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Frost hardiness vs. growth performance in trembling aspen: an experimental test of assisted migration

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Summary

1. According to the range limit hypothesis, the distribution of many temperate species is restricted by a trade-off between their capacity to survive winter extremes in the north (or high elevation) and their ability to compete with better-adapted species in the south (or low elevation range limits). This trade-off has important implications in forestry, particularly in the context of managed seed movement under climate change.

2. In this study, we aim to quantify trade-offs among growth, frost hardiness and timing of leaf senescence and bud break in populations of trembling aspen, *Populus tremuloides* Michx., which were observed in a large reciprocal transplant experiment across five planting sites in western Canada, including additional provenances from Minnesota.

3. After 10 years, we found pronounced increases in productivity as a result of long-distance transfers in a north-west direction. For example, provenances moved 1600 km north-west from Minnesota to central Alberta (a shift of 7° latitude to the north) produced almost twice the biomass of local sources. Similarly, provenances moved 800 km from central Alberta to north-east British Columbia (4° latitude north) also produced twice the biomass of local sources.

4. We further found that increased growth was not associated with lower survival rates. Bud break in provenances transferred north-west generally occurred slightly later than in local sources, suggesting decreased risk of spring frost injury. Leaf abscission was later in provenances transferred in a north-west direction, but they appeared to be very frost hardy, well ahead of very rare early fall frost events.

5. *Synthesis and applications*. This study demonstrated that assisted migration prescriptions have considerable potential to enhance forest productivity. In the case of aspen, even long-distance seed transfers in a north-west direction were successful. We conclude that benefits in productivity outweigh potential risks associated with northward transfer of aspen planting stock under both current and projected future climate conditions.

Key-words: bud break, frost risk, leaf senescence, phenology, *Populus tremuloides*, provenance trial, seed transfer

Introduction

Populations of widespread forest trees are typically adapted to a variety of local climate conditions in which they occur. As climate changes, locally adapted genotypes may become increasingly mismatched with their local environments, potentially leading to reduced productivity and forest health (Gray *et al.* 2011). This problem can be reduced with human-aided movement of reforestation stock to appropriate climate environments, and large-scale reforestation programes offer an opportunity to implement such a climate change adaptation strategy cost-effectively (Gray *et al.* 2011; Pedlar *et al.* 2012). However, such prescriptions, especially those that aim to pro-actively match planting stock to anticipated future climates, run the risk of mal-adaptation under current conditions, with frost damage the most obvious risk (Howe *et al.* 2003; Savolainen, Pyhäjärvi & Knürr 2007).

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In North America, trembling aspen, *Populus tremuloides* Michx., is one of the most widespread and genetically diverse tree species. It is most abundant in the boreal forests of north-east British Columbia, northern and central Alberta and central Saskatchewan. Here, aspen covers an area of approximately 60 million hectares of boreal mixed wood forest, providing habitat for a variety of mammals, birds and insects, as well as other plant species (Stelfox 1995; Canadian Forest Service 2011). Aspen is also an important commercial forest resource in this region, accounting for approximately half of the annual forest harvest, and is primarily processed into oriented strand board (OSB) for construction purposes and pulp for paper products. More recently, aspen has also been used for conversion to biofuels and other biomaterials (Balatinecz, Kretschmann & Leclercq 2001; Sannigrahi, Ragauskas & Tuskan 2010).

Given current and predicted climate change for western Canada (Christensen *et al.* 2007; Mbogga, Hamann & Wang 2009), this important renewable forest resource appears to be under considerable threat. Over the last two decades, loss of forest productivity and dieback of aspen and other tree species has been well documented along the southern fringe of the boreal forest and further south in the United States (Hogg, Brandt & Michaelian 2008; Allen *et al.* 2010; Peng *et al.* 2011; Anderegg *et al.* 2012). Michaelian *et al.* (2011) conducted a detailed survey covering an area of 11·5 million hectares in western Canada to assess the impact of drought-induced aspen dieback. They report 45 megatonnes of dead above-ground biomass, which represented 20% of the total above-ground biomass (226 megatonnes) in the surveyed area. Climate change towards warmer and drier conditions appears to be the primary driver of the observed aspen decline, amplified by other factors such as forest pests, fire suppression policies and other management practices (Marchetti, Worrall & Eager 2011; Anderegg *et al.* 2012; Worrall *et al.* 2013).

One way to address these issues is to afforest the affected areas with different species, or differently adapted planting stock of the same species to better match current and anticipated climate conditions. In a study with lodgepole pine, Rehfeldt, Wykoff & Ying (2001) suggest that adapting to global climate change requires a major redistribution of forest tree species and genotypes across the landscape. They report, for example, that genotypes which are best suited to future climates in north-east British Columbia (latitude 60°) are currently located as much as 9° latitude to the south. Similar work for aspen indicates that relocating aspen planting material northwards by 1–2° latitude is required just to account for climate change observed over the last two decades (Gray *et al.* 2011).

Any movement of planting stock, however, could increase the risk of freezing injury if migrated genotypes are not synchronized with the local growing season (Aitken & Hannerz 2001). Frost hardening and de-hardening coincides with leaf senescence in autumn and bud break in spring. Early spring growth is particularly susceptible to late spring frosts, since tissues are actively growing and not lignified. Bud break is primarily a response to temperature and is initiated after a certain heat sum is acquired (Hunter & Lechowicz 1992; Li, Wang & Hamann 2010). In contrast, autumn leaf senescence in most species, including aspen, is triggered by photoperiod (Horvath *et al.* 2003; Keskitalo *et al.* 2005; Fracheboud *et al.* 2009). Notably, the trigger for the onset of cold hardiness (day length) is decoupled from the actual selective environmental factor (frost events). This poses a special concern when moving seed because a given day length may not correspond to the same frost risk in different geographic locations.

The distribution of many temperate tree species is thought to be determined by their adaptive capacity to survive winter extremes in the north or at high elevation, and their ability to compete with better-adapted species in the south or at low elevation range limits (MacArthur 1984; Woodward 1987). This is a consequence of trade-offs between maximizing growth by fully utilizing the available growing season, and avoiding injury or mortality due to late spring or early autumn frosts (Loehle 1998; Aitken & Hannerz 2001; Leinonen & Hänninen 2002; Koehler, Center & Cavender-Bares 2012). According to Loehle (1998), frost protection requires significant plant resources, being achieved by structural investments (e.g. increased lignification, thicker leaves and cell walls), physiological responses (e.g. accumulation of lipids, sugars or membrane proteins) and conservative growth strategies (e.g. early autumn leaf senescence and late bud break).

This paper aims at developing recommendations for moving planting stock, considering such trade-offs in growth and adaptive traits. Hence, the objectives of the present study are (1) to assess the impact of moving aspen seed sources throughout western Canada on growth and survival in a large-scale reciprocal transplant experiment; (2) to investigate geographic patterns of genetic variation in adaptive traits, including the timing of bud break and leaf senescence, and the onset and degree of frost hardiness; (3) to quantify frost risk environments in early autumn and late spring to which local and transferred aspen populations need to be adapted; and (4) to assess risks and potential benefits of seed movement throughout the western boreal forest. This information could in principle be used to develop sophisticated climate change adaptation strategies that account for uncertainty in future climate projections. For example, we could potentially lower risks (e.g. due to variable future climate), by sacrificing some growth potential (e.g. through a more conservative growth strategy). However, to keep the scope of the study manageable, we do not model performance and trade-offs under uncertain future environments. Instead, this paper aims at management recommendations that enhance health and productivity of planted aspen forests in response to recent climate change trends.

