New evidence for the importance of soil nitrogen on the survival and adaptation of silver birch to climate warming

B. J. H. M. Posseen,1,† M. Rousi,2 S. Keski-Saar,3 T. Silfver,4 S. Kontunen-Soppela,3 E. Oksanen,3 and J. Mikola4

1Ecology Section, Royal HaskoningDHV, Larixplein 1, Eindhoven 5616 VB The Netherlands
2Vantaa Research Unit, Natural Resources Institute Finland, P.O. Box 18, Vantaa 01301 Finland
3Department of Environmental and Biological Sciences, University of Eastern Finland, P.O. Box 111, Joensuu 80101 Finland
4Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, University of Helsinki, Niemenkatu 73, Lahti 15140 Finland

Citation: Posseen, B. J. H. M., M. Rousi, S. Keski-Saar, T. Silfver, S. Kontunen-Soppela, E. Oksanen, and J. Mikola. 2021. New evidence for the importance of soil nitrogen on the survival and adaptation of silver birch to climate warming. Ecosphere 12(5):e03520. 10.1002/ecs2.3520

Abstract. Strong seasonality in the subarctic causes unfavorable conditions for plant growth driving strong latitudinal clines in growth onset and cessation related to temperature and photoperiodic cues. Results from controlled experiments indeed show such clines, but results from field experiments seem to indicate that such clines may depend on site characteristics, suggesting that environmental variation, other than temperature and photoperiod, is relevant under climate change. Here, we increase our understanding of the effects of climate change on survival, height growth, and the phenological cycle by investigating their inter- and intrapopulation variation using three common gardens and six silver birch (Betula pendula) populations (each represented by up to five cloned genotypes) spanning the Finnish subarctic. We found clinal south–north variation among populations in survival and growth and in spring and autumn phenology to be largely absent. Sapling survival decreased with a transfer of over five degrees of latitude southward, but growth and phenology showed little evidence for adaptation to the local climate. Instead, ample genetic variation and plastic responses were found for all traits studied. Higher soil N availability increased sapling survival and growth, and phenology seemed to be adapted to soil N and day length rather than to temperature. Our results suggest that the climatic conditions predicted for the end of this century may, at least for poor soils, reduce the survival of northern silver birch trees in their early growth. However, those saplings that survive seem to have sufficient phenotypic plasticity to acclimatize to the changing climate. Along with climate, soil fertility plays a significant role and clearly warrants inclusion in the future tests of the effects of climate warming on tree growth and survival.

Key words: climate change; common garden; height growth; local adaptation; silver birch; soil nitrogen.

Received 6 October 2020; revised 10 January 2021; accepted 15 January 2021; final version received 24 March 2021. Corresponding Editor: Theresa M. Crimmins.

Copyright: © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† E-mail: boy.posseen@rhdhv.com

INTRODUCTION

The present speed of climate warming is exceeding that recorded for earlier periods of warming (IPCC 2014, Luoto et al. 2018). High latitudes, such as the subarctic tree line where the heat sum of the growing season is predicted to increase by 50% by the end of this century, are expected to warm most (Ruosteenoja et al. 2011). There is evidence that trees have been able to adapt to changing temperatures in the past (Shaw and Etterson 2012) and clinal trait
variation shows that trees are able to adapt to climatic gradients (Raulo and Koski 1977, Rehfeldt et al. 1999, Savolainen et al. 2007).

Strong seasonality in the subarctic causes unfavorable conditions for plant growth. In such environments, a correct timing of phenological events is of critical importance for growth and survival of trees (Sarvas 1972, 1974, Koski and Sievänen 1985). Genetic adaptation to local climate conditions in the timing of phenological events is therefore considered to be of great importance for survival and growth of trees (Tang et al. 2016), and their populations are assumed to be adapted to latitude-specific combinations of seasonal temperature variation and photoperiod (Savolainen et al. 2011, Alberto et al. 2013). Heat sum appears to be the environmental cue driving bud break in spring, at least in early successional species such as hazel (Corylus), aspen (Populus), and birch (Betula; Rousi and Heinonen 2007, Hänninen and Tanino 2011, Hawkins and Dhar 2012, Basler and Körner 2012, Fu et al. 2016), while growth cessation has generally been considered to follow photoperiodic cues (Mikola 1982, Howe et al. 2003, but see Michelson et al. 2018).

Since in trees the period of time favorable for growth is suggested to be directly linked to realized growth (Oleksyn et al. 2001, Heide 2003), there should be selective pressure toward optimal use of the period favorable for growth, while avoiding spring and autumn frosts (Larcher 2003, Polgar and Primack 2011, Hänninen 2016). Therefore, genetic adaptation to new photoperiodic conditions is considered critical for survival and growth under climate warming (Savolainen et al. 2007), although photoperiodic control over the timing of phenological events is known to be modified by temperature (Hänninen 2016).

However, while temperature and photoperiod are clearly the main factors governing the phenophases in trees, other factors such as epigenetics, nutrient status of the soil, nutrient status of the plant, soil moisture or air humidity, and insect herbivory also influence the timing of the different phenophases (Pääkkönen and Holopainen 1995, Sigurdsson 2001, Wielgolaski 2001, Nord and Lynch 2009, Laube et al. 2014, Arend et al. 2016, De Barba et al. 2016, Heimonen et al. 2017, Lloret et al. 2018). For example, late bud burst is commonly associated with a higher degree of herbivory (Aizen and Patterson 1995, Mopper and Simberloff 1995, Heimonen et al. 2017), although consequences for growth and survival are not straightforward (Carmona et al. 2011, Possen et al. 2014b, 2015).

Notwithstanding, the results from commercial forestry and common garden experiments indicate large acclimation capacity (i.e., nongenetic acclimation to prevailing environmental conditions) for photoperiod (Han et al. 1985, Rousi et al. 2012, Hayatgheibi et al. 2019, Spiecker et al. 2019) and for many species rapid evolutionary change should be possible in response to warming (Berteaux 2004, Hamrick 2004). In this context, the genetic composition of natural populations is essential for adaptation (i.e., genetic adaptation to environmental conditions), with high genetic variation facilitating rapid adaptation to new conditions (Hamrick et al. 1992, Mueller et al. 2017).

Silver birch (Betula pendula) is a light-demanding pioneer species with a sympodial growth pattern that will grow at most sites, but thrives only on fertile, well-aerated soils and is among the most common broad-leaved tree species in Europe, extending from the Mediterranean up to a latitude of 68° N (Atkinson 1992). It has shown remarkable acclimation capacity to both light and temperature conditions in transplant experiments (Han et al. 1985, Rousi et al. 2012), and much of its genetic variation is found within populations (Rusanen et al. 2003, Salojärvi et al. 2017). Growth onset in silver birch is driven by heat sum accumulation (Rousi and Heinonen 2007), not modified by photoperiod (Basler and Körner 2012, Hawkins and Dhar 2012), and the heat sum requirement for both bud break and flowering is similar across Finland from 60° to 68° N (Rousi et al. 2019).

For species such as silver birch, growing in areas where the growing season follows a regular pattern and longitudinal and altitudinal variation is small, steep latitudinal clines in the timing of growth onset and cessation are considered typical (Savolainen et al. 2007). Greenhouse experiments have indeed shown strong latitudinal clines such that compared with southern populations, northern populations start growth at lower temperature sums in spring (Mykking and Heide 1995) and cease growth earlier in autumn (Li et al. 2005, Viherä-Aarnio et al. 2005).
However, results from field experiments are less clear (Raulo and Koski 1977, Han et al. 1985, Hannah 1987, Rousi et al. 2012, Viherä-Aarnio et al. 2013, Michelson et al. 2018). Han et al. (1985), Hannah (1987), Raulo and Koski (1977), and Rousi et al. (2012) found no effect on growth and survival after a transfer of up to 24° latitude, whereas Viherä-Aarnio et al. (2013) found a sharp decrease in survival and growth after a transfer of 2° latitude, with the response strongly modified by the common garden site. Thus, photoperiodic control of growth cessation in silver birch can be modified by other environmental cues, still allowing timely winter hardening, survival, and growth. More importantly, clines indicating local adaptation may depend on site characteristics (Viherä-Aarnio et al. 2013). This suggests that environmental variation other than temperature and photoperiod should be considered when evaluating tree performance under changing climatic conditions (Tang et al. 2016). Indeed, we recently showed a strong effect of soil fertility on the acclimation capacity of Scots pine (Pinus sylvestris L.) populations at the subarctic tree line (Rousi et al. 2018) and earlier results of site-specific transfer responses in silver birch (Han et al. 1985, Viherä-Aarnio et al. 2013) clearly indicate relevance for silver birch.

Here, we increase our understanding of the effects of climate change on trees by investigating the inter- and intrapopulation variation of survival, growth, and phenology, using silver birch as a model species. Using three common gardens and six populations (or provenances, each represented by up to five cloned genotypes) latitudinally covering the subarctic region, we aim at imitating the changes in climatic conditions that trees in the subarctic are likely to experience in the future (Ruosteennoja et al. 2011).

An important aspect of our study is to try and understand how site-specific environmental characteristics other than climate, specifically soil nitrogen, affect tree responses to climate change. We aim to reveal to what extent the growth of transplanted silver birch genotypes and populations is related to the response of their phenological traits—bud break, growth cessation, and growing season length—and how this is affected by future climatic conditions. Finally, we want to shed light on the role of genotypic variation within and among silver birch populations in their responses to climate warming.

We expect silver birch to show not only (1) acclimation capacity, that is, increasing growth with decreasing latitude due to a warmer climate in the south, but also (2) local adaptation, that is, the best growth and survival for each population in the common garden closest to its site of origin. Besides acclimation capacity, we expect silver birch to show (3) high adaptation capacity, that is, significant intrapopulation genotypic variation in growth and phenology. Of the three phenological traits, we expect (4) the length of the growing season to best explain growth responses, both at the phenotypic (across individual trees) and genotypic (across genotype means) levels. Finally, we expect (5) soil fertility to play a significant role in explaining the variation in clinal trends and the growth and survival responses to a warmer climate.

