From the Arctic Circle to the Canadian Prairies – a Case Study of Silver Birch Acclimation Capacity

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Earlier provenance research has indicated poor success even in short distance transfers (> 2–3° latitude) of silver birch (*Betula pendula* Roth) southward from their origin. These results may indicate poor adaptability of silver birch to a warming climate. Some of the scenarios for a warming climate in Finland suggest effective heat sums are likely to double in the north and increase 1.5 fold in the south for the period of 2070–2099. Consequently, the outlook for silver birch appears bleak. To study the acclimation of birch to this projected change we established a provenance trial in northeastern Alberta, Canada, at the temperature area currently predicted for Central Finland (lat. 64–66°N) at the turn of this century (1400 dd). Our 10-year experiment showed that all the Finnish provenances (origins 61–67°N) have acclimated well to the warmer growth conditions experienced in Alberta at 54°N. These results suggest that silver birch has the potential to acclimate to thermal conditions predicted for Finland at the end of the 21st century. Our results also indicate that silver birch has the potential as a plantation species in Canada, where the Finnish birch grew faster in the boreal forest region of Canada than local paper birch (*Betula papyrifera* Marsh.) provenances.

Keywords acclimation, *Betula papyrifera*, *Betula pendula*, birch adaptability, critical night length, provenance transfers
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1 Introduction

Long term effects of global climate change on tree growth and survival are difficult to predict since the environmental impacts on the annual growth cycle in boreal trees is still poorly understood (Hänninen 2006). According to recent modeling work the three dominant tree species in Finland (*Picea abies* L., *Pinus sylvestris* L. and *Betula pendula* Roth) should respond positively to warmer growing season temperatures (Briceño-Elizondo et al. 2006). Results from long term provenance trials on the other hand, indicate that a short transfer of approximately 2° latitude (~200 km) north increases volume, whereas southward transfers often lead to a decrease in performance (Johnsson 1976, Stener 1997, Viherä-Aarnio and Velling 2008). Southward transfers of 3° latitude have shown a 50% reduction in volume (Viherä-Aarnio and Velling 2008, but see Raulo and Koski 1977). Recent results by Mäenpää et al. (2011) however, showed that moderately elevated temperatures increased growth of silver birch (*Betula pendula*) saplings.

Provenance experiments under conditions outside the natural distribution range of the species under study provide an excellent system to study acclimation responses of trees under relatively natural conditions (Ghannoum and Way 2011). Estimating the acclimation capacity of trees to a warming climate from the results of provenance trials may, however, be confounded by the lack of synchrony in photoperiod. Although early successional species such as silver birch are photoperiod insensitive in their spring phenologies (Rousi and Heinonen 2007, see also perspective by Körner and Basler 2010), in autumn, the main signal for growth termination is thought to be critical night length (CNL, see Tanino et al., 2010 for references). Furthermore, an interaction between CNL, temperature (e.g. Koski and Sievänen 1985, Tanino et al. 2010) and ontogeny (Junttila and Nilsen 1993, Viherä-Aarnio et al. 2005) has been proposed. For silver birch from northern provenances (lat. 60–67°N) CNLs have been determined to vary between 3.1–6.3 hrs (Viherä-Aarnio et al. 2006). Therefore, there is a possibility that the positive effects of increased temperature in some provenance trials are hampered by the wrong photoperiodic cues, especially if transfer distances are greater than 2–3° latitude.

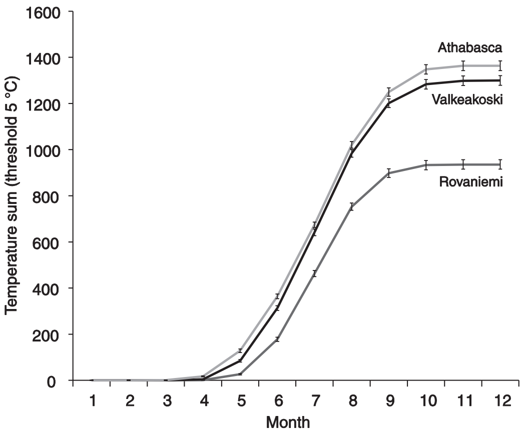

Fig. 1. Temperature sum accumulations (degree days 5°C threshold) for the experimental site (Athabasca, Canada, lat. 54°N) and for the southernmost (Valkeakoski, lat. 61°N) and northernmost (Rovaniemi, lat. 67°N) Finnish provenance of *B. pendula*. Data from Finnish Meteorological Institute and Weather Office Canada for the period of 1971–2000.

