



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

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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.

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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 (Myking 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 (Ruosteenoja 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°0' 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* Ehrh.), 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 Heino (2007)—summed over a year and expressed in degree-days, DD).

Table 1. Latitude and longitude, the number of genotypes representing each population, mean annual temperature (T), temperature sum (Tsum in degree-days, DD with a threshold of 5°C), and precipitation for the three common garden sites (mean of years 2011–2013) and six populations (mean of years 1981–2010), calculated using daily measurements available in a 10 × 10 km grid in the records of the Finnish Meteorological Institute (Venäläinen et al. 2005).

Location	Latitude	Longitude	Genotypes	T (°C)	Tsum (DD)	Tsum ₂₀₃₉ (DD)	Tsum ₂₀₆₉ (DD)	Precipitation (mm)	Soil N (mg/L)	Soil P (mg/L)	pH
Common garden sites											
Kolari (north)	67°21' N	23°49' E		1.1	995	800–900	1000–1100	599	3.9 (3.2–5.1)	20.8 (17.6–24.6)	5.2 (4.9–5.5)
Joensuu (central)	62°36' N	29°43' E		4.0	1427	1200–1300	1400–1500	685	7.3 (4.9–11.3)	9.0 (8.4–10.1)	6.1 (6.0–6.1)
Tuusula (south)	60°21' N	25°0' E		6.1	1682	>1400	>1600	711	3.4 (3.0–3.9)	1.5 (1.5–1.5)	4.6 (4.6–4.7)
Populations											
Kittilä (67° KI)	67°44' N	24°50' E	5	−0.5	776	800–900	900–1000	448			
Rovaniemi (66° RO)	66°27' N	24°14' E	5	1.0	984	1000–1100	1200–1300	504			
Posio (65° PO)	65°53' N	27°39' E	5	0.7	914	900–1000	1000–1100	579			
Vehmersalmi (62° VE)	62°45' N	28°10' E	5	3.3	1274	1200–1300	1400–1500	569			
Punkaharju (61° PU)	61°48' N	29°19' E	2	3.9	1348	1300–1400	>1600	528			
Loppi (60° LO)	60°36' N	24°25' E	4	4.5	1293	>1400	>1600	615			

Notes: The predicted temperature sum values Tsum₂₀₃₉ and Tsum₂₀₆₉ are from Ruosteenoja et al. (2011). Soil mineral N (soil N), soil P content, and pH give the mean and range of values among the replicate blocks.

Temperature sum is commonly used to estimate the amount of thermal energy available for the development of the phenological cycle, and in a common garden setup, temperature sum can be used to illustrate the difference between current and future climatic conditions. For example, the climate experienced by our northern populations in the central common garden is approximately equivalent to the climate they are likely to experience in their own growing sites somewhere between 2040 and 2069 (Ruosteenoja et al. 2011).

In addition to climate, soil fertility differs among our common gardens in terms of phosphorous (P, as total P in mg/L) and nitrogen (N, as total N in mg/L) availability (Table 1), which allows a test of the role of soil fertility (these data 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 (Ryyänen 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 Heino 2007, Basler and Körner 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 micro-propagated 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 \times 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

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		<i>P</i>
	df	Wald Chi ²	
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.

