Adaptation of white spruce to climatic risk environments in spring: Implications for assisted migration

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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, we 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. We 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. Our 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, we 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, we conclude that assisted migration northward, compensating for approximately 2° C warming, is safe and yields higher growth rates for white spruce.

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 and 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 and 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 species with moderate shade tolerance such as white spruce (Richardson and O'Keefe, 2009) or if the growing season is generally short in cold regions (Morin et al., 2007; Dantec et al., 2015).

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 (Laube et al., 2014; Fu et al., 2015; 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 0–5 °C). Once a specific heat sum requirement is fulfilled, apical growth begins (Körner, 2006; Hänninen and Tanino, 2011). Photoperiod can have a small moderating effect on the timing of bud burst in spring, but it is generally negligible compared to temperature (Laube et al., 2014; Rossi, 2015).

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 (Menzel et al., 2001; Jeong et al., 2011; Chen et al., 2019). 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 (Beaubien and Hamann, 2011; Augspurger, 2013; Zohner et al., 2020a) and can exacerbate dieback and mortality together with other stress factors (Wolken et al., 2009; Kharuk et al., 2015; Vanoni et al., 2016). 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 (Heide, 2003; Fu et al., 2015; Chen et al., 2019).

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 (Nienstaedt, 1967; Olson et al., 2013; Ford et al., 2016). However, an early budbreak, with higher frost risks, to take advantage of a short growing season, may not be advantageous under climate warming, when 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 (Corlett and Westcott, 2013; Cooper et al., 2019). Synchronized timing of bud break is particularly important for understory species that have a narrow window of sunlight to capitalize on before the overstory canopy develops (Richardson and O'Keefe, 2009). Assisted migration of southern populations northward to track changing climate can increase productivity (Schreiber et al., 2013; Etterson et al., 2020), 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, we 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. We 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. Our 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. Materials and methods

2.1. 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.

The sampling design for the heat sum versus chilling experiments differed due to logistical constraints as the trial was located 200 km 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 two randomly selected trees 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 × 2 trees per block × 5 blocks × 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 (±1°C stdev) and average humidity of 37 % (±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 h day length regime with a light intensity of ~ 45 μmolm^{-2}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).

2.2. 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 20 km from the genetic trial site (Rock Island Lake auto weather
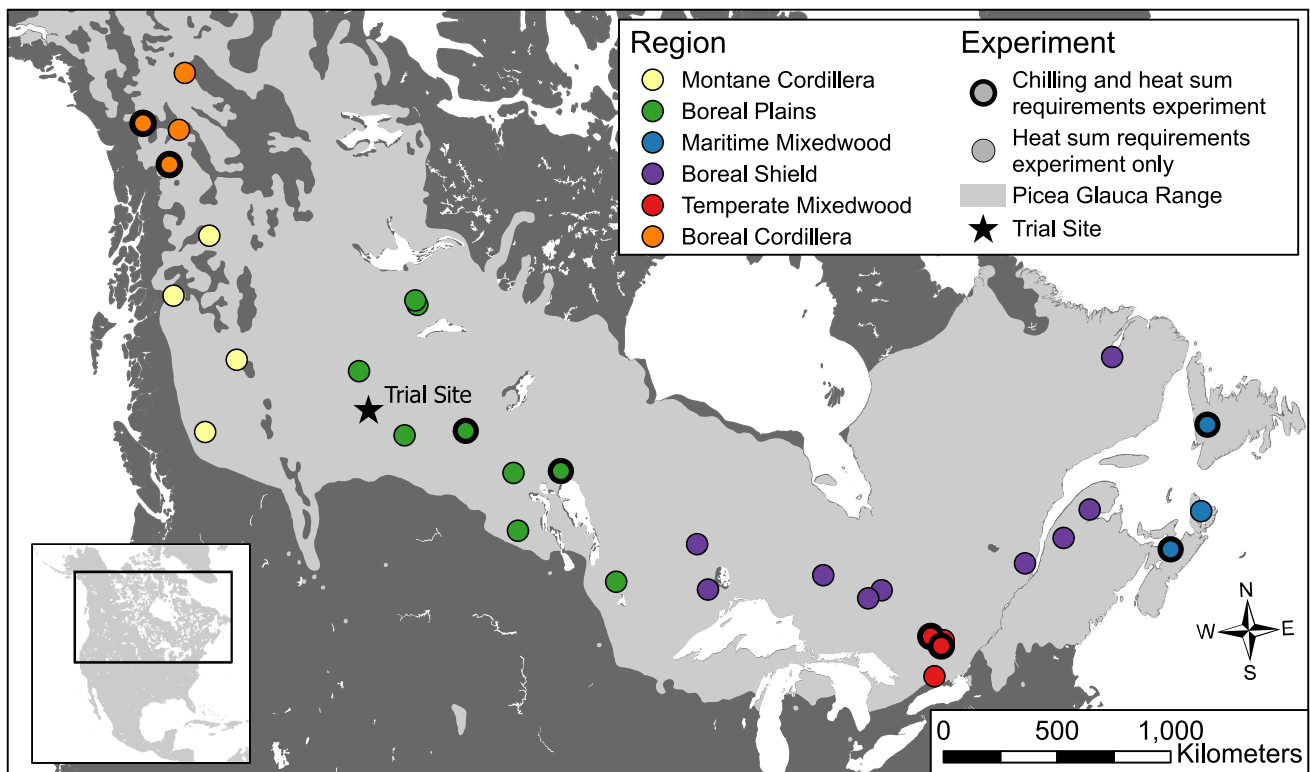
Fig. 1. Locations of 33 provenances collections used in this study to estimate heat sum requirements, and a subset of 8 provenances to assess chilling requirements. Colors indicate ecozones of provenance origins, according to the Canadian ecozone classification system.

