Variation in Bud Set Process Among Eight Genetically Improved White Spruce Seed Sources From Eastern Canada

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Abstract

A strong differentiation of bud set among natural populations may lead to limited adaptive capacity of seed sources during assisted population migration. The present study aimed to fill gaps regarding the dynamic nature of bud set and its variation among genetically improved white spruce (*Picea glauca* [Moench] Voss) seed sources used in the reforestation program in Québec, Canada. Bud set phases of seedlings from eight white spruce seed sources were monitored during the first growing season on a test plantation site. Results showed that bud set phases were interdependent but did not vary significantly among seed sources. Bud set timing was unrelated to the latitude or longitude of geographic origin. The lack of significance in bud set timing among tested seed sources may indicate low potential risk associated with the transfer of southern seed sources to the northern locations.

Introduction

Bud set is a complex physiological process representing the transition phase from active growth to dormancy (Cooke et al. 2012). Because bud formation is accompanied by growth cessation, the timing of bud set represents a trade-off between the active growth duration and the cold hardiness acquisition (Aitken et al. 2008, Howe et al. 2003, Savolainen et al. 2007). Natural selection has led to genetic differentiation and clinal variation in phenological traits such as bud set in boreal and temperate tree species. The resulting local adaptation enables populations to synchronize bud set with local climate conditions (Aitken et al. 2008, Beaulieu et al. 2004, Howe et al. 2003, Savolainen et al. 2007). For this reason, one may expect limited adaptation to climate change due to strong genetic control of phenological traits, and that this would be more obvious under restricted phenotypic plasticity and epigenetic memory to bud set expression. Assisted population migration (APM), which aims to move tree populations to sites where the future climate is similar to that of their origin, has been proposed as a forest management practice that can potentially mitigate the adverse effects of climate change on forest plantations (Aitken and Whitlock 2013, Pedlar et al. 2011). This practice is already implemented for some tree species (O'Neill et al. 2008, Pedlar et al. 2012). Therefore, the assessment of bud set process and its variation among genetic populations is of great interest for successful APM.

In indeterminate species, bud set initiation is induced by a critical photoperiod and low temperature (Cooke et al. 2012, Maurya and Bhalerao 2017). In contrast, environmental cues (photoperiod and temperature) are not as essential for the initiation of bud formation for determinate species (Bigras and D'aoust 1992, Cooke et al. 2012). For these species, bud set is initiated once the elaboration of all pre-formed stem units (during the last growing season) is completed (Cooke et al. 2012, El Kayal et al. 2011). However, temperature, photoperiod, and their interactions may nevertheless affect onset and duration of the bud set process (Bigras and D'aoust 1992, El Kayal et al. 2011, Hamilton et al. 2016, Singh et al. 2017). Several studies showed that short-day or blackout treatments resulted in the induction of bud formation, cessation of height growth, and significant increases in carbohydrate content, root nutrient contents, and root dry mass (Colombo et al. 2001, Lamhamedi et al. 2013).

White spruce (*Picea glauca* [Moench] Voss), a determinate species, is one of the most commercially important tree species in Canadian boreal forests (Beaulieu et al. 2009). Genetic variation in the timing of bud set has been found among natural populations of white spruce in the eastern part of the boreal forest (Li et al. 1993, 1997; Jaramillo-Correa et al. 2001). A similar trend was observed for the sympatric black spruce (*Pica mariana* [Mill.] BSP) (Beaulieu et al. 2004, Perrin et al. 2017) and for interior spruce (*Picea glauca engelmannii* complex) in Western Canada (Liepe et al. 2016).

Reforestation programs in Eastern Canada typically use genetically improved stock (up to 90 percent in the province of Quebec) and until now, no results on the investigation of the genetic variation in the timing of bud set was reported for this type of material under plantation site conditions. Also, bud set has generally been assessed only as a single stage or an index (Bousquet 1984, Jaramillo-Correa et al. 2001, Li et al. 1993) and sometimes inferred from growth cessation. Growth studies, however, have shown that bud set is a complex and dynamic sequence of events (Cooke et al. 2011, El Kayal et al. 2011, Perrin et al. 2017, Rohde et al. 2011). It remains unknown whether these events are highly correlated, and if they involve independent environmental cues and different levels of genetic control (Perrin et al. 2017).