**Materials and Methods**

**Common gardens**

Three common gardens were established (Table 1) in southern (S), central (C), and northern (N) Finland (Heimonen et al. 2015a). The southern garden was established near Tuusula (60°21’ N, 25°00’ E) on a clear-cut, surrounded by silver birch; the central garden on the grounds of the botanical garden of the University of Eastern Finland Joensuu campus (62°36’ N, 29°43’ E), with some scattered mature trees growing nearby; and the northern garden on an abandoned agricultural field near Kolari (67°21’ N, 23°49’ E), surrounded by mixed Scots pine, birch (B. pendula and B. pubescence Ehr.), and aspen (Populus tremula L.) forest. The gardens were established on sandy till soils, except the central garden, where the soil type was a fine sandy till. All gardens were fenced to prevent herbivory by mammals, but insect herbivory was as in nature. The three common gardens span a cline of approximately seven degrees latitude, or 780 km, and have widely different abiotic conditions (Table 1), most notably temperature sum (i.e., the daily mean temperature above a threshold value—here 5°C following Rousi and Heinonen 2007—summed over a year and expressed in degree-days, DD).
Natural regeneration in silver birch is such that birch populations and micropropagation were available as replicate block means). As N is the primary growth-limiting nutrient in terrestrial ecosystems, we chose to include N in our statistical analysis.

**Birch populations and micropropagation**

The procedures followed for selecting and producing the plant material are described in detail in Heimonen et al. (2015b). In brief, late winter 2009 (February–March), branches were collected from six naturally regenerated populations of silver birch, ranging from 60° to 67° N (Table 1). Natural regeneration in silver birch is such that suitable areas are quickly colonized with high seeding densities (Kinnaird 1974, Atkinson 1992), resulting in high mortality and even-aged stands (Kinnaird 1974). Within populations, randomly selected, single-stemmed, well-spaced mature trees were used for micropropagation.

Using standard micropropagation protocols (Ryynänen 1996), dormant vegetative buds were used to replicate the randomly chosen mother trees (genotypes) for each population. At the end of the propagation process, each population was represented by two to five genotypes and a total of 26 genotypes were included in the study.

Once rooted, the plantlets were individually planted in plastic trays filled with fertilized peat and grown according to standard nursery protocols in a greenhouse in the Haapastensyrjä Unit of the Natural Resources Institute Finland in Loppi (60° N). After being allowed to acclimatize to outdoor conditions, 10 saplings per genotype were planted in each common garden in July 2010. Within each garden, the saplings were randomly allocated to five replicate blocks (two saplings per genotype in each block) with a planting distance of 1.2 m. All common gardens were fenced to protect the saplings from mammal herbivory.

**Observations of survival, plant height, and phenology**

For spring phenology, five subsequent buds along a randomly selected branch (starting from...
the tip of the branch) were evaluated in each sapling during 2011–2013. Annually, the branches were selected and marked before the onset of growth. Bud break was monitored daily (including weekends), starting before any buds had opened and continuing until all buds had opened. Following the protocol developed by Rousi and Pusenius (2005), buds were considered open once the protective bud scales were clearly separated and the emerging leaf was visible. The day of the year when all monitored buds had opened was considered the start of the growing season for a sapling. This was further turned into temperature sum needed for bud break (bud break DD) using daily temperature data obtained from the records of the Finnish Meteorological Institute (Venäläinen et al. 2005). DD provides a meaningful scale of measurement for silver birch spring phenology (Rousi and Heinonen 2007, Basler and Korner 2012, Hawkins and Dhar 2012).

Growth cessation was monitored in autumn by measuring the height of the main stem of the saplings twice a week to the nearest centimeter. Using a ruler and starting before growth cessation could be expected (beginning of June in the northern site and beginning of July in the central and southern sites), measurements continued until the height was not found to change over three consecutive measurements. The first day of the year with no change in height was taken as the end of the growing season. This measurement also gave the estimate of the final height for the year.

The difference in days between the end and the start of the growing season was taken as the length of the growing season.

To estimate the survival rate for the different populations in the three common gardens, dead saplings were counted throughout the experiment. Here, we use the data from the last survey (autumn 2013).

**Environmental data and transfer distance**

To approximate the climatic conditions to which the original populations and their micropropagated offspring were adapted to, the mean annual temperature and growing season DD were calculated for a 30-yr period (1981–2010) for each population (origin) using daily records available as a 10 × 10 km grid from the Finnish Meteorological Institute (Venäläinen et al. 2005). All genotypes within a population originate from the same grid cell and therefore received the same value. To describe the conditions the saplings experienced during the experiment, mean climatic conditions were calculated for the common gardens for the duration of the experiment (2011–2013) using the same approach and dataset.

Given the profound effect of temperature on the phenological cycle of trees, the distance of transfer between the original growing site and the common garden is expressed in DD. This is particularly appropriate in Finland, where the lack of meaningful altitudinal differences means that latitudinal transfer in kilometers is highly correlated with DD transfer (in our case, Spearman’s $\rho = -0.97$, $P < 0.001$, $n = 18$). DD transfer was calculated by subtracting mean growing season DD calculated for a population from the mean growing season DD calculated for a common garden. This gives a negative value for a northward transfer and a positive value for a southward transfer.

**Statistics**

All statistical analyses were carried out using the IBM SPSS Statistics package (version 24, SPSS, Chicago, Illinois, USA).

To identify the factors controlling sapling survival, the effects of soil N, common garden site, linear and quadratic DD transfer (DD transfer raised to the power of two), population, genotype, and field replicate block on the number of saplings that died in the sapling pairs were analyzed using a generalized linear model with the Poisson probability distribution and log-link function. Genotype, block, and site × population interaction had no effect and were excluded from the final model, as supported by comparisons of model AIC values.

Sapling height and phenology data were analyzed using the same predictors, but as means of the two saplings in a replicate block. Models (repeated-measures linear mixed model type I ANOVA) including all three study years showed a significant interaction effect of year with most explanatory variables for all response variables (Appendix S1: Table S1), warranting analysis of each year’s data separately. In the annual data, the effects of the predictors were tested by means
of type I ANOVA models. The quadratic DD transfer was included in the models to test a curvilinear response of sapling height and phenology to DD transfer as a testimony of their local adaptation. To evaluate whether the assumptions of ANOVA were met, visual methods such as Q-Q plots and histograms of residual variation were used (Zuur 2009).

The approach based on type I ANOVA, which allocates variation to explanatory variables in their order of appearance, has earlier proved valuable in disentangling the various effects in a comparable common garden setup (Rousi et al. 2018). As an example, to be able to estimate the effect of DD transfer, any effects of common garden site needs to be removed from the data first by means of allocating variation to common garden site before DD transfer. Otherwise, the transfer effect could be confounded by common garden attributes (e.g., a northward transfer into colder climate could appear positive if the northern site happened to have more fertile soil). In the ANOVA models, common garden site and population were treated as fixed factors and genotype and block as random factors. Genotype was nested within population and block within common garden site. Soil N (consisting of block means), and the linear and quadratic DD transfer (all genotypes and individuals within a population had equal transfer) were included in the models as covariates.

To be able to visually interpret the results here, the effects of common garden site, DD transfer, population, and genotype are illustrated in the figures using model residuals instead of original data (Rousi et al. 2018). This way the effect of population, for example, can be clearly illustrated as the effects of soil N, common garden site, and transfer are removed from the data and no longer confounded with the population effect. Figures were drawn using R version 3.5.1. (R Core Team 2018) and the packages developed by Wickham (2016) and Graumann and Cotton (2018).

To examine the common garden site × population interaction effect on sapling height and phenology in more detail, three post hoc tests were used: First, the significance of the south–north trend or cline of population origin was tested for each common garden separately using linear regression analysis; second, the difference between the southern and northern populations was tested for each common garden separately using a Mann-Whitney test; and third, the differences among common garden sites were tested for the southern and northern populations separately using SNK pairwise comparisons. Populations were grouped based on their latitude of origin, such that populations from Kittilä (67°N), Rovaniemi (66°N), and Posio (65°N) were considered as “northern populations” and populations from Vehmersalmi (62°N), Punkaharju (61°N), and Loppi (60°N) as “southern populations,” as in Tenkanen et al. (2020). The difference between the northern and southern populations is 3–7° latitude, while within groups the difference between populations is 1–2° latitude. The temporal (among years) and spatial (among common gardens) consistency of genotypic variation in phenology and sapling height, as well as the phenotypic and genotypic correlations between height and phenology, was tested using Spearman’s rank correlation.

**RESULTS**

**Survival**

The number of dead saplings was significantly affected by soil N, common garden site, and linear DD transfer (Table 2). When the effects are illustrated as sapling survival rate (Fig. 1), survival was generally higher with higher soil N availability (the mean soil mineral N content in Tuusula, Joensuu, and Kolari was 3.4, 7.3, and 3.9 mg/L, respectively; Table 1). After considering the effect of soil N, survival was still significantly lower in the southern site, compared with the central and northern sites, and was negatively affected by a southward transfer as illustrated by the lower survival of northern populations in the southern site (Fig. 1). Survival rate of saplings for single genotypes within the northern populations in Tuusula was 60–80% for 65°PO, 30–80% for 66°RO, and 40–70% for 67°KI, while the survival for genotypes within the southern populations was 70–100% for 60°LO, 80–100% for 61°PU, and 70–100% for 62°VE.

**Sapling height**

Variation in sapling height (Fig. 2A) was significantly explained by all predictors, and the proportion of total variation explained by the
ANOVA model increased from 30% in 2011 to 54% in 2013 (Table 3). Soil N, common garden site, and linear DD transfer were the best predictors for sapling height, especially in 2012 and 2013 (each explaining 10–20% of variation; Table 3).

The effect of soil N increased over time (Table 3), and sapling height was always strongly positively associated with greater availability of soil N (Fig. 3A; Table 3).

After removing the effect of soil N and transfer distance (allowing for the evaluation of the population effect), no south–north cline appeared for populations ($P > 0.05$ in regression analysis in each site), but the saplings with a northern origin ($65°$ PO, $66°$ RO, $67°$ KI) were always shorter.

Table 2. General linear model results with degrees of freedom (df), Wald Chi², and $P$ values for the effects of soil N, common garden site, DD transfer (including both linear and quadratic responses), and population on the number of dead saplings (0, 1, or 2) in 2013 in sapling pairs planted for each genotype in each population, replicate block, and site ($N = 390$).

| Predictor          | Source of variation | df | Wald Chi² | $P$   |
|--------------------|---------------------|----|-----------|-------|
| Soil N             |                     | 1  | 19.4      | <0.001|
| Common garden site |                     | 2  | 30.4      | <0.001|
| DD transfer (linear)|                   | 1  | 12.4      | <0.001|
| DD transfer (quadratic)|               | 1  | 0.02      | 0.880 |
| Population         |                     | 4  | 7.31      | 0.120 |

*Note:* Values of $P < 0.05$ are in bold.