For Finland, the climate change scenario with the largest greenhouse gas emissions is projected to increase thermal sums in most of southern Finland to 1400°C (the threshold +5°C) days by 2040–2069 (Ruosteenoja et al. 2010), a 200–400°C day increase compared to current conditions and corresponding to a transfer of 4–5° latitude south (see Fig. 1). Thus, based on the provenance trials with silver birch, the outlook appears bleak, although an earlier experiment in Korea suggested that some Finnish silver birch provenances may acclimate well to these long distance transfers (Han et al. 1985).

We established a field experiment in northeastern Alberta, Canada where environmental conditions in terms of thermal sums are close to the worst-case scenario projected for central Finland at the turn of the 21st century. Our overall aim was to study the acclimation of silver birch (or European white birch) to heat sums predicted for Finland and compare the growth of Finnish silver birch to local Canadian paper birch (or North American white birch; *Betula papyrifera*

Marsh). To gain insight into these questions we studied 1) the capacity for acclimation (survival and growth) of Finnish birch provenances in a Canadian experiment growing under higher temperature conditions than those experienced presently in Finland; and 2) we compared growth and survival of Finnish birches growing in field trials in Canada and in Finland to gain insight into the magnitude of their capacity to acclimate.

Finnish silver birch might be a commercially viable alternative in Canada if growth/quality is better compared to the local white birch or other native species. Silver birch is already used as an ornamental species because of its white trunk and apparent rapid growth. Thus, we also had two practical goals: first, to compare the growth of Finnish silver birch and Canadian paper birch in Alberta. Secondly, comparisons were made between second-generation (seed) orchard seed lots of silver birch and stand collected silver and paper birch for consideration as an alternative species in high production forest plantations in Canada.

2 Material and Methods

2.1. Provenances and Seed Lots

Silver birch has a geographical distribution in Europe ranging from the Mediterranean to well above the Arctic Circle (Atkinson 1992). North American paper birch also shows a wide distribution, and is found in most provinces and territories of Canada, as well as the northern continental United States. These two species of white birch are closely related (Järvinen et al. 2003, Schenk et al. 2008).

The material in our experiment represents three groups of white birch: 1) Finnish silver birch provenances, representing the best stands (based on phenotype) selected for commercial seed use in Finland. The northernmost provenance (Rovaniemi) is from the heat sum area of 940 degree days (1971–2000 averages) and the southernmost provenances from 1100–1230 dd; 2) Finnish seed orchard material, selected to represent the main distribution areas of silver birch in Finland. The material was collected from plastic house orchards, including the southernmost and northernmost Finnish orchards containing 1st, 2nd and 3rd generation breeding material. The material (plus-tree grafts) was collected from the heat sum areas 1126–1238 dd (averages for genotypes in seed orchards 363, 379, 385, 387) and 938 dd (average for genotypes in seed orchard 390), and 3) paper birch provenances from Alberta and British Columbia, Canada from an average heat sum area of 1400 dd. In Alberta, very little work on the genetics of paper birch has been done, although several experiments have been installed by Alberta-Pacific Forest Industries Inc. (Al-Pac) in recent years. The material thus represents average, non-selected provenances. Five seed origins (provenances or orchard seed lots) represent each group of white birch. The collection year for the seeds of Finnish provenances (1) was 1989, and for the orchard seed lots (2) 1989–95. The Canadian material (3) was collected between 1999 and 2001.