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

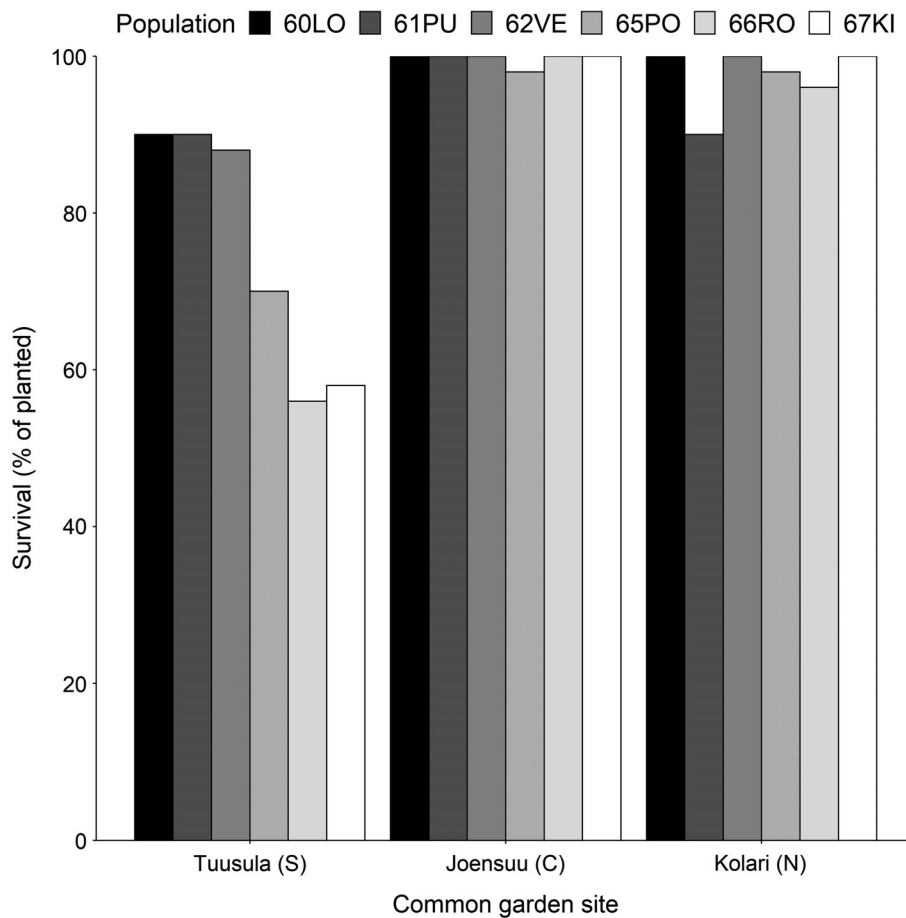


Fig. 1. Survival rate (percentage of planted individuals) in 2013 for saplings originating from the six populations (from the southernmost 60° LO to the northernmost 67° KI) and growing in the southern Tuusula, central Joensuu, and northern Kolari common gardens.

