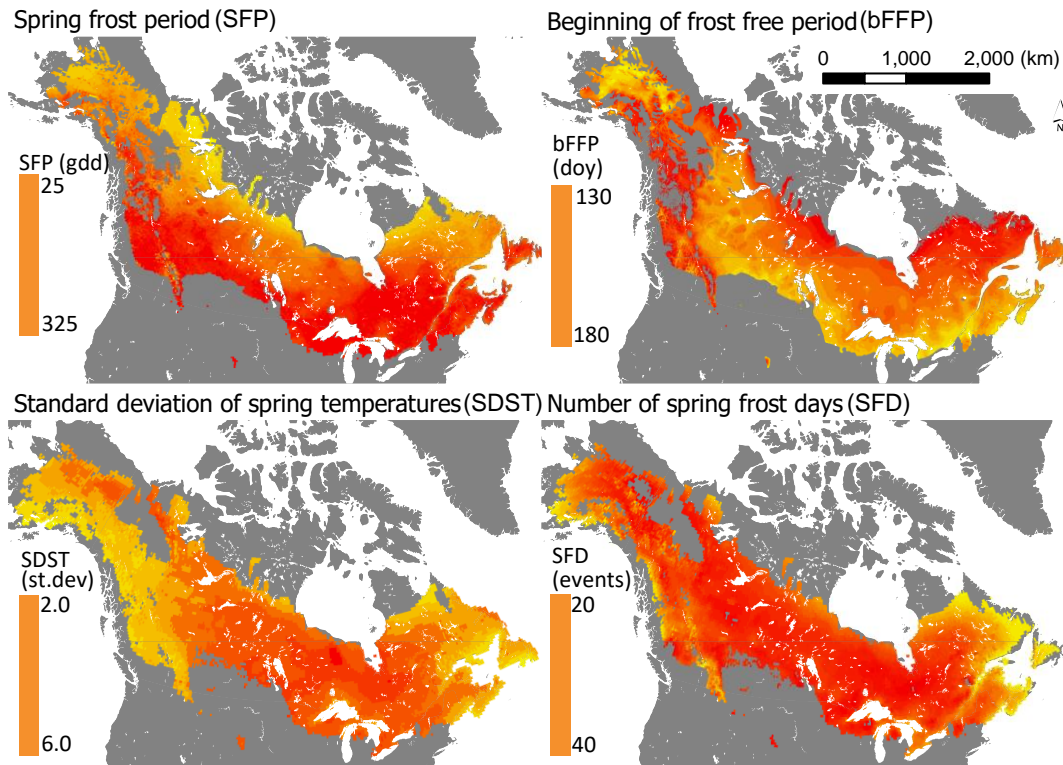


Fig. 6. Geographic patterns in climatic variables across the range of white spruce that describe spring frost risk and growing season environments. Variables shown include the length of the spring frost period after temperatures first reach 0°C (SFP), the date of the beginning of frost free period (bFFP), the standard deviation of spring temperatures prior to budbreak (SDST) and the number of frost days in spring prior to budbreak (SFD)

5. Discussion

5.1. Genetic adaptation to a restricted growing season

The low heat sum requirements found in northern populations of white spruce in this study suggest local adaptation of populations to the climatic conditions of higher latitudes. I propose two possible explanations for why lower heat sum requirements improve the fitness of northern populations. First, northern regions have faster transitions to frost-free growing conditions, thus not requiring heat sum requirements as high as in southern regions. Second, lower heat sum requirements allow earlier bud break, taking better advantage of a short growing season, even if this involves some exposure to late spring frosts (Leinonen & Hänninen, 2002, Silvestro *et al.*,

2019). In other words, the trade-off between survival risks versus adaptations that maximize growth is shifted towards accepting higher frost risks to take full advantage of a highly restricted growing season for the most northern populations. Either mechanism would lead to populations from northern locations to have lower heat sum requirements than southern populations to align bud break timing with local spring climate.

This study is not specifically designed to distinguish between the alternative hypotheses (1) a more rapid transition from cold conditions to suitable growing conditions during a shorter spring period, and (2) shifting the risk balance to take advantage of a short growing season, to explain lower heat sum requirements of northern populations. However, there is empirical evidence that favors the first hypothesis. The SFP metric had by far the highest correlation with heat sum requirements of populations, indicating that this transition speed during the spring period is a selective factor in determining the optimal date of bud break. In contrast, commonality analysis that describe the growing season length (NFFD) and cumulative growing degree days (GDD) did not explain any unique variance components that were not also explained. To my knowledge this is the first study that establishes a link between the length of the spring transition period and heat sum requirements.

