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ORIGINAL PAPER

High-acclimation capacity for growth and role of soil fertility after long-range transfer of *Betula pendula* and *B. pubescens* between Finland and Italy

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Abstract The acclimation capacity of *Betula pendula* and *Betula pubescens* was studied over 4 years in common gardens in central Italy (43° N) and southern (61° N) and northern Finland (67° N), representing drastically different photoperiod and climate in temperate, boreal and subarctic vegetation zones. Two study sites that differed in soil fertility were established at each location, giving a total of six common gardens. The birch material was micropropagated from naturally regenerated stands of *B. pendula* and *B. pubescens* from Susa Valley and Rochemolle Valley in northern Italy, Punkaharju in southern Finland and Kittilä in northern Finland. The plants were measured for height growth, stem diameter, leaf chlorophyll content, leaf herbivory and pathogen damage. The effects of soil fertility on the common garden results were also analyzed. The results showed high acclimation capacity of *B. pendula* and *B. pubescens* after a long-range transfer from southern to northern Europe, despite the major shift in climate and photoperiod. First-year growth on average was best in boreal southern Finland for all origins. *Betula pendula* grew more than *B. pubescens* in Italy and southern Finland, while *B. pubescens* grew more in northern Finland and better tolerated the northward transfer. The height growth of origins showed a clear latitude gradient from slowly growing northern to fast growing southern origins in the nursery and laboratory, but not in the field. Soil fertility explained a significant part of variation among locations not only for growth variables, but also for leaf chlorophyll content and leaf herbivory and pathogen damage. Leaf herbivore and pathogen damage was greatest in southern Finland. Our results demonstrate good survival of birch from northern Italy in Finnish conditions and support the possibility of long-range south-to-north transfer of *Betula* species to provide resistant planting material in boreal forests for the rapidly changing climate.

Oksanen Elina and Silfver Tarja are co-first authors and made equal contributions to this paper.

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Introduction

Climate warming will be faster in boreal forests than in any other forest biomes; by the end of this century, boreal forests are expected to warm by 4–11 °C (Gauthier et al. 2015). Evidence from Alaska suggests that *Pinus* and *Picea* are more sensitive to warming than deciduous species (Reich et al. 2022). Major changes in tree species composition may therefore take place in Fennoscandia, northwestern Europe, where forests are dominated by *Pinus sylvestris* and *Picea abies*. In Fennoscandian forests, conifers often grow with two white birch species, *Betula pendula* Roth (silver birch) and *B. pubescens* Ehrh. (downy birch) (e.g., Hetemäki et al. 2022). Both species are considered critical for enhancing biodiversity (Nieuwenhuis and Barrett 2002; Kuuluvainen et al. 2017; Salemaa et al. 2023) and soil nutrient mineralization in the nutrient-poor northern ecosystems (Kanerva and Smolander 2007; Kanerva et al. 2008; Mikola et al. 2018). However, contrasting information on the capacity of birches to acclimate to fast environmental changes (Savolainen et al. 2007; Rousi et al. 2019) highlights the need for further research to design the best strategies for tree migration and breeding programs.

Betula pendula and *B. pubescens* are widely distributed in Eurasia, extending from eastern Siberia to Atlantic coastal area and covering subarctic, boreal, and temperate zones (Atkinson 1992). Their distribution is largely overlapping, and they often grow in common stands in natural forests. In the southern part of this range, the species are mainly found at high elevation in the mountains, and where the natural distribution extends to Italy, both species grow in the Alps. Only *B. pendula* reaches the southernmost regions with scattered populations in the Apennines, a few relicts at lower elevation and an isolated population on Mount Etna in Sicily (Morrocchi et al. 1997; Leonardi et al. 2012; de Dato et al. 2020). In Finland, slash and burn agriculture continued until the twentieth century, favoring birches as pioneer species. In 1920s, the first birch plywood mills were established, and high demand for construction material and furniture diminished the high-quality birch phenotypes in forests. It soon became clear that for Finnish plywood production, the growth and trunk form of *B. pendula* was superior to that of *B. pubescens*, and experiments on *B. pendula* regeneration, silviculture and breeding started in late 1940s (Sarvas 1947, 1952, 1956). Birches are also widely cultivated in Baltic countries (particularly Latvia), but in other European countries they are not as important for the economy as in Finland (Liepins 2011; Willoughby et al. 2019; Liziniewicz et al. 2022). In the southernmost parts of its distribution (e.g., in Tuscany, Italy), *B. pendula* is grown as an ornamental tree.

Greenhouse experiments have suggested strict local adaptation for *B. pendula* since the timing of winter hardening is determined by critical night length (3.1 h for northern provenances at 68° N and 6.3 h for southern provenances at 61° N) (Viherä-Aarnio et al. 2006). Provenance transfer experiments have further supported these results (Viherä-Aarnio et al. 2013), and accordingly, local seed is used in Finland and the maximum transfer is ± 100 km on the north–south axis (Äijälä et al. 2019). However, there is also evidence of exceptionally high *B. pendula* plasticity: In a 10-year study in Alberta, Canada, Finnish *B. pendula* (from latitudes 61°–63° N) grew faster than the local birches and showed high survival at 54° N (Rousi et al. 2012). Finnish *B. pendula* trees have also been successfully transferred as far as 37° N in South Korea (Han et al. 1985), and recent studies in Finland show *B. pendula* winter hardening is plastic and affected by factors such as soil fertility and autumn temperatures (Possen et al. 2021).

Because the experimental evidence on the acclimation capacity of *B. pendula* is contradictory and basically nonexistent for *B. pubescens*, new common garden experiments are warranted. In this study, we extended the latitudinal range for the birch provenances (populations) and common garden locations by including plant material and growing sites from temperate Italy to subarctic Finland. Our main aim was to investigate the limits and acclimation capacity of birch provenances to very long transfer distances and thus to drastically different climatic conditions and to compare the growth performance (height and stem diameter growth) of the two species and to disentangle the effects of soil and climatic conditions across the south-north gradient. To better understand the factors potentially influencing birch growth across the sites, we also measured leaf chlorophyll concentration and leaf herbivore and pathogen damage.

As recently shown for *B. pendula* (Salojärvi et al. 2017; Oksanen 2021; Possen et al. 2021), we hypothesized that the acclimation capacity, as estimated by growth, of both birch species is high. In more detail, we hypothesized that (H1) the annual growth rate of both species increases as the origin is farther to the south, (H2) soil fertility explains a great share of growth differences among common garden locations, and (H3) northward transfer has no drastic effects on survival and growth, despite a major change in the photoperiod. Since herbivore damage tends to be greater in warmer climates (Kozlov et al. 2013, 2015; Redondo et al. 2015), we hypothesized that (H4) leaf damage increases toward southern locations and that the northern provenances are most susceptible to herbivory when subjected to high temperature and water deficit in southern locations (Cohen and Leach 2020; Raza and Bebber 2022).

Materials and methods

Common garden setup and field site characteristics

The common gardens were established at three locations in temperate central Italy, boreal southern Finland and subarctic northern Finland (Fig. 1; Table 1). At each location, a common garden was established at two sites (giving a total of six common gardens): sites A and B in Italy, C and D in southern Finland, and E and F in northern Finland (Table 2). In Italy, the two sites are 100 km apart (A in Florence, B in Belagaio). Both belong to the temperate, submediterranean bioclimate (Pesaresi et al. 2017) in the Worldwide Bioclimatic Classification System (WBCS; Rivas-Martínez et al. 2011) and to the climate type Csa in the Köppen-Geiger (KGCC) climate classification. In southern Finland, the sites are 1 km apart (both in Punkaharju, boreal subcontinental bioclimate in WBCS, Dfb in KGCC) and in northern Finland 10 km apart (both in Kolari, boreal hypercontinental bioclimate in WBCS, Dfc in KGCC).

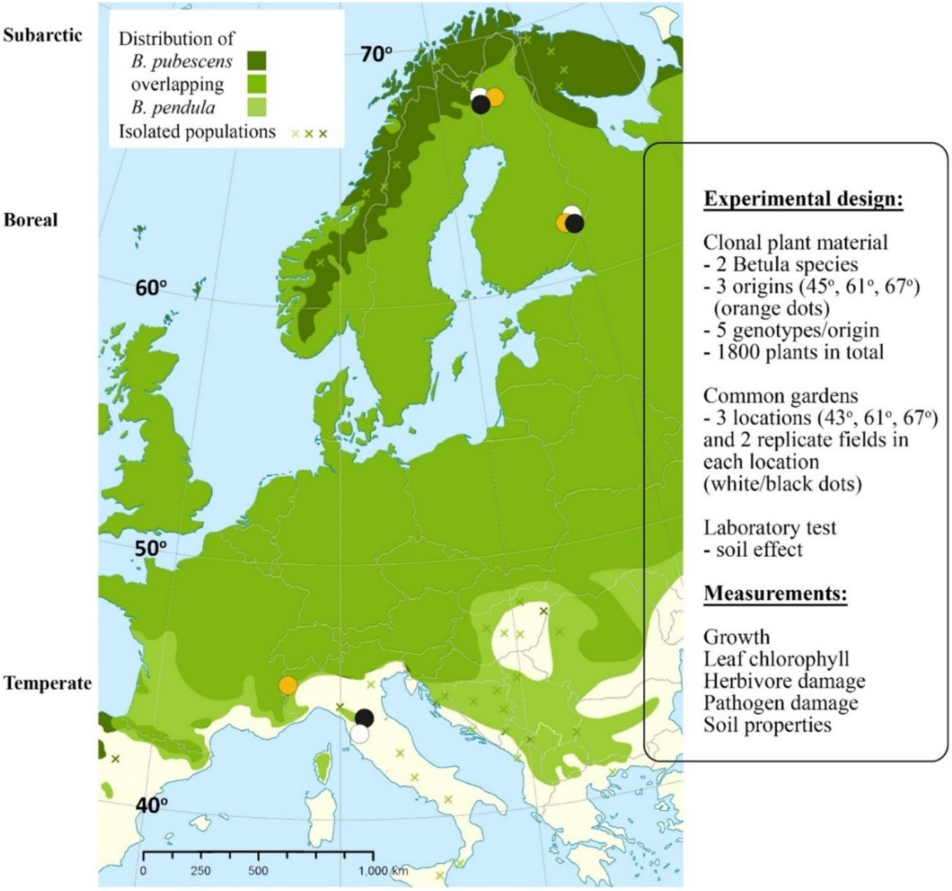

Fig. 1 Layout of the common garden study, extending from northern Finland to central Italy