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 and 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, we 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 1 km resolution was obtained to characterize long-term climate conditions to which local populations are adapted. For this purpose, we 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 *https://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 1 km resolution was used to better describe frost risk environments. This data, obtained from *https://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). We 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, we 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.

2.3. 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 we 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, we 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).

3. Results

3.1. 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).

With regards to variables derived from daily climate data that

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 bud break (SMT); the standard deviation of spring temperatures prior to bud break (SDST); the number of frost days in spring prior to bud break (SFD); and the length of the spring frost period after temperatures first reach 0 °C (SFP).

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.

3.2. Genetic differentiation in heat sum and chilling requirements

We find significant genetic population differentiation in heat sum requirements ranging from 390 to 450°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.

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.

3.3. 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
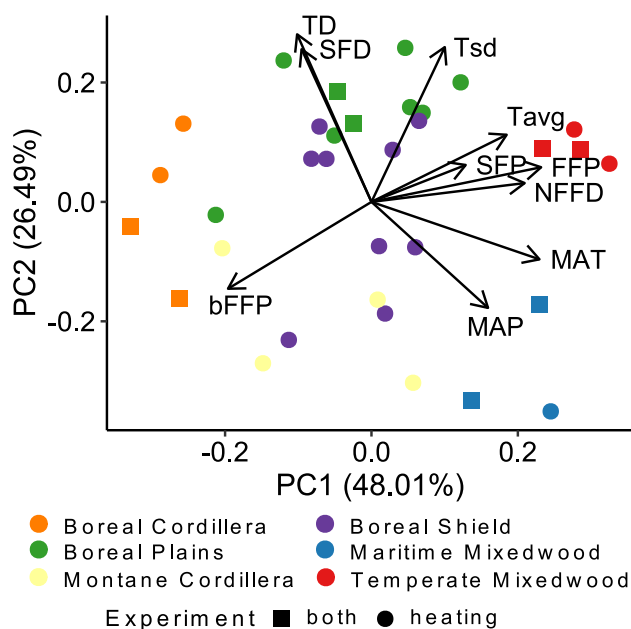
Table 1
Regional means of heat sum requirements in units of growing degree days for stage 4 bud break (new bud visible through bud scales). N refers to the number of provenances that represent each region, and standard errors are given in parentheses, and letters indicate statistically significant differences 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.

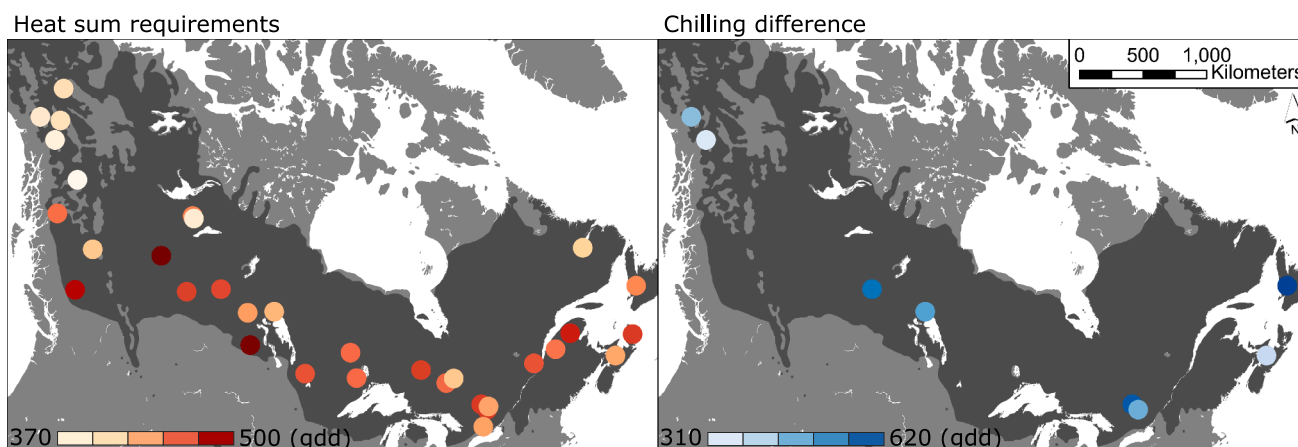| Region	N	Heat sum requirement (gdd)
Boreal Cordillera	4	390 (13)[a]
Montane Cordillera	4	429 (13)[ab]
Maritime Mixedwood	3	444 (16)[ab]
Boreal Shield	9	445 (9)[b]
Boreal Plains	9	447 (13)[ab]
Temperate Mixedwood	4	450 (9)[b]

