Survival, growth and cold hardiness tradeoffs in white spruce populations: Implications for assisted migration

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ABSTRACT

Human assisted movement of reforestation stock poleward or upward in elevation has been proposed as a tool to address climate change in regular reforestation programs. However, moving warm adapted seed sources to colder environments could carry the risk of frost damage if seed sources are moved too far. Here, we assess genetic differentiation in growth potential, survival and cold hardiness of a wide-ranging tree species, white spruce (*Picea glauca* [Moench] Voss). We use data from a 34-year-old common garden experiment planted in the approximate center of the species range. Cold hardiness was negatively related to growth and positively to survival. Generalized additive models identified mean coldest month temperature and latitude (as a proxy for the day length regime) as an exceptionally good predictor for the onset of cold hardiness ($R^2_{adj} = 0.91$). The results suggest that day length, an environmental factor that is not influenced by climate change, is an important factor controlling the timing of the onset of hardiness. Survival was only moderately well predicted, primarily by precipitation of the provenance origin ($R^2_{adj} = 0.36$) indicating that other adaptive traits besides cold hardiness should be considered in assisted migration prescriptions. Survival of seed sources appears primarily compromised when transplanting sources from wet origins to a dry location. Nevertheless, acceptable migration distances without significant tradeoffs were up to 500 km north and 1500 km west towards a central planting location.

1. Introduction

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

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

Population differentiation in growth and adaptive traits can be studied with common garden experiments, usually referred to as provenance trials in a forestry context. Historically, provenance trials have been established for many commercial forestry species to identify fast growing seed sources, and they have now also become ideal climate change laboratories, where we can observe how exposure of

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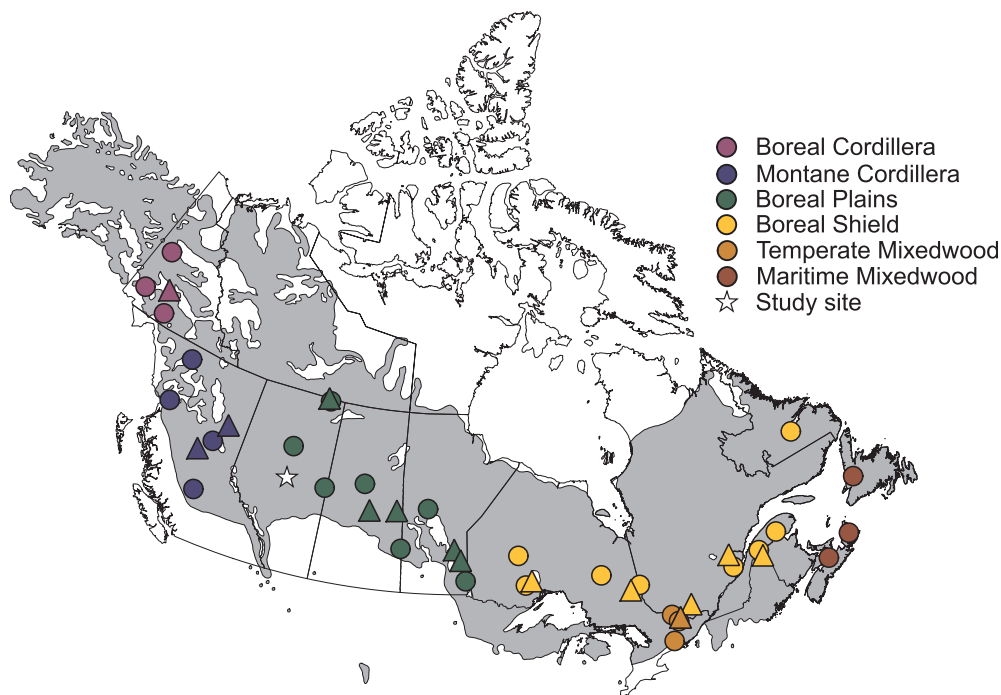 *E-mail address:* jaime4@ualberta.ca (J. Sebastian-Azcona).