Table 1 Coordinates, altitude, annual and June–August mean temperature (±SD), annual and June–August precipitation (±SD), and mean June day length at the common garden locations in 2016–2020 (Finnish data: www.ilmatieteenlaitos.fi, Italian data: nearest weather station in Servizio Idrologico Regione Toscana, DATI/Archivio storico, http://www.sir.toscana.it/consistenza-rete)

Common gardens sites	Coords	Site descriptors					
		Altitude (m a.s.l.)	Annual mean temperature (°C)	June–August mean temperature (°C)	Annual precipitation (mm)	June–August precipitation (mm)	June day length (h)
Florence, Central Italy	43° 77′ N, 11° 17′ E	36	15.0 ± 6.0	23.8 ± 3.3	732 ± 39	112 ± 51	15.3
Belagaio, Central Italy	43° 07′ N, 11° 21′ E	411	15.3 ± 7.2	23.7 ± 1.7	651 ± 39	89 ± 39	15.3
Punkaharju, Southern Finland	61° 48′ N, 29° 19′ E	90	5.0 ± 7.2	16.0 ± 1.1	600 ± 93	232 ± 80	19.5
Kolari, Northern Finland	67° 44′ N, 24° 50′ E	170	0.6 ± 14.0	13.4 ± 1.0	544 ± 36	203 ± 60	24.0

Table 2 Habitat and soil properties for each of the common gardens (A–F) in central Italy and southern and northern Finland

Site		Habitat	Soil type	Conductivity (×10 mS cm^{-1})	pH	Property N (%)	C (%)	C/N ratio	P (mg L^{-1})	K (mg L^{-1})	Ca (mg L^{-1})	Mg (mg L^{-1})	S (mg L^{-1})	B (mg L^{-1})
Central Italy	A	Nursery grassland	Fine-sandy moraine	1.8	7.3	0.14	1.9	14	250	210	5100	240	8.6	1.3
	B	Temperate forest (Castanea, *Quercus*, *Pinus pinaster*)	Fine-sandy moraine	2.6	7.5	0.18	2.4	13	2.9	100	21,000	93	18.7	0.6
Southern Finland	C	Boreal forest (*Betula*, *P. abies*, *P. sylvestris*)	Fine-sandy moraine	0.6	5.8	0.26	4.2	16	< 1.5	110	970	99	10.7	0.3
	D	Boreal forest (*Betula*, *P. abies*, *P. sylvestris*)	Sandy-moraine	0.4	4.9	0.18	4.9	27	< 1.5	43	250	37	15	<0.15
Northern Finland	E	Boreal forest (*Betula*, *P. sylvestris*)	Sandy-moraine	0.2	5.4	0.03	1.1	43	9	54	210	28	41.9	0.2
	F	Boreal forest (*Betula*, *P. sylvestris*)	Sandy-moraine	0.2	5.3	0.01	0.8	64	4.7	26	74	<20	25.3	<0.15

Mean annual temperature, mean June–August temperature and precipitation follow the latitudinal gradient across the locations, being highest in Italy and lowest in northern Finland (Table 1). Mean annual precipitation does not differ much among the locations, but summer precipitation and June day length show clear gradients, being lowest in Italy (Table 1). Comparing the growing conditions between Finland and Italy is not straightforward, however, because in Italy spring (from late February to late May) and late autumn (September–October) can be more favorable for growth than summer, when plants are often water-stressed due to high temperatures and drought. Therefore, changes in precipitation and temperature along seasons are also shown using Walter-Lieth diagrams (Fig. S1), which reveal the unfavorable periods (yellow color in diagrams) in the Italian sites between June and August.

To distinguish the effect of soil from the effect of climate across the south-north gradient of the locations, the two sites within each location were selected to be as different as possible in terms of their soil characteristics. In Italy, site A was established in an experimental nursery of a research station, and site B was established in a forest; differences in soil characteristics were obvious (Table 2). In both locations in Finland, however, the two sites were established in forest ground, and soils were tested in up to five sites before two with different soil characteristics could be chosen. For soil analysis, five subsamples of soil were collected from random spots in each site. The subsamples were pooled and homogenized and analyzed by Eurofins Agro Fertility service (Eurofins Viljavuuspalvelu, https://www.eurofins.fi/agro) except for total N, which was analyzed at the University of Helsinki using a LECO CNS-2000 analyzer (LECO Corp., USA). For soil solution conductivity and pH, the difference between sites (i.e., within a location) was smaller than the mean difference among locations, but for all nutrients, the difference between sites was similar or bigger than the mean difference among locations (Table 2). The portion of the soil sample that was not used for soil analysis was stored in a freezer until used for the laboratory trial of soil effects on plant traits. At each site, except for Florence, trees were harvested before the common gardens were set up.

Plant material

The plant material, described in detail later, was collected from randomly selected, mature birch trees in naturally regenerated stands in winter 2015, except in southern Finland, where *B. pendula* material was collected from a common garden that had been established in 1999 using micropropagated plantlets from a naturally regenerated stand (Silfver et al. 2009). Although the physical appearance of *B. pendula* and *B. pubescens* is rather similar, interspecific hybrids are rare because the species have different number of chromosomes (*B. pendula* is diploid, $N = 28$; *B. pubescens* is tetraploid, $N = 56$) (Johnsson 1945; Hagman 1971). When Johnsson (1945) tried to hybridize *B. pendula* and *B. pubescens*, even single hybrids were hard to obtain after reciprocal crosses, indicating strong incompatibility between the species. Previous studies have confirmed the existence of hybrids between the two species (Brown et al. 1982), but Rousi et al. (2019) concluded that interspecific hybridization is an unlikely mechanism of adaptation for *B. pendula* and *B. pubescens* because there is no significant overlap in flowering in northern latitudes (60°–68° N). For the present plant material, the genomes were sequenced by Salojärvi et al. (2017) who found no species misidentification or hybridization in any of the birch genotypes. Differences in leaf shapes between the species and populations in the present study are illustrated in Fig. S2.

In Italy, materials for both species were collected in the northern part of the country from western sites of the Alps, where they are present in natural stands (Terzuolo et al. 2002). *Betula pendula* was collected on the slopes of Colle del Lys (Rubiana, Torino, 45° 9′ 16″ N, 7° 21′ 50″ E, 1100 m a.s.l., Cfb in KGCC) and *B. pubescens* in Rochemolle (Bardonecchia, Torino, 45° 8′ 11″ N, 6° 46′ 39″ E, 2150 m a.s.l., Dfc in KGCC)) from local populations included in the European Commission Forest Reproductive Material Information System (2021/IT/BETUL_PUB/IT/BPU/1/A100/PIE/0094, https://ec.europa.eu/forematis/). In southern Finland, *B. pendula* was collected in Kuikanniitty (61° 47′ N, 29° 21′ E, 90 m a.s.l.) and *B. pubescens* in Selkälahti (61° 48′ N, 29° 21′ E, 90 m a.s.l.), both in the Punkaharju municipality (Dfb in KGCC)). In northern Finland, both species were collected in Sätkenä in the Kittilä municipality (67° 44′ N, 24° 50′ E for *B. pendula*, 67° 43′ N, 24° 51′ E for *B. pubescens*, 170 m a.s.l., Dfc in KGCC)).

Five healthy trees, representing five genotypes in the local population, were chosen from each stand for both species, and branches were collected from the southern side of the upper third of the canopy. The branches were transferred to the laboratory at the Haapastensyrjä Unit of the Natural Resources Institute Finland, where buds were used to produce 1440 micropropagated (clonal) plantlets for the field experiment (5 genotypes × 3 origins × 2 species × 8 blocks × 2 sites × 3 locations) and 180 plantlets for the laboratory experiment (5 genotypes × 3 origins × 2 species × 2 sites × 3 locations). Standard tissue-culture procedures were used for cloning (Ryynänen 1996). The plantlets were potted into nursery peat (Kekkilä OPM 420 W) before being planted to field sites and used in the laboratory trial in 2016.