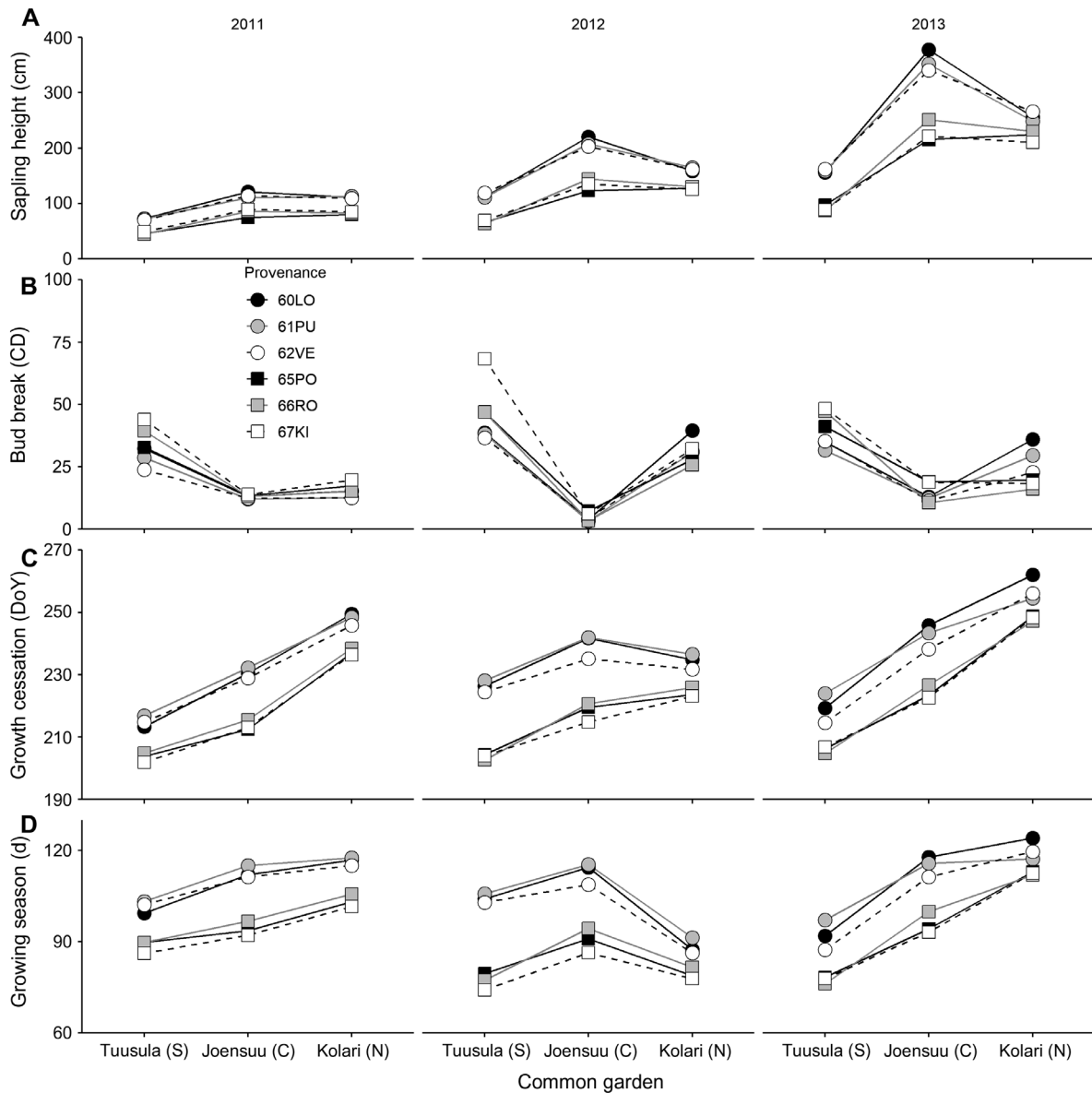


Fig. 2. Reaction norms (means, $n = 8-25$ for populations within a common garden) of (A) sapling height in cm, (B) temperature sum needed for bud break (DD with a 5°C threshold), (C) growing season length in days, and (D) growth cessation (calendar day; DoY) for the six populations (ranging from 60° LO to 67° KI) growing at the three common garden sites in 2011–2013.

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

Table 3. 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) on sapling height growth 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		SS	<i>F</i>	<i>P</i>	Percentage of total SS
	df _{predictor}	df _{error}				
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

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).