Fig. 1. Location of the common garden experiment (star) and the origin of seedlots used in this study. The number of provenances for lab assessments (circles) were a subsample of the provenances in the field trial (circles and triangles). The area in grey delineates the species range of white spruce.

populations to different climatic conditions can influence tree growth and survival (Mátyás, 1994). Generally, provenance trials have shown that population survival is limited by cold temperatures for sources that originate from the cold edge of the species range (Woodward, 1990) and by a combination of biotic and abiotic factors for populations from the warm edge of the species range (Cahill et al., 2014). These limitations suggest a tradeoff between growth potential and cold hardiness (Loehle, 1998; Howe et al., 2003). Northern populations limit their growth by adapting to a shorter growing season and spending their resources into thicker and more rigid cell walls that give structural stability to the leave tissues and by producing cryoprotectant substances, such as lipids, proteins or carbohydrates, which protect the cell structures from frost damage (Sakai and Larcher, 1987; Zwiazek et al., 2001).

Frost hardiness can be evaluated through various protocols, including experimental freeze testing and evaluation of cellular damage (Burr et al., 2001), as well as morphological properties of needles and hydraulic tissue (Schreiber et al., 2013; Montwé et al., 2018). The amount of resources invested in the needles can be estimated with the ratio of projected leaf area to dry mass, or specific leaf area. The expectation is that specific leaf area is lower in plants growing under more adverse or extreme growing conditions that also result in lower growth rates (Poorter et al., 2009). Thus, a comparatively low specific leaf area in a common garden experiment indicates a tradeoff between growth potential and investing more resources to produce persistent leaves that ensure higher survival rates.

White spruce (*Picea glauca* [Moench] Voss) is one of the most important commercial species in Canada and significant efforts have been made to understand how climate change might impact its growth and survival. An artificial warming experiment with open-top chambers showed that a warmer climate can enhance white spruce growth under subartic climate conditions (Danby and Hik, 2007). Increased growth rates were also observed in a dendrochronology study in Alberta for the last part of the 20th century, but the unusually dry conditions experienced after 2001 induced a decrease in growth (Hogg et al., 2017). Several provenance trial experiments have been conducted to study genetic population differentiation. Seedling experiments in eastern

Canada observed that southern provenances had a higher growth potential (Li et al., 1997; Lesser and Parker, 2004; Prud'homme et al., 2017). Similar results were obtained in mature, range-wide provenance trials (Rweyyongeza et al., 2011; Lu et al., 2014), showing that southern sources had the fastest growth. Based on a large set of provenance and progeny trials 7 to 32 years of age, Gray et al. (2016) concluded that short northward transfers are generally beneficial in a regional study for the province of Alberta. Most of these authors cautioned against long distance transfers because of the risk of maladaptation to cold temperatures.

In this paper we contribute a comprehensive cold hardiness assessment for white spruce that covers provenance from throughout the species distribution, including a wide range of source climate conditions. Cold hardiness assessments include experimental freeze testing as well as morphological characteristics of needles. This data is evaluated in the context of long-term growth and survival observed in a 34-year-old field trial. Cold hardiness is measured experimentally through freeze tests. Specifically, we (1) investigate geographic patterns of genetic differentiation among provenances; (2) identify possible tradeoffs between frost hardiness, growth and survival; (3) analyze the association of climate and latitude at the origin of seed sources (as a proxy for day length regime) with growth, survival and frost hardiness observed in the common garden trial; and (4) quantify the impact of long distance transfers to identify seed sources with good hardiness characteristics as well as good growth performance as a recommendation for assisted migration prescriptions.

2. Methods

2.1. Field trial and measurements

The common garden experiment includes bulk seed collections from 43 natural stands of white spruce across the Canadian distribution of the species (Fig. 1). Seeds were collected between 1959 and 1976, and planted in 1982 as four-year-old seedlings in central Alberta, Canada (55°17′N, 113°10′W). The experimental layout of the provenance trial was a randomized complete block design of five blocks with five trees

per provenance planted in each block in a row plot with 2.5 × 2.5 m spacing. Provenances were grouped by Canadian ecozones (Ecological Stratification Working Group, 1995) to calculate summary statistics for this analysis, indicated by different colors in Fig. 1. Height and survival of all trees was assessed in 2014 after 32 growing seasons in the field trial. Tree height was measured with a telescopic measuring pole and survival was calculated as the proportion of live trees to the total number of trees planted.