Field planting and measurements

For planting, each field site was divided into 5–8 replicate blocks. One plantlet of each genotype was randomly allocated to each block in each site and planted 2 m apart, giving 30 plantlets per block (2 species × 3 origins × 5 genotypes), 150–240 plantlets per site and 300–480 plantlets per location. In northern Finland, the plantlets were planted on July 25, in southern Finland on August 9 and in central Italy on September 12 (Florence) and December 5, 2016 (Belagaio). The plantlets allocated to Belagaio were kept in pots in Florence and watered when needed (at the same time as the already-planted Florence plantlets) until the dry and hot summer season was over and no watering was needed for plantlets to survive.

The height of plantlets at the time of planting followed the sequential planting dates, with plantlets in northern Finland being shortest and plantlets in Italy being tallest when planted (Fig. 2). The origin also had a significant influence ($F = 43.4$, $P < 0.001$) on planting height: the plantlets of northern Finland (NF) origin were shortest, the plantlets of Italian origin tallest and the plantlets of southern Finland (SF) origin in-between those of the other two origins at the time of planting (Fig. 2). The difference between origins did not depend on species (origin × species interaction effect on planting height $F = 1.32$, $P = 0.289$), neither did the two species differ from each other ($F = 2.03$, $P = 0.169$) (Fig. 2).

During the first growing season 2017, plant height was measured in June and October, and leaf chlorophyll content and damage indices were assessed approximately 2 months after bud burst, i.e., on May 7–10 in Italy and on July 4–7 in Finland. Buds opened between February 27 and March 13 in Italy, between May 5 and May 26 in southern Finland and between May 23 and June 15 in northern Finland. For leaf chlorophyll content, one to five topmost full-grown leaves were measured for each experimental plantlet using a CCM-200 (Opti-Sciences, Hudson, NH, USA), and plantlet means were used for statistical tests. Leaf herbivory and pathogen damage were monitored on all leaves of each plantlet, except for particularly large plantlets for which only leaves in the top branch and two side branches were monitored. Damage caused by the pathogen *Melampsoridium betulinum* was recorded separately. Leaf damage was scored using a modified Schreiner-type method (Fritz et al. 1998; Silfver et al. 2015), where a damage index ranging from 0 to 100 is produced by multiplying two scores: (1) the average percentage of total area damaged per leaf (0 = 0%, 1 = 1%–4%, 5 = 5%–20% and 25 = 21%–100% of leaf area eaten or damaged) and (2) the percentage of total leaves damaged (0 = 0%, 1 = 1%–25%, 2 = 26%–50%, 3 = 51%–75% and 4 = 76%–100% of all leaves damaged).

Few plants in Belagaio survived the heat wave that hit Tuscany in 2018 (Copernicus Climate Change Service 2019), so the 4-year survival, height growth and stem diameter were measured in October 2020 at the Finnish sites only.

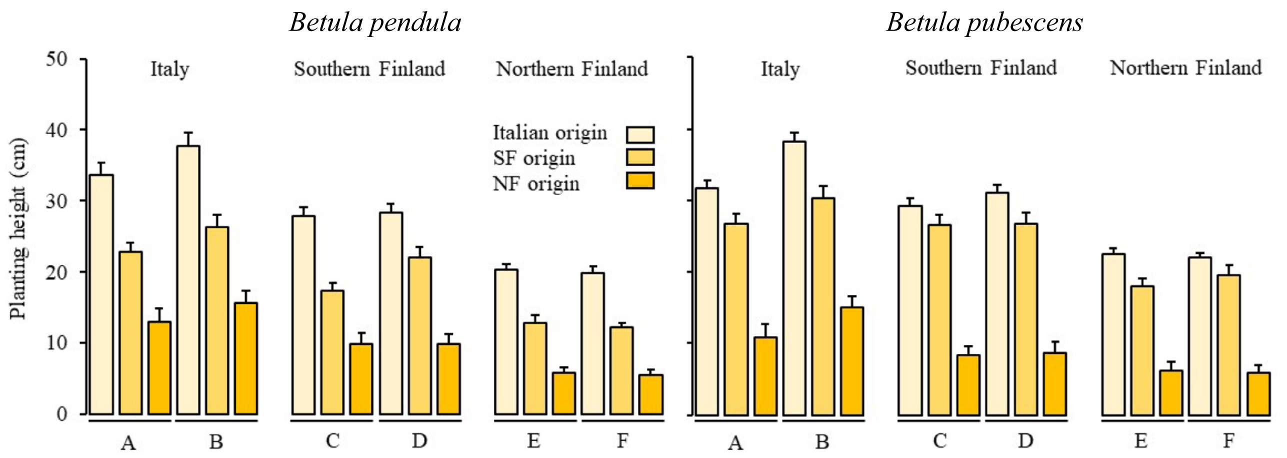

Fig. 2 Height (mean + SE) of *B. pendula* and *B. pubescens* plantlets from three origins (Italian, SF = southern Finland, NF = northern Finland) at the time of planting (year 2016) to common gardens at the two sites in Italy (A and B, on September 12 and December 5, respectively), southern Finland (C and D, on August 9 at both sites) and northern Finland (E and F, on July 25 at both sites). See Table S2 for samples sizes for plantlets at each site

Laboratory test of soil fertility effects on plant performance

Soils collected from the six field sites (Table 2) were randomly placed in seedling trays (Plantek 64F, 8 × 8 cells per tray, cell size 46 × 46 × 73 mm^3; 30 cells with soil of each site). One to three micropropagated birch plantlets of 2–5 genotypes per species per origin were then randomly allocated and planted to cells of each soil type on May 9, 2016 (180 total plantlets, but since not all plantlets in each genotype were sufficiently fit for planting, the number of plantlets varied among genotypes). At planting, the roots of plantlets were gently washed and their stem height, length of the longest root, root system density (classified into three categories) and leaf area were quantified as initial sizes. The seedling trays were placed in a growth chamber (Weiss Technik, Lindenstruth, Germany; 16 h day with PAR of 350 µmol m^{-2} s^{-1}, 20 °C day/12 °C night) for 1 week and then moved to a greenhouse in ambient temperature and light. The plants were watered using tap water every 1–2 days, and at each watering, the trays were rotated.

At the end of laboratory test (June 22, 2016), height and dry mass of each plantlet was measured. The chlorophyll content of the three topmost leaves, excluding the youngest leaf, was measured for each plantlet (except for nine plantlets that had leaves too small for measurements) 2 days before harvest using a Dualex polyphenol and chlorophyll meter (ForceA, Orsay, France). Plantlet means for leaf chlorophyll content were used in statistical tests. Leaf N content was measured for each origin of both species and for each soil type only (36 total estimates); leaves of individual plantlets were ground to a powder, then pooling all leaves within the same origin and grown in the same soil type, and measuring N using the LECO CNS-2000 analyzer (LECO Corp., St. Joseph, WI, USA).

Statistical analyses

For the laboratory data, the effects of soil (sites A–F), species (*B. pendula* and *B. pubescens*), origin (Italy, southern Finland, northern Finland) and genotype (2–5 genotypes per origin) on plantlet height growth, total biomass, leaf chlorophyll content and leaf N concentration were tested using type III ANOVA models (see Table S1 for the number of plantlets in the treatment levels and level combinations of ANOVA effects in the original setup). Soil, species, and origin were treated as fixed factors and genotype as a random factor. Genotype was nested within origin, and when testing for a genotype effect, origin was further nested within species, while in other parts of the models, origin (i.e., the site where the plant material was collected) was considered as independent of species. The genotype effect on leaf N was not tested because leaf N was analyzed using pooled samples. The initial stem height, leaf area, root length and root density were used as covariates, but if not statistically significant, were removed from final models. When covariates remained in the final model (height growth and biomass), estimated marginal means were produced by the fitted model for each soil. These were then used as proxies of soil fertility when analyzing the field data. When no covariates remained (leaf chlorophyll and N content), mean values of soils were used as proxies. The ANOVA assumption of normal data distribution was checked using histograms of residual distribution and the data were transformed when necessary (logarithm transformation for height growth and total biomass, square-root transformation for leaf N concentration, 1/*x* transformation for leaf chlorophyll content). Correlations between soil N concentration and plantlet attributes were tested using Pearson correlation tests.

For field data, the effects of soil fertility proxy (the laboratory estimate for the soils of six sites), location (Italy, southern Finland, northern Finland), site within location (two sites in each location), block within site (5–8 blocks in each site), species (*B. pendula* and *B. pubescens*), origin (Italy, southern Finland, northern Finland) and genotype (3–5 genotypes in each origin) on the first-year growth in height, total growth in height over 4 years, stem diameter, leaf chlorophyll content and leaf herbivory and pathogen indices were tested using type I ANOVA models (see Table S1 for the number of plantlets in the treatment levels and level combinations of ANOVA effects in the original setup). Location, site, species and origin were treated as fixed factors, block and genotype as random factors. Site was nested within location, block within site and genotype within origin, and as with the laboratory data, when testing the genotype effect, origin was further nested within species. Planting height and the soil fertility proxies measured in the laboratory test were treated as covariates and placed in the beginning of ANOVA models. Their effects are illustrated in Figs. 3, 4, 5 and 6 and Fig. S3 by presenting residual data devoid of covariate effects (blue bars) with the original data (yellow bars). The ANOVA model assumption of normal data distribution was checked using histograms of residual distribution and the data were transformed when necessary (square root transformation for height growth, and logarithm transformation for stem diameter, leaf chlorophyll content and leaf damage indices). Plantlets whose first-year height decrease was more than 2 cm were considered broken and were excluded from the first-year growth data. The 4-year survival data were analyzed using a generalized linear mixed model with binomial probability distribution and complementary log–log link function. The explanatory variables followed those used in the ANOVA models except that no covariates were included.