The present study is part of a research project on assisted migration initiated in 2013 by the Quebec Ministry of Forests, Wildlife, and Parks to assess local genetic adaptation and phenotypic plasticity of functional traits of various genetically improved white spruce seed sources. The overall goal is to refine their deployment under climate change (Benomar et al. 2015, 2016, 2018; Otis Prud'homme et al. 2018; Villeneuve et al. 2016). Results reported so far have shown the existence of clinal variation in height growth, which was partially driven by the trade-off between photosynthetic rate and water use efficiency, mediated by genetic variation in stomatal conductance. Furthermore, genetically improved white spruce seed sources in Quebec exhibit a similar level of phenotypic plasticity for several functional traits. In the present study, we focus on bud phenology by (1) assessing the variation in bud set phases among eight genetically improved white spruce seed sources and its association with height growth and geographical origin, and (2) examining the level of interdependency among bud set phases.

Material and Methods

Genetic Material and Experimental Design

The study was carried out using eight white spruce seed sources from six first-generation and two second-generation clonal seed orchards (table 1).

Table 1. Geographic coordinates of the centroid of plus-trees (i.e., the location of the parent trees) that make up the eight white spruce seed sources used in this study.

Seed source	Locality	Latitude (°N)	Longitude (°W)	Target ecological region*
S01-1	Wendover	46.39	71.94	2b, 2c
S01-2	Fontbrune	46.43	75.74	1, 2, 3, 4
S01-3	Baby	47.75	78.47	3aS, 4a, 4b, 4c, 5a, 5b, 5cT
S01-4	Desroberts	48.76	77.86	5a, 5b, 5cS, 5cT, 6a, 6c, 6e
S01-5	Robidoux	48.55	65.59	4g, 4h, 5h, 5k
S01-6	Falardeau	48.54	71.73	4c, 4d, 4e, 5dM, 5dT095, 5dT096, 5dT097, 5dT098, 5dT099, 5cM, 5cT
S02-1	Berthierville	46.08	73.18	1, 2, 3, 4aT037, 4bM, 4bT039, 4bT041
S02-2	Sainte-Luce	48.35	68.35	4, 3dS, 3dT, 5cM, 5dM, 5eT, 5h

*Ecological regions are described in Saucier et al. (2009).

Figure 1. Seedlings performance and bud set timing were evaluated at the Watford plantation site (Photo by Mohammed S Lamhamedi, April 2016).

The first-generation seed orchards are the most commonly used for reforestation in Québec, Canada, and were established about 30 years ago using phenotypically plus-trees selected in local natural forests from distinct regions. The second-generation seed orchards were established more recently using grafts of plus-trees selected from the top-performing, open-pollinated families from across Québec and Ontario and assessed in a series of genecological tests (Beaulieu et al. 2009).

Open-pollinated seeds were collected from each seed orchard for 2 consecutive years (2008 and 2009). Seedlings were produced from the mixed seed collections for each seed orchard in the State forest nursery of St-Modeste Québec, Canada (47.50 °N, 69.23 °W) using Québec's standard nursery cultural practices (Lamhamedi et al. 2006, Villeneuve et al. 2016).

A genetic field test was established using a randomized complete block design with four blocks; each block being partitioned into eight plots in which the eight seed sources (SO) were assigned randomly. The size of each plot was about 730 m2 (0.18 ac) and contained 144 trees (12 by 12 rows of trees) (figure 1). The plantation site was located in the Eastern Canadian forest near the locality of Ste-Rose de Watford, Québec, Canada (46.30°N, 70.40°W) in the sugar maple-yellow birch domain on loamy soil. The 2-year-old seedlings were planted at 2.25 m by 2.25 m (7.38 by 7.38 ft) spacing during the last week of May 2013.