Cold hardiness measurements were performed once in spring (May 12–14, 2016) and at four dates in fall (August 25–27, September 9–11, September 23–25 and October 7–9, 2016). Because of limitations on processing and freeze testing within a given time, we sampled only 28 of the 43 provenances for cold hardiness assessments (Fig. 1, circles). Six trees per provenance and date were chosen at each date (one from each block, and one block sampled twice). To avoid excessive damage to trees, a different tree was chosen from each 5-tree row plot within each block for different sampling dates. During each of the three-day field visits, we collected healthy, sun-exposed branches from the upper part of the crown, approximately 60 cm long to provide enough material for freeze testing at multiple temperatures. Branches were labeled and stored in plastic bags with wet paper towels to maintain humidity, and transferred to a cold room ($+4°C$) on the same day.

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

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

2.2. Climate data

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

MAP*1000, summer heat-moisture index (SHM) calculated as MWMT/MSP*1000, chilling degree-days below $0°C$ (DD0), growing degree-days above $5°C$ (DD5), frost-free period (FFP), day of year at which the frost-free period begins (FFPB) and ends (FFPE), and Hargreaves' climatic moisture deficit (CMD).

2.3. Statistical analysis

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

Because different trees were sampled at each date for the assessment of the onset of fall cold hardiness, only provenance averages were used for calculating the values of $D50_{-30}$ and $D50_{-40}$. However, for all other measurements (height, mortality, specific leaf area and spring cold hardiness), we took advantage of the experimental design to reduce the error of the estimate, using linear mixed-effect models, treating block and rowplot within block as random effects. To estimate mortality of provenances, we used a generalized linear mixed-effect with the logit link function for a binomial distribution. The general linear mixed model was implemented with the *lmer* function, and the generalized logit model were implemented with the *glmer* function of the *lme4* package (Bates et al., 2014) for the R programming environment (R Core Team, 2017). Subsequently, best linear unbiased estimates with their standard errors of provenance means for fixed effects (height, mortality, specific leaf area and spring cold hardiness) were extracted from *lmer* and *glmer* objects with the *lsmeans* package (Lenth, 2016). We tested for statistically significant differences among regions using a Tukey adjustment for multiple inferences with the *cld* function of the *lsmeans* package. Correlations between growth and adaptive traits were analyzed with the Pearson correlations, based on provenance means.

To test associations between the climate condition at the provenance source locations and hardiness, height and mortality assessments, we used generalized additive models (GAM) using the *gam* function of the package *mgcv* (Wood, 2017) for the R programming environment (R Core Team, 2017). GAMs are flexible in that they fit cumulative curves for each independent variable, without assuming any prior shape by fitting splines. We specified the Gaussian identity link function as an option in the GAM model for normally distributed errors in height and hardiness variables, and the logit function for the binomial distributed error of mortality. We used a low basis dimension ($k = 3$) to restrict the shape of the splines to straight lines or simple curves, to avoid overfitting the data. The adjusted R^2 for the models was calculated as the proportion of variance explained, where original variance and residual variance are both determined through unbiased estimators. The R^2 value for mortality is a pseudo-R^2 for non-normal errors, calculated as the proportion of the null deviance explained. Statistically significant variables for each model were determined by assigning penalties to smoothing parameter estimation of individual predictor variables, which can completely remove terms from the model. If the smoothing parameter is set to zero (i.e. the model term is removed), the individual variable penalty is also set to zero, thereby avoiding overfitting not only by restricting the number of basis dimensions, but also by restricting the number of predictor variables. This selection method was performed with the *select* option from the *gam* function. The contribution of
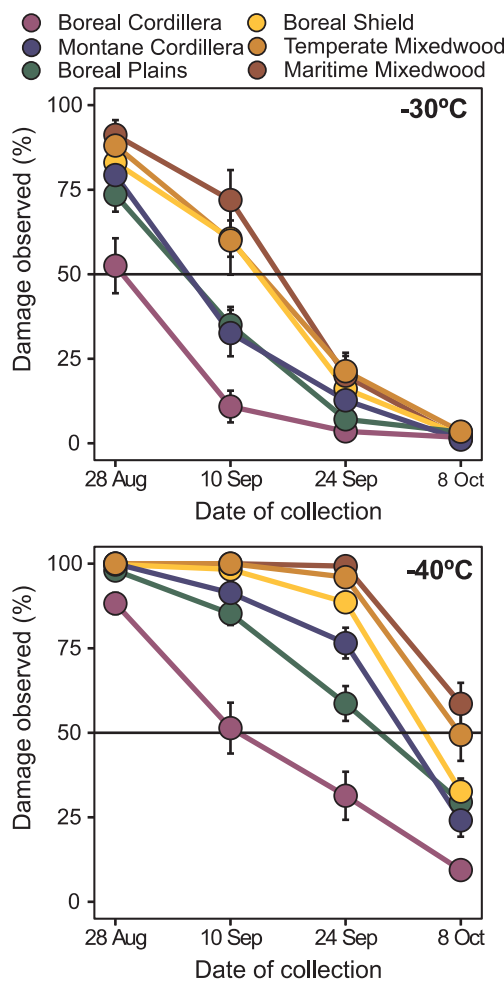
Fig. 2. Percentage of observed damage in needle tissue at each collection date for the two freeze test temperatures (−30 and −40 °C). Error bars represent the standard error of the means.