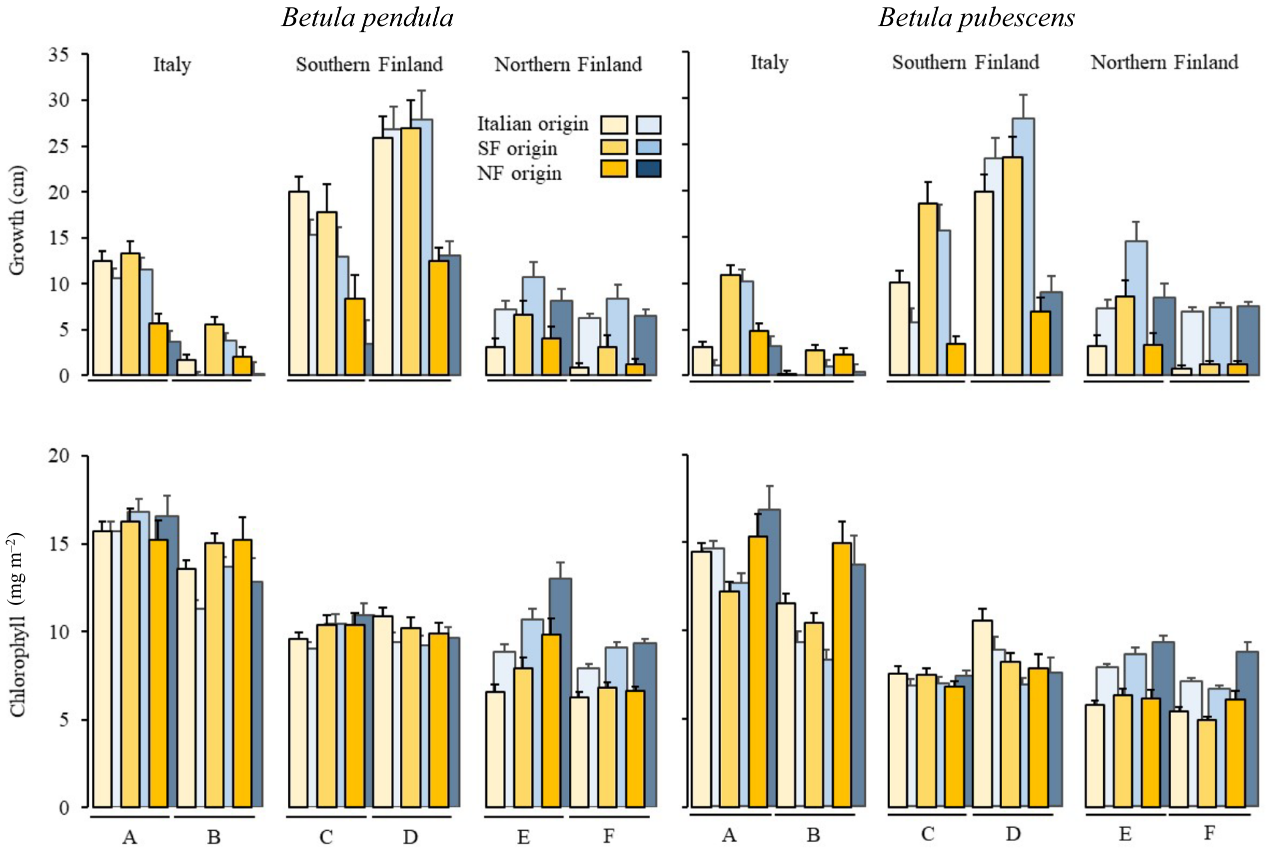

Fig. 3 Growth in height and leaf chlorophyll content (yellow bars in the front; mean + SE), and their residuals devoid of soil effect (blue bars in the back), for *B. pendula* and *B. pubescens* plantlets from three origins (northern Italy, SF = southern Finland, NF = northern Finland) growing in common gardens at two sites in central Italy (A and B), southern Finland (C and D) and northern Finland (E and F). For comparison of original values and residuals, the range of values on the vertical axis is equal for both, and the residual mean (0) and the grand mean of original values (9.79 cm for height growth, 9.85 mg m^{-2} for leaf chlorophyll content) are aligned. See Table S2 for sample sizes of plantlets for each bar

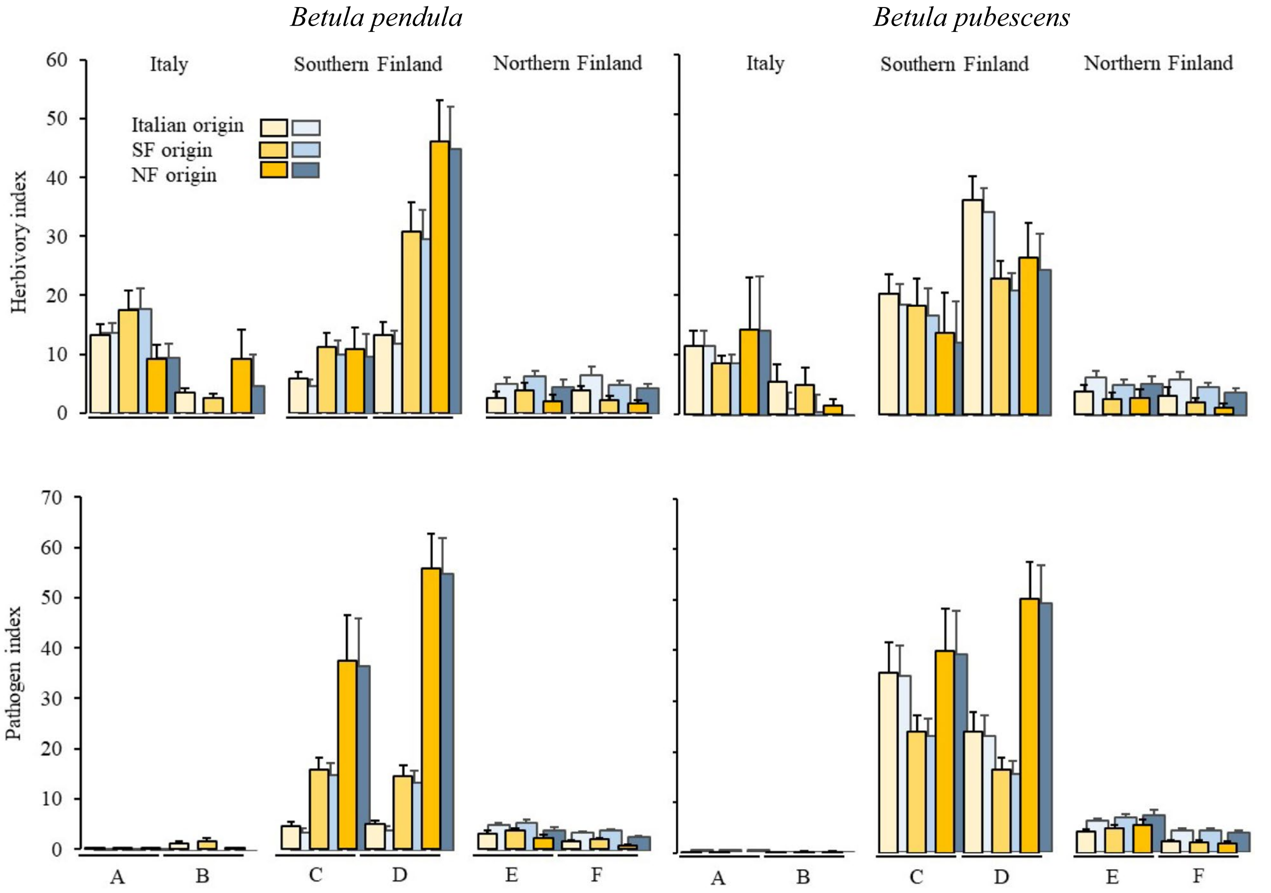

Fig. 4 Herbivory and pathogen indices (yellow bars in the front; mean + SE), and their residuals devoid of soil effects (blue bars in the back), for *Betula pendula* and *B. pubescens* plants from three origins (northern Italy, SF = southern Finland, NF = northern Finland) growing in common gardens at two sites in central Italy (A, B), southern Finland (C, D) and northern Finland (E, F). For comparison of original values and their residuals, the range of values on the vertical axis is equal for both, and the residual mean (0) and the grand means of original values (9.46 and 7.10 for herbivory and pathogen, respectively) are aligned. See Table S2 for sample sizes for each bar