Fig. 1. Survival rate (percentage of planted individuals) in 2013 for saplings originating from the six populations (from the southernmost $60°$ LO to the northernmost $67°$ KI) and growing in the southern Tuusula, central Joensuu, and northern Kolari common gardens.
than those with a southern origin (60° LO, 61° PU, 62° VE) in the central and northern sites. In the southern site, instead, no difference was found in 2011 and 2012, and in 2013, the northern saplings were the tallest (Fig. 4A). The central common garden produced the tallest saplings in all years when the southern populations were considered, whereas for northern saplings, growth was better in the southern and central sites (Fig. 4A).

After removing the effect of soil N and common garden site, sapling height decreased with increasing southward transfer (Fig. 5A). The significance of the quadratic response to DD
transfer increased over time, but remained weak, and in 2013, the tallest saplings were found at a −194 DD (northward) transfer.

After removing the effects of soil N, common garden site, transfer distance, and population (leaving only the genotypic effect), intrapopulation genotypic variation, that is, the genotype effect, was present in all years (Table 3) and both the variation among and within genotypes increased over time (Fig. 6A). Genotypic variation was temporally consistent as the rank of genotype means for sapling height residuals (i.e., data devoid of other effects) correlated positively among years ($\rho = 0.79$, $P < 0.001$, for 2011 vs. 2012 comparison; $\rho = 0.72$, $P < 0.001$, for 2012 vs. 2013 comparison). The variation was also spatially consistent between the northern and central common garden sites, whereas in the southern garden, the genotype rank did not closely follow the rank in other sites (Table 4).

| Predictor            | df | df_predictor | df_error | SS   | F    | P    | Percentage of total SS |
|----------------------|----|--------------|----------|------|------|------|------------------------|
| 2011                 |    |              |          |      |      |      |                        |
| Soil N               | 1  | 74           | 35885    | 176  | <0.001 | 7.4 |
| Common garden site   | 2  | 285          | 66821    | 195  | <0.001 | 13.9 |
| DD transfer (linear) | 1  | 311          | 6196     | 383  | <0.001 | 1.3 |
| DD transfer (quadratic) | 1  | 311         | 651      | 4.0  | 0.046 | 0.1 |
| Population           | 4  | 20           | 12929    | 3.8  | 0.018 | 2.7 |
| Site × population    | 9  | 325          | 2478     | 1.7  | 0.095 | 0.5 |
| Genotype             | 20 | 314          | 16901    | 5.2  | <0.001 | 3.5 |
| Block                | 11 | 311          | 4122     | 2.3  | 0.010 | 0.9 |
| Error                |    |              |          |      |      |      | 336178 |
| Percentage of total SS explained by the model | | | | | | | 30.3 |
| 2012                 |    |              |          |      |      |      |                        |
| Soil N               | 1  | 69           | 145970   | 244  | <0.001 | 9.1 |
| Common garden site   | 2  | 279          | 186950   | 189  | <0.001 | 11.6 |
| DD transfer (linear) | 1  | 311          | 228938   | 494  | <0.001 | 14.2 |
| DD transfer (quadratic) | 1  | 311         | 3189     | 6.9  | 0.009 | 0.2 |
| Population           | 4  | 20           | 26293    | 4.0  | 0.015 | 1.6 |
| Site × population    | 9  | 322          | 31565    | 7.5  | <0.001 | 2.0 |
| Genotype             | 20 | 314          | 32849    | 3.5  | <0.001 | 2.0 |
| Block                | 11 | 311          | 12529    | 2.5  | 0.006 | 0.8 |
| Error                |    |              |          |      |      |      | 941262 |
| Percentage of total SS explained by the model | | | | | | | 41.5 |
| 2013                 |    |              |          |      |      |      |                        |
| Soil N               | 1  | 64           | 531874   | 421  | <0.001 | 12.5 |
| Common garden site   | 2  | 272          | 938101   | 458  | <0.001 | 22.1 |
| DD transfer (linear) | 1  | 311          | 529726   | 556  | <0.001 | 12.5 |
| DD transfer (quadratic) | 1  | 311         | 21573    | 23   | <0.001 | 0.5 |
| Population           | 4  | 20           | 33415    | 1.9  | 0.150 | 0.8 |
| Site × population    | 9  | 324          | 129807   | 15   | <0.001 | 3.1 |
| Genotype             | 20 | 315          | 88119    | 4.6  | <0.001 | 2.1 |
| Block                | 11 | 311          | 27612    | 2.6  | 0.003 | 0.6 |
| Error                |    |              |          |      |      |      | 1951721 |
| Percentage of total SS explained by the model | | | | | | | 54.1 |
Fig. 3. Relationship between soil mineral N content (measured separately for each replicate block at each
Timing of bud break (Fig. 2B) was affected by all predictors included in the ANOVA model, except for the main effect of population (Table 5). Soil N, common garden site, genotype, and the quadratic response to DD transfer explained the largest proportion of the variation, while the model itself explained 31–43% of the total variation over the years (Table 5).

Fig. 4. Means of residuals (±1 SE, n = 8–25 for a population within a common garden) of (A) sapling height in cm, (B) temperature sum needed for bud break (DD with a 5°C threshold), (C) growing season length in days, and (D) growth cessation calendar day in 2011–2013 (n = 361; lines represent linear regressions and are shown for statistically significant effects).
Fig. 5. Relationship between transfer distance (in DD with a 5°C threshold) and residuals of (A) sapling height in cm, (B) temperature sum needed for bud break (DD with a 5°C threshold), (C) growing season length in days,
and (D) growth cessation calendar day in 2011–2013 ($n = 361$; dotted lines show statistically significant linear effects and solid curves show statistically significant quadratic effects, residuals are devoid of soil N and site effects).

The DD needed for bud break was lower with higher availability of soil N in all years (Fig. 3B, Table 5). A significant site × population interaction effect was also found in all years (Table 5), suggesting that neither the site nor the origin of the population had an unambiguous

Fig. 6. Means of residuals (±1 SE; $n = 5$ for a genotype) of (A) sapling height in cm, (B) temperature sum needed for bud break (DD with a $5^\circ$C threshold), (C) growing season length in days, and (D) growth cessation calendar day for genotypes within the six populations, ordered from south to north, in 2011–2013 (residuals are devoid of soil N, common garden site, population, and both DD transfer effects).
main effect on DD needed for bud break. When the interaction was examined further, no statistically significant south–north population cline or trend in bud break emerged for any common garden in any year (Fig. 4B).

After removing the effect of soil N and common garden site, the DD needed for bud break increased with increasing southward transfer in 2011 and 2012, but this effect was weak and disappeared in 2013 (Fig. 5B, Table 5). The quadratic response to DD transfer, in contrast, got stronger over time (Table 5) and the regression curve drawn on model residuals suggests that the DD needed for bud break increased with both southward DD transfer and northward DD transfer, thus suggesting local adaptation (Fig. 5B). The minimum DD needed for bud break was near zero DD transfer in 2011 (C0 DD), but substantially higher in 2012 (193 DD) and 2013 (236 DD; Fig. 5B).

Genotypic variation (after removing the effect of all other predictors) was found in all years and became stronger over time (Table 5, Fig. 6B). Comparing the intrapopulation (Fig. 6B) and interpopulation (Fig. 4B), variation in the timing of bud break supports the absence of a significant population main effect: There was more genotypic variation within populations than among populations.

Genotypic variation was temporally and spatially consistent as the ranks of genotype means for bud break residuals correlated positively among the years (p = 0.78, P < 0.001, for 2011 vs. 2012; p = 0.89, P < 0.001, for 2012 vs. 2013 comparison) and sites (Table 4), except for the comparison of the northern and southern sites in 2012.

**Growth cessation in autumn**

The variation in growth cessation (Fig. 2C) was consistently and significantly explained by common garden site, linear DD transfer, and genotype, while soil N, quadratic DD transfer response, and population were weaker and more transient predictors (Table 6). Over the years, the ANOVA model explained 25–55% of the total variation (Table 6).

In 2011 and 2012, growth cessation was weakly correlated with soil N, but this effect disappeared in 2013 (Fig. 3C, Table 6). As with bud break DD, the southern and northern populations differed in the timing of growth cessation, but no significant south–north population cline appeared at any site (Fig. 4C).

Growth cessation had a strong linear relationship with DD transfer in all years, and the day of the year at which growth ceased was advanced with an increasing southward transfer (Table 6, Fig. 5C). A weak quadratic response to DD transfer appeared in 2012 (Table 6, Fig. 5C).

Within-population genotypic variation was significant in all years (Table 6, Fig. 6C), and the

---

**Table 4.** Spearman's rank correlations (p: n = 26) and their P values (P; values of P < 0.05 are in bold) of genotype means of residuals (devoid of soil N, common garden site, DD transfer, and population effects) of temperature sum needed for bud break (DD with a 5°C threshold), growth cessation calendar day, growing season length (days), and sapling height (mm) between the three common garden sites for each study year.

| Phenophase     | Year | Kolari (N) vs. Joensuu (C) | Kolari (N) vs. Tuusula (S) | Joensuu (C) vs. Tuusula (S) |
|---------------|------|---------------------------|---------------------------|----------------------------|
|               | p    | P                         | p                         | P                          |
| Bud break     | 2011 | 0.68 <0.001               | 0.45 0.021                | 0.70 <0.001                |
|               | 2012 | 0.70 <0.001               | 0.30 0.131                | 0.46 0.018                 |
|               | 2013 | 0.77 <0.001               | 0.55 0.004                | 0.66 <0.001                |
| Growth cessation | 2011 | 0.52 0.007                | 0.31 0.118                | 0.51 0.007                 |
|               | 2012 | 0.37 0.065                | 0.23 0.257                | 0.15 0.454                 |
|               | 2013 | 0.30 0.133                | 0.05 0.805                | 0.19 0.357                 |
| Growing season length | 2011 | 0.57 0.002                | 0.35 0.077                | 0.44 0.024                 |
|               | 2012 | 0.31 0.121                | 0.22 0.292                | 0.11 0.583                 |
|               | 2013 | 0.28 0.175                | 0.08 0.701                | 0.13 0.542                 |
| Sapling height | 2011 | 0.68 <0.001               | 0.26 0.201                | 0.48 0.013                 |
|               | 2012 | 0.54 0.004                | 0.26 0.204                | 0.17 0.418                 |
|               | 2013 | 0.61 0.001                | 0.29 0.146                | 0.23 0.260                 |
rank of genotypes was consistent in time as the genotype means of growth cessation residuals correlated positively among the years ($r = 0.82$, $P < 0.001$, for 2011 vs. 2012 comparison; $r = 0.63$, $P < 0.001$, for 2012 vs. 2013 comparison). Rank correlations of genotype means across the sites were, in contrast, mostly not statistically significant, although all positive (Table 4).