Present data can be compared with two 10-year old Korean experiments with Finnish silver birch at the same latitude as Seoul (37°30'N) (Han et al. 1985). Two origins of Finnish silver birches grew faster than local white birches (*Betula platyphylla* Sukaczev) in a Pyeongchang county Kangwon province experiment, located at 600 m elevation. The average daily temperatures (Korea Meteorological Administration, means of 1981–2010) below zero measured monthly from December–March were –4.4°C, –7.7°C, –5.5°C, –0.5°C, respectively. Average temperatures from April–October are higher than in Finland at 7.0°C, 11.9°C, 15.7°C, 19.1°C, 19.1°C, 14.1°C 8.3°C, respectively and November is the transition month between growing season and winter dormancy with a 1.9°C average temperature. Average yearly precipitation is 1898 mm, primarily occurring as summer rains during May–October (122 mm, 201 mm, 327 mm, 421 mm, 307 mm and 125 mm, respectively). In the other experimental site in Hwaseong county, Kyeonggi province, silver birch grows somewhat more poorly than the local white birches. The soil at the second site was sandier (sand content 62 vs 29% in Pyeongchang-site, see Han et al. 1985), and the site was located at a much lower elevation (60 m) resulting in a somewhat warmer climate.

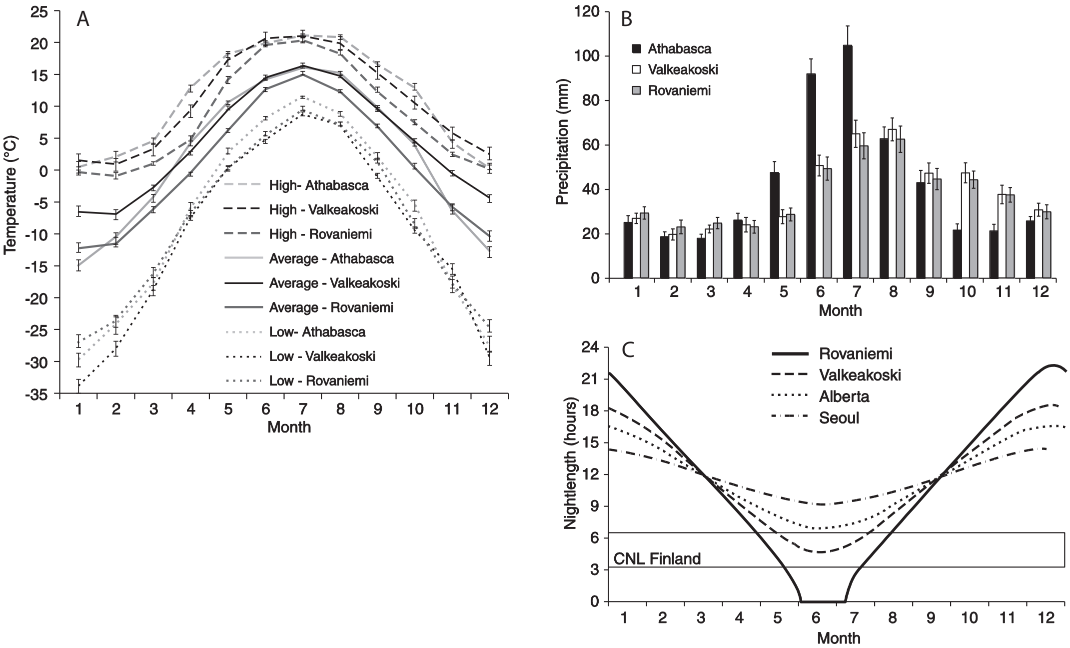

Fig. 2. Monthly Climate normals for the experimental site (Athabasca, Canada), for the southernmost (Valkeakoski) and northernmost (Rovaniemi) Finnish provenances of *Betula pendula* for the period of 1971–2000. 2A: Highest average, and lowest temperatures (mean in °C ± S.E.). 2B: precipitation (mean in mm ± S.E.) (Data from: Venäläinen, Tuomenvirta, Pirinen and Drebs. A basic Finnish climatic data set and illustrations. Finnish Meteorological Institute. Reports 2005:5, and http://www.climate.weatheroffice.gc.ca/climate_normals/results_e.html?stnID=1535&autofwd=1&month1=0&month2=12). 2C: Night length in hours for the experimental site (Alberta, Canada), the southernmost (Valkeakoski) and northernmost (Rovaniemi) Finnish provenances of *B. pendula* and Seoul (South Korea) and the critical night length (CNL) range for growth termination in Finland. Nightlength data from http://aa.usno.navy.mil/data/docs/Dur_OneYear.php, CNL range from Viherä-Aarnio et al. 2006.