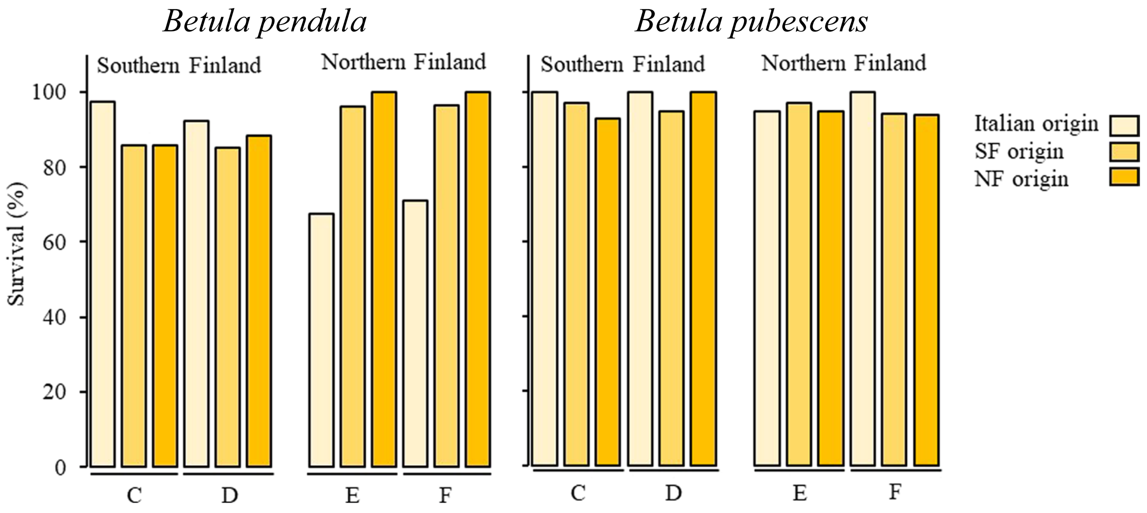

Fig. 5 Four-year survival rate (% of original plants) of *B. pendula* and *B. pubescens* plants from three origins (northern Italy, SF = southern Finland, NF = northern Finland) in common gardens at two sites in southern (C, D) and northern Finland (E, F)

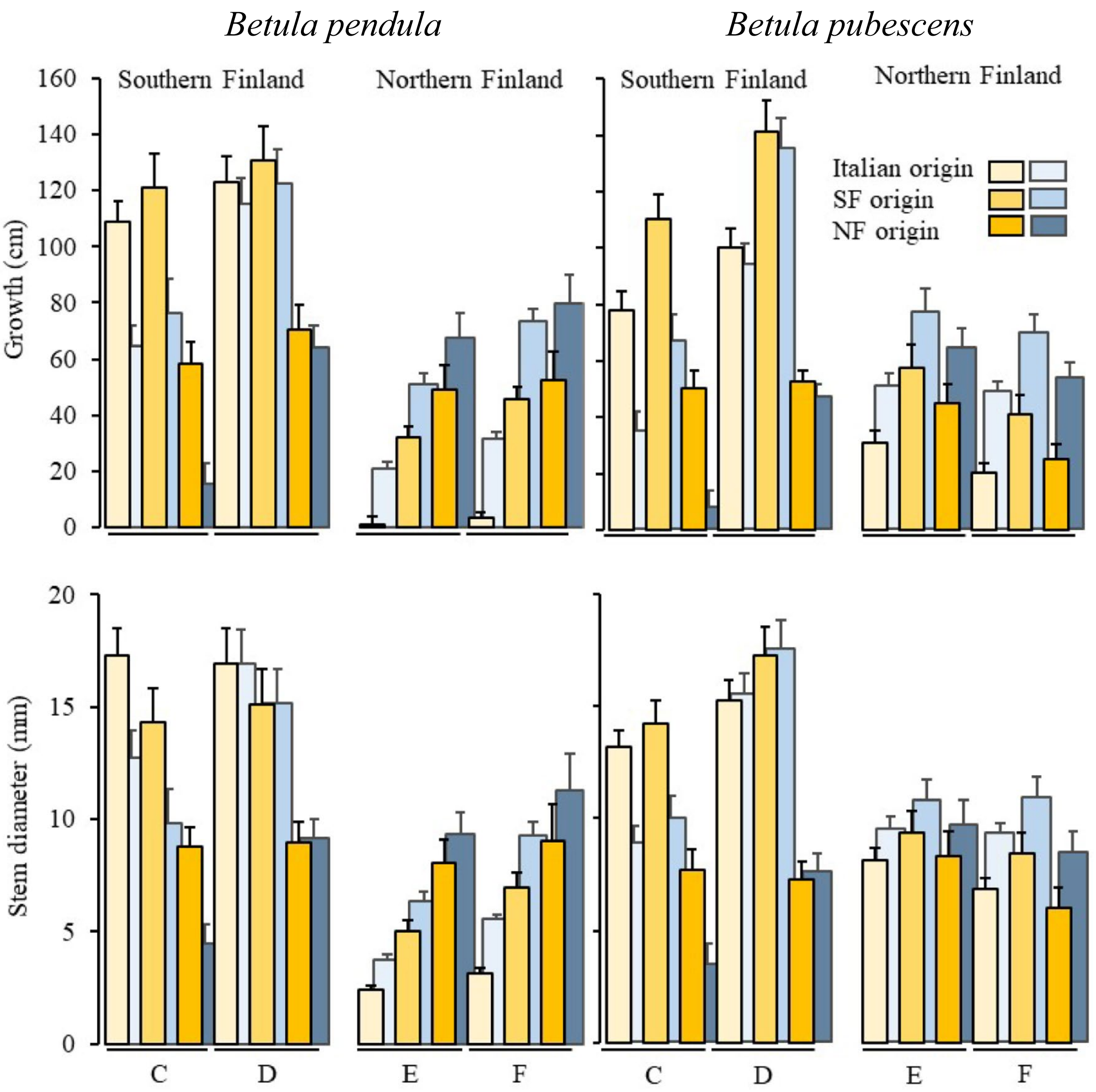

Fig. 6 Four-year height growth and stem diameter (yellow bars; mean + SE), and their residuals devoid of soil effects (blue bars), of *B. pendula* and *B. pubescens* saplings from three origins (northern Italy, SF = southern Finland, NF = northern Finland) growing in common gardens at two sites in southern (C, D) and northern (E, F) Finland. For comparison of original values and their residuals, the range of values on the vertical axis is equal for both, and the residual mean (0 cm) and the grand mean of original values (6.9 cm for growth and 10.7 mm for stem diameter) are aligned. See Table S2 for all sample sizes

Results

Growth and leaf attributes in the laboratory test

In the laboratory test, common garden soil had a significant effect on plantlet growth (height growth: $P = 0.038$, biomass: $P = 0.002$), leaf chlorophyll content ($P < 0.001$) and leaf N concentration ($P < 0.001$) (Table 3; see Figs. S3 and S4, and Tables S3 and S4 for the complete data and analysis). Soil N concentration correlated positively with plantlet growth (height growth: $r = 0.951$, $P = 0.004$, $N = 6$; biomass: $r = 0.913$, $P = 0.011$), leaf N concentration ($r = 0.782$, $P = 0.066$) and leaf chlorophyll content ($r = 0.820$, $P = 0.045$).

First-year growth and leaf chlorophyll content in common gardens

Common garden location had a significant influence on first-year growth and explained 23% of variation (Fig. 3, Table 4). Height growth was on average greatest in southern Finland (SF) (17.9 cm), intermediate in Italy (6.7 cm) and smallest in northern Finland (NF) (3.2 cm) (Fig. 3). Height growth in the laboratory (Table 3), used as a proxy of soil fertility,

Table 3 Growth in height, biomass (shoot and root combined), leaf chlorophyll content and leaf N concentration of birch plantlets (mean ± SE, $N=28$–30 for growth, biomass and leaf chlorophyll content, $N=6$ for leaf N concentration) growing in the soils collected from the two common garden sites in central Italy, southern Finland and northern Finland

Soil origin	Site	Growth in height (cm)	Biomass (g)	Leaf chlorophyll (mg m^{-2})	Leaf N (%)
Italy	A	0.78 ± 0.07	0.472 ± 0.01	11.25 ± 0.49	0.74 ± 0.04
	B	0.77 ± 0.07	0.479 ± 0.01	13.46 ± 0.86	0.91 ± 0.09
Southern Finland	C	0.92 ± 0.07	0.524 ± 0.01	12.30 ± 0.60	0.79 ± 0.05
	D	0.67 ± 0.07	0.452 ± 0.01	13.21 ± 1.39	0.80 ± 0.08
Northern Finland	E	0.50 ± 0.07	0.435 ± 0.01	9.63 ± 0.28	0.66 ± 0.05
	F	0.44 ± 0.07	0.419 ± 0.01	10.21 ± 0.47	0.65 ± 0.03

Growth in height and biomass are estimated marginal means produced by the fitted statistical models in Table S3. Means and errors were back-transformed from log-transformed data

Table 4 Effects of growth in height/leaf chlorophyll content in the laboratory (used as proxies of soil fertility), initial planting height, common garden location (central Italy, southern Finland, northern Finland), site within location (two sites in each location), block within site (5–8 blocks in each site), species (*Betula pendula* and *B. pubescens*), origin (northern Italy, southern Finland, northern Finland) and genotype within origin within species (3–5 genotypes in each origin) on the growth in height and leaf chlorophyll content of field grown birch plantlets in a type I ANOVA test