Prior to outplanting (in 2012 at the end of the second nursery growing season), characteristics were assessed on a sample of 15 seedlings from each seed orchard. Average values ranged from 33.5 cm (1.1 ft) to 41.9 cm (1.36 ft) for height, 11.9 g (0.41 oz) to 15.5 g (0.55 oz) for total dry mass, and 1.5 to 1.68 percent for shoot nitrogen concentration.

Additional information regarding soil characteristics of the planting site and morphophysiological variables under forest nursery and site conditions can be found in Otis Prud'homme et al. (2018) and Villeneuve et al. (2016). At the end of the first growing season at the planting site, survival averaged 98 percent (Villeneuve et al. 2016).

Bud Set Monitoring

Apical bud set was monitored in summer 2013 from July 7 (DOY 188) to September 11 (DOY 254). Monitoring was done every 2 days except for the last 2 weeks, when data were collected every 3 days. Monitoring observations were made on the 15 central seedlings within each plot for a total of 480 seedlings (15 trees x 4 blocks x 8 seed sources). Five bud set phases were defined according to Dhont et al. (2010): phase 1 (white bud); phase 2 (beige bud); phase 3 (brownish bud); phase 4 (visible brown bud); and phase 5 (opaque brown, clearly visible bud). Bud set phase was assessed using binoculars for the two first phases and by visual inspection for the later phases. Photos showing the different bud phases are described and illustrated by Dhont et al. (2010).

For each seed orchard within each block, the timing of each bud set phase was estimated as the time at which 50 percent of seedlings reached that phase (BS50). The cumulative frequency of bud set was calculated using the following logistic regression curve:

$$Y = \frac{1}{1 + e^{a(X - BS_{50})}} \qquad \textbf{1.}$$

where Y is the cumulative frequency of X, X is the timing of seedling bud set within the plot, and a is a parameter representing the rate of the process.

The time at which 25 (BS25) and 75 (BS75) percent of seedlings reached each bud set phase was also estimated as in equation (1).

Climate Data During the Sampling Year

A weather station was installed on the plantation site after planting. The station was supplied with a shielded air temperature and relative humidity sensor (HMP50, Vaisala, Helsinki, Finland), PAR sensors (Li 190 Campbell Scientific, Logan, UT, USA), pluviometer, and soil temperature sensors (figure 2). Data were recorded hourly throughout the growing season using a datalogger (CR10X, Campbell Scientific, Logan, UT, USA).

The data were used to estimate the accumulation of chilling hours (ACHs) according to Lamhamedi et al. (2005) as:

$$ACHs = \sum_{j=182}^{j=300} \cdot \sum_{i=1}^{i=24} (T_r - T_h) \ and \ (T_r - T_h) > 0 \qquad \textbf{2.}$$

where Tr, is the reference temperature (=5°C), Th is the hourly temperature, i is the hour of the day,

Figure 2. A permanent meteorological station was installed April 2013 at the Watford plantation site (Photo by Mohammed S. Lamhamedi, July 2013)

and j is the day of the year. The July 1 (DOY=182) was used as the starting day for calculation of ACHs which corresponds to one week before bud set measurements began.

Statistical Analyses

Data were analyzed using the SAS/STAT software version 9.4 (SAS Institute, Cary, NC, USA). Bud set (BS50) was subjected to repeated-measures analysis of variance (Proc Mixed) using the following linear mixed model:

$$Y_{SPB} = \mu + \beta_s + \beta_P + \beta_{SP} + v_B + e \qquad \textbf{3.}$$

Where Y_{SPB} is the timing of bud set; μ is the grand mean; β_p is the fixed effect of seed source; β_s is the fixed effect of bud set phase; β_{SP} is the fixed effect of the interaction between seed source and bud set phase; v_B is the random effect of block; and e is the residual error.