each predictor variable was further quantified by an effect size measure, calculated as the difference between the maximum and minimum value of individual splines across the range of the predictor variable. The concurvity of the predictor variables was calculated to account for the correlation between these variables with the *concurvity()* function of the *mgcv* package.

3. Results

3.1. Population differentiation in cold hardiness

We found significant population differentiation in the onset of cold hardiness for the main test temperatures (−30 and −40 °C) that were evaluated at all four assessment dates (Fig. 2, Table 1). When plotting damage scores over test temperature separately for each measurement date, the September and October dates at colder temperatures (−50 and −60 °C) also showed pronounced differentiation among provenances in the absolute cold hardiness values in fall (Fig. S1). In all cases, we observed a similar genetic cline, with the most northern region (Boreal Cordillera) showing the earliest resistance to frost damage and the highest absolute resistance values, followed by the two regions from central latitudes (Montane Cordillera and Boreal Plains). The provenances in the south and east of the distribution (Boreal Shield, Temperate Mixedwood and Maritime Mixedwood) were the most vulnerable for both absolute hardiness values and the timing of onset in the last measurement (Fig. 2, Fig. S1).

Table 1
Best linear unbiased estimates of mixed-effect models for regional means of tree height, mortality, cold hardiness and specific leaf area. Standard errors of the estimates are given in parenthesis. Mean estimates for regions with the same letter were not significantly different at p < 0.05, using a Tukey adjustment for multiple comparisons. The number of provenances per region for lab assessments were a subsample of the number of provenances in the field trial, and the number of trees was 25 per provenance for field assessments (height and mortality) and 6 per provenance for lab assessments (specific leaf area and cold hardiness variables).

Region	Number of provenances for field assessments	Number of provenances for lab assessments	Height (m)	Mortality (%)	Temperature causing 50% damage in spring (°C)	Date at which −30 °C caused 50% damage (Days)	Date at which −40 °C caused 50% damage (Days)	Specific leaf area (cm²/g)
Boreal Cordillera	4	3	5.4 (2.3) a	3.9 (2.0) ab	−27.1 (0.7) a	28 Aug (2.6) a	9 Sep (3.3) a	44.2 (4.2) a
Montane Cordillera	6	4	8.0 (2.1) b	5.5 (2.1) ab	−27.9 (0.4) a	2 Sep (2.2) ab	29 Sep (2.9) bc	51.1 (3.9) a
Boreal Plains	12	7	9.5 (1.7) c	2.9 (1.0) a	−27.2 (0.4) a	3 Sep (1.7) ab	25 Sep (2.0) b	41.7 (3.2) a
Boreal Shield	13	8	9.6 (1.6) c	7.5 (1.6) ab	−27.0 (0.8) a	10 Sep (1.6) c	2 Oct (2.2) bc	43.8 (3.0) a
Temperate Mixedwood	4	3	9.6 (2.2) c	12.6 (3.2) bc	−26.7 (0.6) a	9 Sep (2.6) bc	6 Oct (3.3) bc	49.5 (4.3) a
Maritime Mixedwood	3	3	7.7 (2.9) b	22.4 (5.2) c	−28.0 (0.6) a	13 Sep (2.6) c	9 Oct (3.3) c	48.7 (4.4) a