Materials and methods

PLANT MATERIAL AND EXPERIMENTAL DESIGN

The effects of moving planting stock to new growing environments were tested with a reciprocal transplant experiment, established by the industrial members of the Western Boreal Aspen Cooperative in 1998. The planting sites and collection locations were chosen to represent forest management areas of the participating Canadian forestry companies, and the management areas in turn reflect ecological zones with relatively homogeneous climatic and physiogeographic conditions (Selby & Santry 1996). The ecological regions include the south-eastern boreal plains of Saskatchewan (SK), the Alberta foothills ecoregion (ABf), the central boreal plains of Alberta (cAB), the northern boreal plains of Alberta (nAB) and the taiga plains of British Columbia (BC). The regions were unequally represented with three to eleven collection locations, reflecting assumptions where productive genotypes for reforestation in western Canada may be found. Also included are five seedlots from the boreal shield ecoregion in Minnesota (MN) for testing in western Canada (Fig. 1, Table 1). Note that there is no corresponding test site for this region.

The experiment comprises five common garden trials, and all seed sources collected for this study were planted at all sites. In total, 43 half-sib families from six regions were tested. Each collection thus represents seed from a single open pollinated female tree. In the subsequent text, we refer to half-sib families from this trial as provenances or collection locations. Trials were established with over-winter dormant stock in spring of 1998 as randomized complete block designs with six replications per seed source, planted in row plots with five trees per plot and surrounded by two rows of border trees. Thus, a total of 6450 seedlings (excluding border trees) were planted in the entire experiment with 1290 trees in each common garden.

Height and diameter at breast height (DBH) measurements for all 6450 trees were taken after one growing season in an outdoor nursery bed and nine growing seasons in the field in the fall of 2006. An additional height measurement was carried out for the central Alberta site in 2008 after eleven growing seasons in the field. Total above-ground biomass for trembling aspen was calculated according to the Canadian national biomass equations in kg dry weight (Ung, Bernier & Guo 2008). For all other physiologic and phenological traits, we had to employ a subsampling strategy to keep the study feasible while trying to capture most of the genetic variation present in this experiment. Phenology observations were carried out for all 1290 trees at the central Alberta test site. Cold hardiness measurements were carried out at the same site on six provenances from three regions (Minnesota, central Alberta and north-east British Columbia), sampling eight trees per provenance (indicated by numbers in Fig. 1). In total, 864 cold hardiness measurements were carried out at three dates for six test temperatures.

PHENOLOGY MEASUREMENTS

Timing of leaf senescence, expressed as day of year was determined based on an eight-level senescence scale according to Fracheboud *et al.* (2009). Scoring was carried out in autumn of 2010 at seven dates: 14, 18, 21, 23, 25, 28 September and 2 October. The day of year at which a senescence score of 5 (all leaves yellow) was reached was subsequently determined as follows for each individual tree: If a score of 5 was recorded on a single date, that date was used. If a score of 5 was recorded on multiple dates, the day of the phenological event was calculated as an average. If a score of 5 was not directly recorded, the day of year was inferred by means of linear regression from the bracketing dates and scores.

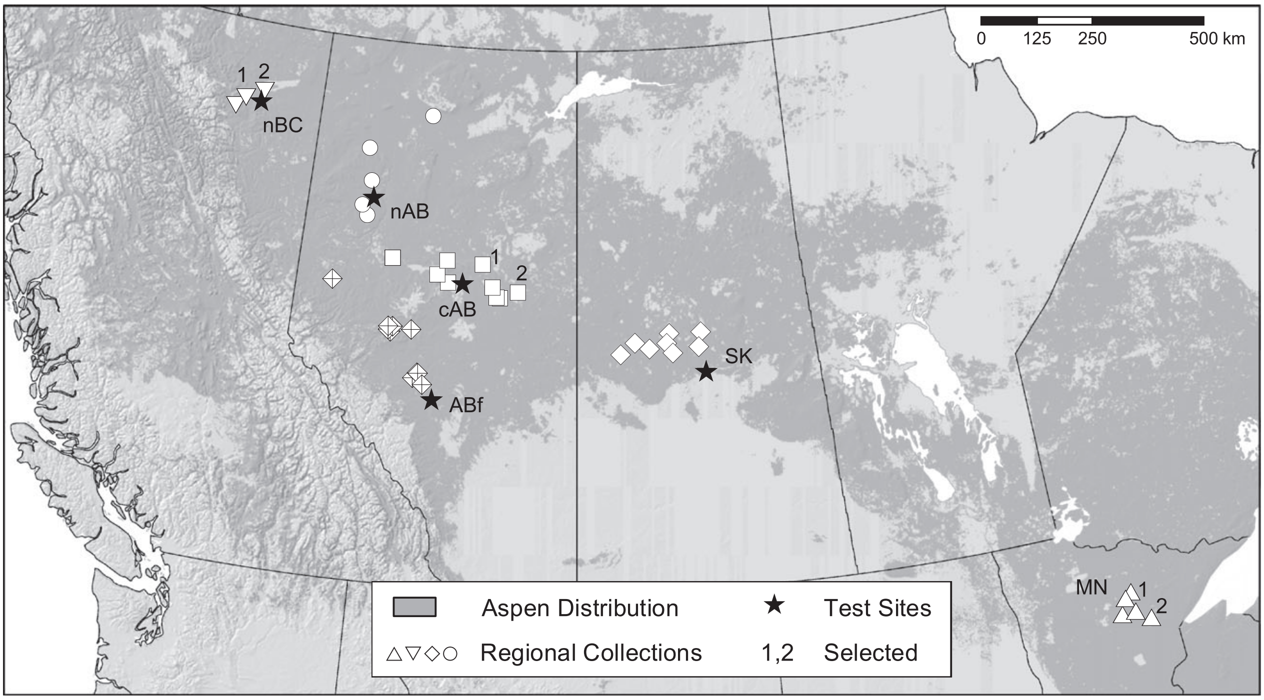

Fig. 1. Collection locations and test sites of the provenance trial series. Genotypes selected for the physiological study are indicated by numbers and are, for example, referred to as MN1 or MN2 in subsequent figures.

Table 1. Regional representation of seed collections, geographic information of test sites, source of weather station data and average temperature values for the 1961–1990 climate normal period

Region	Number of provenances	Test site coordinates			Weather stations*	Temperature (°C)†			
		Latitude	Longitude	Elevation (m)		EMT	$T_{\min}01$	$T_{\max}07$	MAT
Minnesota (MN)	5	–	–	–	216612	−42·2	−20·2	27·2	4·9
Saskatchewan (SK)	8	53°20′N	105°36′W	480	4056240	−49·4	−26·1	24·2	0·6
Alberta Foothills (ABf)	11	52°44′N	114°47′W	970	3015520-3	−44·1	−18·2	21·8	2·6
Central Alberta (cAB)	11	54°53′N	113°18′W	570	3060321	−46·1	−20·6	22·3	1·8
Northern Alberta (nAB)	5	56°46′N	117°28′W	525	3075040	−48·9	−22·9	22·4	0·8
North-east British Columbia (BC)	3	58°32′N	122°20′W	335	1192940	−47·2	−26·3	23·0	−1·0

*Weather station IDs according to (http://www.climate.weatheroffice.gc.ca) for Canada and according to (http://www.noaa.gov/) for Minnesota.