**Length of the growing season**

The variation in the length of the growing season (Fig. 2D) was best explained by common garden site, linear DD transfer, and genotype, while other predictors (including soil N and population) were weaker and more transient (Table 7). The proportion of total variation explained by the model increased over time and while linear DD transfer explained the biggest proportion of the variation in 2011 and 2012 (~15%), common garden site explained over 30% in 2013 (Table 7).

Soil N had a considerable effect on growing season length in 2012 only; the growing season was longer with better soil N availability.

---

**Table 5. Analysis of variance with degrees of freedom, sum of squares (SS), $F$ statistic, and $P$ values ($P$) for the effects of soil N, common garden site, DD transfer (including both linear and quadratic responses), population, genotype (nested within population), and field replicate block (nested within site) needed for bud break in 2011–2013 (values of $P < 0.05$ are in bold; percentage of total SS denotes the proportion of total variance explained by the predictor).**

| Predictor                  | df | df<sub>predictor</sub> | df<sub>error</sub> | SS    | $F$   | $P$   | Percentage of total SS |
|---------------------------|----|------------------------|-------------------|-------|-------|------|------------------------|
| **2011**                  |    |                        |                   |       |       |      |                        |
| Soil N                    | 1  | 150                    | 6767              | 242   | <0.001| 5.6  |                        |
| Common garden site        | 2  | 318                    | 19,174            | 57    | <0.001| 15.8 |                        |
| DD transfer (linear)      | 1  | 311                    | 2218              | 8.7   | <0.001| 1.8  |                        |
| DD transfer (quadratic)   | 1  | 311                    | 343               | 0.8   | 0.003 | 0.3  |                        |
| Population                | 4  | 20                     | 684               | 6.2   | 0.540 | 0.6  |                        |
| Site × population         | 9  | 323                    | 2220              | 5.5   | <0.001| 1.8  |                        |
| Genotype                  | 20 | 313                    | 4288              | 1.2   | <0.001| 3.5  |                        |
| Block                     | 11 | 311                    | 513               | 1.1   | 0.294 | 0.4  |                        |
| Error                     |    |                        |                   | 54,776|       |      |                        |
| Percentage of total SS explained by the model | 29.9 |

| **2012**                  |    |                        |                   |       |       |      |                        |
| Soil N                    | 1  | 47                     | 56,208            | 458   | <0.001| 19.4 |                        |
| Common garden site        | 2  | 233                    | 43,501            | 241   | <0.001| 15.0 |                        |
| DD transfer (linear)      | 1  | 311                    | 1799              | 22    | <0.001| 0.6  |                        |
| DD transfer (quadratic)   | 1  | 311                    | 7277              | 90    | <0.001| 2.5  |                        |
| Population                | 4  | 20                     | 954               | 0.5   | 0.718 | 0.3  |                        |
| Site × population         | 9  | 327                    | 3753              | 5.0   | <0.001| 1.3  |                        |
| Genotype                  | 20 | 316                    | 9100              | 5.6   | <0.001| 3.1  |                        |
| Block                     | 11 | 311                    | 3185              | 3.6   | <0.001| 1.1  |                        |
| Error                     |    |                        |                   | 1,64,131|      |      |                        |
| Percentage of total SS explained by the model | 43.4 |

| **2013**                  |    |                        |                   |       |       |      |                        |
| Soil N                    | 1  | 111                    | 14,728            | 185   | <0.001| 6.3  |                        |
| Common garden site        | 2  | 309                    | 23,287            | 159   | <0.001| 9.9  |                        |
| DD transfer (linear)      | 1  | 311                    | 149               | 2.1   | 0.149 | 0.1  |                        |
| DD transfer (quadratic)   | 1  | 311                    | 7253              | 102   | <0.001| 3.1  |                        |
| Population                | 4  | 20                     | 930               | 0.2   | 0.910 | 0.4  |                        |
| Site × population         | 9  | 332                    | 2700              | 4.0   | <0.001| 1.1  |                        |
| Genotype                  | 20 | 313                    | 19,109            | 13    | <0.001| 8.1  |                        |
| Block                     | 11 | 311                    | 1251              | 1.6   | 0.098 | 0.5  |                        |
| Error                     |    |                        |                   | 1,65,930|      |      |                        |
| Percentage of total SS explained by the model | 29.5 |
Table 6. Analysis of variance with degrees of freedom, sum of squares (SS), F statistic, and P values for the effects of soil N, common garden site, DD transfer (including both linear and quadratic responses), population, genotype (nested within population), and field replicate block (nested within site) on growth cessation calendar day in 2011–2013 (values of P < 0.05 are in bold; percentage of total SS denotes the proportion of total variance explained by the predictor).

| Predictor                        | df | df<sub>predictor</sub> | df<sub>error</sub> | SS    | F       | P       | Percentage of total SS |
|----------------------------------|----|------------------------|-------------------|-------|---------|---------|------------------------|
| 2011                             |    |                        |                   |       |         |         |                        |
| Soil N                           | 1  | 166                    | 390               | 9.6   | 0.002   | 0.2     |                        |
| Common garden site               | 2  | 320                    | 63,597            | 789   | <0.001  | 37.5    |                        |
| DD transfer (linear)             | 1  | 311                    | 14,010            | 349   | <0.001  | 8.3     |                        |
| DD transfer (quadratic)          | 1  | 311                    | 12                | 0.3   | 0.581   | 0.0     |                        |
| Population                       | 4  | 20                     | 716               | 1.0   | 0.411   | 0.4     |                        |
| Site x population                | 9  | 321                    | 817               | 2.2   | 0.020   | 0.5     |                        |
| Genotype                         | 20 | 313                    | 3444              | 4.3   | <0.001  | 2.0     |                        |
| Block                            | 11 | 311                    | 471               | 1.1   | 0.388   | 0.3     |                        |
| Error                            |   |                        |                   |       |         |         | 86,197                 |
| Percentage of total SS explained by the model |   |                        |                   |       |         |         | 49.2                   |
| 2012                             |    |                        |                   |       |         |         |                        |
| Soil N                           | 1  | 108                    | 1404              | 18    | <0.001  | 0.8     |                        |
| Common garden site               | 2  | 308                    | 10,862            | 78    | <0.001  | 5.9     |                        |
| DD transfer (linear)             | 1  | 311                    | 25,209            | 374   | <0.001  | 13.6    |                        |
| DD transfer (quadratic)          | 1  | 311                    | 166               | 24    | <0.001  | 0.1     |                        |
| Population                       | 4  | 20                     | 2102              | 2.6   | 0.068   | 1.1     |                        |
| Site x population                | 9  | 320                    | 998               | 1.6   | 0.106   | 0.5     |                        |
| Genotype                         | 20 | 313                    | 4061              | 3.0   | <0.001  | 2.2     |                        |
| Block                            | 11 | 311                    | 1214              | 1.6   | 0.088   | 0.7     |                        |
| Error                            |   |                        |                   |       |         |         | 1,39,462               |
| Percentage of total SS explained by the model |   |                        |                   |       |         |         | 24.8                   |
| 2013                             |    |                        |                   |       |         |         |                        |
| Soil N                           | 1  | 56                     | 50                | 0.7   | 0.391   | 0.0     |                        |
| Common garden site               | 2  | 256                    | 93,253            | 898   | <0.001  | 43.8    |                        |
| DD transfer (linear)             | 1  | 311                    | 14,732            | 310   | <0.001  | 6.9     |                        |
| DD transfer (quadratic)          | 1  | 311                    | 76                | 1.6   | 0.206   | 0.0     |                        |
| Population                       | 4  | 20                     | 2369              | 3.2   | 0.034   | 1.1     |                        |
| Site x population                | 9  | 324                    | 1559              | 3.6   | <0.001  | 0.7     |                        |
| Genotype                         | 20 | 315                    | 3697              | 3.9   | <0.001  | 1.7     |                        |
| Block                            | 11 | 311                    | 1583              | 3.0   | 0.001   | 0.7     |                        |
| Error                            |   |                        |                   |       |         |         | 95,714                 |
| Percentage of total SS explained by the model |   |                        |                   |       |         |         | 55.1                   |

(Table 7, Fig. 3D). No south–north population cline of growing season length appeared at any common garden site (Fig. 4D). Instead, the southern populations had a longer season than the northern populations in 2011 (except in the southern site) and 2012 and a shorter season than the northern populations in 2013 (except in the central site; Fig. 4D).

Growing season length was explained best by the linear DD transfer in all years, and following the trend in the timing of growth cessation, a southward transfer resulted in a shorter growing season (Table 7, Fig. 5D). Also, as in the case of growth termination, the quadratic response to DD transfer appeared in 2012 only (Table 7), when growing season length was longest near the zero DD transfer (−24 DD; Fig. 5D).

Intrapopulation genotypic variation was significant in all years (Table 7, Fig. 6D), and the rank of genotype means of growing season residuals was consistent across the years (ρ = 0.71, P < 0.001, for 2011 vs. 2012 comparison; ρ = 0.60, P < 0.001, for 2012 vs. 2013 comparison). Rank correlations across the sites were also
positive, but statistically significant in 2011 only (Table 4).

**Phenotypic and genotypic correlations between growth and phenology**

When phenotypic correlations were tested using values of individual saplings, sapling height was significantly and positively correlated with both date of growth cessation and growing season length, with Spearman’s $\rho$ varying between 0.48 and 0.86 among the years and growing sites (Table 8A). Phenotypic correlations of height with the DD needed for bud break were generally negative (except for two years in Kolari), but not as strong as for the two other variables (Table 8A).

Genotypic correlations, calculated using genotype means of residuals devoid of all other effects (including population mean differences), were less consistent (Table 8B). Genotype means for date of growth cessation and growing season length were consistently, positively, and significantly correlated with the genotype means of sapling height in the central Joensuu site only.