The observed regional differences were statistically significant for the fall hardiness assessments, but not for spring cold hardiness (Table 1, indicated by letters). Provenance variation of hardiness within regions was relatively homogeneous, with standard deviation of the onset of cold hardiness typically around ± 4 days (data not shown). The most resistant provenances, from the northern edge of the distribution were resistant to 50% damage in the needles as early as August 27th for a test temperature of −30 °C, and at September 3rd for a temperature of −40 °C. The least resistant provenances on the other hand had a much later onset of cold hardiness, becoming 50% resistant to −30 °C in September 18th and to −40 °C in October 13th (data not shown).

3.2. Growth, survival and their relation with adaptive traits

We also observed significant differences between regions of seed origin in growth and survival (Table 1). For tree height, we found three groups that were clearly differentiated, with differences between their means of about 2 m each. The superior growing group was comprised of the central and southern regions, followed by the two coastal regions that showed intermediate growth. The lowest tree growth was found in the most northern region. The region with the best survival was the Boreal Plains from the central part of the distribution, which recorded less than 5% mortality in all its provenances except for one source (16%). The region with the highest mortality was the Atlantic coast (Maritime Mixedwood), where provenances showed mortality rates between 16 and 28% when grown at a central location. There were no significant differences among regions for specific leaf area due to high within-region and within-provenance variability.

When evaluating correlations between growth and adaptive traits, we found that populations that were most vulnerable to cold damage in fall (D50−40) also showed the best growth (Fig. 3a). The same result was obtained for the D50−30 measurement with a Pearson's r of 0.54 (p = 0.003). Trees that became resistant to low temperatures later in the fall also showed higher mortality than those that started its cold adaptation earlier (Fig. 3b). However, mortality was not linearly correlated to the onset of cold hardiness, but showed a significant curved response after fitting a GAM (R^2_{adj} = 0.18, p < 0.001, Fig. 3b). Spring cold hardiness, measured as the temperature causing 50% damage, showed weak associations with growth and survival (Pearson's r = −0.20, p = 0.306 for height and r = −0.21, p = 0.290 for mortality), meaning a tendency of hardier provenances having better growth and lower survival. However, these relationships were not statistically significant.

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

3.3. Association with the climate of provenance origin

We analyzed relationships of traits with the climate of origin of the provenances to infer genetic adaptation of white spruce populations to climate. The climate of provenance origin explained a large proportion of the variance in height, mortality and fall cold hardiness observed in the common garden experiment. For both cold hardiness models, latitude was the predictor variable that explained the highest amount of variance (Table 2). The selected model for the onset of cold hardiness represented by the D50−40 measurement, included the predictor variables latitude and mean coldest month temperature, and were able to explain 91% of the among provenance variance (Table 2, Fig. 4). For the D50−30 measurement, only latitude resulted a significant predictor variable with a lower proportion of the variance explained by the model than for D50−40. We used the D50−40 model to make spatial prediction from gridded climate data for the onset of cold hardiness across Canada (Fig. 5). Using an interval size of one week difference in the onset of cold hardiness, we obtain five fall hardiness zones for areas covered by
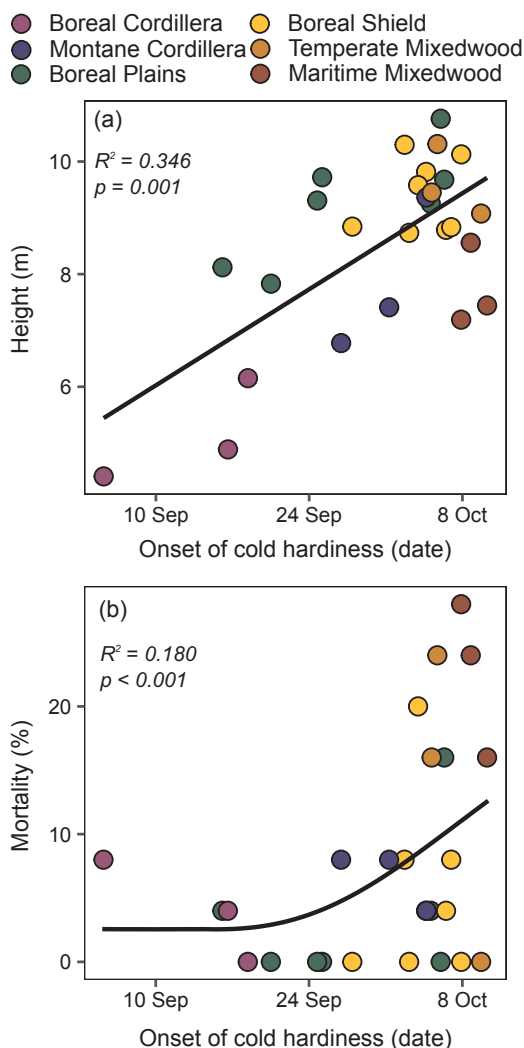