†All temperature values based on the 1961–1990 climate normal period. EMT, 30-year extreme minimum temperature; $T_{\min}01$, mean monthly minimum temperature for January; $T_{\max}07$, mean monthly maximum temperature for July; MAT, mean annual temperature.

The corresponding day length (*DL*) for the day of year (*DoY*) when a score of 5 was reached was calculated as a function of latitude and *DoY* according to Forsythe *et al.* (1995):

$$DL = 24 - \frac{24}{\pi}\cos^{-1}\left[\tan\frac{\mathrm{LAT}\pi}{180}\tan\phi\right]$$

where ϕ is the declination angle of the sun, calculated as:

$$\phi = \sin^{-1}[0\cdot 3979\cos\theta]$$

and where θ is the revolution angle, calculated as:

$$\theta = 0\cdot 2163 + 2\tan^{-1}\left[0\cdot 9671\tan[0\cdot 0086 \times (DoY - 186)]\right]$$

Assuming that leaf senescence is primarily controlled by day length, which is well documented for temperate tree species including poplars (Kriebel *et al.* 1976; Kriebel 1993; Horvath *et al.* 2003; Keskitalo *et al.* 2005; Fracheboud *et al.* 2009), we inferred differences in the day of leaf senescence for provenances based on the latitude of the other four planting sites. These estimates are meant to broadly characterize the average date of leaf senescence. We note that there may be temperature-modulated year-to-year variations in the date of leaf abscission, but for the purpose of interpreting geographic patterns of adaptive genetic variation, these were not considered relevant.

Bud break scores, calculated similarly to the leaf senescence data described above, were obtained from a previous study using the identical plant material from the central Alberta test site (Li, Wang & Hamann 2010). Here, we re-analysed these data in a different research context, inferring the average day of bud break (score 3: buds broken and leaves extending) for the six regions of our study design, using daily weather station data for the 1961–1990 normal period. The expected date of bud break for each individual tree was calculated according to a model optimized for aspen in the boreal forest (Beaubien & Hamann 2011). Required heat sums for bud break were determined as the daily sum of average temperatures with a start date set as January 1st and a threshold value set as 0°C. This summation continues up to the day at which a bud break score of 3 was reached, yielding a required heat sum statistic for the observed event. Based on the well-supported assumption that bud break is determined by a genetically controlled heat sum requirement (Lechowicz 1984; Hunter & Lechowicz 1992), an expected date of bud break could then be estimated for all provenances at all test sites.

COLD HARDINESS MEASUREMENTS

Cold hardiness was measured using the electrolyte leakage method (Zhang & Willison 1987; Morin *et al.* 2007), which quantifies frost damage by measuring the leakage of cell sap into the extracellular space due to ruptured plasma membranes. Plant material was sampled at the central Alberta test site from six provenances within three regions (Minnesota, central Alberta and north-east British Columbia) representing the full geographic extent of the experiment. For each provenance, we randomly selected eight trees from which we sampled one current year twig per freezing treatment. The collection was repeated three times in autumn 2011: on 22 August, 12 September and 10 October. All twigs were cut into 5 cm pieces and placed in 30-mL high-density polyethylene bottles (Fisherbrand, Fisher Scientific). Adding 5 mL of deionized water to the samples before freezing treatments was applied to ensure ice formation. The freezing treatments were 8°C (control), −5°C, −10°C, −20°C, −30°C on 22 August; 8°C (control), −10°C, −30°C, −50°C, −60°C on 12 September; and 8°C (control), −30°C, −60°C, −70°C, −80°C on 10 October. A programmable freezer (Model 85-3·1A, Scientemp Corp., Adrian, MI, USA) cooled the samples at a rate of 5°C per hour, holding the target temperature for 1 h, before re-warming to 8°C. Each segment was subsequently cut into 5-mm pieces, topped up with 20 mL deionized water, stored for 20–24 h at 8°C and manually shaken three times during storage. The amount of electrolyte leakage was measured at room temperature (approximately 20°C) using a conductivity meter (Oakton Acorn CON 6 Meter, Oakton Instruments, Vernon Hills, IL, USA). Conductivity readings were taken before (c1) and after (c2) all samples were boiled at 100°C for 50 min. Cell lysis (*L*) was calculated as:

$$L = \mathrm{REL} - \frac{\overline{\mathrm{REL}_C}}{100 - \overline{\mathrm{REL}_C}} \times 100$$

where REL is the relative amount of electrolyte leakage of the sample undergoing freezing treatments calculated as (c1/c2) × 100, and REL_c is the mean value of the control samples.

STATISTICAL ANALYSIS

Statistical analyses were performed using the R programming environment (R Development Core Team 2011), and graphics were prepared with the R package *ggplot2* (Wickham 2009).

Growth traits and phenology traits were analysed in a two-step process. First, means of provenances were separately estimated with a mixed effects model implemented with the *lmer()* function of the *lme4* package (Bates, Maechler & Bolker 2011). Blocks were treated as a random effect and provenance as a fixed effect, and row-plot means were considered the experimental units.

Second, regional means and standard errors of regional means were calculated in a second step from provenance means. Standard errors of regional means were used to calculate effect size statistics, that is, the probability that a transferred provenance matches or exceeds local sources at each test site. We used the *pt()* function, which integrates the area under a t-distribution, used for small sample sizes. To give an example, for an observed regional mean of 5·0 m height based on three provenance samples with a standard error of 0·25, the probability of matching or exceeding a reference value of 4·7 m is calculated as *pt*((5·0–4·7)/0·25, 3–1), resulting in an estimate of 82% confidence.

For frost hardiness measurements, standard null-hypothesis testing was carried out to detect significant differences in the degree of cold hardiness. To take advantage of the blocked experimental design, these data were analysed using a mixed effects model implemented with the *lmer()* function available through the R package *lme4* (Bates, Maechler & Bolker 2011). The fixed effects in this model were the selected regions MN, cAB, BC, and the random terms were block and provenance. Experiment-wise *P*-values were calculated using Tukey's adjustment for multiple mean comparisons.

CLIMATE DATA AND FROST RISK ASSESSMENT

In order to assess current frost risk environments to which plant populations are putatively adapted, we used daily weather station data for the 1961–1990 normal period from the National Climate Data and Information Archive for Canada (Environment Canada; http://www.climate.weatheroffice.gc.ca) and the Minnesota Climatology Working Group for historical climate data for Minnesota, USA (University of Minnesota; http://climate.umn.edu/doc/historical.htm) (Table 1). Frost risks for three regions sampled for frost hardiness measurements were derived by first calculating means and standard deviations for daily minimum temperatures for each day of the year of the 1961–1990 normal period. The probability of a frost event was then estimated based on a normal distribution characterized by daily means and standard deviations. Frost thresholds of interest (−5, −10, −20, −30 and −40°C) were first converted to *z*-scores, by subtracting the mean daily minimum temperatures and subsequently dividing by the daily standard deviations. The probability of a frost event equal or exceeding a given frost threshold was then calculated for each day as an integral under the normal distribution, using the function *pnorm()* of the R programming environment (R Development Core Team 2011). The resulting time series were subsequently smoothed with a 7-day moving average, since day-to-day variation simply reflects variability in daily climate data and not true day-to-day variation in frost risk.