My results with respect to low heat sum requirements in far northern populations is consistent with findings for other boreal tree species (e.g., Li *et al.*, 2010b, Rossi, 2015), and provides additional evidence for the general expectation that far northern (and very high elevation) populations generally have lower heat sum requirements than populations originating further south (Hänninen & Tanino, 2011, Nienstaedt, 1967). Regarding the response of populations to a

warming climate, higher spring temperatures can lengthen the growing season, and could therefore increase productivity for all populations (Ford *et al.*, 2016). Dow *et al.* (2022), however found that warming trends only shifted the growing season forward, with summer temperature limitations preventing overall increases in productivity. However, if very low heat sum requirements lead to a faster advance of bud break than the rate receding risk of late spring frosts, then late spring frost damage can increase and cause reproductive failure or reduced productivity (Zohner *et al.*, 2020b).

5.2. Chilling requirements do not compromise response to climate warming

I do not find evidence of high chilling requirements in white spruce, or a clear regional population differentiation. Although the most contrasting climate environments from this range wide provenance trial were sampled, only a moderate species-level chilling requirement was detected. These results are consistent with single provenance experiments for white spruce (Man *et al.*, 2017). Chilling requirements appear to be fully met in fall across the species range, around early as October in central Alberta (this study) or late-October in Ontario as shown by Man *et al.* (2017). While white spruce does not appear to have high chilling requirements or geographic population differentiation in chilling requirements, Thibault *et al.* (2020) could document that chilling requirements decrease with latitude in *Populus balsamifera* across a comparable range as in this study. Also, higher heat sum requirements are generally expected for populations or species that reside in milder climates that still experience significant frost periods in winter, such as temperate maritime climates (Leinonen, 1996). Here, forcing conditions with growing degree days above 5°C may occur mid-winter, and high chilling requirements protect plants from premature bud break under those conditions.

Although not observed in this study, high chilling requirements can pose a problem under anthropogenic climate warming, when they are no longer met at the correct time to transition to heat sum accumulation for a timely bud break. This has been documented as a potential problem for trembling aspen (*Populus tremuloides*) which has chilling requirements over 500 chilling hours. In southern Ontario, these chilling requirements are currently met mid-December but could be delayed under warming conditions and lead to later bud break (Man *et al.*, 2017). The potential for delayed bud break, when in fact an earlier date of bud break due to climate warming may optimize the fitness of populations, has also been documented for other tree species (Fu *et al.*, 2015, Laube *et al.*, 2014). For white spruce, this study suggests that chilling requirements only serve to prevent a second bud break late in the same growing season if fall conditions are unusually warm. Warming trends should not cause delayed dormancy release in spring for this species, as chilling requirements are already met in fall.

5.3. Implications for forest management under climate change

Provenance trials, as used in this study, are essentially transplant experiments that can provide insight for the safety of human assisted migration prescriptions to address climate change. Generally, in areas where the warming signal over the last decades has been high, seed sources from more southern locations transferred north exhibit a higher growth potential (Aitken & Bemmels, 2016, Etterson *et al.*, 2020, Gray *et al.*, 2011, Thomson & Parker, 2008). This has also been observed for white spruce (Lu *et al.*, 2014; Rweyongeza *et al.*, 2007). However, potential benefits of increased growth of sources that have been moved northward needs to be weighed against potential risks associated with their physiological traits, such as phenology, cold

hardiness, or drought resistance. Adaptive traits should either match among source and target locations, or their values should indicate reduced risks of transferred material relative to local populations.

Regarding drought resilience, Montwé *et al.* (2015) showed that migration from warm and moist to colder and drier environments in coastal Douglas-fir (*Pseudotsuga menziesii*) would compromise drought resilience. In contrast, assisted migration would be beneficial for interior sources of lodgepole pine (*Pinus contorta*), as northern populations lack physiological adaptations to drought (Isaac-Renton *et al.*, 2018). For white spruce, Sang *et al.* (2019), showed minimal population differentiation in drought resilience across the range of the species, suggesting that assisted migration should not have important effects on this trait. Nevertheless, a cautious approach would avoid transfer from moist to dry sites.

Another important adaptive trait is fall phenology, specifically the timing of the onset of cold hardiness. For white spruce, population differentiation in fall phenology might pose a problem for assisted migration, because southern sources, transferred north, initiate cold hardiness later than local sources (Lu *et al.*, 2003, Sebastian-Azcona *et al.*, 2020, Sebastian-Azcona *et al.*, 2018). Similar results were also documented for lodgepole pine (Montwé *et al.*, 2018). Nevertheless, a moderate northward transfer of 300-400 km compensating for 2° C warming appears safe for forestry species in western Canada (Sang *et al.*, 2021).