Four covariance structures were tested: Heterogeneous Banded Toeplitz (TOEPH), Autoregressive(1) (AR[1]), Compound Symmetry (CS), and Heterogeneous AR(1) (ARH[1]). The latter was chosen because it had the lowest Akaike information criterion (AIC) value. Comparisons of means were performed using the Tukey's range test, and differences were considered significant at $P < 0.05$. The relationships between bud set phases and between the first bud set phase and geographic variables (latitude and longitude) of seed source origins were tested using Proc Corr.

Results

Mean daily temperature from July to mid-September averaged 17.1 ± 3.2 °C (62.8 ± 5.7 °F) on the plantation site with a coefficient of variation of 19 percent (figure 3a). The accumulation of chilling

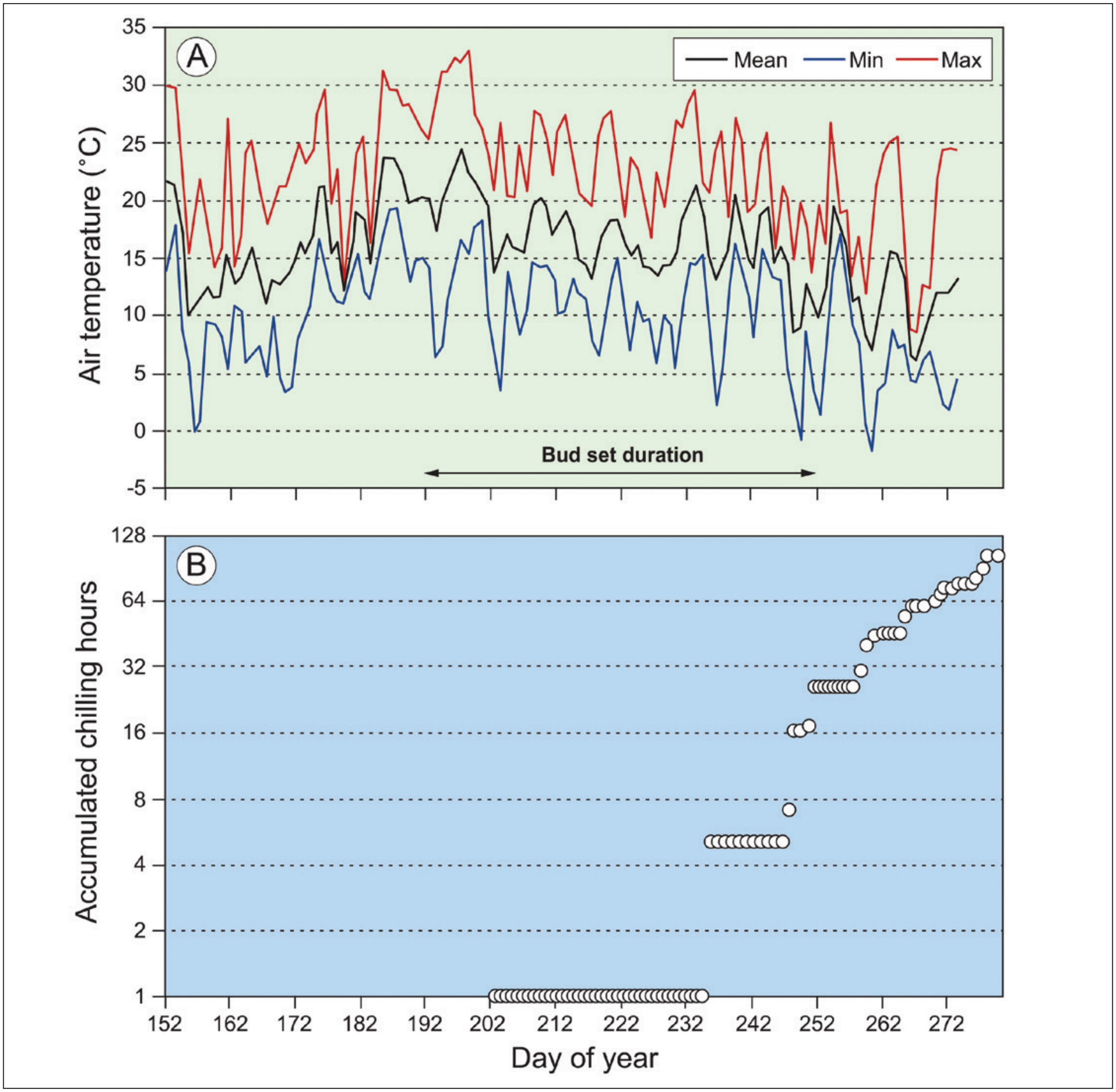

Figure 3. (a) Mean, minimum, and maximum daily air temperature and (b) accumulation chilling of hours during the first growing season at the Watford plantation site. July 1 (DOY=182) was used as the starting day for calculation of chilling hours.

Table 2. The effect of seed source on bud set for white spruce seed sources from the first- and second-generation seed orchards at the end of the first growing season in the Watford forest plantation site.

		BS50		BS25		BS75	
	DF	F value	P value	F value	P value	F value	P value
First-generation seed orchards (n=6)							
Seed source	5	1.70	0.185	1.17	0.360	1.92	0.141
Phase	4	2484.60	<0.001	1725.19	<0.001	2096.55	<0.001
SS*P	20	0.83	0.669	0.79	0.713	1.17	0.305
Second-generation seed orchards (n=2)							
Seed source	1	1.56	0.258	2.10	0.197	0.56	0.483
Phase	4	561.97	<0.001	375.85	<0.001	331.73	<0.001
SS*P	4	0.89	0.487	0.75	0.567	0.86	0.501
Combined first- and second-generation seed orchards							
Seed source	7	1.74	0.124	1.17	0.358	1.52	0.210
Phase	4	3009.53	<0.001	2040.10	<0.001	2190.60	<0.001
SS*P	28	1.07	0.397	0.76	0.791	0.90	0.610