Results

GROWTH DATA

After nine growing seasons in the field, we found pronounced increases in productivity of aspen trees as a result of long-distance seed transfers in a north-west direction. For example, provenances moved 1600 km north-west (and 7° latitude north) from Minnesota to central Alberta were 34% taller and had 84% more biomass than local sources (Table 2, see Table S1, Supporting information). Similarly, provenances moved approximately 800 km north-west (and 4° latitude north) from central Alberta to north-east British Columbia produced twice the biomass compared with local sources and were 15% taller. The farthest seed transfer tested in our design, which was from Minnesota to north-east British Columbia (2300 km north-west and 11° latitude north), still outperformed local sources by 17% in height and had more than twice the biomass. Increased performance as a result of north-west transfers was not associated with reduced survival. Minnesota provenances had survival rates similar to local sources at all sites. The next most southern group, the Alberta Foothills provenances, had better survival rates at all northern test sites relative to other sources than at its own

Table 2. Height (m) and survival (%) of provenances grown in the reciprocal transplant experiment after nine growing seasons in the field. Test sites are ordered along a north-west gradient. Local sources are marked in bold, and standard errors are given in parenthesis

	Test site				
Origin of seed source	SK	ABf	cAB	nAB	BC
Height (m)					
Minnesota (MN)	4·0 (0·06)	4·0 (0·23)	6·9 (0·23)	5·0 (0·11)	3·0 (0·08)
Saskatchewan (SK)	**3·3 (0·14)**	3·5 (0·09)	5·6 (0·08)	5·0 (0·16)	2·9 (0·07)
Alberta Foothills (ABf)	3·1 (0·12)	**3·1 (0·11)**	5·2 (0·15)	5·1 (0·16)	2·8 (0·14)
Central Alberta (cAB)	3·4 (0·11)	3·4 (0·11)	**5·2 (0·15)**	5·1 (0·11)	2·9 (0·09)
Northern Alberta (nAB)	3·1 (0·15)	2·9 (0·16)	5·0 (0·09)	**5·3 (0·06)**	3·6 (0·11)
North-east British Columbia (BC)	2·5 (0·15)	1·6 (0·24)	3·7 (0·11)	4·4 (0·12)	**2·5 (0·11)**
Survival (%)					
Minnesota (MN)	61·6 (6·01)	76·4 (6·96)	91·8 (1·53)	92·8 (1·36)	87·8 (2·24)
Saskatchewan (SK)	**66·0 (4·72)**	89·0 (2·00)	94·5 (1·43)	95·9 (1·43)	92·4 (2·07)
Alberta Foothills (ABf)	67·3 (4·54)	**74·2 (3·95)**	88·9 (3·91)	90·7 (3·11)	80·9 (2·90)
Central Alberta (cAB)	72·4 (2·19)	79·5 (5·18)	**94·8 (1·68)**	95·4 (1·61)	87·5 (2·29)
Northern Alberta (nAB)	73·6 (2·40)	78·8 (1·62)	92·0 (3·13)	**92·2 (2·63)**	90·0 (1·34)
North-east British Columbia (BC)	65·3 (3·53)	44·7 (4·41)	84·7 (2·33)	97·7 (2·33)	**77·7 (5·21)**

local planting site, where it ranked second lowest. Similar to Minnesota provenances, survival rates of the Saskatchewan and central Alberta provenances were comparable to local sources when transferred to the northern Alberta or north-east British Columbia test sites (Table 2).

Conversely, southward transfer of northern sources consistently resulted in decreased productivity. The north-east British Columbia and the northern Alberta provenances always ranked as the lowest and second lowest group of provenances at more southern planting sites. For example, the north-east British Columbia provenances were 16%, 28% and 50% smaller in height than the local sources at the northern Alberta, central Alberta and the Alberta Foothills test site, respectively (Table 2). Furthermore, north-east British Columbia provenances showed only 45% survival at the Alberta Foothills test site, which represents the warmest of all test sites with a mean annual temperature of 2·6°C (Table 1). The northern Alberta provenances showed only somewhat reduced height of 5% and 8% at the central Alberta and Foothills test sites, respectively.

SPRING AND AUTUMN PHENOLOGY

At the central Alberta test site, where phenology was recorded, the sequence of leaf senescence started with the most northern provenances (BC and nAB), followed by mid-latitude provenances (cAB, ABf and SK), and ended with Minnesota provenances turning yellow 10 days later than the first provenances from the north (Table 3). For the inferred day of leaf senescence at other planting sites, using day length as a presumed trigger, we found no discernible difference in sequence or dates of leaf senescence. Bud break occurred latest for the central Alberta and Saskatchewan provenances, while the north-east British Columbia provenances consistently broke bud earliest with the Minnesota provenances having an intermediate date of bud break (Table 3). Inferred bud break dates for 1961–1990 normal climate differed only by a few days, with provenances flushing first at the central Alberta site, followed by the Saskatchewan, Alberta Foothills and northern Alberta sites, and last at the north-east British Columbia site.

The above observations are also reflected in a relatively strong correlation between height and leaf senescence at the central Alberta test site, where phenology measurements were carried out (R^2 = 0·36, P < 0·0001). This correlation appears to be driven by early leaf senescence of the northern British Columbia sources and late leaf senescence of the Minnesota sources, when transferred to the central Alberta test site (Fig. 2a). For bud break, a strong latitudinal differentiation was not apparent (Fig. 2b). Sources from north-east British Columbia had the lowest heat sum requirements and broke bud first, but otherwise there was more within- than among-regional variation in the date of bud break, which could not explain variation in height (R^2 = 0·07). There is also no correlation between height and the utilized growing season, calculated as the day of leaf senescence minus the day of bud break (R^2 = 0·002, P = 0·78, data not shown).

COLD HARDINESS

The amount of freezing injury, measured as electrolyte leakage, revealed a general trend in which trees from Minnesota appear to be more vulnerable than trees from central Alberta and trees from north-east British Columbia, where the onset of frost hardiness occurs first (Fig. 3a). Our cell lysis data suggest clear regional differences with very little variation of frost hardiness within regions (Table 4, see also Fig. S1, Supporting information). At the August sample date, the −10 and −20°C treatments resulted

Table 3. The inferred average date of leaf senescence for four test sites based on a day length trigger measured at the cAB planting site in autumn 2011, and the average date of bud break for the 1961–1990 climate normal conditions inferred from heat sum requirements observed at the cAB planting site in spring of 2009. Test sites are ordered along a north-west gradient. The response in the native environment are marked in bold, and standard errors are given in parenthesis

	If transferred to				
Origin of seed source	SK	ABf	cAB	nAB	BC
Leaf senescence (day of year)					
Minnesota (MN)	269 (0·3)	269 (0·3)	270 (0·3)	269 (0·2)	269 (0·2)
Saskatchewan (SK)	**262 (0·2)**	262 (0·2)	263 (0·2)	263 (0·2)	263 (0·2)
Alberta Foothills (ABf)	262 (0·3)	**262 (0·3)**	263 (0·3)	262 (0·2)	263 (0·2)
Central Alberta (cAB)	263 (0·2)	262 (0·2)	**264 (0·2)**	263 (0·2)	263 (0·2)
Northern Alberta (nAB)	259 (0·4)	259 (0·4)	260 (0·4)	**260 (0·3)**	261 (0·3)
North-east British Columbia (BC)	259 (0·8)	258 (1·0)	260 (0·8)	260 (0·7)	**260 (0·8)**
Bud break (day of year)					
Minnesota (MN)	134 (0·7)	134 (0·7)	131 (0·7)	133 (0·7)	136 (0·7)
Saskatchewan (SK)	**140 (0·9)**	141 (1·1)	137 (1·0)	140 (1·0)	142 (1·0)
Alberta Foothills (ABf)	137 (0·8)	**137 (0·9)**	134 (0·9)	137 (0·9)	139 (0·9)
Central Alberta (cAB)	139 (1·0)	140 (1·2)	**137 (1·1)**	140 (1·1)	142 (1·1)
Northern Alberta (nAB)	134 (0·9)	135 (1·0)	132 (1·0)	**135 (1·0)**	137 (1·0)
North-east British Columbia (BC)	129 (0·7)	128 (0·3)	126 (0·3)	128 (0·3)	**131 (0·3)**