---

**Table 7. Analysis of variance with degrees of freedom, sum of squares (SS), $F$ statistic, and $P$ values for the effects of soil N, common garden site, DD transfer (including both linear and quadratic responses), population, genotype (nested within population), and field replicate block (nested within site) on the length of the growing period (measured in days) in 2011–2013 (values of $P < 0.05$ are in bold; % of total SS denotes the proportion of total variance explained by the predictor).**

| Predictor | df | df$_{\text{error}}$ | SS   | $F$   | $P$   | Percentage of total SS
|-----------|----|---------------------|------|-------|-------|-------------------------|
| **2011**  |     |                     |      |       |       |                         |
| Soil N    | 1  | 157                 | 31   | 0.7   | 0.405 | 0.0                     |
| Common garden site | 2  | 319                 | 10,867 | 124 | $<0.001$ | 8.4     |
| DD transfer (linear) | 1  | 311                 | 19,192 | 441 | $<0.001$ | 14.9    |
| DD transfer (quadratic) | 1  | 311                 | 1.5 | 0.0 | 0.851 | 0.0                     |
| Population | 4  | 20                  | 444  | 0.6 | 0.673 | 0.3                     |
| Site × population | 9  | 321                 | 764  | 1.9 | $0.047$ | 0.6     |
| Genotype | 20 | 313                 | 3766 | 4.3 | $<0.001$ | 2.9     |
| Block | 11 | 311                 | 539  | 1.1 | 0.340 | 0.4                     |
| Error | 93,112 |                     |      |      |       |                         |
| Percentage of total SS explained by the model | | | | | | 27.7 |
| **2012**  |     |                     |      |       |       |                         |
| Soil N    | 1  | 162                 | 7142 | 91   | $0.001$ | 3.2     |
| Common garden site | 2  | 320                 | 11,352 | 73 | $0.001$ | 5.1     |
| DD transfer (linear) | 1  | 311                 | 30,122 | 389 | $0.001$ | 13.5    |
| DD transfer (quadratic) | 1  | 311                 | 4128 | 53  | $0.001$ | 1.9     |
| Population | 4  | 20                  | 1591 | 2.1 | 0.115 | 0.7                     |
| Site × population | 9  | 318                 | 882  | 1.3 | 0.258 | 0.4                     |
| Genotype | 20 | 313                 | 3750 | 2.4 | $0.001$ | 1.7     |
| Block | 11 | 311                 | 928  | 1.1 | 0.368 | 0.4                     |
| Error | 16,2493 |                     |      |      |       |                         |
| Percentage of total SS explained by the model | | | | | | 26.9 |
| **2013**  |     |                     |      |       |       |                         |
| Soil N    | 1  | 55                  | 1000 | 14   | $0.001$ | 0.5     |
| Common garden site | 2  | 255                 | 57,290 | 510 | $0.001$ | 30.8    |
| DD transfer (linear) | 1  | 311                 | 15,674 | 305 | $0.001$ | 8.4     |
| DD transfer (quadratic) | 1  | 311                 | 461  | 9.0 | $0.003$ | 0.2     |
| Population | 4  | 20                  | 190  | 2.2 | 0.107 | 0.1                     |
| Site × population | 9  | 324                 | 2112 | 4.5 | $0.001$ | 1.1     |
| Genotype | 20 | 315                 | 4212 | 4.1 | $0.001$ | 2.3     |
| Block | 11 | 311                 | 1724 | 3.1 | $0.001$ | 0.9     |
| Error | 1,03,604 |                     |      |      |       |                         |
| Percentage of total SS explained by the model | | | | | | 44.4 |
and virtually no significant genotypic correlation existed between the DD needed for bud break and sapling height (Table 8B).

**DISCUSSION**

We show that under field conditions survival of silver birch may decrease in northern populations if the heat sum increases twofold. For growth and phenology, adaptation to local temperature sums may be of lesser importance compared with the random variation in soil N availability. Our results reveal high intrapopulation genotypic variation for growth and phenological traits, indicating high adaptability and high acclimation capacity. In line with earlier work (Hawkins and Dhar 2012, Rousi et al. 2012), these results suggest that silver birch is likely to cope well with a projected increase in temperature.

**Survival**

Compared to the central and northern common gardens, where survival was high for all populations, the southern site had a slightly lower survival rate for the southern populations and a significantly lower survival rate for the northern populations. This suggests that there was no south–north cline in survival among the populations. Apparently, no adaptation to photoperiod was necessary for good survival rates as the southern populations showed high survival in the northern site.

Instead, survival was positively related to soil N. The southern site had generally lower survival and a long (>5 latitudes) southward transfer, which doubled the typical heat sum for northern populations, and further reduced survival. The higher mortality at the southern site is likely linked to a less fertile soil, which may have intensified the stress experienced by the saplings originating from northern populations. For these same trees, the incidence of leaf herbivory (which could not be controlled for in our experiment), but not insect herbivore density or community composition, has been shown to be slightly more severe for northern populations (Heimonen et al. 2015a, b, 2017) and therefore may have affected the survival of the saplings. Soil fertility is known to affect the growth response of silver birch to insect herbivory such that total biomass decreases more

| Phenophase                        | Year | Kolari  | Joensuu | Tuusula |
|-----------------------------------|------|---------|---------|---------|
| DD needed for bud break           |      |         |         |         |
| 2011                              | 0.40 | <0.001  | <0.001  | <0.001  |
| 2012                              | 0.14 | 0.111   | 0.002   | 0.008   |
| 2013                              | 0.12 | 0.192   | 0.001   | 0.44    |
| Growth cessation date             |      |         |         |         |
| 2011                              | 0.58 | <0.001  | <0.001  | 0.69    |
| 2012                              | 0.57 | <0.001  | 0.81    | <0.001  |
| 2013                              | 0.50 | <0.001  | 0.85    | <0.001  |
| Growing season length             |      |         |         |         |
| 2011                              | 0.61 | <0.001  | 0.71    | <0.001  |
| 2012                              | 0.52 | <0.001  | 0.83    | <0.001  |
| 2013                              | 0.48 | <0.001  | 0.86    | <0.001  |
in response to defoliation under nutrient-poor compared with nutrient-rich conditions (Hjalten et al. 1993, Anttonen et al. 2002). Also, insect herbivory may lead to increased investment in leaves (Vamagiryte-Kabasinskiene et al. 2016) altering the N cycle in the saplings. However, there is no general threshold for the effects of defoliation (Anttonen et al. 2002, Huttunen et al. 2013) and effects may be either favorable or negative (Hjalten et al. 1993) and are usually not observed for clipping or perforating of leaves (Vamagiryte-Kabasinskiene et al. 2016), which is comparable to insect herbivory in our experiment (Heimonen et al. 2015a). This, combined with our observation that the northern saplings were on average taller compared with the southern saplings in the southern common garden where soil fertility was lowest, suggests that insect herbivory did not affect our results in terms of survival.

Also, the comparatively young age of our saplings should be taken into account (Possen et al. 2014a). As a light-demanding pioneer species (Atkinson 1992), seeds able to germinate in open soil and able to sustain more height growth compared with the surrounding vegetation will establish successfully (Kinnaird 1974, Lintunen and Kaitaniemi 2010).

Importantly, in the southern site survival was lower in all genotypes of northern populations in comparison with the genotypes of southern populations, which suggests that there is no major genotypic variation in tolerance to warmer climate in northern populations. This may hinder adaptation in northern populations. Given that Tenkanen et al. (2020)—consistent with previous studies (e.g., Rusanen et al. 2003, Salojärvi et al. 2017)—showed the relatedness of our genotypes to be high and we consistently show high intrapopulation variation in our measured traits, this finding is unlikely to be caused by lower genetic variation in northern (marginal) populations. However, caution is needed as the number of genotypes in our trial was comparatively low and the common garden sites within climatic regions were not replicated.

**Height growth is controlled by adaptation to the soil environment**

We found that sapling height growth had a strong, positive correlation with soil N availability. This agrees well with the general notion that silver birch performs best in fertile sites (Atkinson 1992) and that its growth is sensitive to soil nutrient status (Ingestad 1970, Helliwell 1974). Considering this and the fact that due to land-use history (e.g., the northern common garden was established on an abandoned agricultural field, while the southern common garden was established on a clear-cut) soil nitrogen among our sites did not follow the general south–north gradient in Finland with soil fertility decreasing toward north (Merilä and Jortikka 2013), it is not surprising that we did not find the highest growth in the warm, southern common garden. Instead, our analyses where individual effects of soil N, common garden site, transfer distance, and population can be disentangled revealed a much more complicated pattern: For southern populations, the southern and northern sites did not differ and both sustained lower growth compared with the central site. Only for northern populations, our prediction was confirmed as the northern site sustained comparatively lower growth.

Such a pattern is likely explained by both the variation in soil fertility among sites and adaptation of southern and northern populations to natural differences in soil fertility (Merilä and Jortikka 2013) although the colonization history of Finnish birches may also play a role here; see Palmé et al. (2002) and Salojärvi et al. (2017). Significance of adaptation to soil conditions is further supported by our observation that the northern saplings were on average taller compared with the southern saplings in the southern site at the end of the experiment (2013; after removing the transfer effect).

These observations suggest that the effect of soil fertility on silver birch growth can overrule the effects of a temperature sum gradient as high as 700 DD. This supports earlier notions that soil fertility may have a significant role in explaining variation in tree growth across temperature gradients (Rousi et al. 2018) and illustrates how differences in growth between southern and northern populations can be modified by local environmental conditions other than temperature. Such modification is a sign of a genotype × environment (G × E) interaction, arising from among-site variation in environmental conditions and genotypic variation. Earlier studies have shown that significant G × E interactions in silver birch growth arise from...
intrapopulation genotypic variation when the quality of growing environments differs significantly (Silfver et al. 2009, Mikola et al. 2014). Our results show that this also holds for interpopulation genotypic variation.

**Weak local adaptation of height growth to temperature with high plasticity and genotypic variation**

We expected to see the best height growth for each population in the common garden site closest to its origin, that is, we expected populations to be locally adapted. The quadratic response to DD transfer became stronger over time and best growth was found near the origin (at –194 DD transfer in 2013), thus supporting local adaptation. However, the response explained only 0.5% of the total variation in growth. This indicates weak local adaptation, at least during early growth, and high acclimation capacity under field conditions.

When site conditions are suboptimal (as indicated by low growth), silver birch has been suggested to exhibit steep local adaptation (Viherä-Aarnio et al. 2013). In our case, we found evidence of adaptation (in terms of growth) to local soil conditions and autumn day length (growth cessation advanced and the growing season shortened with southward transfer) rather than to local climatic conditions. High acclimation capacity of silver birch has been reported earlier. Finnish silver birch survived better and grew taller compared with local birches when transplanted 6–13° latitude into wetter summer and warmer spring conditions in Alberta, Canada (Rousi et al. 2012), or Korea (Han et al. 1985), and silver birch saplings were able to acclimate to strongly contrasting temperature and soil moisture conditions realizing equal growth under such conditions (Possen et al. 2015).