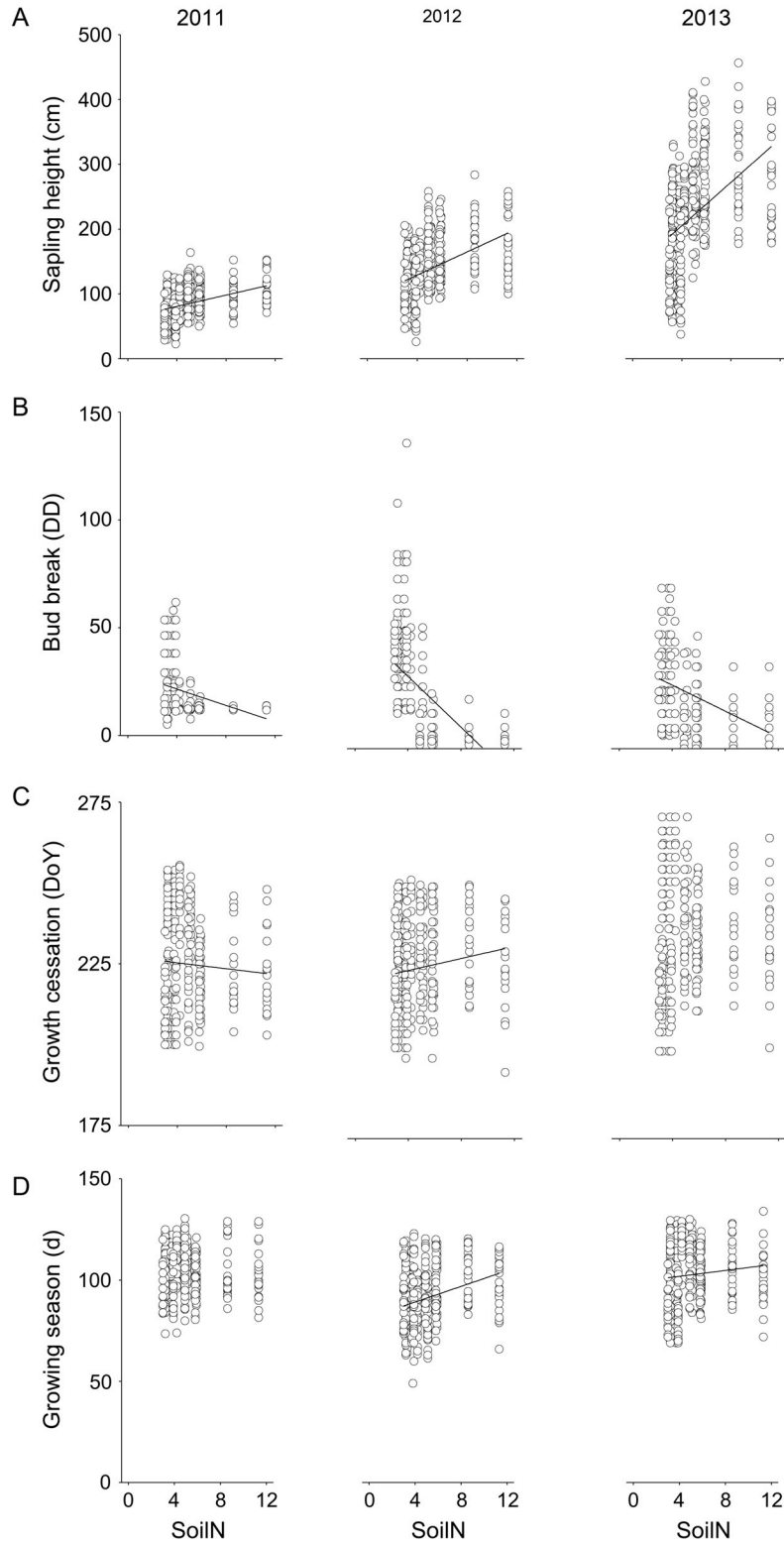


Fig. 3. Relationship between soil mineral N content (measured separately for each replicate block at each

(Fig. 3. Continued)

common garden site) and (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).

Bud break

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).