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.
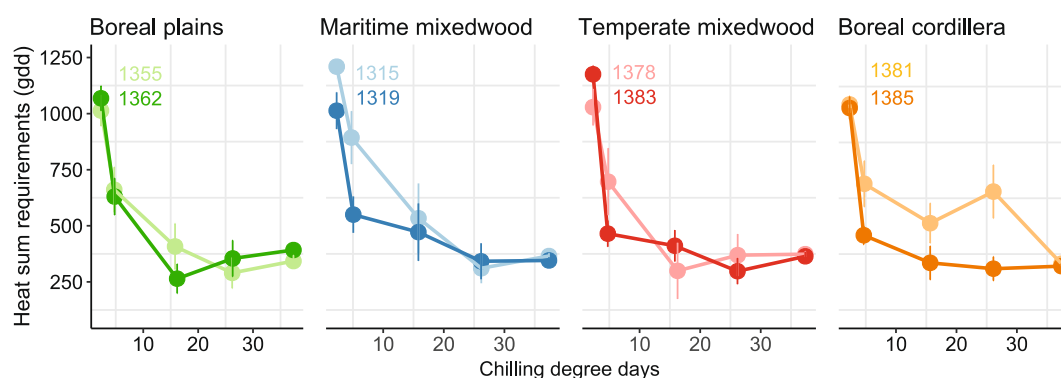

Fig. 4. Chilling requirements illustrated as plots of heat sum requirements for bud break observed in forcing experiments, after provenances were exposed to five different amounts of chilling degree days in the field at consecutive sampling dates in fall and spring (last measurement). Each line represents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

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.

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

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.

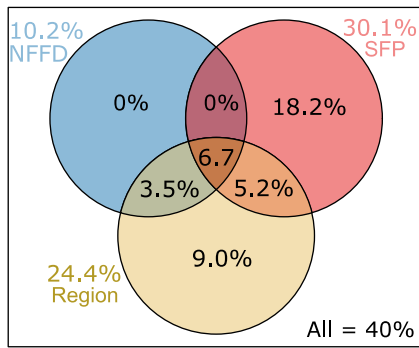| Bud break stage	Growing season descriptors				Frost risk descriptors			
	bFFP	FFP	NFFD	GDD5	SFP	SFD	SMT	SDST
1	−0.02	0.1	0.13	0.06	0.43*	−0.28	0.01	0.11
2	−0.03	0.13	0.15	0.09	0.41*	−0.31*	0.03	0.11
3	−0.2	0.28	0.24	0.23	0.50**	−0.35*	0.11	0.22
4	−0.38*	0.41*	0.32	0.37*	0.57***	−0.31*	0.19	0.36*
5	−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 heat sum of populations by three predictor variables: number of frost free days (NFFD), spring frost period (SFP), and region of the provenance of origin. Autocorrelations among predictors leads to overlap in the variance components explained, illustrated with a Venn diagram.

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.

4. Discussion

4.1. Genetic adaptations 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. We 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, to take better advantage of a short growing season, even if this involves some exposure to late spring frosts (Leinonen and 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.