In agreement with the low level of local adaptation to temperature in silver birch populations, we found large intrapopulation variation, allowing for the possibility of rapid genotypic change in populations. This confirms our hypothesis and supports the recent genome analysis of silver birch by Salojärvi et al. (2017). It should be noted, however, that the number of genotypes included for each population is on the low side for firm conclusions with respect to genotypic variation, although intrapopulation variation is found consistently for silver birch phenology, physiology, herbivory, and N cycling (e.g., Rousi and Heinonen 2007, Silfver et al. 2009, Possen et al. 2014, 2015, Mikola et al. 2018) and for silver birch most variation is found within populations (Rusanen et al. 2003, Salojärvi et al. 2017).

Nonetheless, supporting earlier findings with silver birch saplings (Mikola et al. 2014), we found that genotypic variation was highly consistent across years. In contrast, variation across sites was inconsistent, a sign of high phenotypic plasticity, and in good agreement with our finding that the rank for sapling growth of southern and northern differed among the common garden sites. It appears local populations maintain genotypes that perform relatively better after a transfer to another environment and are thus currently not growing in their optimal environment (Possen et al. 2015). As high intrapopulation variation is important for maintaining species distributions under climate change (Peñuelas et al. 2013), our results predict no major withdrawal in silver birch distribution under the warming climate.

**No consistent latitudinal variation in spring and autumn phenology**

Increasing air temperature, summarized by accumulation of temperature sum expressed as DD, is thought to be the main driver for silver birch spring phenology (Rousi and Heinonen 2007, Basler and Körner 2012). Here, we show that the DD needed for bud break is affected by site conditions as more DD was needed for bud break in the warmer southern common garden in comparison with other sites. For many species, populations from cooler environments are suggested to start growth in spring at lower temperature sums (Hänninen 2016 and references therein), a sign of local adaptation. Supporting this, we found that northern silver birch populations required less DD and thus started growth earlier compared with southern populations, but this difference was clear in the central common garden only. This suggests that there is no consistent south–northcline for population origin with respect to the temperature sum required for bud break in silver birch, in line with Rousi et al. (2019). Instead, the pattern seems to vary from site to site depending on local environmental conditions.

Although, to our knowledge, this is the first time clinal variation in spring phenology has been
evaluated for silver birch under field conditions in terms of temperature sum, there is earlier evidence from other tree species that clinal variation in spring phenology is not guaranteed. For instance, Hawkins and Dhar (2012) show that the DD requirement of a population of paper birch (B. papyrifera Marsh.) differs among common gardens, supporting the importance of random environmental variation, and Soolanayakanahally et al. (2013) report similar results for Populus balsamifera L. Of the eight species included in their meta-analysis, Alberto et al. (2013) found no south–north cline for population origin for four species and a cline where southern populations required less DD for three species, two of the latter being broadleaves. In other words, there appears to be no common cline in spring phenology across years, tree species, or growing sites when evaluated on the basis of temperature sum. This agrees with the notion that spring phenology exhibits a large degree of phenotypic plasticity (Kramer 1995, Vitasse et al. 2010) and clearly warns against drawing conclusions from single-year experiments or experiments conducted under controlled conditions (Poorter et al. 2016).

What is remarkable, however, is that in spite of great phenotypic plasticity, we found differences among silver birch genotypes in the timing of bud break to be much more persistent across years and common garden sites than for growth or any other phenophases we measured. This indicates that genotypic variation is more conserved for bud break than for other phenophases. A reason why intrapopulation genotypic variation remains high and is not eroded by selection could be that bud break in spring is not closely linked to the period of carbon gain as differences in bud break are compensated for during leaf development (Possen et al. 2014b). In other words, there may be little penalty for comparatively late bud break in spring.

According to the literature, northern populations should cease growth earlier (in terms of calendar days) compared with southern populations, at least when grown at the same sites. Isolating the population effect, we found no support for such cline in our populations. Instead, it appeared that growth cessation did not follow any consistent pattern across sites or years. For instance, growth ceased earlier in southern populations compared with northern populations in the southern and northern common garden sites, but not in the central common garden in 2011 and 2013, and in 2012, this pattern was reversed. Similarly, the saplings with a northern origin ceased growth earlier in the northern common garden site in 2012, but later in 2011 and 2013. Since the timing of growth cessation among common garden sites differed among years, the effects of other factors—night temperature in particular (Fu et al. 2016)—cannot be excluded. On the other hand, when the population effects were removed, we found a southward transfer to consistently lead to earlier growth cessation, further reflected in a shorter growth season, which likely is a result of northern genotypes on average being adapted to cease growth at longer days.

**Soil N sustains height growth, but also affects the timing of bud break**

In line with our hypothesis, we found that N availability in the soil not only sustained growth, but also affected the timing of bud break. The DD needed for bud break was significantly lower when soil N concentrations were high. Work on this subject is limited, but there is evidence that soil fertility can affect spring and/or autumn phenology in silver birch (Pääkkönen and Holopainen 1995) and in some other deciduous tree species (Sigurdsson 2001, Arend et al. 2016). This suggests the association of soil N availability and timing of bud break may apply to trees in general, which agrees well with the finding that, especially in the subarctic, those biosphere models that include climate-N cycle feedbacks perform significantly better in explaining vegetation responses to climate warming than those that do not (Guenet et al. 2013, Tang et al. 2016).

One potential mechanism to explain this link is that higher availability of storage compounds (apparently sustained by high soil fertility) facilitates earlier bud break in spring (Beauvieux et al. 2018). This effect could be further strengthened by lower N resorption from senescing leaves in autumn in environments where N is available in abundance (Yuan and Chen 2015), allowing an extension of the growing period and synthesis of more storage compounds before dormancy (Luoranen 2000). Supporting this idea, Pääkkönen and Holopainen (1995) showed delayed growth cessation in silver birch as a consequence of increased N availability. Although, in our study, soil N had a minor influence on growth cessation, these results together
suggest that in addition to controlling tree growth (Pääkkönen and Holopainen 1995, Rousi et al. 2018), soil N can affect the timing of phenophases.

**Height growth has a genotypic association with growing season length in favorable sites**

In line with our expectations, sapling height was strongly and positively associated with growing season length at the phenotype level (i.e., among individual plants) across all sites and years. This seemed to be mainly because late growth cessation was positively associated with growth, but early bud break also had a constantly positive effect on growth in the central and southern growing sites. In contrast, sapling height had a strong and positive genotypic correlation with growing season length in the central site only, with the southern and northern sites showing significant correlations for some years only. Also, these genotypic correlations seemed to be entirely explained by late growth cessation as timing of bud break appeared to have no consistent genotypic association with sapling height.

These results have two general implications. First, the phenotypic correlations show that early bud break and late growth cessation, for genetic or environmental reasons, lead to a longer growing season and better growth in almost any environment and year. This would suggest that climate warming, which can lead to both an earlier start of growth in spring and later growth cessation in autumn (Piao et al. 2007, Buitenwerf et al. 2015), should significantly increase the indeterminate growth of silver birch in the boreal forest zone. Second, the genotypic correlations show that these associations are only partly governed by direct genotypic links and that the positive correlations of late growth cessation and growing season length with growth only emerge when both climate and soil fertility are favorable, as was the case in the central site. In the northern site (with a harsher climate) and in the southern site (with poorer soil), these genotypic links seem to break down, presumably due to other genetically controlled plant traits becoming more important for sustaining good growth. As a result, natural selection on late growth cessation and a long growing season is likely to occur in the most optimal sites only. This apparently contributes to maintaining the high genotypic variation of these traits that we found in local populations in our study.

**CONCLUSION**

Using three common gardens, six populations each represented by up to five cloned genotypes latitudinally covering the subarctic, we show that clinal south–north variation in height growth and survival, as well as in spring and autumn phenology, is largely absent in silver birch when grown in field conditions. In line with our expectation, we found evidence for adaptation to local climatic conditions in sapling survival, which decreased when the growing heat sum doubled, but little evidence for such adaptation in growth and phenology. There we found ample genotypic variation and plasticity. As high intrapopulation variation is important for maintaining species distributions under climate change, our results predict no major distribution shifts in silver birch due to changes in temperature. Furthermore, survival and acclimation capacity in height growth and phenology to a warmer climate were substantially modified by soil N availability.

Following the natural subarctic south–north cline in soil fertility, our results suggest that northern, subarctic silver birches are adapted to less fertile soils compared with those growing in central and southern subarctic soils. We found that sapling height growth had a strong, positive correlation with soil N availability and that the effects of soil fertility can overrule the effects of a temperature sum gradient as high as 700 DD.

As genotypic associations between growth and phenology depended on soil N, in line with the notion that biosphere models including climate-N cycle feedbacks perform significantly better in explaining vegetation responses to climate warming, soil properties should be considered in both short-term phytotron experiments and long-term common garden experiments aiming at clarifying the effects of climate change on survival, height growth, and the phenological cycle of trees.

**ACKNOWLEDGMENTS**

The staff of the Natural Resources Institute Finland, Luke (the former Finnish Forest Research Institute, METLA), in Kolari (K. Ranta, J. Unga, I. Heikkilä), Punkaharju (H. Sikanen), and Haapastensyrjä (P. Kanonen, A. Leppänen, S. Vanhakoski, M. Pekonen), and the staff of the University of Eastern Finland in Joensuu (H. Hakulinen, A. Tenkanen, M. Deepak, A.
Taimioja, H. Korhonen, R. Khajvand, V. Vilkman, and K. Heimonen) helped in selecting the birch populations, micropropagated the plant material, helped in establishing the experiments, and collected the data. K. Heimonen is further acknowledged for assistance in data preparation. S. Ruotsalainen for his help in accessing the meteorological data and commenting on an earlier version of the manuscript, and C. Roeper and J. Versnel for help in accessing SPSS. B. Possen personally acknowledges S. den Held for making the work possible. The experimental work was supported by the strategic funding of the University of Eastern Finland (Project 931060), R&D budget was invested by Royal HaskoningDHV, the data were analyzed, and the manuscript was written under the Academy of Finland Project ’BETUMICS, Towards more efficient Arctic research using dominant Betula species, spectromics and genomics’ (decision #285030), in memory of Tom.

LITERATURE CITED

Aizen, M. A., and W. A. Patterson. 1995. Leaf phenology and herbivory along a temperature gradient: a spatial test of the phenological window hypothesis. Journal of Vegetation Science 6:543–550.

Albeto, F. J., et al. 2013. Potential for evolutionary responses to climate change - evidence from tree populations. Global Change Biology 19:1645–1661.