2.2 Climatic Conditions Predicted and Present

The magnitude of the projected change in the thermal season depends strongly on the magnitude of predicted greenhouse gas emissions. In the worst case scenario the predicted heat sum for 2040–2069 is 1400 dd for most of Southern and Central Finland, and for Rovaniemi area, even 1300 dd is possible by 2070–2099 (Ruosteenoja et al. 2010). The nearest weather station to the experiment in Canada is situated in Athabasca, Alberta (54.7°N, 113.3°W, 514.7 m elevation), approximately 50 km west of the test site, with an average heat sum of 1370 dd. Comparisons of 1971–2000 climate normals in the experimental site indicate warmer springs (May–April) compared to Finland (Fig.2A). In addition, summer (May–July) precipitation is higher in Canada (Fig. 2B).

2.3 Experimental Design

The experiment in Alberta was planted in spring of 2001 at the Al-Pac mill site, Field 23 (54°N, 112°W) using one-year-old dormant seedlings. The trial has a randomized complete-block-design with eight blocks, 15 seed lots and 6-tree row plots of each seed lot in each block, with a spacing of 1.5 m x 3 m for 48 trees/ seed lot and a total of 720 trees in the trial. To prevent an edge effect, two border rows of excess seedlings were also planted around the experiment at the time of trial establishment. Unbleached pulp sheet mats were placed around each tree at the time of planting to remove competition. The area between the rows was planted with grass. The height and diameter of seedlings was measured annually from 2001–2003, 2005, and the last measurement was at the end of the 2010 growing season. The site is an orthic grey luvisol with a clay loam texture in the A horizon. The organic matter content of the A horizon is approximately 3.7% with a pH of 6.8 in the A horizon and 7.2 in the B horizon.

To compare the growth of silver birch in Finland and Canada, we used additional data from three experiments by the Finnish Forest Research Institute established with provenances from Varkaus, Pielavesi and Lieksa (Finland). Two of the experiments are located in Pieksämäki (62°N, 13-yr-old) and one in Maaninka (63°N, 13-yr-old). Spacing was either 2.25 m x 2.25 m or 2.5 m x 2.5 m. These three experiments are all located on high fertility sites. Additionally, we used data from two 10-yr-old Finnish experiments, one situated in Punkaharju and one in Parikkala (both at 62°N) containing birch plantlets micropropagated from a single natural population (see Laitinen et al. 2000 for details). The Punkaharju experiment was established on a fertile site (an abandoned field) and the Parikkala experiment was planted on a typical yet not optimal site for birch (*Vaccinium myrtillus* forest type) with a spacing of 2 m x 2 m. The soil type for both of these sites was a fine sandy till. Growth curves of these two trials are based on mean growth of all 24 genotypes in the experiments. Growth of micropropagated plantlets does not differ from that of seed-born material (Viherä-Aarnio and Velling 2001).

2.4 Statistics

We constructed and used Linear Mixed Models (SPSS 17.0; SPSS, Chicago, IL, USA), since these models also allow for modelling of the variances (that are allowed to be correlated). The average height for each 6-tree plot per measured year was used for repeated measures analysis. A heterogeneous covariance structure for the repeated effect gave the strongest models (by AI-criteria). Block and origin of the material were used to model the covariance structure of the dependent variable (height), again based on the AI-criteria of the model.

The height of the Finnish provenance experiments (Varkaus, Pielavesi and Lieksa) was measured after 13 years of growth in the field, while the same material growing in the Canadian trial was measured after 10 years of growth. In order to be able to compare the height growth of Finnish material in Canada to the same material growing in Finland, we extrapolated the Canadian growth data from 10 to 13 years of growth using simple linear regression to construct the relationship between years of growth and height for each seed origin and calculate an expected height for 13 years of growth for the material growing in Canada.