Fig. 3. Association of height (a) and mortality (b) with the onset of frost hardiness, measured as the date at which 50% of the needles were damaged at a test temperature of −40 °C. A later date indicates that the provenance is more vulnerable to frost damage. The R² value for mortality is a pseudo-R² (the proportion of the null deviance explained).

Table 2
Generalized additive models for mean height, mortality and fall cold hardiness as a function of climate variables and latitude as a proxy for the day length regime. Effect size is the difference between the maximum and minimum predicted value by the individual splines across the range of the predictor variable. Sample size was 43 provenances for height and mortality and 28 for cold hardiness. The R² value for mortality is a pseudo-R² (the proportion of the null deviance explained).

Model	R^2_{adj}	Variables	Cumulative R^2_{adj}	Effect size	P-value
Height	0.83	Latitude	0.65	5.9 (m)	< 0.0001
		MAP	0.12	2.8 (m)	< 0.0001
		MAT	0.05	3.2 (m)	< 0.0001
		FFP	0.02	1.8 (m)	0.0256
Mortality	0.36	MAP	0.31	6.8 (%)	< 0.0001
		MAT	0.13	3.6 (%)	0.0051
D50−30	0.64	Latitude	0.64	20 (days)	< 0.0001
D50−40	0.91	Latitude	0.83	23 (days)	< 0.0001
		MCMT	0.07	13 (days)	< 0.0001

D50−30 = date at which a −30 °C freeze treatment caused 50% damage, *D50−40* = date at which a −40 °C freeze treatment caused 50% damage. *MAT* = mean annual temperature, *MCMT* = mean coldest month temperature, *MAP* = mean annual precipitation, *FFP* = frost-free period.
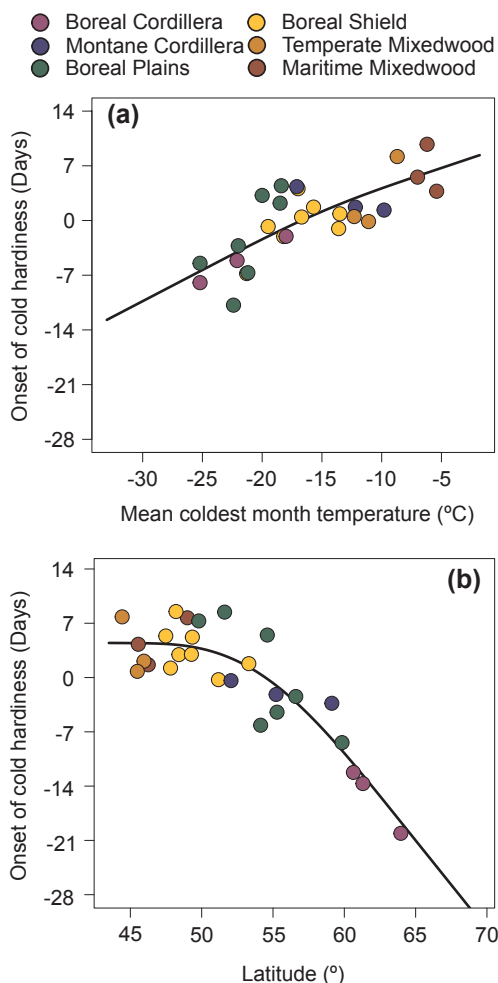
Fig. 4. Visualization of the individual predictor variable effects in the variance of the onset of cold hardiness (Table 2, R^2_{adj} = 0.91). The onset of frost hardiness was measured as the date at which 50% of the needles were damaged at a test temperature of -40 °C. A later date indicates that the provenance is more vulnerable to frost damage. Climate variables are represented in the X-axes and their individual model effects on tree height are shown in the Y-axis. The x-axes of mean coldest month temperature and latitude were expanded to cover the values extrapolated values in the prediction of Fig. 5.

the sampled provenances, plus two extrapolated zones north and south of our data coverage for the range of the species.