DF = degrees of freedom

hours (ACHs) during the monitoring period reached only 4 hours (figure 3b). The mean July temperature in 2013 was 19.9 °C (67.8 °F), which was 1.5 °C (2.7 °F) above climate normals (1981 to 2010). Also, 2013 was the warmest and wettest year from 2010 to 2017 at the plantation site.

Average bud set initiation (BS50) was DOY 200 ±2 (July 19), and the first phase was completed within 12 days. The average date of the last phase, which corresponds to complete bud development was DOY 240 (August 28). None of the five bud set phases differed by seed source (tables 2 and 3). Similarly, BS25 and BS75 for the five phases were similar among seed sources. Bud set duration averaged 38 days (from the first to the fifth phase) and did not differ among seed sources (P=0.32). Intra-seed source variance for each bud set phase was similar between first- and second-generation seed orchards and averaged (2.3 day). This variance was also unrelated to both latitude and longitude ranges of plus-trees of the six first-generation seed orchards (table 3, figure 4).

The occurrence of each bud set phase was dependant on the occurrence of the previous phase (table 4). The strength of this interdependency was higher for the first

Table 3. Mean day of year (DOY± standard deviation) when 50 percent of seedlings from each of the eight seed sources reached each bud set phase (BS50).

Source	Phase 1	Phase 2	Phase 3	Phase 4	Phase 5
S01-1	200±2.91	204±2.02	215±2.93	225±2.19	239±2.35
S01-2	200±1.51	205±0.91	214±1.43	225±0.47	237±1.08
S01-3	200±1.28	205±1.09	213±1.64	225±0.83	238±1.18
S01-4	201±1.19	204±1.48	214±2.03	225±0.24	237±0.92
S01-5	199±2.15	203±1.35	213±3.1	223±2.31	236±3.13
S01-6	199±0.68	203±1.51	212±1.26	224±1.53	236±2.01
S02-1	199±1.55	204±2.52	213±2.18	225±0.81	237±2.36
S02-2	201±1.41	205±1.79	214±2.64	226±1.58	237±4.07

For all phases, means were similar at α=0.05.