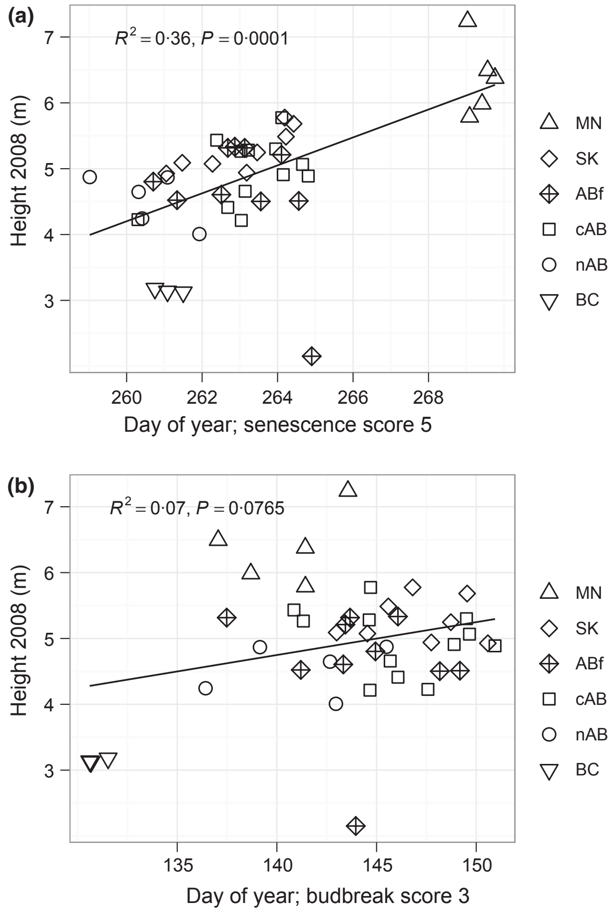

Fig. 2. Regression of 11-year height and timing of leaf senescence (a) and bud break (b). Shapes represent regions ordered along a north-west gradient.

in significantly higher vulnerability of Minnesota sources. Regional differences were most pronounced at all freezing treatments in September, with a sequence of increasing vulnerability from British Columbia to Alberta to Minnesota. At the October sample date, all sources showed generally low amounts of cell lysis, even under −80°C freezing treatments. However, trees from Minnesota were still the most vulnerable (Table 4, Fig. 3a).

The onset of frost hardiness also showed a strong correlation with leaf senescence (Fig. 3b). Trees from Minnesota were the least hardy and senesced the latest. On the other hand, the British Columbia provenances showed a high degree of hardiness and also were the first to turn uniformly yellow. The central Alberta provenances ranked in between, however showing a rather large spread of approximately 12% in cell lysis.

PHENOLOGY, HARDINESS AND FROST RISKS

A joint representation of phenology and regional frost risks is shown in Fig. 4. Generally, the probability of frost curves indicates a progression from relatively mild winters in Minnesota, to more severe winters in Alberta and British Columbia. For example, the British Columbia planting site has a 30–40% chance of a −30°C or colder frost event at any given day in January, whereas the corresponding probability in Minnesota is about 10–15%. Nevertheless, the time where mild frost events of −5°C or colder can be expected at the three planting sites is remarkably similar, although the probability increases much faster in autumn and decreases more rapidly in spring at the northern test sites.

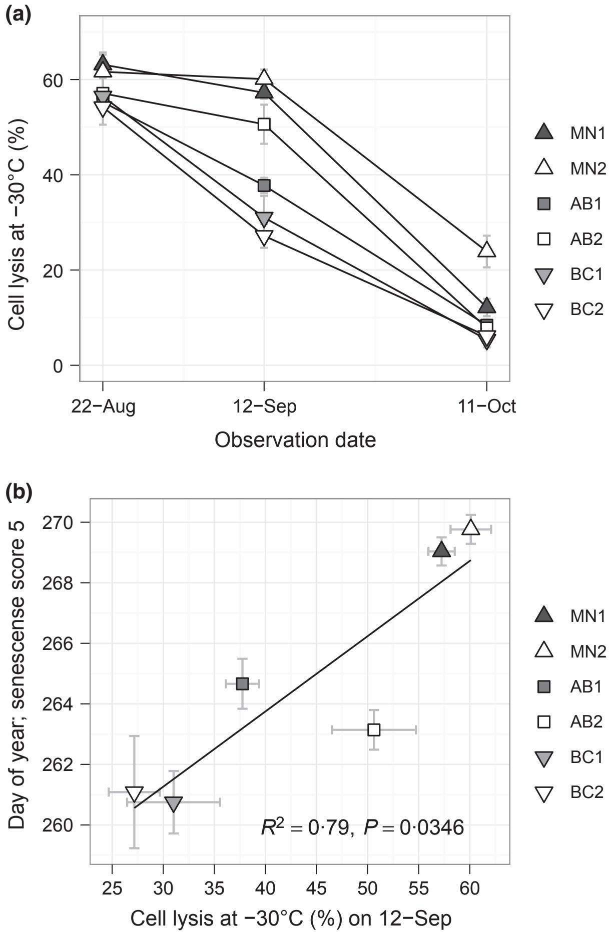

Fig. 3. Cell lysis at −30°C for six different aspen provenances measured on three dates in late summer and autumn in 2011 (a). Regression of the day of year of leaf senescence and cell lysis at −30°C for 12 September (b). Symbols and shading represents regions and genotype within region ordered along a north-west gradient.

The phenology of local provenances further appears to be remarkably well attuned to the frost risks of their local environments. The central Alberta provenances appear to perfectly avoid any frost risk without sacrificing the available growing season at their local central Alberta test site. The British Columbia provenances start growing very early in spring, but still avoid spring frost risks well in their local environment and in central Alberta. Regarding the date of leaf senescence, Minnesota provenances are the latest to turn yellow in fall. However, by mid-September, when −5°C frost risks start to appear at all

Table 4. Differences in frost hardiness measured as percentage cell lysis among the regions Minnesota (MN), central Alberta (cAB) and north-west British Columbia (BC), based on data shown in Fig. S1 (Supporting information)

	Cell lysis by region of origin (%)		
Freezing treatment	MN	cAB	BC
August			
−5°C	1·4 (0·6)^{A}	1·5 (0·5)^{A}	0·4 (0·2)^{A}
−10°C	49·6 (3·8)^{A}	31·2 (3·6)^{B}	22·7 (3·3)^{B}
−20°C	52·7 (4·1)^{A}	31·7 (3·9)^{B}	23·0 (4·1)^{B}
−30°C	62·4 (2·1)^{A}	56·2 (1·8)^{A}	55·3 (1·9)^{A}
September			
−10°C	21·2 (1·8)^{A}	10·9 (1·7)^{AB}	8·0 (3·8)^{B}
−30°C	58·7 (1·2)^{A}	44·2 (2·7)^{B}	29·1 (2·6)^{C}
−50°C	58·8 (1·2)^{A}	40·2 (4·4)^{B}	21·0 (2·5)^{C}
−60°C	66·0 (1·2)^{A}	44·9 (2·9)^{B}	32·1 (3·7)^{C}
October			
−30°C	18·0 (2·4)^{A}	8·1 (0·8)^{B}	5·8 (1·1)^{B}
−60°C	28·2 (3·5)^{A}	13·3 (0·9)^{B}	13·0 (1·6)^{B}
−70°C	18·0 (1·7)^{A}	10·4 (1·2)^{AB}	9·9 (1·2)^{B}
−80°C	18·8 (1·5)^{A}	11·5 (0·8)^{A}	12·1 (1·9)^{A}