The selected model for tree height included latitude, mean annual temperature, mean annual precipitation and frost free period, and explained 83% of the variance (Table 2). Latitude was the most important predictor variable with the highest variance explained and the largest effect size of all four variables (5.9 m), with southern provenances growing significantly better than northern provenances (Fig. S2). Precipitation had a negative effect with provenances from wetter origins growing worse than provenances from drier origins after other effects have been accounted for. Annual temperature was optimal at levels close to the study site, with provenances from warmer or colder origins performing worse after other effects have been accounted for by the GAM. Provenances with longer frost free periods in their climate of origin also performed better than provenances with shorter ones, but this variable had the lowest effect size (Table 2, Fig. S2).

The climate variables that best explained tree mortality were mean annual precipitation and mean annual temperature, although tree mortality was much less related to the climate of origin than tree height and cold hardiness with a pseudo R^2 of 0.36 for this model (Table 2, Fig. S3). Mean annual precipitation was the most important variable of the

model, with an effect size of 6.8% (p < 0.0001). As for the height model, provenances with mean annual temperature similar to that of the test site were optimal for tree survival. Precipitation had a negative effect, with provenances with high precipitation in the environment where they originated showing higher mortality.

4. Discussion

4.1. Tradeoffs between growth and adaptive traits

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

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

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

4.2. Environmental drivers of population differentiation

The environmental regulation of the onset and release of cold hardiness can explain the different degree of genetic differentiation observed in fall and spring cold hardiness timing. Bud flush and the release of cold hardiness in spring is mainly regulated by temperatures (Nienstaedt, 1966; Saxe et al., 2001). First, a certain amount of time with temperatures between 0 °C and 5 °C is needed to satisfy chilling requirements. Subsequently, growth initiation occurs in response to accumulation of degree days above a certain threshold. As a result release of dormancy is a highly plastic trait that strongly responds to year to year variation in spring temperature, and may therefore not require
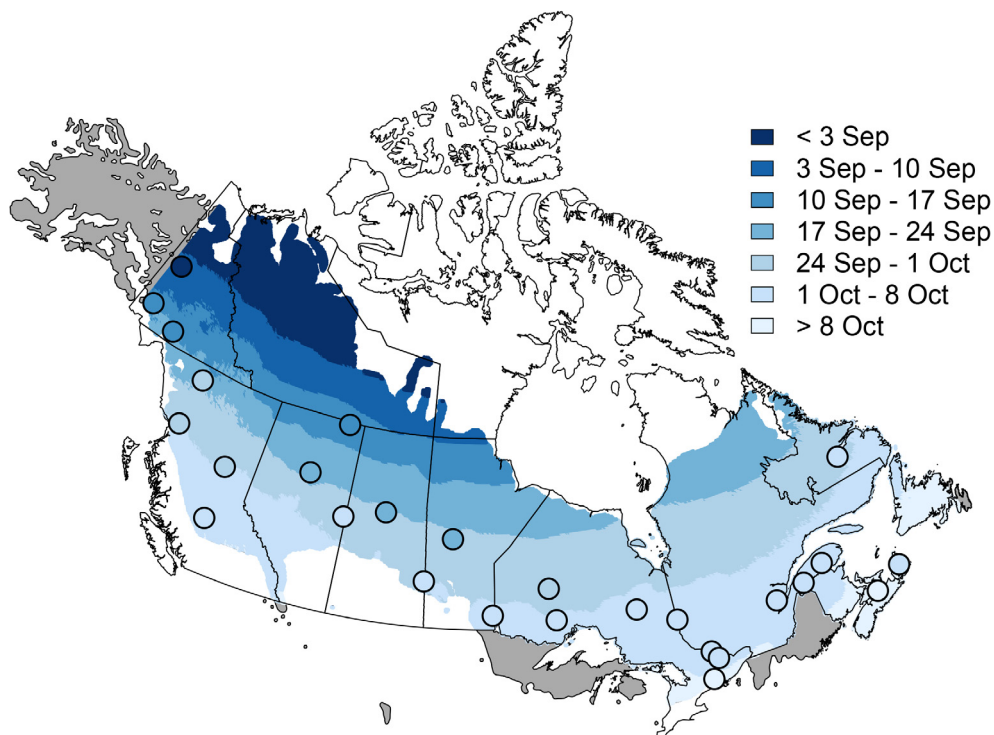
Fig. 5. Cold hardiness zones inferred by one week intervals in the onset of frost hardiness. The onset of cold hardiness observed for provenances (circles) was predicted by a generalized additive model using latitude and mean coldest month temperature as the best predictor variables (Table 2, $R_{adj}^2 = 0.91$). The dates represent the time at which 50% of needles were damaged at a test temperature of $-40\,°C$.