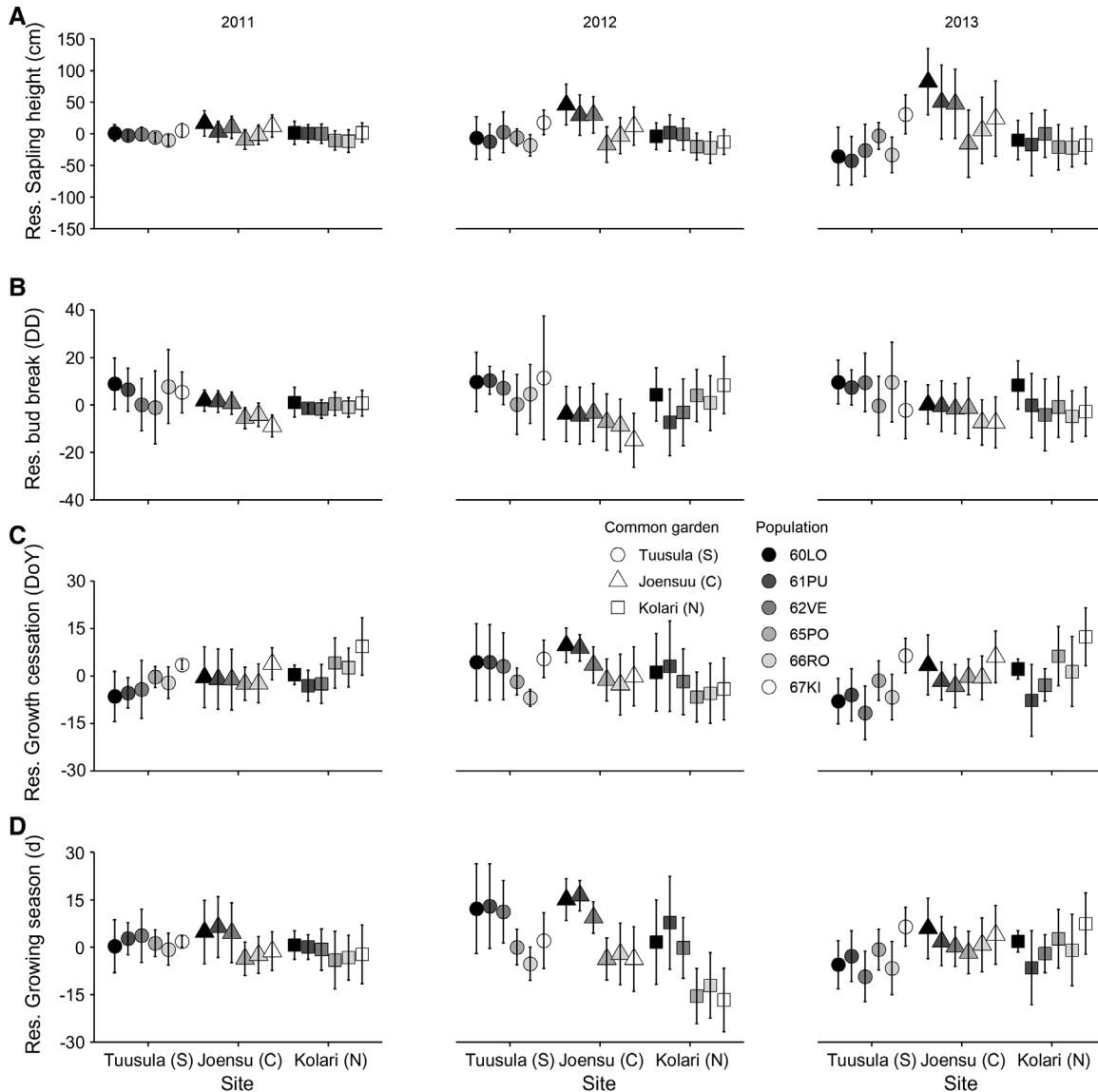


Fig. 4. Means of residuals (± 1 SE, $n = 8$ –25 for a population within a common garden) of (A) sapling height in cm, (B) temperature sum needed for bud break (DD with a 5°C threshold), (C) growing season length in days, and (D) growth cessation calendar day for the six populations (ranging from 60° LO to 67° KI) growing at the three common gardens in 2011–2013 (residuals devoid of soil N and both DD transfer effects).