Explanatory variable	Growth in height				Leaf chlorophyll concentration			
	df	F	P	R^2	df	F	P	R^2
Lab plant growth/leaf chlorophyll	1, 40	134	< 0.001	14	1, 51	127	< 0.001	12
Initial planting height					1, 51	92.2	< 0.001	8.8
Location	2, 39	112	< 0.001	23	2, 44	169	< 0.001	33
Site (Location)	2, 45	32.5	< 0.001	6.3	2, 41	9.05	< 0.001	1.8
Block (Site(Location))	42, 815	2.09	< 0.001	4.2	42, 844	2.88	< 0.001	4.1
Species	1, 21	9.15	0.007	1.5	1, 20	39.6	< 0.001	6.0
Origin	2, 21	15.4	< 0.001	5.0	2, 23	1.04	0.369	0.3
Genotype (Origin (Species))	22, 794	3.33	< 0.001	3.5	22, 823	3.99	< 0.001	3.0
Species × Location	2, 794	5.20	0.006	0.5	2, 823	0.47	0.626	< 0.1
Species × Site (Location)	3, 794	1.35	0.258	0.2	3, 823	3.20	0.023	0.3
Origin × Location	4, 794	14.7	< 0.001	2.8	4, 823	4.76	< 0.001	0.6
Origin × Site (Location)	6, 794	1.84	0.089	0.5	6, 823	3.44	0.002	0.7
Origin × Species × Location	4, 794	2.21	0.067	0.4	4, 823	4.42	0.002	0.6
Origin × Species × Site (Location)	6, 794	2.05	0.057	0.6	6, 823	1.71	0.117	0.3
Total % of variation explained				63				72

R^2 gives the percentage of variation explained by each variable

was positively associated with the growth in the field (Fig. S5) and explained 14% of variation (Table 4). When this effect was removed from the data (blue bars in Fig. 3), the average growth in Italy was lower than in northern Finland, and the difference in growth between southern and northern Finland decreased.

A species × location interaction appeared in growth (Table 4) because *B. pendula* grew more than *B. pubescens* in Italy and southern Finland, but not in northern Finland (Fig. 3). The origin × location interaction was because the growth of plants from Italian and NF origins was on average similar and around a half of the growth of plants from SF origin in Italy and northern Finland, but not in southern Finland, where the plantlets from Italian origin grew significantly more than those from NF origin, approaching the growth of those from SF origin (Fig. 3).

Common garden location had a major effect on leaf chlorophyll content, explaining 33% of variation (Fig. 3, Table 4). The chlorophyll content was highest in Italy, intermediate in southern Finland and lowest in northern Finland (Fig. 3). Laboratory leaf chlorophyll content (Table 3), a proxy of soil fertility, was positively associated with chlorophyll measurements in the field (Fig. S6) and explained 12% of variation (Table 4). Height at the time of planting was also positively associated with leaf chlorophyll concentrations in the field (Fig. S6), explaining 8.8% of variation (Table 4). When both these effects were removed from the data, mean concentrations in southern and northern Finland did not differ but were still only around half of those in Italy (blue bars in Fig. 3). *Betula pendula* had on average higher leaf chlorophyll concentration than *B. pubescens* (Fig. 3), the species explaining 6.0% of variation, but several interactions between species, origin, location and site also appeared (Table 4).

First-year leaf herbivory and pathogen occurrence in common gardens

On average, 92–93% of birch plantlets had leaves damaged by herbivory, 71–81% by pathogens other than *M. betulinum* and 34–41% by *M. betulinum* (Table 5). All types of damage were most frequent in southern Finland, where 99.3%, 99.6% and 79% of plantlets had herbivory, unidentified pathogen and *M. betulinum* damages, respectively (Table 5). Herbivory damage was somewhat more frequent in Italy than in northern Finland, whereas pathogen damage was clearly more frequent in northern Finland than in Italy. *Melampsoridium betulinum* damage was almost absent in Italy but found on 31% of plantlets in northern Finland (Table 5).

Common garden location had a major influence on leaf herbivory damage, explaining 34% of the variation (Table 6, Fig. 4). However, sites also differed (Table 6), especially in Italy and southern Finland, and although leaves in southern Finland on average had more herbivory damage than in Italy, leaf damage did not differ between site C in southern Finland and site A in Italy (Fig. 4). Initial planting height had no effect, but the laboratory leaf N concentration, a proxy of soil fertility, was positively associated with leaf herbivory index (Fig. S7), explaining 2.7% of variation (Table 7). When this effect was removed from the data, herbivory damage in northern Finland was on average higher than in site B in central Italy (blue bars in Fig. 4). The species × location interaction effect on herbivory index (Table 6) appeared because *B. pendula* and *B. pubescens* plantlets were equally damaged in northern Finland, *B. pendula* was on average more damaged than *B. pubescens* in Italy and *B. pendula* was less damaged than *B. pubescens* in southern Finland (Fig. 4).

Location explained 70% of total variation in pathogen (excluding *M. betulinum*) index (Table 6), and the differences among index values between locations were clear (Fig. 4) (see *M. betulinum* results in Fig. S8 and Table S5). Planting height had no effect, but the laboratory leaf N concentration was weakly positively associated with the pathogen damage index (Fig. S7), explaining 2.5% of variation (Table 6). When this effect was removed from the data, the pathogen damage index increased in northern Finland and decreased in southern Finland, but the order of locations in pathogen load did not change (blue bars in Fig. 4). The significant origin × species × location interaction effect was because the differences between the origins in pathogen damage differed for the two species in southern Finland:

Table 5 Percentage of birch plants that had leaves damaged by herbivores, pathogens (excluding *Melampsoridium betulinum*) and *M. betulinum* for each species, origin, common garden location (C Italy = central Italy, N Italy = northern Italy, S Finland = southern Finland, N Finland = northern Finland) and site

Location (Site)	Origin	Herbivory damage (% of plants)		Pathogen damage (% of plants)		*M. betulinum* damage (% of plants)	
		B. pendula	*B. pubescens*	*B. pendula*	*B. pubescens*	*B. pendula*	*B. pubescens*
C Italy (A)	N Italy	100	97	39	3	0	3
	S Finland	100	100	30	19	0	0
	N Finland	91	100	18	0	0	9
C Italy (B)	N Italy	97	94	78	34	3	0
	S Finland	96	79	100	29	4	3
	N Finland	92	58	46	17	0	8
S Finland (C)	N Italy	100	100	100	100	85	78
	S Finland	100	100	100	100	78	78
	N Finland	100	91	100	96	56	64
S Finland (D)	N Italy	100	100	100	100	88	92
	S Finland	100	100	100	100	89	85
	N Finland	100	100	100	100	79	67
N Finland (E)	N Italy	92	90	97	100	3	63
	S Finland	80	85	100	100	44	35
	N Finland	71	74	94	100	53	58
N Finland (F)	N Italy	92	100	92	97	0	37
	S Finland	93	100	100	97	15	21
	N Finland	78	82	67	88	17	35
Average		93	92	81	71	34	41

Table 6 Effects of initial planting height, laboratory plant leaf N concentration (a proxy of soil fertility), common garden location (central Italy, southern Finland, northern Finland), site within location (two sites in each location), block within site (5–8 blocks in each site), species (*Betula pendula* and *B. pubescens*), origin (northern Italy, southern Finland, northern Finland) and genotype within origin within species (3–5 genotypes in each origin) on leaf herbivory and pathogen (excluding *Melampsoridium betulinum*) indices of field-grown birch plantlets in type I ANOVA tests. R^2 gives the percentage of variation explained by each variable

Explanatory variable	Leaf herbivory index				Leaf pathogen index			
	df	*F*	*P*	R^2	df	*F*	*P*	R^2
Planting height	1, 32	3.74	0.062	0.5	1, 29	3.41	0.075	0.2
Lab plant leaf N concentration	1, 31	59.4	< 0.001	2.7	1, 38	55.4	< 0.001	2.5
Location	2, 32	371	< 0.001	34	2, 38	774	< 0.001	70
Site (Location)	2, 30	19.1	< 0.001	1.7	2, 37	20.1	< 0.001	1.8
Block (Site(Location)	41, 811	0.72	0.904	1.9	41, 811	2.32	< 0.001	1.8
Species	1, 21	3.63	0.071	0.8	1, 21	1.14	0.299	0.1
Origin	2, 24	0.21	0.810	0.1	2, 23	1.30	0.293	0.2
Genotype (Origin (Species))	22, 790	3.03	< 0.001	4.3	22, 790	4.87	< 0.001	2.0
Species × Location	2, 790	9.43	< 0.001	1.2	2, 790	67.4	< 0.001	2.5
Species × Site (Location)	3, 790	1.23	0.297	0.2	3, 790	10.8	< 0.001	0.6
Origin × Location	4, 790	2.20	0.068	0.6	4, 790	28.0	< 0.001	2.0
Origin × Site (Location)	6, 790	1.04	0.400	0.4	6, 790	2.25	0.037	0.2
Origin × Species × Location	4, 790	1.74	0.139	0.5	4, 790	13.4	< 0.001	1.0
Origin × Species × Site (Location)	6, 790	0.70	0.647	0.3	6, 790	1.96	0.069	0.2
Total % of variation explained				49				86