3 Results

The transfer of 6–13° latitudes to the south did not prevent Finnish silver birch from matching the performance of local paper birch provenances in Canada (Fig. 3). Finnish seed orchard seed lots (selected trees) outperformed local Canadian provenances ($p < 0.0001$) after only one year in the field, while this took three years for the wild collected Finnish provenances to outperform local Canadian seed lots. Mortality after 10-years was a single tree in the trial.

After one year of growth in the nursery, the Canadian paper birch seedlings were roughly the same size as the Finnish birch of which the northernmost Finnish provenance (Rovaniemi) was the smallest. After 10 years of growth, most of the Finnish orchard seed lots and the best Finnish provenances were approximately 1.5 m taller than the wild stand collected Canadian paper birch (Fig. 3). A significant difference in height growth among Finnish birch provenances was also found ($p < 0.0001$) with the southern provenances growing the fastest ($p < 0.0001$), a trend which is clearly seen in the comparatively poor performance of the northernmost provenance and orchard seed lot (Fig. 3). Significant differences in height growth between the Canadian provenances was also found ($p < 0.0001$). Similar results were obtained for diameter growth (results not shown).

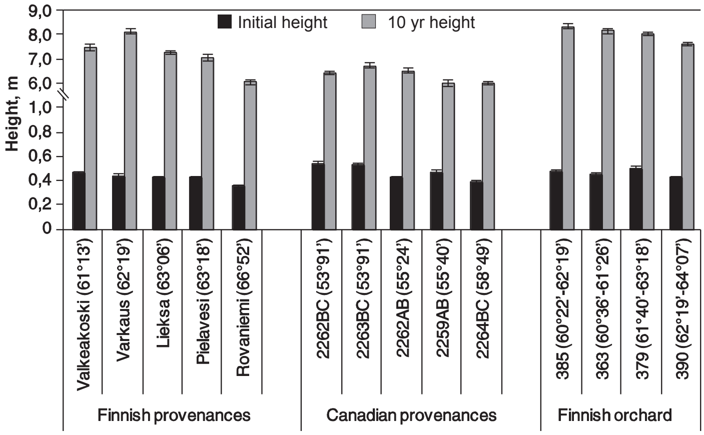

Fig. 3. Initial and 10-yr height of *Betula pendula* and *B. papyrifera* provenances and *B. pendula* orchard seed lots in the Canadian field experiment. For orchard seed lots the latitudinal range of graft material is given. The seedlings were 1-yr-old when planted in the field (Initial Ht). *B. papyrifera* provenances were from British Columbia (BC) or from Alberta (AB). Data are means ± SE.

Table 1. Height of *B. pendula* provenances in three Finnish provenance trials after 13 years of growth (mean ± SE). All the trials and origins are from 62°20'N–63°10'N.

Provenance trial site	Provenance	Height (m)
Pieksämäki 138601	Varkaus	12.02±0.34
	Lieksa	11.35±0.45
Maaninka 148303	Varkaus	12.07±0.56
	Pielavesi	11.91±0.48
Pieksämäki 148301	Varkaus	12.53±0.34
	Pielavesi	12.34±0.40

After 13 years of growth the trees from Varkaus, Pielavesi and Lieksa provenances reached an average height of 12.2, 12.1 and 11.4 m respectively (averaged across all Finnish field trials, Table 1). Linear extrapolation (R^2 for each origin > 0.97) indicates that the trees from these origins growing in Canada can be expected to reach a height of approximately 10.5, 9.2 and 9.4 m (Varkaus, Pielavesi and Lieksa provenances, respectively) after 13 years of growth in the field, indicating that the performance of the trees growing in Canada can be expected to be somewhat lower compared to the performance of the same material growing in Finland.