Legend:
- < 3 Sep
- 3 Sep – 10 Sep
- 10 Sep – 17 Sep
- 17 Sep – 24 Sep
- 24 Sep – 1 Oct
- 1 Oct – 8 Oct
- > 8 Oct

the same degree of genetic differentiation as the onset of fall hardiness.

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

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

Because day length regimes are not affected by climate change, a mismatch between climate and photoperiod is likely to occur in natural populations. However, this issue is not associated with a risk of fall cold injury but rather with a missed opportunity to take advantage of suitable growing conditions in fall. This mismatch should therefore be considered in tree breeding programs and assisted migration prescriptions. If southern provenances with late growth cessation are moved northwards, the change in the photoperiod regime will result in an even later cessation at their new location (Way and Montgomery, 2015). The latitudinal effect observed in both fall cold hardiness and tree height models in our study (Table 2) conforms to a strong influence of photoperiod on the timing of growth cessation and onset of cold hardiness.

Collinearity among predictor variables should be taken into consideration when interpreting results, and in this case the appropriate measure is concurvity for GAM splines. We find low to moderately high concurvity (Latitude-MAT = 0.80, Latitude-MAP = 0.72, Latitude-FFP = 0.61, MAT-MAP = 0.52, MAT-FFP = 0.68, MAP-FFP = 0.27, Latitude-MCMT = 0.52) and where concurvity is high, other interpretations of the data should be considered. The latitude-temperature association is certainly an intrinsic feature of adaptation. The adaptation targets synchronization of the growth period with the available growing season (i.e. temperature), but because of the strong association with day length (and therefore latitude), dormancy triggered by day length appears to be the proximate mechanism to control this adaptation.

4.3. Other tradeoff mechanisms

Besides latitude, we found significant relationships of tree height and mortality with mean annual precipitation and temperature. Both mortality and height models had similar patterns for temperature and precipitation, with an optimal temperature of source origin close to that of the study site and a negative effect of precipitation in both cases. These results suggest that adaptation to drought may explain this relationship. Specifically, the eastern Maritime Mixedwood provenances (and to some degree the most southern provenances from the Temperate Mixedwood) lack drought adaptations that lead to higher mortality and lower growth when transplanted to a central boreal site. That said, other southern provenances from the Boreal Shield, often with origin climates that were much wetter than the central test site, did not appear to be compromised in growth or mortality (Table 1).

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

4.4. Management implications

An important application of adaptation to cold is the delineation of plant hardiness zones. These hardiness zones are developed to predict areas where a plant can survive and have been traditionally used in horticulture to safely introduce non-native ornamental species (McKenney et al., 2007). With data of population differentiation from common garden experiments, hardiness zones could also be used to limit the distance of seed transfers within the species range (Fig. 5).

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

The best performing provenances in this trial came from the southern central part of the distribution (South East Manitoba), about 500 km south and 1500 km east of the study site and a region with warmer summers and similar winter temperatures and precipitation. These climatic conditions are consistent with the expected climate change at the test site, and therefore assisted migration prescriptions of moderate distance (up to 500 km north) seem well supported by this study.

Declarations of interest

None.

Appendix A. Supplementary material

All data presented in the main text were deposited on figshare with the DOI: https://doi.org/10.6084/m9.figshare.7268723.v1. Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.10.046.

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