Table 7 Effects of laboratory plant growth (a proxy of soil fertility; growth in height used for growth in height, biomass for stem diameter), common garden location (southern Finland, northern Finland), site within location (two sites in each location), block within site (5–8 blocks in each site), species (*Betula pendula* and *B. pubescens*), origin (northern Italy, southern Finland, northern Finland) and genotype within origin within species (3–5 genotypes in each origin) on the growth in height and stem diameter of 4-year-old, field-grown birch saplings in a type I ANOVA test

Explanatory variable	Growth in height				Stem diameter			
	df	*F*	*P*	R^2	df	*F*	*P*	R^2
Lab plant growth	1, 28	242	< 0.001	26	1, 28	146	< 0.001	17
Location	1, 26	128	< 0.001	14	1, 26	128	< 0.001	15
Site (Location)	1, 28	3.42	0.075	0.4	1, 29	0.22	0.645	< 0.01
Block (Site (Location)	28, 580	1.62	0.025	3.0	28, 589	1.60	0.026	3.2
Species	1, 21	< 0.01	0.967	< 0.01	1, 21	5.10	0.035	1.9
Origin	2, 21	13.3	< 0.001	5.4	2, 22	2.32	0.122	1.6
Genotype (Origin (Species)	22, 563	2.98	< 0.001	4.3	22, 567	4.97	< 0.001	7.5
Species × Location	1, 563	17.5	< 0.001	1.1	1, 567	50.2	< 0.001	3.4
Species × Site (Location)	2, 563	5.40	0.005	0.7	2, 567	6.43	0.002	0.9
Origin × Location	2, 563	48.0	< 0.001	6.3	2, 567	56.2	< 0.001	7.7
Origin × Site (Location)	4, 563	0.37	0.831	0.1	4, 567	1.95	0.101	0.5
Origin × Species × Location	2, 563	10.3	< 0.001	1.3	2, 567	18.4	< 0.001	2.5
Origin × Species × Site (Location)	4, 563	0.39	0.816	0.1	4, 567	0.36	0.836	0.1
Total % of variation explained				63				61

R^2 gives the percentage of variation explained by each variable

the pathogen damage index of plants from Italian origin was 69% and 90% lower than the index of plants from SF origin and NF origins, respectively, for *B. pendula*, but 48% higher and only 34% lower, respectively, for *B. pubescens* (Fig. 4).

Four-year survival and growth in Finnish common gardens

The 4-year survival was affected by an origin × species × location interaction effect ($P=0.009$; see Table S6 for full statistical analysis). This interaction was mainly because the survival of plants from the Italian origin depended both on species and location: For *B. pubescens*, survival was equal or slightly better than the survival of plants from SF and NF origins at both Finnish locations, whereas for *B. pendula* the survival was on average 9%-unit higher than the survival of plants from SF and NF origins when grown in southern Finland and 29%-unit lower than the survival of those from SF and NF origins when grown in northern Finland (Fig. 5). Moreover, for *B. pendula*, the survival of plants from SF and NF origins was 12%-unit higher in northern Finland than in southern Finland, but similar between the locations for *B. pubescens* from these two origins (Fig. 5). On average, survival of *B. pubescens* was 8%-unit higher than that of *B. pendula* (Fig. 5).

The 4-year height growth was significantly affected by location, which explained 14% of the variation (Table 7). Growth in southern Finland was on average triple the growth in northern Finland (Fig. 6). However, laboratory height growth, a proxy of soil fertility, was positively associated with field growth (Fig. S5), explaining 26% of the variation (Table 7), and when this effect was removed from the data (blue bars in Fig. 6), mean growth in northern Finland was higher than the growth in site C in southern Finland. The origin, species and location effects interacted strongly (Table 7). The NF-origin plants grew on average 50% less than those from SF origin in all species × location combinations except for *B. pendula* growing in northern Finland, where *B. pendula* plants from NF origin grew 31% more than those from SF origin (Fig. 6). Also, for *B. pubescens* the Italian-origin saplings grew on average 35% less than those from SF origin in both locations, whereas for *B. pendula* the Italian-origin saplings grew 8% and 95% less than those from SF origin in southern and northern Finland, respectively (Fig. 6).

The results of stem diameter resembled in many ways the results of height growth (Table 7, Fig. 6), including the positive association of stem diameter with laboratory plant biomass (Fig. S9) and the consequently smaller differences in residual stem diameter, devoid of soil effects, between southern and northern Finland (blue bars in Fig. 6). The main differences, in comparison to the height growth, were that stem diameter in southern Finland was only double that in northern Finland and that the Italian-origin saplings performed relatively better in comparison to those from Finnish origins (Fig. 6). For example, in southern Finland, the Italian-origin *B. pendula* plants produced 20% thicker stems than those from SF origin (Fig. 6).

Discussion

Birch acclimation thrives across 20° latitudinal gradient

This is the first study, to our best knowledge, that provides evidence of the high acclimation capacity of *B. pendula* and *B. pubescens* when transferred between the extremes of the geographical range wider than 20° latitude: The first-year growth was on average best for all origins in boreal southern Finland and no drastically negative effects on first-year growth appeared when saplings from each origin were transplanted across the whole gradient. The only clearly negative effect was the lowered 4-year survival and growth of Italian *B. pendula* (but not *B. pubescens*) in subarctic Finland. These results suggest that birches cope well with the photoperiodic change. As we predicted, plantlet growth rate increased toward southern origins in the nursery and laboratory, but not in the field, where the growth rates of saplings from NF and Italian origins approached each other. As we expected, soil fertility explained a significant share of growth variation among locations; in fact, the difference in growth between Italy and northern Finland (better growth in Italy) reversed in the data devoid of the soil fertility effect (better growth in northern Finland). Against our assumption, leaf herbivore and pathogen damages did not increase toward the south but were instead highest in southern Finland. Neither did saplings from any of the origins differ in herbivore damage.

Acclimation capacity of birch species

Although common gardens with trees from different latitudes are widely used as a tool in forest research (e.g., Heimonen et al. 2015; Rousi et al. 2018; Tullus et al. 2021), forest managers and tree breeders avoid transfers over excessive distances due to reported adverse effects on the growth, quality and survival of seedlings (Viherä-Aarnio et al. 2006, 2013; Heimonen et al. 2015). Southward transfer of birch from northern origins leads to early cessation of height growth due to adaptation to frost that in the north appears at shorter critical night lengths (Viherä-Aarnio et al. 2006; Luquez et al. 2008; Possen et al. 2021). In our experiment, this effect was visible as less 4-year growth of the NF provenance (after correction for soil fertility effect) in southern Finland than in northern Finland.

The results from Viherä-Aarnio et al. (2013) and Lee et al. (2015) indicate that height and volume growth of *B. pendula* are greatest when the latitudinal transfer is between zero and two latitude degrees north, while Tedla et al. (2019) reported an increase in height and biomass of *B. papyrifera* Marsh. (white birch) when shifted northward up to four latitude degrees. Our results support the studies by Han et al. (1985) and Rousi et al. (2012) that demonstrated potential for even more extensive transfer. In particular, our results show that a northward transfer of ca. 16 latitude degrees from northern Italy to southern Finland did not harmfully affect the 4-year survival of plantlets of either species, despite the drastic change in photoperiod and growth season. Also, although the 4-year height growth of the Italian provenances in southern Finland was slightly lower than those of local origins, stem diameters were larger. Since the soils in the two common garden sites at each location were in our experiment chosen to be as different as possible, our results can be safely generalized beyond the sites used in the experiment. The next step could be a transfer of birch material from Baltic countries and Central Europe to Scandinavia to see whether it has an acclimatization capacity similar to that of the Italian genotypes. When comparing our results to those in the literature, it should be noted that many previous studies used seedlings, plant material characterized by a higher genetic variability than the micropropagated cloned material used in our present study, which in turn lends greater strength to statistical testing.

Latitude and soil fertility effects on growth and leaf chlorophyll

Our results show that the growth of both birch species was affected by the latitudinal location, and in general, southern Finland seemed to have the best environmental conditions, in accordance with the positive correlation of mean annual temperature and *B. pendula* performance reported for Fennoscandia between 63° and 67° N (Tullus et al. 2021). In central Italy, the greatest resource limitation is the lack of water during the summer drought (Fig. S1), which can severely affect young birches (Kou et al. 2023). In comparison to other *Betula* species, *B. pendula* is less able to maintain turgor at low leaf water potentials, resulting in a drastic drop in photosynthesis already under mild water stress (Ranney et al. 1991). The high leaf chlorophyll content for plants in central Italy could be a result of N-use optimization under water stress because N allocation to leaves increases in herbaceous and woody species during drought (Weih et al. 2011; Luo et al. 2023; Medina and Craig 2024).