We found some indication that growth of Finnish trees growing in Canada tended to be faster during the first five years compared with the birch growing in Finland (Fig. 4, $p < 0.0001$ for origin x years of growth). After 10 years

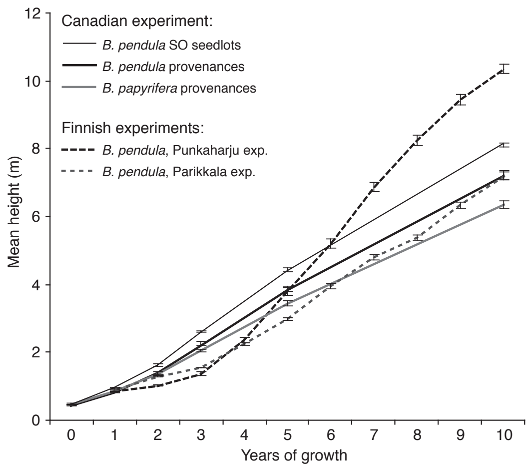

Fig. 4. Height of white birch in the Canadian (Athabasca) experiment (*Betula pendula* and *B. papyrifera*) and Finnish field experiments (*B. pendula*). The measurements in the Canadian experiment were done at the time of planting (0 yrs of growth) and after 1, 2, 3, 5 and 10 years of growth, the data for the Finnish experiment is based on yearly measurements. Data are means (± SE).

of growth micropropagated material growing in Punkaharju (better site) was on average 25% taller ($p < 0.0001$), but in Parikkala (poorer site) results were similar compared to Finnish orchard seed lots growing in Canada.

4 Discussion

Good growth and close to 100% survival in our 10-year Canadian field experiment indicate that silver birch has the capacity to acclimate to novel environmental conditions, including the largest projected thermal changes in Finland for the next 30–50 years (Ruosteenoja et al. 2010). Birch from the northernmost provenance (Rovaniemi) showed good acclimation to temperatures exceeding the largest projected increases until the end of this century in the Arctic Circle region. Canadian climate normals (1971–2000) show shorter transfer periods during both the onset and termination of growth (more continental climate) and larger inter annual temperature variation during the active growing season compared to the present climate of Finland (see Fig. 2A and B).

Finnish silver birch have also grown well in earlier experiments in Vermont, USA (Hannah 1987). Good performance of Finnish silver birch has also been reported from much warmer and more rainy conditions in South Korea (Han et al. 1985), where some of the birch provenances from southern Finland have not only survived a southward transfer of 25° latitude, but have also shown the capacity to outgrow local *B. platyphylla* (Japanese white birch, a close relative of silver birch) provenances. Additional evidence of acclimation capacity of silver birch comes from practical experience: for more than 40 years birch seed production in Finland has been based on plastic house orchards, where heat sum is 11% higher and the growing season two weeks longer compared to outdoor conditions (Pertti Pulkkinen, FFRI, unpublished results) still no acclimation problems have been noticed. Consequently, we suggest that silver birch may acclimate to various temperature and precipitation regimes, and that the capacity of silver birch to acclimate is underestimated in most of the earlier research, which has warned of a steep decrease in performance in southward transfers (Johnsson 1976, Kleinschmit and Otto 1980, Stener 1995, 1997, Viherä-Aarnio and Velling 2008). Survival in our experiment was also much higher (99.9%) compared to earlier research (e.g. 30–87% in Viherä-Aarnio and Velling 2008). Different outcomes in experiments may be more likely explained by cultural conditions in the field (e.g. density, spacing, vegetation control) than differences among genotypes in their capacity to acclimate.

The 6–13° latitude transfer south from Finland to Alberta resulted in differences in several environmental factors such as night length (Fig. 2C). The critical night length for autumn growth termination of Finnish silver birch is much shorter (6.3 hrs for local origins at 60°N, 3.1 hrs at 67°N, see Viherä-Aarnio et al. 2006) than any of the night lengths experienced in Canada at 54°N. Success of silver birch in South Korea (lat 37°30’N), where nights are always longer than nine hours gives an additional indication of highly flexible winter hardening in various temperature and night length regimes (Fig. 2) (see also Koski and Sievänen 1985, Tanino et al. 2010).