Different letters in rows indicate significant differences at $P < 0·05$, and standard errors are given in parenthesis.

planting sites, they are already well hardened against −10°C frosts (Table 3). By mid-October, when −10°C frost risks start to appear with very low probabilities, Minnesota provenances are similarly hardened against −30°C to −80°C freeze events. That said, overall cell lysis values indicate that British Columbia and Alberta provenances were always more hardened at any given time than Minnesota sources. For example, British Columbia provenances sustained the same level of damage at −50°C that Minnesota sources sustained at −10°C in mid-September (around 20%).

Discussion

Adaptations for growth optimization vs. survival optimization are normally expected to be important trade-offs for temperate tree species (Leinonen & Hänninen 2002). Fitness of trees from high-latitude ecosystems should be strongly influenced by their ability to withstand harsh frost, whereas trees from milder climates should be favoured by natural selection based on higher growth rates and competitive fitness (Loehle 1998). By moving trees north out of their local habitat, one would generally expect an increasing risk of frost damage in autumn due to delayed growth cessation (Howe *et al.* 1995). This is broadly what we found in the current study with Minnesota provenances or Alberta sources moved to more northern positions showing a delay in the timing of leaf senescence, and a lesser degree of cold hardiness than local sources. However, this did not compromise survival, and the timing of the onset of dormancy and frost hardiness suggests that there should be no severe risks involved with moderate northward transfers of planting material.

Spring phenology was quite similar across all provenances observed at the central Alberta test site, except for the northern Alberta provenances. It is not uncommon that provenances from very high latitudes or very high elevation are adapted to make the most out of a short period of favourable temperatures and extended photoperiods and tend to be less conservative in utilizing the available growing season (Beuker 1994; Aitken & Hannerz 2001). In our case, this means that a northward movement of more southern provenances would typically lead to similar or slightly delayed onset of growth of introduced genotypes relative to local provenances, and therefore, northward transfers would not pose additional risks.

Another interesting observation is that the inferred dates of bud break and leaf senescence (for the regions BC, nAB, ABf, SK, MN) were not drastically different from the common garden site at which they were all observed (cAB), and this may have two explanations: while the risk of severe frost increases from south-east to north-west, there are virtually no differences in the frost-free period from Minnesota to north-east British Columbia (Fig. 4). Secondly, the date of leaf senescence of aspen populations coincides exactly with the inflection point of the day length curve (see Fig. S2, Supporting information). This means that although the day length trigger is temperature-decoupled, it will nevertheless work more or less appropriately under latitudinal transfers, because the day length does not vary with latitude around the date of the southern equinox (22 September), which coincides with the observed leaf senescence in aspen. The true critical day length that initiates senescence must be somewhat earlier than the date where we observe leaf senescence, so there may be small shifts in the timing of senescence under long-distance transfers. However, we find these quite small in absolute terms. For example, Minnesota provenance senesced six days later than the local sources when moved over 7° of latitude to the central Alberta planting site (Table 3).

Perhaps the most striking result of this large-scale transplant experiment is that moving aspen as far as 2300 km north-west from Minnesota to north-east British Columbia did not result in higher mortality rates or inferior growth. In fact, trees from Minnesota outperformed all local sources at Saskatchewan, Alberta and north-east British Columbia test sites. It seems that moving aspen as far as 2300 km north-west was not enough to reach the cold tolerance limit of aspen from Minnesota. That said, we should acknowledge that there are clearly discernible differences in frost hardiness from south-east to north-west, suggesting a typical trade-off between investments in growth (Minnesota sources) vs. investments in cold resistance (north-east British Columbia sources). However, when looking at the corresponding risk environments, investments in cold resistance appear nonoptimal for current climate conditions, that is, too conservative (Fig. 3b). All provenances appear to be sufficiently hardy early enough to withstand extremely unlikely cold events, for example −30°C in mid-September.

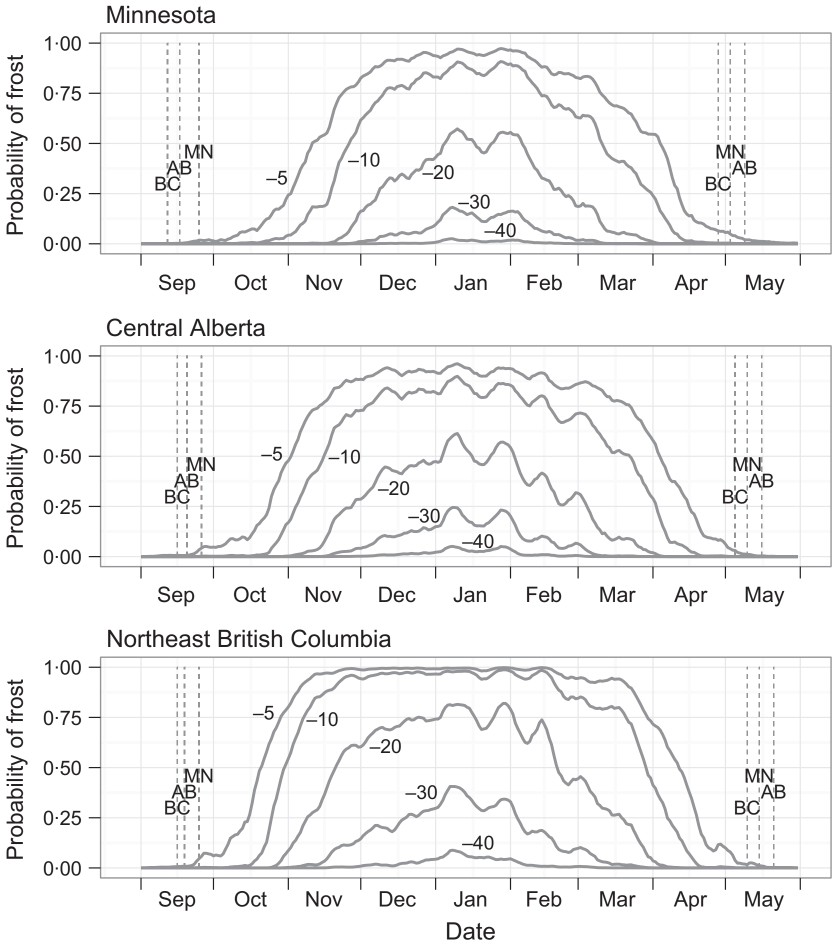

Fig. 4. Probability of a frost event being equal or exceeding a certain threshold value for any given day between 1 September and 31 May at the Minnesota (top) central Alberta (middle), and north-east British Columbia (bottom) planting sites. The expected day of bud break calculated for 1961–1990 normal climate and the expected day of leaf senescence for the latitude of planting sites are indicated by vertical lines for provenances from central Alberta, north-east British Columbia and Minnesota.