Synthesizing the results of knowledge on growth and adaptive traits for white spruce, including this study, it appears that a moderate northward transfer appears safe, and is expected to yield

higher growth rates of transferred provenances relative to local sources. This study contributed a spring phenology analysis that showed higher heat sum requirements of southern populations, transferred north, reduces risks of spring frost damage. Further, lack of geographic population differentiation in chilling requirements implies no significant concerns for this trait.

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Appendix

Table S1. Heat sum requirements for each stage of budbreak obtained from curve-fitting experimental data to sigmoidal functions for each of the sampled provenances including their location of origin (standard error calculated using bootstrap methods). Cells are shaded with darker colors indicating higher values of budbreak relative to other values in the same column.

| Provenance | Lat | Long | Stage 1 | Stage 2 | Stage 3 | Stage 4 | Stage 5 | Stage 6 |
|---------------------------|--------|----------|----------|----------|----------|----------|----------|-----------|
| Boreal Cordillera | | | | | | | | |
| 1386 | 59.883 | -111.717 | 196 (22) | 315 (23) | 315 (19) | 397 (12) | 488 (16) | 580 (29) |
| 1387 | 54.633 | -110.217 | 257 (15) | 346 (13) | 346 (12) | 395 (12) | 446 (16) | 497 (21) |
| 1385 | 56.633 | -114.583 | 213 (21) | 321 (18) | 321 (13) | 388 (11) | 458 (23) | 529 (37) |
| 1381 | 53.333 | -60.417 | 243 (18) | 332 (14) | 332 (11) | 382 (13) | 433 (19) | 484 (28) |
| Boreal Plains | | | | | | | | |
| 15 | 49.017 | -57.617 | 279 (13) | 388 (17) | 388 (20) | 498 (14) | 640 (18) | 781 (36) |
| 1365 | 46.267 | -60.617 | 277 (12) | 392 (16) | 392 (16) | 497 (11) | 626 (18) | 754 (34) |
| 12 | 45.567 | -63.167 | 243 (13) | 360 (17) | 360 (18) | 461 (11) | 583 (24) | 704 (46) |
| 1362 | 47.833 | -68.350 | 283 (20) | 392 (18) | 392 (15) | 460 (14) | 532 (24) | 605 (35) |
| 1352 | 48.417 | -66.250 | 253 (17) | 373 (19) | 373 (15) | 457 (11) | 552 (30) | 647 (52) |
| 1380 | 48.217 | -79.483 | 225 (18) | 343 (24) | 343 (25) | 442 (14) | 562 (29) | 681 (58) |
| 1363 | 47.500 | -71.000 | 241 (29) | 357 (32) | 357 (25) | 433 (23) | 516 (63) | 599 (107) |
| 1355 | 44.433 | -77.833 | 225 (29) | 343 (33) | 343 (26) | 424 (19) | 514 (47) | 604 (84) |
| 10 | 48.033 | -80.367 | 212 (15) | 320 (13) | 320 (11) | 386 (9) | 456 (11) | 526 (16) |
| Boreal Shield | | | | | | | | |
| 1325 | 49.367 | -89.750 | 265 (17) | 384 (18) | 384 (14) | 469 (12) | 563 (32) | 658 (55) |
| 1350 | 51.200 | -90.200 | 256 (11) | 376 (12) | 376 (10) | 463 (8) | 560 (13) | 658 (22) |
| 1331 | 49.300 | -82.700 | 247 (20) | 367 (25) | 367 (22) | 457 (13) | 561 (35) | 664 (63) |
| 1335 | 49.817 | -95.3333 | 236 (13) | 337 (15) | 337 (21) | 452 (15) | 608 (29) | 765 (61) |
| 1349 | 54.167 | -99.167 | 246 (15) | 366 (16) | 366 (14) | 451 (14) | 548 (25) | 644 (40) |
| 1338 | 55.317 | -106.083 | 258 (32) | 374 (31) | 374 (24) | 451 (19) | 536 (38) | 621 (65) |
| 1321 | 53.917 | -102.383 | 279 (28) | 384 (25) | 384 (19) | 447 (16) | 514 (21) | 581 (32) |
| 1327 | 51.633 | -101.667 | 250 (30) | 354 (26) | 354 (17) | 417 (41) | 482 (85) | 548 (133) |
| 1314 | 55.250 | -123.083 | 227 (13) | 337 (12) | 337 (10) | 406 (9) | 480 (13) | 553 (20) |
| Maritime Mixedwood | | | | | | | | |
| 1317 | 56.333 | -129.250 | 253 (13) | 373 (14) | 373 (12) | 463 (9) | 566 (14) | 669 (23) |
| 1315 | 59.167 | -129.250 | 250 (15) | 365 (14) | 365 (13) | 440 (11) | 522 (14) | 604 (21) |
| 1319 | 52.083 | -122.933 | 227 (16) | 346 (20) | 346 (14) | 429 (14) | 523 (44) | 617 (77) |