Elevated temperature (ambient +1°C, i.e. close to present Alberta temperatures) has been found to increase photosynthesis, canopy duration and growth of silver birch under Finnish field conditions (Mäenpää et al. 2011). Generally, effects of temperature not only on photosynthetic biochemistry but also on respiratory and stomatal processes are complicated (Lin et al. 2012). In silver birch, for example, the response to rising nighttime temperatures consists of a genotype-specific interplay between temperature, light and diurnal oscillations – including growth regulators and feedback from carbon source- sink processes (Mäenpää et al. 2012). The low and high estimates for the largest greenhouse gas emissions suggest growth in southern Finland to terminate 14–41 days later and in extreme cases, winter may not be detected at all (Ruosteenoja et al. 2010). A shorter period of freezing temperatures might resemble the growing season in the present climate of South Korea, where Finnish silver birch have also thrived (Han et al. 1985). However, caution is needed in our conclusions. For example, extreme autumn solar radiation conditions found at high latitudes (Fig. 2C) in combination with drastic lengthening of the thermal growing season might lead to plant responses that are hard to predict. However, the uncertainty levels for predictions of future climates, such as for the length of the growing season, are large (Ruosteenoja et al. 2010) and regional changes are hard to predict (see e.g. Schmittner et al. 2011).

Two-year-old Finnish birch outgrew the local white birch in the Canadian experiment and the relative differences between the two species remained roughly the same suggesting acclimation of silver birch to the Canadian photoperiod during the first years of growth. Growth of silver birch in Canada may not be radically different compared to growth in Finland, although at the best Finnish sites, height growth after 10 years was 20–30% greater. The comparison of growth curves in Finland and Canada suggest, however, some caution in our conclusions: the growth in Canada may be slowing down at an earlier age than occurs in Finland. Removal of competition (use of pulp mats around seedlings) may partly explain the faster early growth in Canada, but other environmental factors (including e.g. insect pests) may also be involved. More experimental evidence is clearly needed for firmer conclusions.

The northernmost provenances and seed orchard seed lots grew more slowly than the southern birches, and anomalies (such as Valkeakoski in Fig. 3) can probably be explained by random factors (including possible inbreeding). Generally, provenance experiments have indicated that populations from milder climates have a higher growth potential, but a lower cold tolerance than populations from the north (Rehfeldt et al. 2002). Recent results have shown, however, that after photoperiodic constraints have been removed, genotypes of balsam poplar (*Populus balsamifera* L.) from high latitudes were capable of equal or greater growth than their counterparts from lower latitudes (Soolanayakanhally et al. 2009). Because of the possible effects of CNL, caution is needed in interpreting the reasons for lower growth of high latitude trees in this experiment, as in most provenance experiments. However, the relative differences in size of Finnish birch seed lots remained the same in the Canadian environment suggesting no latitudinal differences in the speed of acclimation.

In general, better growth for orchard seed lots compared to southern Finnish provenances could be expected. Orchard seeds are derived from crossings in plastic houses, thus in addition to genetic superiority, epigenetic reasons (see e.g. Raj et al. 2011) may also explain faster growth in the warmer summers of Alberta. Epigenetic effects may also have partly determined the poor growth of the Rovaniemi provenance (Arctic Circle conditions during seed formation) during the first year of growth, and may have continued to influence performance. Clearly, more experiments are needed to give more reliable estimates of the growth differences of various seed lots and provenances and limits of their acclimation capacity.

Silver Birch as a Commercial or Ornamental Species in Canada

Growing silver birch in Canada as an ornamental species or by the forest industry (e.g. plywood and pulp) seems promising according to our preliminary results. Generally, seed orchard material showed somewhat better growth compared to southern provenances, and, due to genetic or epigenetic effects, the improved performance may be due to a higher efficiency in converting resources (light, water, nutrients) into growth (e.g. Binkley et al. 2010). The length of the growing period of silver birch is genetically determined and strongly connected to the height growth (Rousi and Pusenius 2005), and it has been shown that there is large within population genetic variation in birch's acclimation to changing climate (Kasurinen et al. 2012). Breeding silver birch genotypes for better growth in Canadian conditions should thus be a very profitable approach and worth further consideration.

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