Anttonen, S., R. Piispapen, J. Ovaska, P. Mutikainen, P. Saranpää, and E. Vapaavuori. 2002. Effects of defoliation on growth, biomass allocation and wood properties of Betula pendula clones grown at different nutrient levels. Canadian Journal of Forest Research 32:498–508.

Arend, M., A. Gessler, and M. Schaub. 2016. The influence of the soil on spring and autumn phenology in European beech. Tree Physiology 36:78–85.

Atkinson, M. D. 1992. Betula pendula Roth (B. verrucosa Ehrh.) and B. pubescens Ehrh. Journal of Ecology 80:837.

Basler, D., and C. Körner. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. Agricultural and Forest Meteorology 165:73–81.

Beauvieux, R., B. Wenden, and E. Dirlewanger. 2018. Bud dormancy in perennial fruit tree species: a pivotal role for oxidative cues. Frontiers in Plant Science 9:657.

Berteaux, D. 2004. Keeping pace with fast climate change: can arctic life count on evolution? Integrative and Comparative Biology 44:140–151.

Buitenwerf, R., L. Rose, and S. I. Higgins. 2015. Three decades of multi-dimensional change in global leaf phenology. Nature Climate Change 5:364–368.

Carmona, D., M. J. Lajeunesse, and M. T. J. Johnson. 2011. Plant traits that predict resistance to herbivores: traits that predict resistance to herbivores. Functional Ecology 25:358–367.

De Barba, D., S. Rossi, A. Deslauriers, and H. Morin. 2016. Effects of soil warming and nitrogen foliar applications on bud burst of black spruce. Trees 30:87–97.

Fu, Y. H., Y. Liu, H. J. De Boeck, A. Menzel, I. Nijs, M. Peaucelle, J. Penuelas, S. Piao, and I. A. Janssens. 2016. Three times greater weight of daytime than of night-time temperature on leaf unfolding phenology in temperate trees. New Phytologist 212:590–597.

Graumann, J., and R. Cotton. 2018. Multipanelfigure: simple assembly of multiple plots and images into a compound figure. Journal of Statistical Software 84:1–10.

Guenet, B., P. Cadule, S. Zaehele, S. L. Piao, P. Peylin, F. Maignan, P. Ciais, and P. Friedlingstein. 2013. Does the integration of the dynamic nitrogen cycle in a terrestrial biosphere model improve the long-term trend of the leaf area index? Climate Dynamics 40:2535–2548.

Hamrick, J. 2004. Response of forest trees to global environmental changes. Forest Ecology and Management 197:323–335.

Hamrick, J. L., M. J. W. Godt, and S. L. Sherman-Broyles. 1992. Factors influencing levels of genetic diversity in woody plant species. Pages 95–124 in W. T. Adams, S. H. Strauss, D. L. Copes, and A. R. Griffin, editors. Population genetics of forest trees. Springer, Dordrecht, The Netherlands.

Han, Y., Y. Lee, K. Ryu, and M. Park. 1985. Growth of European white birch (Betula pendula Roth) introduced from Finland at age 11 in Korea. Pages 73–77. Institute of Forest Genetics Suwon Korea, Suwon, South Korea.

Hannah, P. 1987. Early growth of planted yellow and paper birch and European birches in Vermont. New Forests 4:343–349.

Hänninen, H. 2016. Boreal and temperate trees in a changing climate. Springer Netherlands, Dordrecht, The Netherlands.

Hänninen, H., and K. Tanino. 2011. Tree seasonality in a warming climate. Trends in Plant Science 16:412–416.

Hawkins, C. D. B., and A. Dhar. 2012. Spring bud phenology of 18 Betula papyrifera populations in British Columbia. Scandinavian Journal of Forest Research 27:507–519.

Hayatgheibi, H., A. Fries, J. Kroon, and H. X. Wu. 2019. Estimation of genetic parameters, provenance performances, and genotype by environment interactions for growth and stiffness in lodgepole pine (Pinus contorta). Scandinavian Journal of Forest Research 34:1–11.

Heide, O. M. 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing...
the effect of climatic warming. Tree Physiology 23:931–936.

Heimonen, K., A. Valtonen, S. Kontunen-Soppela, S. Keski-Saari, M. Rousi, E. Oksanen, and H. Roininen. 2015a. Insect herbivore damage on latitudinally translocated silver birch (Betula pendula) – predicting the effects of climate change. Climatic Change 131:245–257.

Heimonen, K., A. Valtonen, S. Kontunen-Soppela, S. Keski-Saari, M. Rousi, E. Oksanen, and H. Roininen. 2015b. Colonization of a host tree by herbivorous insects under a changing climate. Oikos 124:1013–1022.

Heimonen, K., A. Valtonen, S. Kontunen-Soppela, S. Keski-Saari, M. Rousi, E. Oksanen, and H. Roininen. 2017. Susceptibility of silver birch (Betula pendula) to herbivorous insects is associated with the size and phenology of birch – implications for climate warming. Scandinavian Journal of Forest Research 32:95–104.

Helliwell, D. 1974. The growth of sycamore (Acer pseudoplatanus L.) and birch (Betula verrucosa Ehrh.) seedlings in 50 different soils. Merlewood Research and Development Paper No. 58. Institute of Terrestrial Ecology, Grange-over-Sands, UK.

Hjalten, J., K. Danell, and L. Ericson. 1993. Effects of simulated herbivory and intraspecific competition on the compensatory ability of birches. Ecology 74:1136–1142.

Howe, G. T., S. N. Aitken, D. B. Neale, K. D. Jermstad, N. C. Wheeler, and T. H. Chen. 2003. From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. Canadian Journal of Botany 81:1247–1266.

Huttunen, L., M. Ayres, P. Niemelä, S. Heiska, R. Tegelberg, M. Rousi, and S. Kellomäki. 2013. Interactive effects of defoliation and climate change on compensatory growth of silver birch seedlings. Silva Fennica 47(3):1–14.

Ingestad, T. 1970. A definition of optimum nutrient requirements in birch seedlings. I. Physiologia Plantarum 23:1127–1138.

IPCC. 2014. Climate change 2013: the physical science basis: working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, USA.

Kinnaird, J. W. 1974. Effect of site conditions on the regeneration of birch (Betula Pendula Roth and B. Pseudopoa Ehrh.). Journal of Ecology 62:467.

Koski, V., and R. Sievanen. 1985. Timing of growing cessation in relation to the variations in the growing season. Pages 167–193 in P. M. A. Tigerstedt, P. Puttonen, and V. Koski, editors. Crop physiology of forest trees. University of Helsinki, Helsinki, Finland.

Kramer, K. 1995. Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. Plant, Cell and Environment 18:93–104.

Larcher, W. 2003. Physiological plant ecology: ecophysiology and stress physiology of functional groups. Fourth edition. Springer, Berlin, Germany.

Laube, J., T. H. Sparks, N. Estrella, and A. Menzel. 2014. Does humidity trigger tree phenology? Proposal for an air humidity based framework for bud development in spring. New Phytologist 202:350–355.

Li, C., A. Welling, T. Puhakainen, A. Vihera-Aarnio, A. Ernssten, O. Junttila, P. Heino, and E. T. Palva. 2005. Differential responses of silver birch (Betula pendula) ecotypes to short-day photoperiod and low temperature. Tree Physiology 25:1563–1569.

Lintunen, A., and P. Kaitaniemi. 2010. Responses of crown architecture in Betula pendula to competition are dependent on the species of neighbouring trees. Trees 24:411–424.

Lloret, A., M. L. Badenes, and G. Rios. 2018. Modulation of dormancy and growth responses in reproductive buds of temperate trees. Frontiers in Plant Science 9:1368.

Luoranen, J. 2000. Control of growth and frost hardening of silver birch container seedlings: growth retardants, short day treatment and summer planting. The Finnish Forest Research Institute Research Papers 777, Helsinki, Finland.

Luoto, T. P., A. E. K. Ojala, L. Arppe, S. J. Brooks, E. Kurki, M. Oksman, M. J. Woolier, and M. Zajaczkowski. 2018. Synchronized proxy-based temperature reconstructions reveal mid- to late Holocene climate oscillations in High Arctic Svalbard: holocene climate oscillations in high arctic Svalbard. Journal of Quaternary Science 33:93–99.

Märlä, P., and S. Jortikka. 2013. Forest condition monitoring in Finland - National report. The Finnish Forest Research Institute, Helsinki. http://urn.fi/Urn:NBN:fi:metla-201305087568

Michelson, I. H., P. K. Ingvarsson, K. M. Robinson, E. Edlund, M. E. Eriksson, O. Nilsson, and S. Jansson. 2018. Autumn senescence in aspen is not triggered by day length. Physiologia Plantarum 162:123–134.

Mikola, J. 1982. Bud-set phenology in relation to the variations in the growing season. Pages 167–193 in P. M. A. Tigerstedt, P. Puttonen, and V. Koski, editors. Crop physiology of forest trees. University of Helsinki, Helsinki, Finland.

Kramer, K. 1995. Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. Plant, Cell and Environment 18:93–104.

Larcher, W. 2003. Physiological plant ecology: ecophysiology and stress physiology of functional groups. Fourth edition. Springer, Berlin, Germany.

Laube, J., T. H. Sparks, N. Estrella, and A. Menzel. 2014. Does humidity trigger tree phenology? Proposal for an air humidity based framework for bud development in spring. New Phytologist 202:350–355.

Li, C., A. Welling, T. Puhakainen, A. Vihera-Aarnio, A. Ernssten, O. Junttila, P. Heino, and E. T. Palva. 2005. Differential responses of silver birch (Betula pendula) ecotypes to short-day photoperiod and low temperature. Tree Physiology 25:1563–1569.

Lintunen, A., and P. Kaitaniemi. 2010. Responses of crown architecture in Betula pendula to competition are dependent on the species of neighbouring trees. Trees 24:411–424.

Lloret, A., M. L. Badenes, and G. Rios. 2018. Modulation of dormancy and growth responses in reproductive buds of temperate trees. Frontiers in Plant Science 9:1368.

Luoranen, J. 2000. Control of growth and frost hardening of silver birch container seedlings: growth retardants, short day treatment and summer planting. The Finnish Forest Research Institute Research Papers 777, Helsinki, Finland.

Luoto, T. P., A. E. K. Ojala, L. Arppe, S. J. Brooks, E. Kurki, M. Oksman, M. J. Woolier, and M. Zajaczkowski. 2018. Synchronized proxy-based temperature reconstructions reveal mid- to late Holocene climate oscillations in High Arctic Svalbard: holocene climate oscillations in high arctic Svalbard. Journal of Quaternary Science 33:93–99.