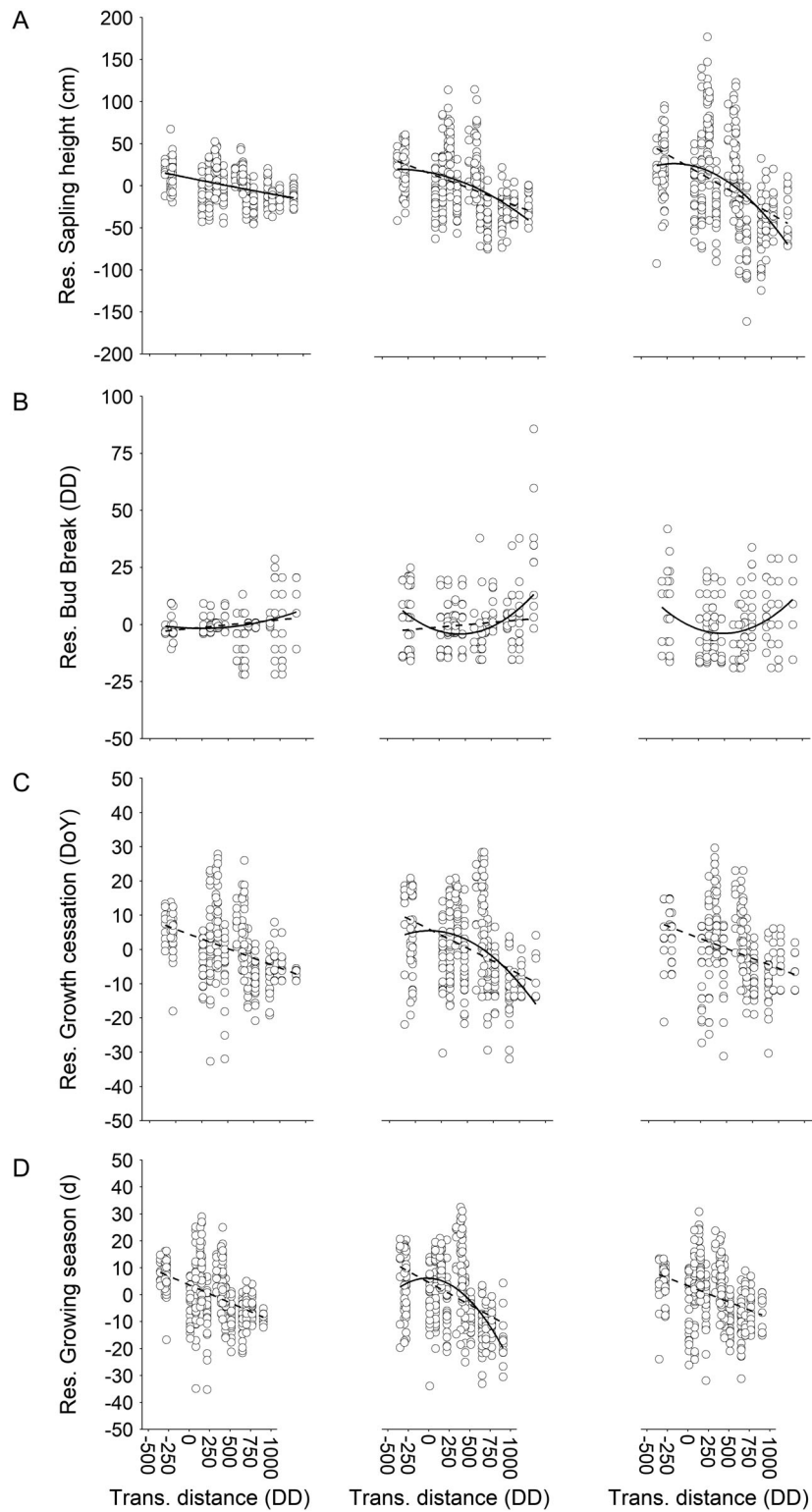


Fig. 5. Relationship between transfer distance (in DD with a 5°C threshold) and residuals of (A) sapling height in cm, (B) temperature sum needed for bud break (DD with a 5°C threshold), (C) growing season length in days,

(Fig. 5. *Continued*)

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 \times 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