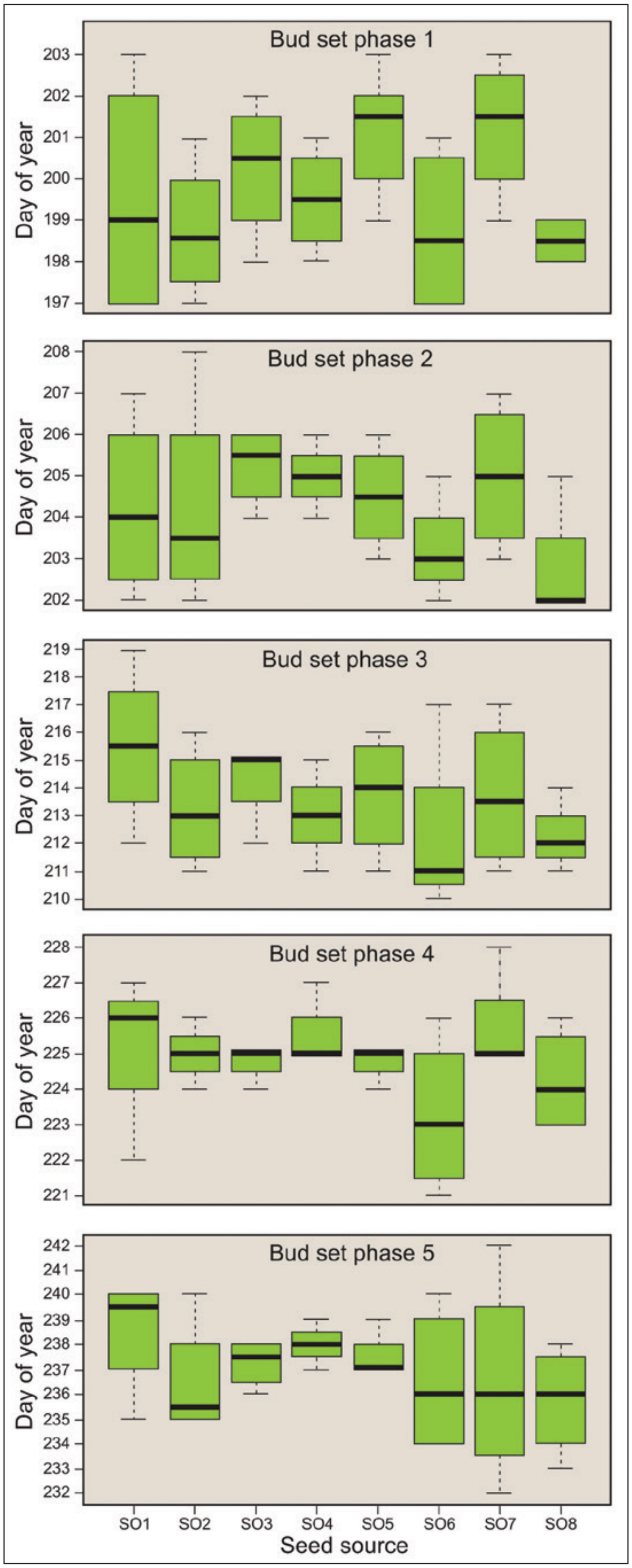

Figure 4. Timing of the five bud set phases of seedling of eight seed sources of white spruce during the first growing season in forest plantation of Watford. The timing of each phase corresponds to the day of the year at which 50 percent of seedlings reached the stage.

three phases and was marginal for the last two phases (table 4). The timing of the first bud set phase was unrelated to the latitude and longitude of seed source origins (figure 5). The relationship between bud set and growth during the first growing season was marginal (P=0.07).