Merilä, P., and S. Jortikka. 2013. Forest condition monitoring in Finland – National report. The Finnish Forest Research Institute, Helsinki. http://urn.fi/Urn:NBN:fi:metla-201305087568

Michelson, I. H., P. K. Ingvarsson, K. M. Robinson, E. Edlund, M. E. Eriksson, O. Nilsson, and S. Jansson. 2018. Autumn senescence in aspen is not triggered by day length. Physiologia Plantarum 162:123–134.

Mikola, J. 1982. Bud-set phenology as an indicator of climatic adaptation of Scots pine (Pinus sylvestris) in Finland. Silva Fennica 18(184).

Mikola, J., U. Paaso, T. Silfver, M. Autelio, K. Koikkalainen, S. Ruotsalainen, and M. Rousi. 2014. Growth and genotype × environment interactions in Betula pendula: Can tree genetic variation be maintained
by small-scale forest ground heterogeneity? Evolutionary Ecology 28:811–828.

Mikola, J., T. Silfver, U. Paaso, B. J. M. H. Possen, and M. Rousi. 2018. Leaf N resorption efficiency and litter N mineralization rate have a genotypic tradeoff in a silver birch population. Ecology 99:1227–1235.

Mopper, S., and D. Simberloff. 1995. Differential heritability in an oak population: the role of plant phenology and insect performance. Ecology 76:1233–1241.

Mueller, L. O., L. C. Breza, M. A. Genung, C. P. Giardina, N. E. Stone, L. C. Sidak-Loftis, J. D. Busch, D. M. Wagner, J. K. Bailey, and J. A. Schweitzer. 2017. Ecosystem consequences of plant genetic divergence with colonization of new habitat. Ecosphere 8:e01743.

Myking, T., and O. M. Heide. 1995. Dormancy release and chilling requirement of buds of latitudinal ecotypes of Betula pendula and B. pubescens. Tree Physiology 15:697–704.

Nord, E. A., and J. P. Lynch. 2009. Plant phenology: a critical controller of soil resource acquisition. Journal of Experimental Botany 60:1927–1937.

Oleksyn, J., P. B. Reich, M. G. Tjoelker, and W. Chalupka. 2001. Biogeographic differences in shoot elongation pattern among European Scots pine populations. Forest Ecology and Management 148:207–220.

Pääkkönen, E., and T. Holopainen. 1995. Influence of nitrogen supply on the response of clones of birch (Betula pendula Roth) to ozone. New Phytologist 129:595–603.

Palmé, A. E., Q. Su, A. Rautenberg, F. Manni, and M. Lascoux. 2002. Postglacial recolonization and cpDNA variation of silver birch, Betula pendula: phylogeography of Betula. Molecular Ecology 12:201–212.

Peñuelas, J., et al. 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere. Global Change Biology 19:2303–2338.

Piao, S., P. Friedlingstein, P. Ciais, N. Voivy, and J. Demarty. 2007. Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades: phenology and carbon cycle. Global Biogeochemical Cycles 21.

Polgar, C. A., and R. B. Primack. 2011. Leaf-out phenology of temperate woody plants: from trees to ecosystems: Tansley review. New Phytologist 191:926–941.

Poorter, H., F. Fiorani, R. Pieruschka, T. Wójciewoński, W. H. van der Putten, M. Kleyer, U. Schurr, and J. Postma. 2016. Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. New Phytologist 212:838–855.

Possen, B., M. Anтонен, E. Оксанен, M. Rousi, J. Heinonen, K. Костиайнен, S. Kontunen-Soppela, J. Heiskanen, and E. Vapaavuori. 2014a. Variation in 13 leaf morphological and physiological traits within a silver birch (Betula pendula) stand and their relation to growth. Canadian Journal of Forest Research 44:657–665.

Possen, B. J. H. M., M. Rousi, T. Silfver, M. J. Anttonen, S. Ruotsalainen, E. Oksanen, and E. Vapaavuori. 2014b. Within-stand variation in silver birch (Betula pendula Roth) phenology. Trees 28:1801–1812.

Possen, B. J. H. M., J. Heinonen, M. J. Anttonen, M. Rousi, S. Kontunen-Soppela, E. Oksanen, and E. M. Vapaavuori. 2015. Trait syndromes underlying stand-level differences in growth and acclimation in 10 silver birch (Betula pendula Roth) genotypes. Forest Ecology and Management 343:123–135.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raulo, J., and V. Koski. 1977. Growth of Betula pendula progenies in southern and central Finland. Communications Instituti Forestalis Fenniae 90:1–39.

Rehfeldt, G. E., C. C. Ying, D. L. Spittlehouse, and D. A. Hamilton. 1999. Genetic responses to climate in Pinus contorta: niche breadth, climate change, and reforestation. Ecological Monographs 69:375.

Rousi, M., and J. Heinonen. 2007. Temperature sum accumulation effects on within-population variation and long-term trends in date of bud burst of European white birch (Betula pendula). Tree Physiology 27:1019–1025.

Rousi, M., B. Possen, R. Hagqvist, and B. Thomas. 2012. From the arctic circle to the Canadian prairies - a case study of silver birch acclimation capacity. Silva Fennica 46:355–364.

Rousi, M., B. J. M. H. Possen, P. Pulkkinnen, and J. Mikola. 2019. Using long-term data to reveal the geographical variation in timing and quantity of pollen and seed production in silver and pubescent birch in Finland: implications for gene flow, hybridization and responses to climate warming. Forest Ecology and Management 438:25–33.

Rousi, M., B. J. M. H. Possen, S. Ruotsalainen, T. Silfver, and J. Mikola. 2018. Temperature and soil fertility as regulators of tree line Scots pine growth and survival-implications for the acclimation capacity of northern populations. Global Change Biology 24:e545–e559.

Rousi, M., and J. Pusenius. 2005. Variations in phenology and growth of European white birch (Betula pendula) clones. Tree Physiology 25:201–210.

Ruosteenoja, K., J. Räisänen, and P. Pirinen. 2011. Projected changes in thermal seasons and the growing season in Finland. International Journal of Climatology 31:1473–1487.
Rusanen, M., P. Vakkari, and A. Blom. 2003. Genetic structure of Acer platanoides and Betula pendula in northern Europe. Canadian Journal of Forest Research 33:1110–1115.

Ryynänen, L. 1996. Survival and regeneration of dormant silver birch buds stored at super-low temperatures. Canadian Journal of Forest Research 26:617–623.

Salojarvi, J., et al. 2017. Genome sequencing and population genomic analyses provide insight into the adaptive landscape of silver birch. Nature Genetics 49:904–912.

Sarvas, R. 1972. Investigations on the annual cycle of development of forest trees - active period. Communicaciones Instituti Forestalis Fenniae 76:1–110.

Sarvas, R. 1974. Investigations on the annual cycle of development of forest trees - autumn dormancy and winter dormancy. Communicaciones Instituti Forestalis Fenniae 84:1–101.

Savolainen, O., S. T. Kujala, C. Sokol, T. Pyhajärvi, K. Avia, T. Knurr, K. Karkkainen, and S. Hicks. 2011. Adaptive potential of northernmost tree populations to climate change, with emphasis on Scots pine (Pinus sylvestris L.). Journal of Heredity 102:526–536.

Savolainen, O., T. Pyhajärvi, and T. Knürr. 2007. Gene flow and local adaptation in trees. Annual Review of Ecology, Evolution, and Systematics 38:595–619.

Shaw, R. G., and J. R. Etterson. 2012. Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics: Tansley review. New Phytologist 195:752–765.

Sigurdsson, B. D. 2001. Elevated [CO2] and nutrient status modified leaf phenology and growth rhythm of young Populus trichocarpa trees in a 3-year field study. Trees 15:403–413.

Silfver, T., H. Roininen, E. Oksanan, and M. Rousi. 2009. Genetic and environmental determinants of silver birch growth and herbivore resistance. Forest Ecology and Management 257:2145–2149.

Soolanayakanahally, R. Y., R. D. Guy, S. N. Silim, and M. Song. 2013. Timing of photoperiodic competency causes phenological mismatch in balsam poplar (Populus balsamifera L.): tree phenology and climate warming. Plant, Cell & Environment 36:116–127.

Spiecker, H., M. Lindner, and J. K. Schuler, editors. 2019. Douglas-fir: an option for Europe. What science can tell us 9. European Forest Research Institute, Joensuu, Finland.

Tang, J., C. Körner, H. Muraoka, S. Piao, M. Shen, S. J. Thackeray, and X. Yang. 2016. Emerging opportunities and challenges in phenology: a review. Ecosphere 7:e01436.

Tenkanen, A., S. Keski-Saari, J. Salojärvi, E. Oksanan, M. Keinänen, and S. Kontunen-Soppela. 2020. Differences in growth and gas exchange between southern and northern provenances of silver birch (Betula pendula Roth) in northern Europe. Tree Physiology 40:198–214.

Varnagiryte-Kabasinskiene, I., V. Araminiene, and V. Stakenas. 2016. Effects of artificial defoliation and simulated insect damage on the growth of Betula pendula saplings. iForest - Biogeosciences and Forestry 9:95–100.

Venäläinen, A., H. Tuomenvirta, P. Pirinen, and A. Drebs. 2005. A basic Finnish climate dataset 1961-2000 - description and illustrations. Page 27. Finnish Meteorological Institute, Helsinki, Finland.

Viherä-Aarnio, A., R. Häkkinen, J. Partanen, A. Luomakoji, and V. Koski. 2005. Effects of seed origin and sowing time on timing of height growth cessation of Betula pendula seedlings. Tree Physiology 25:101–108.

Viherä-Aarnio, A., K. Kostiainen, R. Piispanen, P. Saranpää, and E. Vapaavuori. 2013. Effects of seed transfers on yield and stem defects of silver birch (Betula pendula Roth). Forest Ecology and Management 289:133–142.

Vitasse, Y., C. C. Bresson, A. Kremer, R. Michalet, and S. Delzon. 2010. Quantifying phenological plasticity to temperature in two temperate tree species: quantifying plasticity of leaf phenology. Functional Ecology 24:1211–1218.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer-Verlag, New York, New York, USA.

Wielgoszaki, F. E. 2001. Phenological modifications in plants by various edaphic factors. International Journal of Biometeorology 45:196–202.

Yuan, Z. Y., and H. Y. H. Chen. 2015. Negative effects of fertilization on plant nutrient resorption. Ecology 96:373–380.

Zuur, A. F., editor. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3520/full