Such observations are normally interpreted as adaptational lag, caused by environmental change that exceeds the speed of evolutionary change (Matyas 1990; Matyas & Yeatman 1992). It is not uncommon that provenances transferred around two degrees north show increases in growth relative to local sources (Namkoong 1969; Mangold & Libby 1978; Morgenstern 1996). What is remarkable in the study is the magnitude of the adaptational lag in aspen, which may be due to the unique life history and regeneration biology of aspen. Aspen predominantly reproduces through vegetative reproduction from the distal portion of the root system, resulting in clones that are the oldest and largest known organisms (Mitton & Grant 1996). Aspen seed are very small and lack endosperm, resulting in a narrow window of viability. Suitable conditions with adequate moisture, bare ground and sufficient light are rarely met, limiting reproduction by seed (Peterson & Peterson 1992). Thus, adaptation through evolutionary processes is expected to be slow, which could explain the unusually large adaptational lag observed in this study.

A strong adaptational lag implies that a species should be more vulnerable to movement in one geographic or climatic direction than the opposite. We do, in fact, find indications that heat tolerances may be exceeded and compromise survival in provenances that were transferred southward. A transfer of the most northern provenances from north-east British Columbia to the warmest test site in the Alberta foothills (ABf being 3·6°C warmer than BC, Table 1) yielded by far the lowest survival of any transfer tested in this experiment (45%, Table 3). The data indicate that northward rather than southward movement of trees would be associated with less risk, which also suggests that inaction in the face of climate change may result in higher mortality.

To support decisions on regional seed transfers, we use means and standard errors for height (Table 2) to calculate the probability of a transferred provenance to match or exceed the productivity of local sources or to exceed predetermined reference values of 10%, 20% or 30% gain over the local sources (Table 5). It should be noted that regional representation from British Columbia is quite low with three provenances (or 90 genotypes per site). However, we only report probabilities for north or northwest transfers and exclude transfer recommendations for British Columbia provenances. Transfers in the opposite directions yield probabilities near zero (data not shown).

When interpreting these probabilities, it is important to keep in mind that these probabilities are based on the ranking of provenances at single test sites. Nevertheless, while different planting sites may strongly influence absolute productivity, the relative ranking of provenances should not change. Only if planting environments are so different from

Table 5. Probability of a transferred provenance to match or exceed the productivity of local sources, based on the means and standard errors for height (Table 2). We only report probabilities for north or north-west transfers. Transfers in the opposite directions yield probabilities near zero

Seed sources from	Transferred to	Probability of match or gain			
		Match	+10%	+20%	+30%
Minnesota (MN)	SK	>0·99	>0·99	0·73	<0·01
	ABf	0·99	0·97	0·85	0·45
	cAB	>0·99	>0·99	0·98	0·71
	nAB	0·03	<0·01	<0·01	<0·01
	BC	>0·99	0·98	0·50	0·02
Saskatchewan (SK)	ABf	>0·99	0·82	0·02	<0·01
	cAB	>0·99	0·09	<0·01	<0·01
	nAB	0·05	<0·01	<0·01	<0·01
	BC	>0·99	0·97	0·10	<0·01
Alberta Foothills (ABf)	cAB	0·50	<0·01	<0·01	<0·01
	nAB	0·12	<0·01	<0·01	<0·01
	BC	0·97	0·64	0·09	<0·01
Central Alberta (cAB)	nAB	0·05	<0·01	<0·01	<0·01
	BC	>0·99	0·94	0·15	<0·01
Northern Alberta (nAB)	BC	>0·99	>0·99	>0·99	0·98

test sites that genotype by environment interactions become a major factor, the regional rankings could change. An example for a site that does not conform to the general pattern of this trial series may be the northern Alberta (nAB) test site in a dry ecoregion, where provenances transferred from more southern or eastern origins have a low probability of matching or exceeding local sources.

There may be other important trade-offs, where more northern sources sacrifice growth and instead invest in resistance mechanisms to biotic or abiotic risk factors that we have not considered. One possible risk factor, drought resistance, was excluded by a related study (Schreiber *et al.* 2011) that showed that the Minnesota provenances tested in this experiment also have small vessel diameters, which conferred adequate drought resistance across all genotypes tested in this experiment. Adaptations to biotic factors such as pests and diseases by northern provenances that are absent in southern sources also appear unlikely. Sources from warmer environments and milder winters would generally be expected to be more exposed and therefore better adapted to pest and disease factors.

CONCLUSIONS

This study evaluated potential trade-offs and risks associated with seed transfer of aspen seedlings for reforestation in western Canada. Gray *et al.* (2011) suggested that in order to adapt to observed and predicted climate warming for western Canada, planting stock should be moved 2–3° of latitude northward. Such a prescription could lead to increased frost damage and a mismatch in the timing of bud break and leaf senescence with the available growing season.

Experimental cold hardiness testing and phenology observations in a common garden experiment revealed that seed transfer to more northern locations results in delayed timing of leaf senescence, but the onset of dormancy and frost hardiness suggests that there should be no severe risks involved with northward transfers of planting material. Northward movement was also associated with a slightly delayed onset of growth of introduced genotypes relative to local provenances and therefore poses no additional risks. We conclude that benefits in growth outweigh potential risks to survival associated with a northward movement of aspen populations in forestry operations. Even extreme long-distance northward movements had positive or neutral effects on growth and survival, while southward movement had clear negative consequences, highlighting the risk of inaction in the face of climate change. We therefore recommend that seed transfer guidelines in western Canada allow a moderate movement of aspen planting stock to account for adaptational lag. As for true long-distance transfers, notably the use of Minnesota sources in western Canada, we encourage forest companies and government agencies to pursue this option first on a relatively small operational scale. General recommendations of long-distance transfers should await results from this test series at rotation age, and concurrent experience from small-scale operational plantations.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. DBH (cm) and total dry mass (kg) of provenances grown in the reciprocal transplant experiment after nine growing seasons in the field