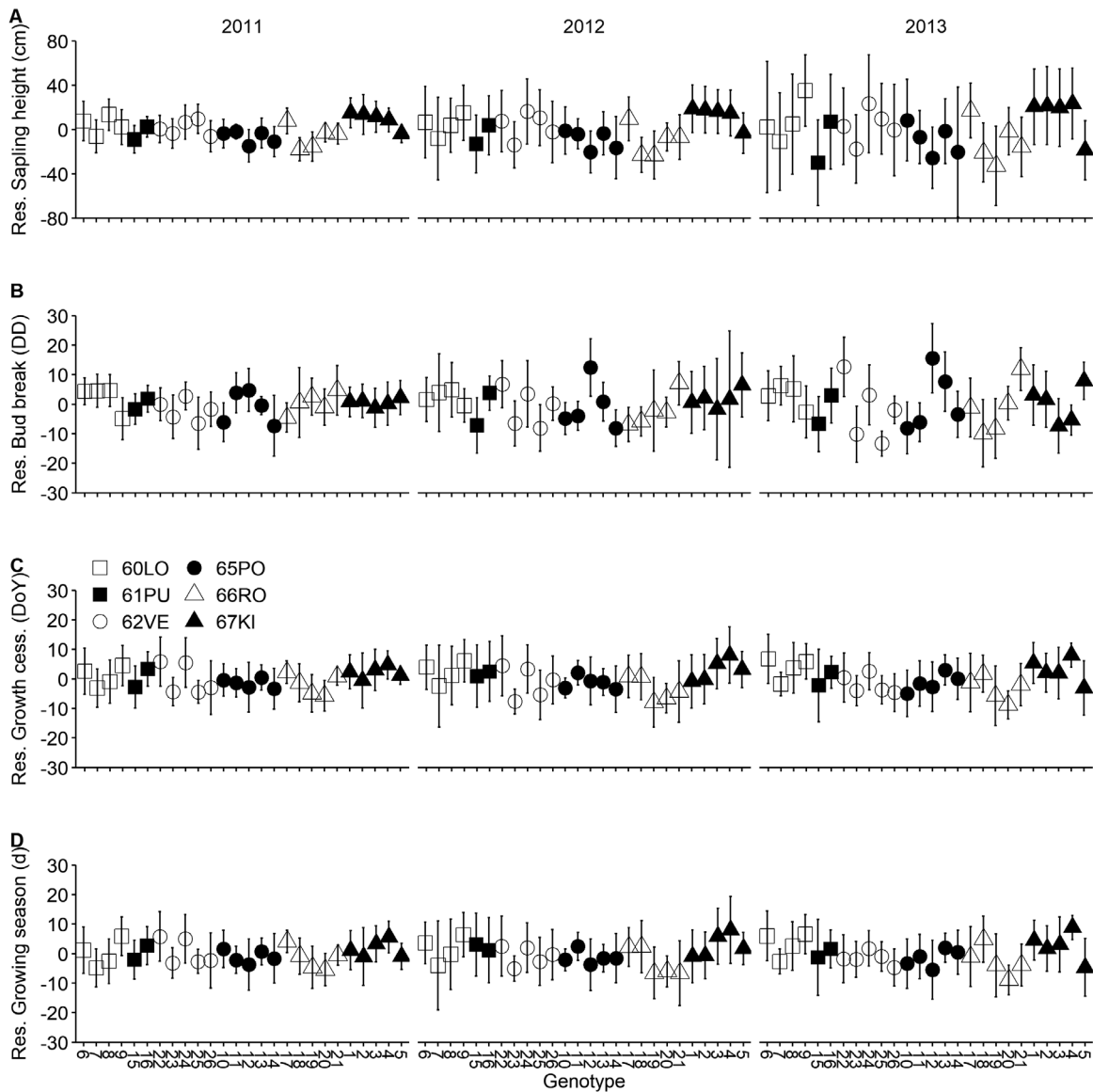


Fig. 6. Means of residuals (± 1 SE; $n = 5$ for a genotype) of (A) sapling height in cm, (B) temperature sum needed for bud break (DD with a 5°C threshold), (C) growing season length in days, and (D) growth cessation calendar day for genotypes within the six populations, ordered from south to north, in 2011–2013 (residuals are devoid of soil N, common garden site, population, and both DD transfer effects).