Discussion

The present study was part of a research project motivated by the urgent need to mitigate climate change effects. The project aimed to fill physiological knowledge gaps to design robust climate-based seed transfer systems for commercial forest tree species in Quebec, Canada. Phenological traits are part of functionals traits involved in tree fitness through the synchronization of a tree's growth cycle with its local environment (Cooke et al. 2012, Savolainen et al. 2004). Our results showed a lack of variation in bud set phenophases among the eight white spruce seed sources most used in Quebec for its reforestation program. Unexpectedly, the variation observed in growth traits during the juvenile phase (Benomar et al. 2016, Otis Prud'homme et al. 2018, Villeneuve et al. 2016) was only marginally explained by the bud set timing.

Clinal variation for phenological traits has been found for several boreal tree species including white and black spruces (Beaulieu et al. 2004; Hurme et al. 1997; Li et al. 1993, 1997; Perrin et al. 2017). In contrast, seed sources in the present study were similar in their bud set timing. These contrasting results may be related to: i) the combined effect of large within-population variation for the measured traits and small ecological distance between tested seed sources; ii) the effect of selection pressure; and/or iii) abnormal climatic conditions at the planting site during the

Table 4. Matrix of phenotypic correlation coefficients between the timing of the five bud set phases of the eight white spruce seed sources tested. Significant correlations (P<0.05) are in bold and marginally significant correlations (P<0.1) are underlined.

	Phase 1	Phase 2	Phase 3	Phase 4	Phase 5
Phase 1		**0.70**	0.39	0.42	0.10
Phase 2			**0.72**	0.53	0.44
Phase 3				0.68	**0.82**
Phase 4					0.62
Phase 5					