Our 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.
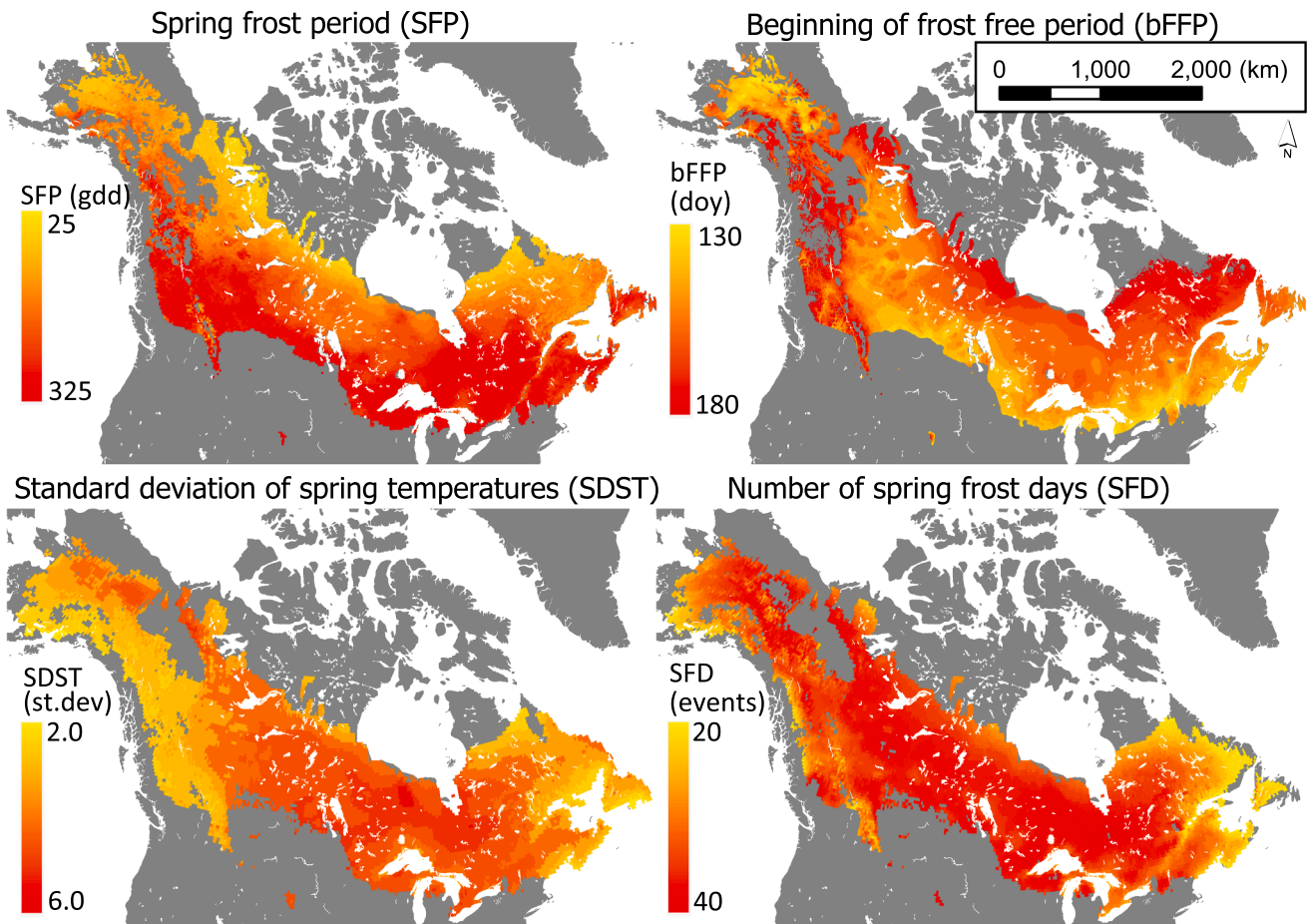

Fig. 6. Geographic patterns in climatic variables across the range of white spruce that describe spring frost risk and growing season environments.

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 already explained. To our knowledge this is the first study that establishes a link between the length of the spring transition period and heat sum requirements.

Our 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., 2010; 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 (Nienstaedt, 1967; Hänninen and Tanino, 2011). 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. Chilling requirements do not compromise response to climate warming

We 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 (Laube et al., 2014; Fu et al., 2015). 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.

6. 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 (Thomson and Parker, 2008; Gray et al., 2011; Aitken and Bemmels, 2016; Etterson et al., 2020). 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., 2018; Sebastian-Azcona et al., 2020). 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 our 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.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Author contributions

MC, AH and UH conceived the study and designed the methodology. MC conducted field and lab work and analyzed the data with advice and support from AH and UH. MC wrote the manuscript with editing contributions from AH and UH.

Declaration of Competing Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability statement

Provenance means of heat sums and chilling requirements, covering all phenology stages, are included as supplementary tables for use in potential future meta analyses. The raw data of bud break score recordings by date are also available from the authors, without undue reservation, to any qualified researcher upon request.

The study was conceived and designed by MC, AH, and UH. UH and AH were responsible for funding acquisition and supervision. MC performed the field work and lab experiments with input from AH and UH. MC conducted the formal data analysis with input from AH. MC wrote the first draft of the paper with editing contributions from AH and UG. All authors approved the final version of the manuscript.

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