Montane Cordillera

| | | | | | | | | |
|------|--------|----------|----------|----------|----------|----------|----------|----------|
| 1376 | 45.967 | -77.433 | 262 (12) | 381 (14) | 381 (13) | 477 (10) | 589 (14) | 700 (24) |
| 1371 | 60.033 | -111.967 | 272 (17) | 382 (15) | 382 (11) | 450 (14) | 522 (25) | 595 (38) |
| 1370 | 60.683 | -135.133 | 248 (20) | 354 (17) | 354 (13) | 417 (14) | 483 (22) | 550 (34) |
| 1373 | 45.500 | -77.017 | 210 (16) | 314 (14) | 314 (11) | 375 (10) | 439 (13) | 504 (18) |

Temperate Mixedwood

| | | | | | | | | |
|------|--------|----------|----------|----------|----------|----------|----------|----------|
| 1383 | 45.683 | -76.800 | 246 (15) | 364 (19) | 364 (19) | 464 (13) | 584 (21) | 703 (39) |
| 1378 | 61.350 | -139.000 | 254 (13) | 374 (14) | 374 (13) | 463 (9) | 564 (11) | 666 (18) |
| 1333 | 64.017 | -139.000 | 214 (11) | 333 (16) | 333 (15) | 431 (8) | 548 (29) | 664 (55) |
| 1384 | 62.050 | -136.233 | 235 (14) | 352 (14) | 352 (12) | 431 (12) | 518 (17) | 605 (25) |

Table S2. Heat sum requirements in units of growing degree days (with standard errors) to reach stage 3 budbreak after different amounts of chilling degree days (CDD) were received at four collection dates.

| Prov | Lat | Long | Elev | Region | Heating sum requirements | | | |
|------|--------|----------|------|------------|--------------------------|-------------------|---------------------|----------------------|
| | | | | | CDD=2 on Sep 18 | CDD=5 on Oct 2 | CDD=16 on Oct 16 | CDD= 26 on Oct 30 |
| 1315 | 49.017 | -57.617 | 45 | East coast | 1014 (69) | 661 (101) | 408 (102) | 290 (69) |
| 1319 | 45.567 | -63.167 | 150 | East coast | 1068 (55) | 630 (82) | 265 (66) | 354 (81) |
| 1355 | 54.167 | -99.167 | 243 | Central | 1209 (52) | 893 (118) | 534 (155) | 311 (67) |
| 1362 | 55.317 | -106.083 | 401 | Central | 1013 (82) | 550 (81) | 472 (128) | 342 (80) |
| 1378 | 45.967 | -77.433 | 170 | S. Ontario | 1175 (39) | 465 (59) | 411 (70) | 298 (58) |
| 1381 | 60.683 | -135.133 | 762 | Yukon | 1029 (82) | 697 (149) | 299 (125) | 369 (94) |
| 1383 | 45.500 | -77.017 | 121 | S. Ontario | 1029 (50) | 459 (41) | 336 (75) | 310 (53) |
| 1385 | 61.350 | -139.000 | 792 | Yukon | 1045 (38) | 690 (103) | 513 (89) | 655 (119) |

Table S3. Chilling difference calculated as difference between required heat sums in fall and spring. The metric was calculated as the difference between the averages of the heat sum requirements to reach stage 3 budbreak for the first two collecting trips and the last two collecting trips.

| Provenance | Latitude | Longitude | Region | Difference |
|------------|----------|-----------|------------|------------|
| 1355 | 54.167 | -99.167 | Central | 469 (85) |
| 1362 | 55.317 | -106.083 | Central | 542 (71) |
| 1319 | 45.567 | -63.167 | East coast | 349 (93) |
| 1315 | 49.017 | -57.617 | East coast | 624 (98) |
| 1383 | 45.500 | -77.017 | S. Ontario | 449 (56) |
| 1378 | 45.967 | -77.433 | S. Ontario | 578 (113) |
| 1381 | 60.683 | -135.133 | Yukon | 306 (87) |
| 1385 | 61.350 | -139.000 | Yukon | 422 (55) |