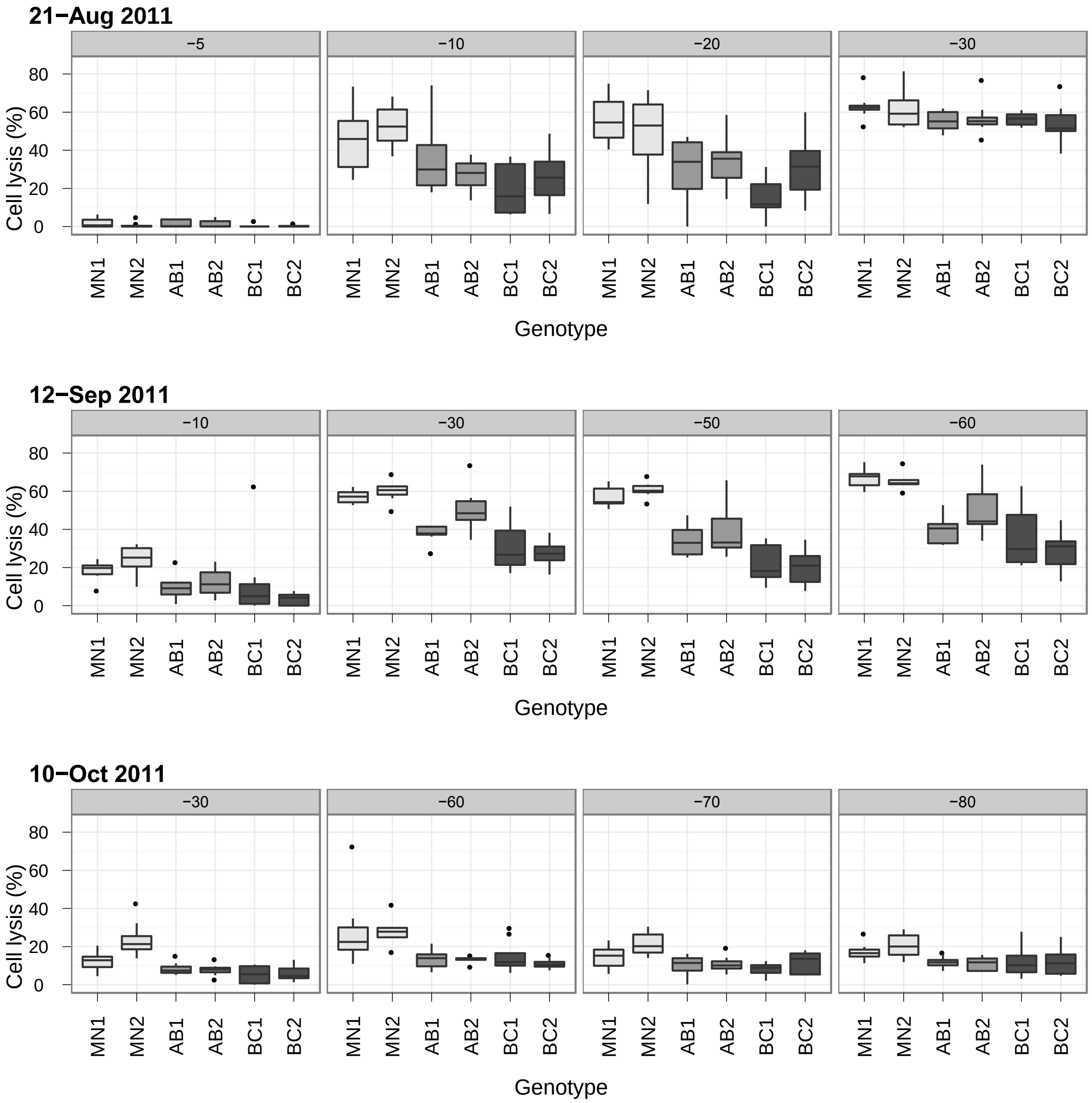
Fig. S1. Frost hardiness assessment for six aspen provenances.

Fig. S2. Changes of day length for the latitudes of the regions Minnesota (MN), central Alberta (cAB), and north-east British Columbia (BC).

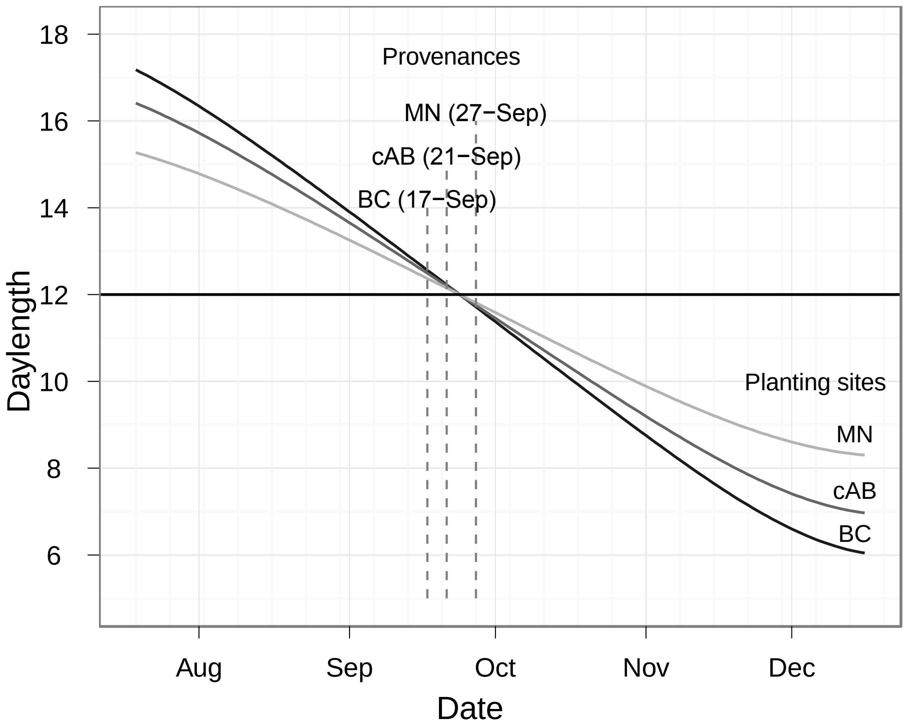
Supporting Information

Supporting Information S1. DBH (cm) and total dry mass (kg) of provenances grown in the reciprocal transplant experiment at age nine. Test sites are ordered along northwest gradient. Local sources are marked in bold, and standard errors are given in parenthesis

	Test site				
Origin of seed source	SK	ABf	cAB	nAB	BC
DBH (cm) at age nine					
Minnesota (MN)	3.14 (0.17)	3.05 (0.2)	7.97 (0.28)	3.21 (0.17)	2.44 (0.13)
Saskatchewan (SK)	**2.39 (0.32)**	2.73 (0.1)	6.72 (0.12)	3.42 (0.16)	2.26 (0.11)
Alberta Foothills (ABf)	2.42 (0.14)	**2.45 (0.12)**	6.93 (0.22)	3.69 (0.15)	2.09 (0.18)
Central Alberta (cAB)	2.68 (0.19)	2.64 (0.13)	**6.65 (0.19)**	3.55 (0.11)	2.25 (0.12)
Northern Alberta (nAB)	2.43 (0.14)	2.09 (0.18)	6.34 (0.11)	**3.65 (0.12)**	2.79 (0.08)
Northeast British Columbia (BC)	2.25 (0.16)	0.99 (0.13)	4.84 (0.11)	2.69 (0.14)	**1.65 (0.17)**
Total dry mass (kg) at age nine					
Minnesota (MN)	1.09 (0.12)	1.05 (0.17)	11.45 (1.13)	1.39 (0.17)	0.52 (0.07)
Saskatchewan (SK)	**0.62 (0.14)**	0.73 (0.06)	6.66 (0.31)	1.6 (0.19)	0.43 (0.05)
Alberta Foothills (ABf)	0.54 (0.07)	**0.56 (0.08)**	6.81 (0.57)	1.92 (0.17)	0.4 (0.08)
Central Alberta (cAB)	0.72 (0.11)	0.69 (0.08)	**6.22 (0.47)**	1.73 (0.14)	0.44 (0.05)
Northern Alberta (nAB)	0.53 (0.08)	0.38 (0.07)	5.33 (0.24)	**1.87 (0.13)**	0.79 (0.06)
Northeast British Columbia (BC)	0.38 (0.07)	0.05 (0.02)	2.43 (0.15)	0.87 (0.11)	**0.21 (0.05)**



Supporting Information S2. Frost hardiness as indicated by for six aspen provenances measured on 21-August (top), 12-September (middle) and 10-October (bottom) in response to different artificial freezing treatments.



Supporting Information S3. Changes of daylength for the latitudes of the regions Minnesota (MN), central Alberta (cAB), and northeast British Columbia (BC). The dates of leaf senescence for the corresponding provenances, observed in a common garden at the central Albert test site, are indicated by vertical lines.