Our study also suggests that a significant part of differences in growth among locations can be explained by differences in their soils, in addition to differences in climate and photoperiod. The laboratory test showed that soil fertility differed among the common garden sites: Plant growth, as well as leaf N and chlorophyll content, differed between the soils collected from the sites, and all plant attributes correlated positively with soil N concentration. These relationships arise from efficient N uptake in birches (van Vuuren et al. 2003) and the fact that the majority of N in a plant is bound to chlorophyll (Valladares et al. 2012). When we included the laboratory results of plant performance, as proxies of soil fertility, in the statistical analyses of field data, they explained a significant proportion of the total variation in growth. Differences between locations decreased and the growth difference between Italy and northern Finland was reversed, while southern Finland still had the greatest growth. These results indicate that the lower growth in northern Finland than in Italy was explainable by soils being more fertile in Italy, whereas the good growth in southern Finland was largely due to the beneficial climate. This finding adds to earlier observations of the importance of soil fertility in explaining and governing tree growth responses to latitudinal transfer and temperature (Rousi et al. 2018; Possen et al. 2021). After 4 years, the height growth in southern Finland was on average almost triple that in northern Finland, but since the soil explained double the amount of variation explained by location, much of the difference in growth between the locations could also then be explained by soil fertility.

In contrast to growth, leaf chlorophyll concentrations showed a latitudinal gradient and increased from northern Finland to Italy. When the soil and planting height effects were removed from the data, mean concentrations in southern and northern Finland did not differ but were still only around half of those in Italy. Thus, the high leaf chlorophyll concentrations in Italy apparently cannot be explained by soil fertility but might be due to acclimation to drought and temperate climate favoring chlorophyll formation (Mohanty et al. 2006; Ogaya et al. 2011), whereas the difference between southern and northern Finland may be explained by soil fertility.

Origin and origin × environment interaction effects on growth and leaf chlorophyll

The growth of our plantlets was clearly affected by their origin, with growth increasing for plantlets from NF to Italian origins in the nursery and laboratory. These results suggest that the earlier finding that southern *B. pendula* populations in Finland have higher growth rates than northern populations (Tenkanen et al. 2020, 2021, 2023) can be extended farther south to the Italian populations and also holds true for *B. pubescens*. However, our results show that this latitudinal gradient of intrinsic, inherited growth rate is highly sensitive to suboptimal growth conditions in the field. The Italian origins had better growth than the NF origins in southern Finland (optimal growth conditions), but not in Italy or northern Finland (suboptimal growth conditions), suggesting that the Italian origins could outperform the NF origins in field growth only in the most favorable environment. These results echo the genotype × environment interactions found for the performance of fast- and slow-growing genotypes of *B. pendula* grown in a nursery and the field (Mikola et al. 2014). Studies of phenotypic trait variation in *Populus* species along latitudinal gradients in North America (Gornall and Guy 2007; McKown et al. 2014; Kaluthota et al. 2015; Soolanayakanahally et al. 2015) and Sweden (Hall et al. 2007; Luquez et al. 2008; Soolanayakanahally et al. 2015) have shown a negative correlation between tree height growth and latitude and higher gas exchange in trees from northern than southern origins. High gas exchange levels have in turn been linked to high leaf N and chlorophyll concentrations (Soolanayakanahally et al. 2009; Kaluthota et al. 2015).

After 4 years of growth in the two Finnish locations, plants from NF origin generally grew less than those from SF origin, except for *B. pendula* in northern Finland, suggesting that *B. pendula* from SF is not adapted to subarctic conditions. For *B. pubescens*, plants with Italian origin grew less than those from SF origin in both locations, whereas for *B. pendula*, those with Italian origin grew almost as well as those from SF origin in southern Finland, but grew very poorly in northern Finland. These results indicate that *B. pendula* plants from the Italian sites can perform well in boreal conditions but lack adaptation to subarctic conditions. The pattern in stem growth mostly followed the pattern in height growth except that differences between southern and northern Finland were less pronounced and plants from Italian origin performed relatively better. It seems that plants from the Italian origins allocate relatively more to stem diameter than height growth, at least at high latitude in the field.

In our laboratory test, plants of both species from NF origin had remarkably more N and chlorophyll in their leaves than those from Italian and SF origin. These results support the view that northern trees accumulate N and chlorophyll in their leaves to acclimate to low temperature and/or to mitigate the constraints due to the cold climate and short growing season (Weih and Karlsson 2001; Tullus et al. 2021). Higher leaf chlorophyll contents in the northern than in the southern Finnish genotypes of *B. pendula* in common garden (Tenkanen et al. 2020) and laboratory (Ndah 2017) studies have also been reported. In our field sites, however, plants from NF origins had higher leaf chlorophyll content than plants from other origins in northern Finland and Italy only (*B. pubescens*) or in northern Finland only (*B. pendula*). These results suggest that the higher leaf chlorophyll content in genotypes from northern Finland in the field mainly appear in suboptimal and low-productivity environments.

Latitude and soil fertility effects on leaf damage

Supporting the idea that leaf herbivory damage levels are positively associated with warmer climate (Kozlov et al. 2013, 2015), an earlier *B. pendula* translocation study in Finland found increasing leaf damage when plant material was moved southward (Heimonen et al. 2015). As a result, we expected that herbivore damage would follow a temperature gradient and be highest in Italy, but this prediction was refuted. Instead, growing conditions in southern Finland seemed to promote higher leaf damage in both species in our experiment. Another explanation is that the common garden sites in Italy were not surrounded by local birch trees, like in Finland, and potential herbivores were not present. We also found that when the soil fertility effect was removed from the data, the difference in leaf herbivory levels between northern Finland and the two other locations decreased, thus suggesting that higher soil N may encourage leaf herbivory by increasing leaf N concentration. Our assumption that plants from NF origins would be most susceptible to herbivory in southern Finland and Italy was also refuted because we did not find a significant origin × location effect on leaf herbivore damage. Altogether, our results suggest that the *B. pendula* and *B. pubescens* genotypes from different origins are well adapted to herbivores in a wide range of locations and neither northern nor southern transfer of trees or herbivores seems to pose a great risk of damage.

As for the pattern in leaf herbivory damage, differences in damage from pathogens were very clear between the locations, but no latitudinal gradient appeared; damage was lowest in Italy and highest in southern Finland. In Italy, the dry weather and lack of local birch trees likely explains the very low number of pathogen attacks, especially for *M. betulinum*, which is a host specialist. In Finland, a clear latitudinal gradient in pathogen damage appeared for both birch species, suggesting that warmer climate in Finland exposes birches to pathogen attack. High variation in leaf chemistry between birch origins, but no clear trends in the south-north axis, has been demonstrated in the Finnish regions (Deepak et al. 2018), but to our knowledge, leaf chemical profiles in trees at boreal-subarctic and at temperate latitudes have never been compared. As in the case of leaf herbivory, our data indicate that a small part of the higher pathogen damage in southern than in northern Finland could be explained by higher leaf N concentration, in line with an earlier finding that *M. betulinum* damage is positively associated with fertilization level (Poteri and Rousi 1996).

Differences between the species

We found that *B. pendula* grew better than *B. pubescens* in Italy and southern Finland, but not in northern Finland, which is in line with observations that *B. pendula* is better adapted to warmer climates and *B. pubescens* to colder and wetter climates (Dubois et al. 2020). Although both birch species are native tree species in large areas of Europe (Atkinson 1992; Dubois et al. 2020), scarce information is available for differences in their growth properties due to the lack of interest in their commercial use (e.g., Nieuwenhuis and Barrett 2002; Dubois et al. 2020). Earlier literature suggests that the growth of the two species in Finland is roughly the same for the first 10–15 years, but the final yield of *B. pendula* may be up to two times higher (Raulo 1977 and references therein). The general assumption of a higher growth rate for *B. pendula* was supported in our study by the finding that leaves of *B. pendula* had on average 7% higher N concentration in the laboratory test and higher chlorophyll content in the field, although the differences between the origins and genotypes were also extensive. Stomatal density is also higher in *B. pendula* leaves, enhancing gas-exchange rates (Pääkkönen et al. 1997).

Our results show surprisingly good performance and survival of *B. pubescens* in northward translocations. Better survival of *B. pubescens* in cool and wet conditions, compared to *B. pendula*, has been explained by formation of temporary fine roots in prolonged wet conditions, high density of nonglandular trichomes in leaves and efficient formation of stem lenticels (Wang et al. 2016). These adaptive morphological traits are especially important in unfavorable waterlogged, anaerobic soils (Wang et al. 2016). Also in warmer areas, as in the Iberian Peninsula in Spain, *B. pubescens* occupies oceanic and western locations while *B. pendula* grows in mesic environments in eastern, southern and mountainous areas (Gomez-Garcia et al. 2010).

Conclusion

Our results provide evidence of high acclimation capacity of *Betula* tree species across Europe, and particularly after a long-range transfer from south to north. High acclimation capacity is important because it provides time for genetic adaptation. Our results also confirm the earlier findings of the importance of soil fertility in modifying the climatic effects on tree performance. Our results are important for future forest breeding and management in Nordic countries, where coniferous tree species, especially *Picea abies*, are challenged by climate change and insect and pathogen attacks (Eriksson et al. 2005; Piri and Valkonen 2013; Hayatgheibi et al. 2021). At fertile sites, *B. pendula* is the only domestic substitute for *P. abies*. Considering that tree diversity is also important for forest soil C and N accrual (Chen et al. 2023), *B. pendula* and *B. pubescens* have potential to become key species in boreal forests. On the basis of our results, we encourage long-range south-to-north transfers with active management to provide high-quality commercial birch material for the rapidly changing climate.

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