Table 4. Spearman's rank correlations (ρ ; $n = 26$) 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)	
		ρ	P	ρ	P	ρ	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

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 (–17 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 ($\rho = 0.78$, $P < 0.001$, for 2011 vs. 2012; $\rho = 0.89$, $P < 0.001$, 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 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		SS	<i>F</i>	<i>P</i>	Percentage of total SS
	df _{predictor}	df _{error}				
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			84,776			
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

rank of genotypes was consistent in time as the genotype means of growth cessation residuals correlated positively among the years ($\rho = 0.82$, $P < 0.001$, for 2011 vs. 2012 comparison; $\rho = 0.63$, $P < 0.001$, 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 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		SS	<i>F</i>	<i>P</i>	Percentage of total SS
	df _{predictor}	df _{error}				
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 × 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 × 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 × 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 clines 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 ($\rho = 0.71$, $P < 0.001$, for 2011 vs. 2012 comparison; $\rho = 0.60$, $P < 0.001$, for 2012 vs. 2013 comparison). Rank correlations across the sites were also

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		SS	<i>F</i>	<i>P</i>	Percentage of total SS
	df _{predictor}	df _{error}				
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

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 ρ 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 8. Spearman’s rank correlations (ρ) between sapling height (cm) and DD needed for bud break, growth cessation date, and growing season length (days) and their P values (values of $P < 0.05$ are in bold) using (A) values of individual plantlets (for Kolari, $n = 129$; for Joensuu, $n = 130$; for Tuusula, $n = 102$) and (B) genotype means of residuals devoid of all other effects in the three common garden sites for each study year (for all sites, $n = 30$).

Phenophase	Year	Kolari		Joensuu		Tuusula	
		ρ	P	ρ	P	ρ	P
(A)							
DD needed for bud break	2011	-0.40	<0.001	-0.33	<0.001	-0.36	<0.001
	2012	0.14	0.111	-0.26	0.002	-0.62	<0.001
	2013	0.12	0.192	-0.30	0.001	-0.44	<0.001
Growth cessation date	2011	0.58	<0.001	0.71	<0.001	0.69	<0.001
	2012	0.57	<0.001	0.81	<0.001	0.81	<0.001
	2013	0.50	<0.001	0.85	<0.001	0.62	<0.001
Growing season length	2011	0.61	<0.001	0.71	<0.001	0.72	<0.001
	2012	0.52	<0.001	0.83	<0.001	0.83	<0.001
	2013	0.48	<0.001	0.86	<0.001	0.66	<0.001
(B)							
DD needed for bud break	2011	0.10	0.596	-0.18	0.347	-0.28	0.129
	2012	-0.16	0.411	0.24	0.207	-0.30	0.105
	2013	-0.26	0.159	-0.41	0.024	-0.23	0.213
Growth cessation date	2011	0.04	0.829	0.44	0.015	0.28	0.141
	2012	0.49	0.007	0.55	0.002	0.45	0.012
	2013	0.53	0.003	0.75	<0.001	0.02	0.906
Growing season length	2011	0.05	0.796	0.47	0.009	0.33	0.071
	2012	0.49	0.006	0.50	0.005	0.55	0.002
	2013	0.53	0.002	0.82	<0.001	0.07	0.722

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

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 (Varnagiryte-Kabašinskiene 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 (Varnagiryte-Kabašinskiene 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 \times environment ($G \times E$) interaction, arising from among-site variation in environmental conditions and genotypic variation. Earlier studies have shown that significant $G \times E$ 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 $6\text{--}13^\circ$ 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–north cline 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.

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SUPPORTING INFORMATION

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