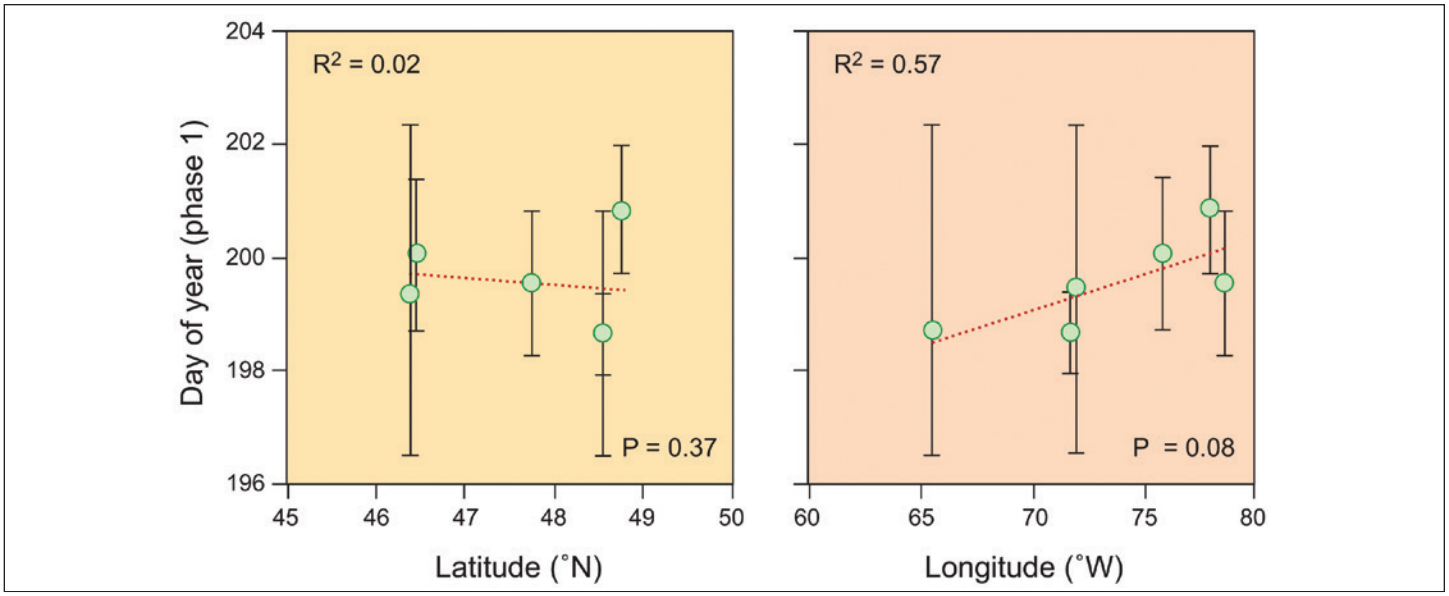

Figure 5. Timing of the first phase of bud set plotted against the latitude and longitude of seed source origin. The correlations were not significant at $P<0.05$. Second generation seed orchards (SO2-1 and SO2-2) were excluded from the regression analysis because they were composed of trees representing multiple widespread provenances from Québec and Ontario, Canada.

measurement period. Each of these are discussed further in the following paragraphs.

First, the extensive genetic variation existing at the intra-population level in white spruce (Bousquet, 1984, Li et al. 1993) constitutes a major challenge when examining genetic differentiation among populations at fine geographical scale as the case herein. Also, the narrow geographical range (2.37° of latitude) and the small number of seed sources tested in the present study may lead to the observed contrasting results with previous range-wide scales studies. In fact, Bousquet (1984) used 91 provenances covering 11.5° of latitude and 62° of longitude, and Li et al. (1993) used 57 provenances from Québec and Ontario covering 6.5° of latitude and 20° of longitude.

Second, breeding programs for white spruce started in 1972 and resulted in the installation of a series of first-generation and second-generation seed orchards. This artificial selection substantially improved white spruce growth. The increase in growth traits by artificial selection may either result from an increased growth rate or from an indirect selection for increased growth duration. The effect of artificial selection on the level of local adaptation of adaptive traits still remains unquantified. For now, MacLachlan et al. (2018) found a similar level of local adaptation for phenological traits between natural and improved seed sources for interior spruce (*Picea glauca* × *P. engelmannii*) in Alberta, Canada. In a previous study (Benomar et al. 2015, 2016), it was found that height growth could be explained by the mean value of photosynthetic-related traits, but the small variation in growth existing between seed sources may suggest an unbalanced effect of selection on bud set timing among seed sources. Further investigations are necessary to confirm this last hypothesis.

Third, the warm conditions during the growing season when data were collected likely delayed bud set and particularly the last phase. Bud set for determinate species such as white spruce, however, is known to be controlled endogenously through preformed growth units related to number of primordia (formed during the previous growing season), and therefore, environmental cues may have little effect on the time course of bud formation.

In contrast with previous findings (Bousquet 1984, Jaramillo-Correa et al. 2001, Li et al. 1993), the timing of bud set in our study explained only a small part of the observed variation of height growth among seed sources. In our previous studies (Benomar et al. 2015, 2016), we found a significant contribution of the CO_2 assimilation rate to variation in height growth among the tested seed sources. Given that, we expect that the variation in growth performance among the seed sources tested in the present study is linked to photosynthetic rate.

Based on these results, a similar timing of dormancy induction and cold tolerance is likely among tested seed sources, and if so, risks of cold injury could be limited for southern seed sources transferred to the northern locations. Our results, however, were obtained at the end of the first growing season on three plantation sites located in different bioclimatic domains in Quebec and revealed a high survival rate (> 98 percent) and complete absence of frost damage on the three sites (Villeneuve et al. 2016). Further investigations of the time course of dormancy and cold hardiness are recommended.

Perspectives

Phenotypic plasticity (i.e., the ability to change the phenotypic expression of a genotype in response to a change in environmental conditions) of bud set and cold hardiness for spruce species still deserves investigation. Better knowledge on bud set plasticity and its variation among seed sources, as well as its relation with frost hardiness, should help elucidate physiological and phenological influences on survival and performance of varying seed sources when transferred to sites that are currently colder but where temperature will increase over time due to climate change.

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